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CHAPTER 4-8
INVERTEBRATES: MOLLUSCS

TABLE OF CONTENTS

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Figure 1. **Slug** on a ***Fissidens*** species. Is it eating, or just a casual visitor? Photo by Janice Glime.

The most familiar of the bryophyte inhabitants among the molluscs are the snails and slugs, but you will see that some bivalves also have an interesting relationship with bryophytes.

Mollusca are considered to be **bilaterally symmetrical** (like humans) (Pratt 1935), but they seem to push the definition to the limit. In bivalves, that is not too difficult to understand, but in snails the twisted body and shell seem to twist the definition as well; even organs normally paired, like kidneys, are not paired (Figure 2).

Gastropoda: Snails and Slugs

Most terrestrial and freshwater snails (**Pulmonata**) have spiral shells and these may be taller than the diameter of the opening (**elongate/conical**; Figure 26) or shorter (Figure 148) (Pratt 1935). The inside body is also a spiral, but it is not the same spiral as the one of the shell. This internal spiral affects the digestive system as well. With its mouth to the ground, the snail is infamous for the positioning of the anus above the mouth on the right side of the head (Figure 2).

In snails, the mantle secretes a shell, and this requires calcium carbonate. For this reason, you will find a number of terrestrial taxa restricted to limestone areas. Slugs (Figure 3), on the other hand, lack shells and exhibit no external twists. Instead they have a thin calcareous plate embedded in the mantle.

Unlike the marine snails, terrestrial gastropods lack an **operculum** to cover the shell opening. Instead, they use a calcified slime (**epiphragm**; Figure 4) for protection in hibernation or aestivation. The **respiratory pore** (Figure 3) is on the right side of the body, and closes to keep out water in aquatic species or to prevent desiccation under dry conditions on land. Both aquatic and terrestrial gastropods have lungs, necessitating return to the surface for aquatic members to get air. Aquatic members have only one pair of non-retractile tentacles, whereas land-dwellers have two pairs and both are retractile. Aquatic species have an eye at the base of each tentacle; the land snails have their eyes on the tips of the rear pair of tentacles.

Most gastropods eat algae and plants, which they scrape with the **radula** (Figure 5), but a few are carnivorous. The radula is made of chitin with rows of minute calcareous teeth. And if you thought bryophytes used minute characters for identification, snail identification is often based on these teeth!

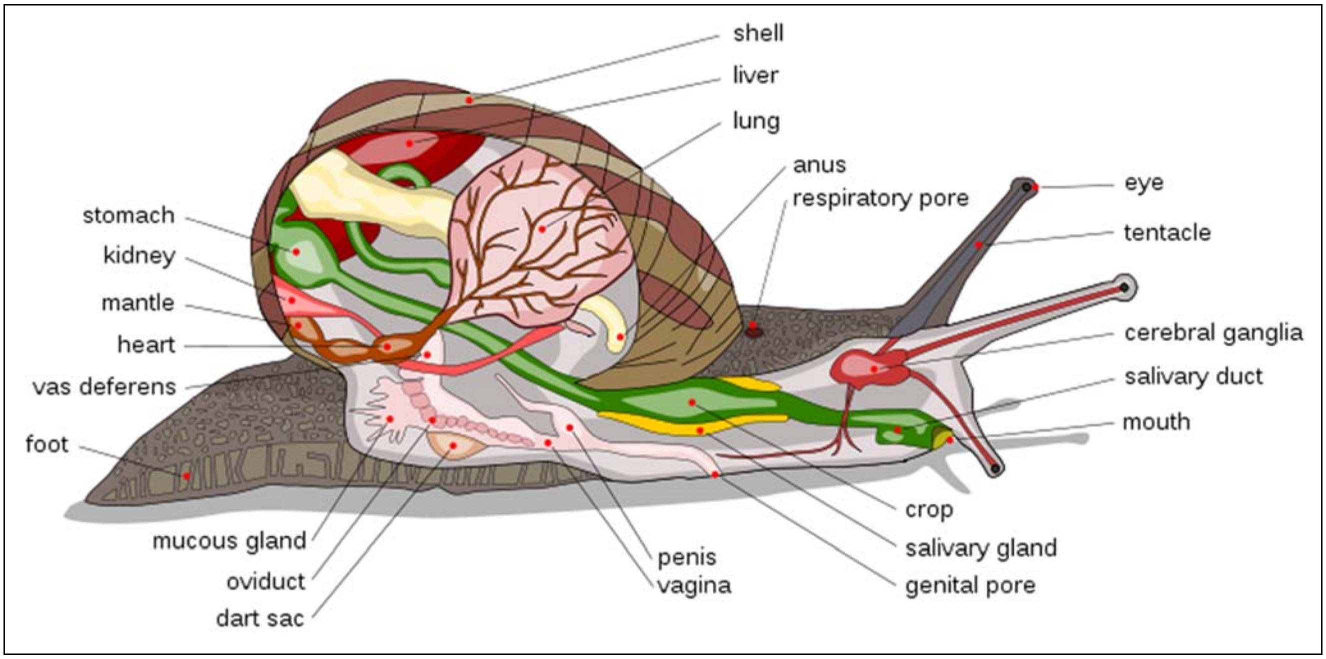

Figure 2. Snail, showing its major internal and external parts. Note the dart sac from which the love dart is ejected. Image from Wikimedia Creative Commons.

Figure 3. Great Red Slug, ***Arion rufus***, dark form, Bishop Middleham Quarry Nature Reserve, Co Durham. Note the large **respiratory pore** on the mantle of this sometimes moss dweller. This snail can travel nearly 0.5 km in search of more suitable conditions (Sandelin 2012). Photo by Brian Eversham, with permission.

Figure 4. *Helix pomatia* **epiphragm**. Photo by Hannes Grobe, through Wikimedia Commons.

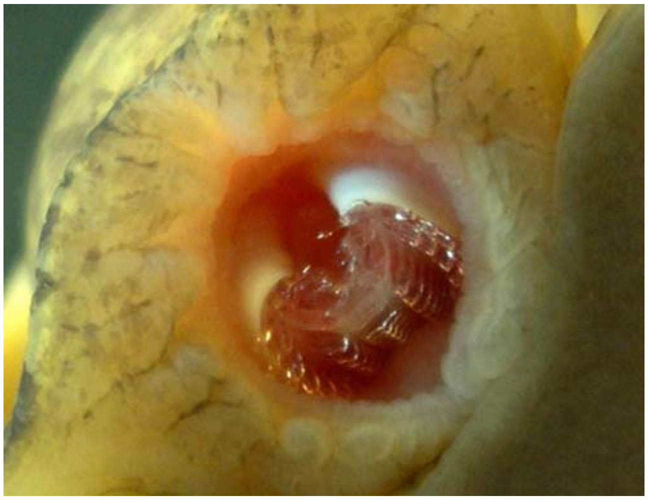

Figure 5. *Pomacea canaliculata* mouth showing **radula**. Photo by S. Ghesquiere, through Wikimedia Commons.

Reproduction

Most terrestrial snails and slugs are **simultaneous hermaphrodites**, mutually exchanging gametes during copulation. This is not true for land-dwelling prosobranch snails (including the Pomatiidae, Aciculidae, Cyclophoridae, and others) – families that have separate sexes (Wikipedia 2012b). The prosobranch snails are the ones that have an **operculum** that can be used to cover the opening when they retreat into the shells.

Some land snails are **sequential hermaphrodites**, being first male, then female (Nordsieck 2012b). Others, such as ***Arianta arbustorum*** (**Helicidae**; Figure 6), a moss-dwelling snail, have a mechanism that prevents sperm cells from fertilizing the snail's own egg cells before they reach the sperm pouch of the mate. In the aquatic **Lymneidae**, snails can reproduce using unfertilized eggs, permitting

them to multiply rapidly in a new location and causing invasive species problems when they are introduced as aquarium pets.

The reproductive anatomy of the snail is a bit peculiar, with the **penis** and **vagina** everting from near the head (Figure 7-Figure 8). In the hermaphrodites, the penes wrap around each other, sometimes extending to great lengths (Figure 9).

Figure 6. ***Arianta arbustorum*** on a bed of mosses and leafy liverworts. Photo ©Roy Anderson, with permission.

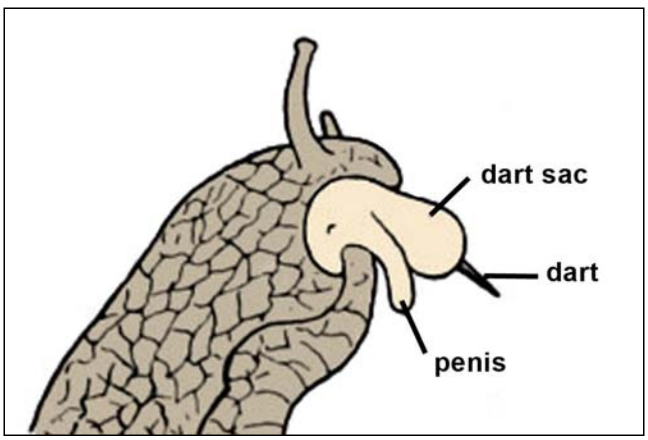

Figure 7. *Helix pomatia* head during mating. Redrawn from Johannes Meisenheimer, through Wikimedia Commons.

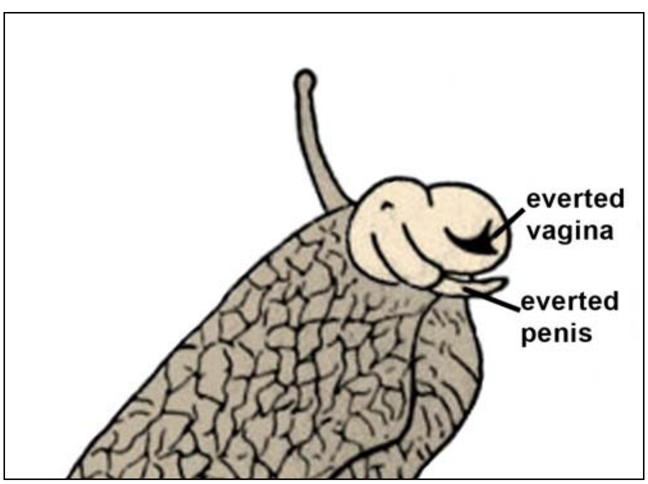

Figure 8. *Helix pomatia* head after mating, showing both male and female parts of this **simultaneous hermaphrodite**. Redrawn from Johannes Meisenheimer, through Wikimedia Commons.

Figure 9. Slugs mating, demonstrating the very long penes. Photo through Wikimedia Commons.

Mating and the Love Dart

The mating process is a combination of love and war (Figure 10). The dart, or more than one in some species, is made of calcium carbonate, chiton, or cartilage (Figure 11). During mating, each snail tries to inject this "dart" into the other snail (Figure 12) (Koene & Chase 1998a; Chase & Blanchard 2006). It might be more appropriate to call this a dagger because it is injected by a thrust, not a shot or a throw. The first mating of a snail stimulates the production of the dart, so it cannot be used until the second mating. Once used, it requires time to generate a new one.

Figure 10. Roman snails (*Helix pomatia*) in full foot contact during mating. This process of contact of foot, lips, and tentacles can take up to 20 hours. Photo through Wikimedia Commons.

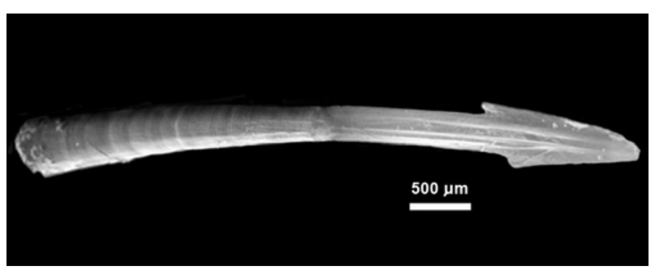

Figure 11. **Love dart** of the snail ***Monachoides vicinus***. Photo by Joris M. Koene and Hinrich Schulenburg through Wikimedia Commons.

Figure 12. Mating garden snails (***Helix aspera***) with **love dart** in snail on right, just above the antenna of the left snail. Photo by Eynar through Wikimedia Commons.

But what does the dart accomplish? Early hypotheses considered it to be a "gift of calcium" to help in the development of the eggs. Leonard (1992) used a theoretical model to support the hypothesis that the love dart induced the partner to act as a male, hence insuring that the thruster would also be fertilized. Koene and Chase (1998a, b) used an experimental approach to disprove the long-held hypothesis of a "gift of calcium."

Through the work of Koene and Chase (1998 a, b), the role of this dart has become clearer. It carries with it a mix of **hormones** that help to move the sperm cells toward the sperm pouch where they are stored until fertilization (Koene & Chase 1998a, b). This is accomplished by causing changes in the structure of the copulatory canal leading ultimately to the sperm pouch. These changes increase the chances, often doubling them, that sperm from that mating snail are successful in fertilizing eggs, since it is likely that the partner will have multiple mating events. But the dart, preferably aimed at the foot, can miss its ideal target and land in a less desirable location, like the base of the antenna. When that happens, the snail is no longer able to retract or extend the antenna.

Each partner goes through gyrations apparently in an attempt to avoid being recipient of the love dart, or at least to avoid receiving it in an undesirable location. So far, Leonard's (1992) hypothesis of stimulating the partner to carry out its male role does not seem to have been tested experimentally, but with the mix of hormones it could still be a viable part of the story. It appears that this love dart, although not understood at the time, could have been the basis for the story regarding Cupid's arrow (Chase 2010).

Egg and Larval Development

Most gastropods lay eggs, with only a few species bearing live young. In aquatic snails, development of the larva occurs as a planktonic stage once it leaves the egg, but in terrestrial pulmonate snails, development is completed within the egg. Some snails (*e.g.* **Clausiliidae**) exhibit **ovoviviparity**, wherein the larvae emerge inside the mother's body and emerge from "her" body as juvenile snails (Nordsieck 2012b). This practice permits these snails to live in dry areas where external eggs could not survive the desiccation. Some species of the **oviparous** (egg-laying) species, such ***Arion flagellus*** (Figure 13), lay their eggs under or among bryophytes (Figure 14).

Figure 13. ***Arion flagellus*** on a sheet of mosses. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 14. ***Arion flagellus*** eggs in Oaks Wood, Cambourne, Cambridgeshire, UK. Note the bit of moss beside the eggs and on the eggs – remnants of the cover that previously protected them. Photo by Brian Eversham, with permission.

Richter (1972) found that the banana slug (***Ariolimax columbianus***, Figure 15) laid 3-4 mm eggs under moss where soil conditions were neither excessively wet nor dry. Placing eggs under mosses and other loose substrata may be an energy-saving strategy for some species. Bauer (1994) considered the behavior of some snails that dig holes to be an investment in **parental care**, but incurring an energy cost. Other than these preparations, snails do not tend their eggs or hatchlings. ***Ariolimax californicus*** (Figure 16) also may occur under bryophytes (Peggy Edwards, pers. comm.).

Figure 15. ***Ariolimax columbianus*** on moss. Photo by Bill Leonard, with permission.

Figure 16. ***Ariolimax californicus*** exiting a mat of mosses, a suitable location for laying eggs. Photo coourtesy of Peggy Edwards.

Bryophyte Interactions

Glistening trails of pearly mucous (Figure 17) 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*** (Figure 18) 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 molluscs simply travelling from one place to another across the moist moss surface, or do they have a more dastardly purpose (as hunters) for traversing these miniature forests?

Figure 17. ***Lehmannia valentiana*** with its slime trail on a moss (upper right) in Swavesey, Cambridgeshire, UK. Photo by Brian Eversham, with permission.

Figure 18. ***Eremarionta immaculata*** in the Riverside Mountains, CA, USA. Photo by William D. Wiesenborn, with permission.

But not all snails and slugs find the bryophyte substrate attractive. Some actually avoid its rough surface. Nevertheless, trails of slime (Figure 19) are not unusual, and we have little insight into the reasons why some find it inviting while others find it repulsive.

Figure 19. Snail or slug trails on ***Dicranum viride*** on big maple trunk. Photo courtesy of Betsy St. Pierre.

Abundance

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. 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).

The study by Grime and Blythe (1969) is helpful in understanding numbers and dynamics of moss-dwelling snail populations, but we need many more studies. They found average morning populations of up to 8.5 per 100 g dry weight of moss in early September for the copse snail ***Arianta arbustorum*** (Figure 20) at Winnats Pass in Derbyshire, England. 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. ***Arianta arbustorum*** numbered 0, 7, 2, and 6 on those days, respectively, with weights of 0.0, 8.5, 2.4, and 7.3 per 100 g dry mass of moss. 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.

Figure 20. The moss-dwelling copse snail, ***Arianta arbustorum***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Nighttime activity by many snails is likely to be greater than that during the day, and little snails may actually seek refuge in mosses during the day (Grime & Blythe 1969). Furthermore, snails like ***Arianta arbustorum*** (Figure 20) typically climb, often to a considerable height, to obtain food. Bryophytes just don't fit as a refuge for larger snails, so the behavior of the larger ***Arianta arbustorum*** may not reflect that of the small snails.

Adaptations

Confusing the Predator

In the Pacific Northwest, USA, unusual jumping slugs in the genus ***Hemphillia*** (Figure 21-Figure 24) prefer coarse woody debris or moss mats on decaying logs (Leonard & Ovaska 2003). They have some remarkable adaptations for their log habitats. One such adaptation appears to be to confuse their predators by smearing their slime trail (Figure 17).

Figure 21. ***Hemphillia glandulosa***, the warty jumping slug, on moss. This and the following photo illustrate the variability in its coloration. Photo by Kristiina Ovaska, with permission.

Jumping to Escape

A second adaptation to avoid predation is to "jump." Jumping slugs (***Hemphillia***; Figure 22) don't actually jump. Instead, when they are approached by a predator snail or other predator, they tighten their muscles, coil up, and straighten rapidly, flopping around on their substrate until they are free of it, and fall. This effects a rapid motion that looks like a jump (Leonard 2011). This activity also breaks the slime trail, facilitating their freedom to "jump." The slow-moving predator snails don't have a chance. Leonard says these slugs are potentially successful dispersers of fungal spores. I would think that would work for dispersing bryophytes as well, for spores, asexual structures, and fragments.

Figure 22. ***Hemphillia glandulosa***, the warty jumping slug, on moss. This and the above photo illustrate the variability in its coloration. Photos by Kristiina Ovaska, with permission.

In Canada, some of these ***Hemphillia*** (Figure 21-Figure 24) species seem safe from extinction due to sufficient abundance, but others are endangered due to increasing patchiness of suitable habitats (Leonard & Ovaska 2003). 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, ***Hemphillia***. ***Hemphillia dromedarius*** (dromedary snail; Figure 23-Figure 24) is officially threatened in both Canada and the United States, where it lives in the state of Washington. Legal 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. Perhaps the novelty of its jumping behavior will increase public interest and sympathy and lead to its protection in yet another way.

Figure 23. ***Hemphillia dromedarius***, the dromedary jumping slug. Photo by Kristiina Ovaska, with permission.

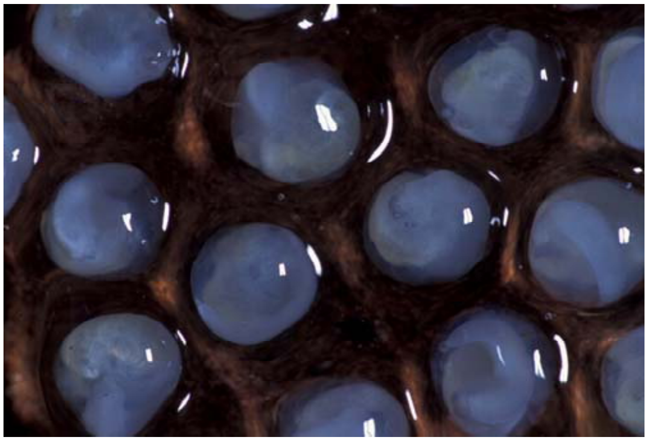

Figure 24. Eggs of ***Hemphillia dromedarius***, the dromedary jumping slug. Photo by Kristiina Ovaska, with permission.

Keeping It Small

If you want to go clambering among the bryophytes, it helps to be small (Figure 26). One would expect that size would also constrain movement among the bryophytes and restrict larger snails to the surface. But some tiny snails actually occur fairly deep within the bryophyte mat. Such is the elongate snail captured by Jan-Peter Frahm deep within a cushion of ***Distichium capillaceum*** (Figure 25).

Figure 25. ***Distichium capillaceum*** with a snail nestled deep within the cushion. Photo by Jan-Peter Frahm, with permission.

Truncatellina cylindrica (Figure 26) is another very small snail. Where it lives at Groomsport, Down, UK, it occurs in yellow dunes among mosses and the roots of vegetation on drier, sunny slopes (Anderson 1996).

Figure 26. ***Truncatella cylindrica*** on ***Tortula*** sp. Note the small size of this conical snail. Photo by Stefan Haller, with permission.

Szlavecz (1986) determined that snail size plays an important role in their behavior, including food searching. Although one might think that larger animals need to eat more, it seems that the larger ***Monadenia hillebrandi mariposa*** (Figure 27) 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 28). This snail lives in cool, mossy forests and sometimes hibernates among mosses, including thick moss on a bigleaf maple branch (Sandelin 2012).

Figure 27. ***Monadenia hillebrandi***, a consumer of the mosses ***Rhytidiadelphus*** sp. and ***Grimmia trichophylla***. Photo by John Slapcinsky, through Creative Commons.

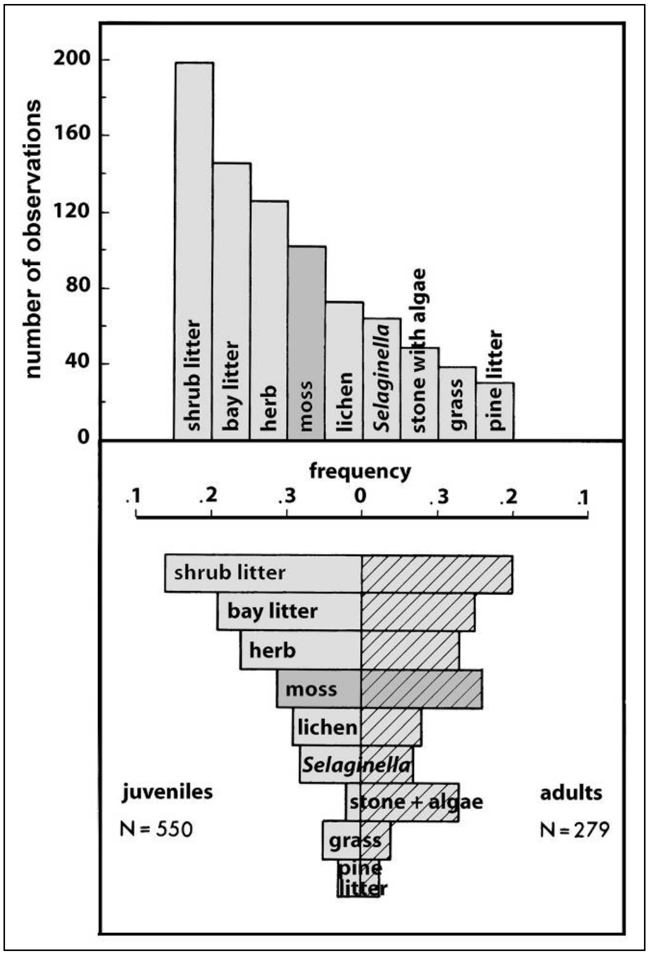

Figure 28. Laboratory selection of foods by the snail ***Monadenia hillebrandi mariposa***. **Upper**: all data combined. **Lower:** juveniles vs adults. Redrawn from Szlavecz 1986.

Monadenia fidelis (Figure 29) lives in dry forests as well as prairie wetlands where its presence is indicative of an unburned prairie (Severns 2005). Loubser *et al*. (2005) found it associated with nearby mosses in 33% of their samples. But like many observations of animals with bryophytes, this may mean that they need bryophytes in their habitat, that they prefer the same habitats as bryophytes, or that the relationship is coincidental – the bryophytes are near something they need. In this case, mosses are one of its winter hibernating sites, where they hibernate under mosses in crotches of maple trees (Monadenia 2016).

Figure 29. ***Monadenia fidelis*** (Pacific sideband snail) on mosses. Photo by Walter Siegmund through Wikipedia Commons.

Conical Shape

The terrestrial conical snails, or at least the smaller of these snails, seem to be more suited to traversing the internal spaces of bryophytes. ***Cochlicopa lubrica*** (Figure 30) and ***Cochlicopa lubricella*** (Figure 31), moss snails, have been known from mosses for a long time. In 1840 Turton reported these snails from mosses and grass on the ground and under stones in the British Isles.

Figure 30. ***Cochlicopa lubrica*** on mosses. Photo by Malcolm Storey, through Creative Commons.

Figure 31. ***Cochlicopa lubricella***, moss snail, on mosses. Photo © Roy Anderson <habitas.org.uk>, with permission.

Turton (1840) also reported another tiny conical snail, ***Ena obscura*** (Figure 32), from mosses and under stones. But this snail has another way to be elusive from would-be predators. It covers itself with mud or debris, rendering it nearly invisible by hiding the shiny shell (The Great Snail Hunt 2012), but might it also provide a means of controlling water loss or temperature?

Figure 32. ***Ena obscura***, a snail that lives in forests or on walls, under stones and moss (Turton 1840) in the Sulehay, Northants, UK. It covers itself with mud as camouflage. Photo by Roger S. Key, with permission.

Avoiding Desiccation

Bryophytes remain moist long after their epiphytic and rock substrata, and even those on dry soil can become moist, collecting fog or light rainfall that never reaches the soil. Hence, they can become a refuge for snails and slugs seeking moisture. Such is often the case for the banana slug, ***Ariolimax columbianus*** (Figure 15), in the Pacific lowlands, USA. This slug leaves its moist cover on a moss-covered fallen log to forage at night, then returns to the moss (Sandelin 2012). Taking advantage of the

moisture at night, this slug can travel nearly 0.5 km in search of more suitable conditions.

The large (up to 13-15 cm) bryophyte-dwelling slug ***Arion ater*** (Figure 33-Figure 35) forms a ball by contracting its body and humping up (Figure 34) (Sandelin 2012). That reduces its surface area and thus reduces water loss. It can also twist on itself to reduce exposed surface area (Figure 35). This twisting ability is probably also helpful as it climbs moss setae and feeds on the capsules.

Figure 33. Black form of ***Arion ater*** in an extended position. Photo by David Perez, through GNU Free Documentation.

Figure 34. Black form of ***Arion ater*** forming a ball by contracting and humping up. Photo by Emőke Dénes, through Wikimedia Commons.

Figure 35. ***Arion ater*** juvenile contracting on itself. Photo © Roy Anderson <habitas.org.uk>, with permission

Bryophytes can offer the snails and slugs yet another means to escape drought and extreme heat or cold. These gastropods can **hibernate** in cold temperatures or **aestivate** in heat or drought (Boss 1974), and this sometimes occurs among bryophytes. Some snails remain dormant for as many as five or six years. Boss suggests that the ability to hibernate and aestivate may play a strong role in the expansion of geographic range, speciation, and extinction.

The European snail species ***Fruticicola fruticum*** (=*Eulota fruticum*, *Bradybaena fruticum*; Figure 36) hibernates from October until a time in spring when the weather is suitable for it to become active (Künkel 1928). It accomplishes this hibernation in dead moss or it may burrow into the ground with its aperture facing upward.

Figure 36. ***Fruticicola fruticum*** with ***Polytrichum*** nearby. Photo by Michael Becker, through Wikimedia Commons.

No Shell – Slugs

Slugs can be somewhat common on bryophytes and seem to have the same adaptations as snails. Their only advantage would seem to be greater flexibility due to the absence of a hardened and bulky shell, but that brings with it a greater chance for desiccation. For that reason, bryophytes may be a source of hydration. For many species, being small helps in permitting them to hide from predators and to maneuver among the bryophytes (Figure 37).

Figure 37. Keeled slug (***Tandonia budapestensis***), common inhabitant of mosses such as this ***Leucolepis*** in the Pacific Northwest, USA. Photo courtesy of Jeri Peck.

The **Limacidae** is a family of slugs, and both common genera (***Deroceras***, ***Limax***) have members that have been found among mosses. In the sub-Antarctic Marion Island, the slug ***Deroceras panormitanum*** (Figure 38; originally described as the separate species ***D. caruanae***) lives in moist bryophyte communities as well as on decaying bryophytes (Smith 1992). With a totally exposed body, slugs in such harsh environments can find shelter and moisture among the bryophytes.

Figure 38. ***Deroceras panormitanum*** on what appears to be a species of the moss ***Campylopus.*** Photo © Roy Anderson <habitas.org.uk>, with permission.

Brain Eversham (pers. comm. 21 March 2012) tells me that the yellow slugs, ***Limax flavus*** (=***Limacus flavus***; Figure 39) and ***L. maculatus*** (Figure 40), live mainly on old walls in Britain, where, like many snails, they are night active. They feed primarily on lichens and algae, but will graze on dead plant material if they run out of lichens. They don't generally eat leafy mosses, but they will browse on the capsules. He has observed ***Tortula muralis*** (Figure 41) and ***Grimmia pulvinata*** (Figure 42) with the setae remaining but all the capsules nibbled off. Ken Adams (Bryonet 18 March 2020) reports that capsules of ***Codonoblepharon forsteri*** (=*Zygodon forsteri*) where he does fieldwork in the UK are mostly eaten before they mature (Figure 43). Eversham suggests that the capsules and spores of bryophytes are more nutritious or more digestible than the leaves and stems.

Figure 39. ***Limax flavus*** on a bed of mosses. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 40. ***Limax maculatus*** on moss at Bridge House, Swavesey, UK. Photo by Brian Eversham, with permission.

Figure 41. ***Tortula muralis***, a species whose capsules serve as food for species of ***Limax***. Photo by Michael Lüth, with permission.

Figure 42. ***Grimmia pulvinata*** with capsules and awns. Photo by Michael Lüth, with permission.

Figure 43. ***Codonoblepharon forsteri*** with young capsules and seta from capsules that were probably lost to herbivory. Photo by Michael Lüth. with permission.

In Search of Food

As just described for two species of ***Limax*** (Figure 39-Figure 40), snails and slugs may browse on bryophytes. They have a rasping tongue (**radula**) that destroys the epidermis of tracheophytes (Grime & Blythe 1969), but what does it do to moss leaves only one cell thick? Apparently in some cases it makes mosses potential food (Szlavecz 1986), and enables some gastropods to consume even the tough capsule (Davidson & Longton 1987, Davidson *et al*. 1990).

Low Palatability?

Often it appears that the palatability index for bryophytes is low (Jennings & Barkham 1975). Furthermore, snails and slugs seem to be less interested in grazing things with awns than those without. Robin Stevenson (pers. comm. January 2008) has seen ***Bryum argenteum*** (Figure 44-Figure 45) that is completely grazed over, but never observed such grazing on an awned ***Grimmia*** species (Figure 42). Could it just be that there is no nutrition in an awn, or do they have trouble gliding across the furry tips of leaves?

Figure 44. ***Bryum argenteum***, a moss with no awns and a food source for snails and slugs. Photo by Michael Lüth, with permission.

Figure 45. ***Bryum argenteum*** showing lack of awns. Photo from UBC website, with permission from Shona Ellis.

But awns, even in ***Grimmia pulvinata*** (Figure 46), may not deter all snails (Figure 46). Szlavecz (1986) was able to identify the awned ***Grimmia trichophylla*** (Figure 47) in feces of the California snail, ***Monadenia hillebrandi mariposa*** (Figure 27) and also demonstrated that the spine tips of the tracheophyte *Selaginella hansenii* (Hansen's spikemoss; Figure 48) did not deter feeding or crawling. Perhaps it depends on the density of the hair tips, since ***Grimmia trichophylla*** (Figure 47) and *S. hansenii* (Figure 48) have much less dense hairs than ***G. pulvinata*** (Figure 46), and on the particular species and size of snail or slug. On the other hand, it appears that the slugs are able to graze the lower margins of a clump, apparently resting on the substrate without the need to traverse the awns (Figure 46).

Figure 46. ***Grimmia pulvinata*** exhibiting grazing that girdles the base of the clump in a pattern typical of snail or slug grazing, but also known for isopods. Photo by Robin Stevenson, with permission.

Figure 47. ***Grimmia trichophylla*** in Bretagne (Brittany), France, showing somewhat less imposing awns than those of ***Grimmia pulvinata***. Photo by Michael Lüth, with permission.

Figure 48. ***Selaginella hansenii***, a spine-tipped tracheophyte eaten by the snail ***Monadenia hillebrandi mariposa***. Photo by J. E. (Jed) and Bonnie McClellan, © California Academy of Sciences, with permission.

Michael Lüth has observed snails grazing on ***Orthotrichum*** (Figure 49) and Terry McIntosh has seen slugs grazing on other bryophytes, with both observers indicating that the damage to the moss was similar to that shown for ***Grimmia pulvinata*** in Figure 46 (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 in this case, after climbing up a bridge coping, the snail or whatever might have found that this moss provided the best choice available.

Figure 49. ***Orthotrichum urnigerum***, member of a genus known to be grazed by snails. Photo by Michael Lüth, with permission.

Low Nutritional Quality?

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 involuta*** (Figure 50). In their laboratory experiments, the snails (***Limicolaria aurora***; Figure 51) gained the most weight when fed with ***Hyophila involuta*** paste. The snails that had only unground moss actually lost weight. Those in the field experiment (restricted to ***Hyophila involuta***) 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 of the moss 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. Rather, the researchers suggest that the snails most likely use the moss as a moist and cool habitat.

Oyesiku and Bello (2012) experimented further with the effect of the moss ***Hyophila involuta*** (Figure 50) as a food for the snail ***Limicolaria aurora*** (Figure 51). The study was based on an interest in including mosses as feed when breeding snails. The moss was mixed in various ratios with corn pap powders (*Zea mays*). Overall, there was a significant correlation with the feed ratios of decreasing order of moss 50%:corn 50% > moss 25%:corn 75% > moss 0%:corn 100% > moss 100%:corn 0% > moss 75%:corn 25%. The highest weight gain of 15 g peaked at the fourth day in ***L. aurora*** fed with moss 50%:corn 50%. Furthermore, the snails exhibited a strong positive weight gain correlation with increasing days of feeding with 25% moss to 75% corn.

Figure 50. ***Hyophila involuta***, with a snail; the snail ***Limicolaria aurora*** can thrive on this moss. Photo by Li Zhang, with permission.

Figure 51. Shell of ***Limicolaria aurora***. Photo by David G. Robinson, USDA APHIS PPQ at Bugwood.org, through public domain.

Chemical Deterrents to Herbivory

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 annual ***Funaria hygrometrica*** (Figure 52) than on perennial ***Brachythecium rutabulum*** (Figure 66) or ***Mnium hornum*** (Figure 80). The phenolic compounds in the latter two species were 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*** supports the general theory that perennials invest more resources in defense against herbivory than do annuals such as ***F. hygrometrica***.

Figure 52. Young sporophytes of ***Funaria hygrometrica*** before spores form. Photo by Michael Lüth, with permission.

Food for Some

Clearly for some slugs and snails there are bryophytes that do indeed seem palatable. Ochi (1960) reported that the thallose liverwort ***Conocephalum conicum*** (Figure 53) served as food for a slug. Merrifield (2000) found evidence of heavy grazing on epiphytic bryophytes, particularly the moss ***Syntrichia laevipila*** (Figure 54), 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 on ***S. laevipila*** may be a response to this grazing.

Figure 53. ***Conocephalum conicum*** showing feeding damage upper middle) by something, perhaps a slug. Photo by John Hribljan, with permission.

Figure 54. ***Syntrichia laevipila*** on bark. Photo by Jonathan Sleath, with permission.

Algae growing on mosses, especially in the aquatic habitat, could be a prominent source of food for gastropods. 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. ***Sphincterochila boissieri*** (Figure 55) feeds on shrubs there, but its feces indicate that it also feeds on the moss ***Tortula atrovirens*** (=***Desmatodon convolutus***; Figure 56) (Yom-Tov & Galun 1971). This is a snail that has color morphs of brown and white, but they apparently don't affect its temperature (Yom-Tov 1971; Slottow *et al*. 1993). However, their rodent predators choose more brown than white snails, enough to exhibit significant differences in their choices (Slottow *et al*. 1993).

Figure 55. ***Sphincterochila boissieri***, a species that is known to eat ***Tortula atrovirens*** in the Negev desert. Photo by Mark A. Wilson, through Creative Commons.

Figure 56. ***Tortula atrovirens***, a moss that is eaten by the Negev Desert snail, ***Trochoidea seetzeni***. Photo by Des Callaghan, with permission.

Szlavecz (1986) examined feeding preferences in 31 individuals of the snail ***Monadenia hillebrandi mariposa*** (Figure 27). Collections of field feces indicated that they consumed the mosses ***Rhytidiadelphus*** sp. (Figure 57) and ***Grimmia trichophylla*** (Figure 58) 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. More green moss than brown occurred in the feces, whereas brown material was more common from consumed tracheophytes (Figure 59).

Figure 57. ***Rhytidiadelphus squarrosus***, a member of a genus that has been found in feces of the snail ***Monadenia hillebrandi mariposa***. Photo by Michael Lüth, with permission.

Figure 58. ***Grimmia trichophylla*** showing awns. Photo by Michael Lüth, with permission.

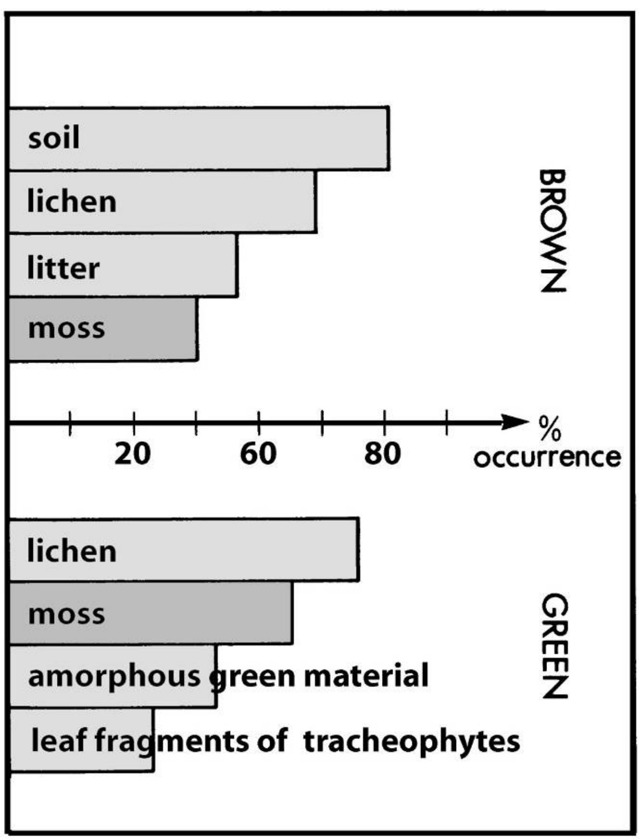

Figure 59. Comparison of green and brown portions of plant material eaten by the **snail *Monadenia hillebrandi mariposa***. Modified from Szlavecz 1986.

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. Studies by Chatfield (1973), Williamson & Cameron (1976), and Richter (1976) indicate that at least juvenile snails might do best on a mixed diet. But for ***Cepaea nemoralis*** (Figure 60-Figure 61), it appears that even though mosses are part of their habitat, they are seldom part of the diet (Williamson & Cameron 1976).

Figure 60. ***Cepaea nemoralis***, banded snail juvenile at Old Sulehay Forest, UK, a species that lives in a mossy habitat but apparently does not eat them. Photo by Brian Eversham, with permission.

Figure 61. ***Cepaea nemoralis***, a species that lives in a mossy habitat but apparently does not eat them. Photo by Stefan Haller, with permission.

In the tropical montane rainforest of Brazil, those small, flattened snails in the **Charopidae** (Figure 62) eat bryophytes (Maciel-Silva & dos Santos 2011). Both ***Canalohypopterygium tamariscinum*** (syn. = ***Hypopterygium tamarisci***; Figure 63) and ***Lopidium concinnum*** (Figure 64) had evidence of leaf herbivory, mostly in the beginning of the rainy season (September to December). A species of snail in the **Charopidae** and a moth larva in the **Geometridae** were the culprits. Using an index of damage (ID) in 2007, 2008, Maciel-Silva and dos Santos found that ***C. tamariscinum*** had higher damage (68%, 35%) than ***L. concinnum*** (38%, 23%) in these two years (Figure 65). These rates were lower than those for

tracheophytes. They found no correlation with phenols, proteins, or the ratio between them (Figure 65).

Figure 62. **Charopidae** feeding on ***Lopidium concinnum*** from an Atlantic Forest, Brazil. Photo by Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

Figure 63. ***Canalohypopterygium tamariscinum***, a food source for **Charopidae**. Photo by Niels Klazenga, with permission.

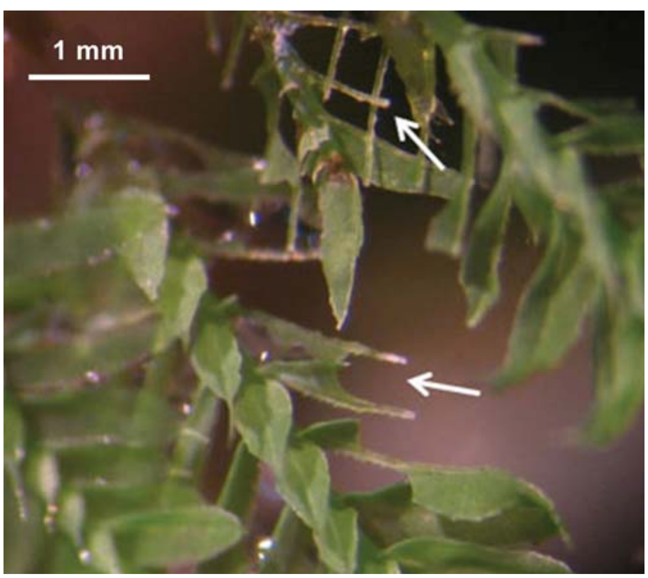

Figure 64. Evidence of **Charopidae** herbivory on ***Lopidium concinnum*** from an Atlantic Forest, Brazil. Photo by Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

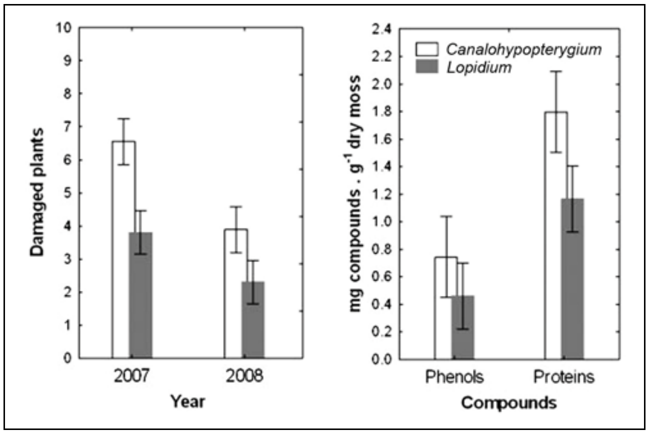

Figure 65. **Charopidae** and **Geometridae** damage to mosses in 10 colonies of plants. Image from Adaises Maciel-Silva and Nivea Dias dos Santos.

An Avoidance of Gametophores?

Davidson and Longton (1985, 1987; Davidson 1988, 1989) reported that several species of generalist slugs consumed bryophytes. In some cases, the **protonema** (threadlike stage that develops from moss spore) is readily consumed (Grime 1979). In Great Britain, capsules and protonemata of several mosses [***Brachythecium rutabulum*** (Figure 66), ***Mnium hornum*** (Figure 67-Figure 68), and ***Funaria hygrometrica*** (Figure 69)] were eaten preferentially to leafy gametophores by slug species in the genus ***Arion*** (Figure 70) (Davidson & Longton 1987; Davidson *et al*. 1990). Cambs (2012) found that the slug ***Limax maculatus*** (Figure 40) likewise would eat capsules, but the leafy parts seemed to serve only as an emergency food. It appears that some may even eat **calyptrae** (covering over capsule; Figure 71). **Ferulic acid**, present in shoots but absent in young capsules of ***Mnium hornum***, is a phenolic compound that is only released after severe hydrolysis. Its antibiotic role as an antifungal agent (Sarma & Singh 2003) and in antiherbivory (Seigler 1983; Smith 2011) may contribute to this preference for capsules, as discussed below. Davidson and coworkers found that older capsules with spores were less preferred than the green ones (Figure 72; Davidson & Longton 1987; Davidson *et al*. 1990).

Figure 66. Slug eating capsules of ***Brachythecium***. Note the number of setae that are missing capsules. Photo by Janice Glime.

Figure 67. Young, green capsules of ***Mnium hornum*** that are preferred by ***Arion* slugs**. Photo by Michael Lüth, with permission.

Figure 68. Mature capsules of ***Mnium hornum***. Photo by Janice Glime.

Figure 69. Capsules of ***Funaria hygrometrica*** – potential snail food. Photo by Michael Lüth, with permission.

Figure 70. ***Arion rufus*** on mosses in a woodland above Poole's Cavern, Buxton, UK. Photo by Brian Eversham, with permission.

Figure 71. Slug on moss calyptra, apparently finding something to eat. Photo courtesy of Sarah Lloyd..

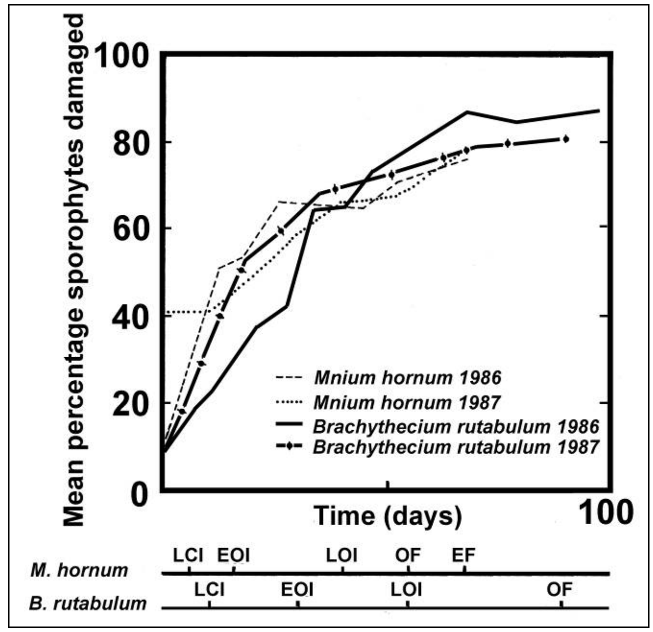

Figure 72. Relative damage by slugs (***Arion*** spp.) of sporophyte stages of two species of bryophytes. n=300-500 at day 0. **LCI** = late calyptra stage; **EOI** = early operculum intact; **LOI** = late operculum intact; **OF =** operculum fallen; **EF** = empty and fresh. Redrawn from Davidson *et al*. 1990.

Davidson (1989) found that slugs consumed only trivial amounts of ***Brachythecium rutabulum*** shoots (Figure 66). ***Mnium hornum*** (Figure 80) was also ignored, but after 5-7 days of starvation ***Arion rufus*** (10-15 cm long; Figure 73) and ***A. subfuscus*** (5-7 cm long; Figure 74) ate significant quantities of shoots of this species. The garden slug ***Arion hortensis*** (Figure 75) still ignored the moss even after 7 days of starvation.

Figure 73. ***Arion rufus*** on a bed of mosses. Photo by Jean Bisetti, with permission.

Figure 74. ***Arion subfuscus***, a slug known to consume ***Mnium hornum***. Photo by Gary Bernon, USDA APHIS at Bugwood.org, through public domain.

Figure 75. ***Arion hortensis*** *s.s.* at Bridge House, Swavesey, UK. Photo by Brian Eversham, with permission.

Given the choice of capsules or vegetative material, both ***Arion rufus*** (Figure 3, Figure 70, Figure 73) and ***A. subfuscus*** (Figure 76) preferred immature capsules (see Figure 77 with a slug on immature capsules of ***Leucolepis acanthoneuron***) of all three mosses, with ***Mnium hornum*** (Figure 80) being top choice (Davidson 1989). Setae were generally ignored, but ***A. subfuscus*** did occasionally eat ***M. hornum*** and ***Brachythecium rutabulum*** (Figure 66) setae. All three slugs also ate protonemata in the laboratory, and for ***B. rutabulum*** and ***Funaria hygrometrica*** (Figure 52) the protonemata were 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 76. ***Arion subfuscus***, a slug that prefers immature capsules. Photo by Sanja 565658, through Creative Commons.

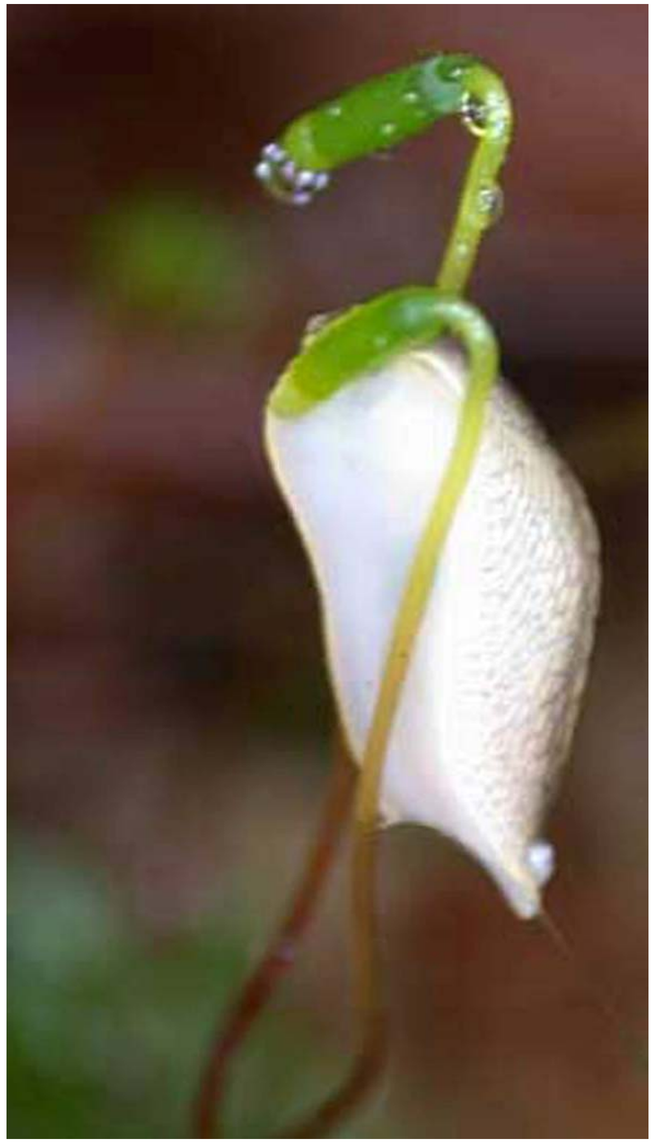

Figure 77. Slug browsing on immature capsule of the moss ***Leucolepis acanthoneuron***. Photo from UBC website, with permission.

Davidson and Longton (1987) suggested that ***Arion hortensis*** (Figure 75) was restricted by the physical structure of the capsule to consuming developing spores from broken capsules in ***Polytrichum commune*** (Figure 78); no spores were eaten from unbroken capsules. When approaching ***Mnium hornum*** (Figure 80), 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*** (Figure 66) 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 acids 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.

Figure 78. ***Polytrichum commune*** capsules showing the persistent hairy calyptra and waxy capsule that is only eaten by snails when the capsule is broken. Photo by Michael Lüth, with permission.

Presence of moss cells of ***Brachythecium rutabulum*** (Figure 79) and ***Mnium hornum*** (Figure 80-Figure 81) in the feces of previously starved ***Arion*** suggest that the leafy mosses are not digested well (Davidson *et al*. 1990). On the other hand, all three species of slugs named above readily consumed ***Funaria hygrometrica*** (0.4-6.5 mg wet weight per slug; Figure 69) in overnight feeding trials. The importance of mosses as food may rest with the organisms living on the mosses – fungi, bacteria, protozoa, rotifers, *etc*., making indigestibility of the mosses inconsequential.

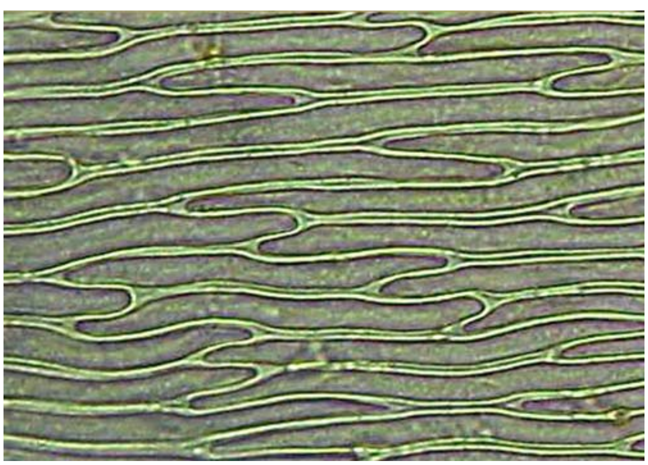

Figure 79. ***Brachythecium rutabulum*** cells as they might be seen in feces. Photo by Tom Thekathyil, with permission.

Mostly indirect evidence suggests that slugs and snails graze capsules of ***Buxbaumia viridis*** (Figure 84) (Gordon Rothero, Birds feeding on moss capsules, Bryonet-l, 10 April 2003; Figure 84). Michael Lüth (Bryonet 23 September 2017) observed and photographed a slug grazing on the capsule of ***Buxbaumia viridis*** (Figure 83). Dave Kofranek reports tasting it – to him it tastes like cucumbers (Bryonet 24 September 2017). Infante Sánchez and Heras Pérez (2015) exlored the herbivory on capsules of ***Buxbaumia viridis*** (Figure 84). They found three types of damage on the sporophytes. In one type the seta and lower part of the capsule remain. For this type, they actually observed slugs feeding on the capsules; the same kind of slug was also feeding on young green capsules of ***Herzogiella seligeri*** (Figure 85). In a second type, the entire capsule is gone, but the seta remains. This could have been slugs as well, but they were unable to observe them and considered that ants or birds might also feed on them. The capsules are grazed in spring before they mature, thus likely being unable to accomplish a successful dispersal. The third type was destruction by a fungus, causing abortion of the capsule development.

Figure 80. ***Mnium hornum*** shoots – a species that was ignored in experiments until the slugs were starved. Photo by Janice Glime.

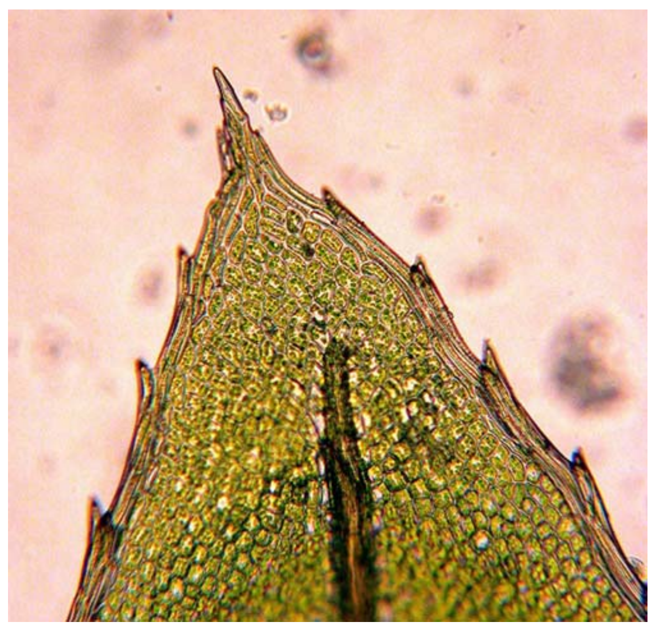

Figure 81. ***Mnium hornum*** leaf tip cells, what one might see in feces. Photo by Bob Klips, with permission.

It is perhaps not surprising that snails eat the capsules of ***Splachnum*** (Figure 82). This genus has odors that attract flies, so they may serve as attractants to gastropods as well. However, no studies have attempted to test this hypothesis with snails.

Figure 82. Snail on setae of ***Splachnum*** capsules in Alaska, eating capsules. Photo courtesy of Blanka Shaw.

Figure 83. ***Buxbaumia viridis*** with slug eating capsule. Photo by Michael Lüth, with permission.

Figure 84. ***Buxbaumia viridis*** capsules. Note that the leafy part belongs to another species of moss. Photo by Adolf Ceska, with permission.

Figure 85. ***Herzogiella seligeri*** with capsules, a species in which young capsules are eaten by slugs. Photo by Hermann Schachner, through Creative Commons.

Guy Brassard reported to me that Stéphane Leclerc has taken a picture of a slug in Quebec, Canada, eating a ***Buxbaumia aphylla*** (Figure 86-Figure 88) capsule!

Figure 86. ***Buxbaumia aphylla*** that are immature and have not been eaten. Photo by Štěpán Koval, with permission.

Stark (1860) relayed a story of the ill fate of collected specimens of ***Buxbaumia aphylla*** (bug-on-a-stick moss; Figure 87) on their journey from Scotland to England. A slug had inadvertently been included in the package and it managed to destroy their prized specimens. On the other hand, ***B. aphylla*** can fool you. After repeated observations with my graduate student, Chang-Liang Liao, we have discovered in the field 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 (Figure 87), and that this occurs on nearly every capsule.

Figure 87. ***Buxbaumia aphylla*** showing exposed green spores in the capsule that has split open. Photo by Janice Glime.

Figure 88. ***Buxbaumia aphylla*** that may have been damaged by a herbivore. Photo by Janice Glime.

Slugs also eat hornworts (**Anthocerotophyta**; Figure 89). Bisang (1996) reported that they especially eat the green sporophytes.

Figure 89. ***Phaeoceros carolinianus***, a hornwort with mostly green sporophytes, a food source for slugs. Photo by Michael Lüth, with permission.

Digestibility

So 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 intact. 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 protonemata seemed to be digestible, resembling the lettuce and carrots in being macerated and colorless or brown.

Caution must be used in conducting laboratory experiments with food choices. 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. The wider range of choices in the field may permit them to avoid the less palatable bryophytes.

Role in Bryophyte Competition with Lichens

Rosso and McCune (2003) found that molluscs 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 mollusc herbivory on lichens (Boch *et al.* 2011) may benefit the bryophytes by contributing to the successful competition of the bryophytes over the lichens in the understory of these forests.

Palatable Gametophytes

Des Callaghan (Bryonet 10 June 2011) reports slugs feasting on the gametophytes of ***Hookeria lucens*** (Figure 90) near a stream. In only six days they completely removed all the plants by dining on them, leaving behind only a stump and a slime trail (Figure 91). This was a research station, so Callaghan needed to find a way to discourage the slugs. Suggestions from Bryonetters included sprinkling ground glass around the study area (Michael Richardson, Bryonet 10 June 2011); putting out cups of beer to attract and drown the slugs or putting curry powder or other hot substance around the mosses (Janice Glime, Bryonet 10 June 2011); copper rings that are effective in gardens and could be made with a coil of wire (David Bell, Bryonet 10 June 2011).

Figure 90. ***Hookeria lucens*** in healthy condition. Photo by Des Callaghan, with permission.

Figure 91. Temperature/humidity data logger with ***Hookeria lucens*** eaten by slugs. Photo by Des Callaghan, with permission.

Annie Martin (Bryonet 11 June 2011) is a professional gardener and described her experience in trying to eliminate slugs. She suggested putting salt on the head (if put on the tail the slug continues to live and eat). Her experience with beer is that it just keeps on attracting snails night after night, even though many of them drown, so it is an ineffective waste of money. Brown mulch seems to provide a favorable habitat, so she eliminated it, a technique that worked, but isn't relevant for discouraging snails on mossy rocks.

Aquatic Grazing

Grazing by gastropods (slugs and snails) can be so severe as to define distribution of a bryophyte species. Lohammar (1954) found that in northern Europe ***Fissidens fontanus*** (Figure 92) was absent in lakes where ***Fontinalis antipyretica*** (Figure 93) was also absent. Gerson (1982) suggested that scarcity of ***Fissidens*** in some places is due to snail grazing. 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 and the density of the ***Fontinalis*** stems.

Figure 92. ***Fissidens fontanus***, a moss that seems to be vulnerable to snail grazing except where it is protected by ***Fontinalis*** species. Photo by Michael Lüth, modified by Janice Glime, with permission.

Figure 93. ***Fontinalis antipyretica***, a moss that apparently protects the smaller ***Fissidens*** from grazing by snails. Photo by Bernd Haynold, through Wikimedia Commons.

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. The thallose liverwort ***Ricciocarpos natans*** (Figure 94) exhibits molluscicidal properties that are active against the snail carrier of **schistosomiasis** (Wurzel *et al*. 1990).

Figure 94. ***Ricciocarpos natans***, a species with molluscicidal properties, floating on the water surface. Photo by Janice Glime.

Bryophyte Antifeedants

Based on the foregoing discussion, it appears that at least some bryophytes are able to discourage browsing by slugs (Frahm & Kirchhoff 2002). Alcohol extracts of the moss ***Neckera crispa*** (Figure 95) and leafy liverwort ***Porella obtusata*** (Figure 96) have antifeedant activity against the slug ***Arion lusitanicus*** (Figure 97). Extracts of 0.5% dry weight of the moss had low activity, whereas

those from the liverwort exhibited moderate activity at only 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 95. ***Neckera crispa***, a moss that has antifeedant activity against the slug ***Arion lusitanicus***. Photo by Michael Lüth, with permission.

Figure 96. ***Porella obtusata***. Photo by Jan-Peter Frahm, with permission.

Figure 97. ***Arion lusitanicus***, a slug that traverses mosses, but finds ***Neckera crispa*** and ***Porella obtusata*** unpalatable. Photo by Mogens Engelund, through Wikipedia Commons.

On the other hand, ***Arion lusitanicus*** (Figure 97), also known as the murder slug, easily eats the thallose liverwort ***Marchantia polymorpha*** (Figure 98) (Nils Cronberg, Bryonet 7 April 2016). Cronberg has observed this species feeding on ***Marchantia*** and has noticed that as the slug had invaded the wetland, ***Marchantia polymorpha*** had disappeared in parallel with the invasion.

Figure 98. ***Marchantia polymorpha*** showing a nibbled thallus on the upper left, about 1/3 down and 1/3 over from the corner. It also has a tear that is not likely the result of herbivory. Photo by James K. Lindsey, with permission.

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 99) leave a trail of mucous as they go, and as you well know if you have handled these molluscs, this secretion can be sticky. It is therefore no surprise that these animals have dispersal abilities.

Figure 99. 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 ***Dicranum flagellare*** (Figure 100) (Kimmerer & Young 1995). 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.

Figure 100. ***Dicranum flagellare*** showing the tight flagellate branches that can be dispersed by **slugs**. Photo by Janice Glime.

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 of spores through the slug's digestive system may enhance germination success. All plates containing mature spores from slug (***Arion*** spp.; Figure 97) fecal pellets produced shoots, whereas only 80% of the plates with uneaten mature ***Mnium hornum*** (Figure 67-Figure 68) spores and 70% of those with uneaten ***Brachythecium rutabulum*** (Figure 101) spores produced shoots.

Figure 101. ***Brachythecium rutabulum***, for which the spores germinate better if they have passed through the gut of a slug (***Arion***). Photo by Michael Lüth, with permission.

For those snails and slugs that nibble on spores, one might assume that not all spores end up inside them. Unless they have perfect aim with that huge foot, their somewhat clumsy feeding method is undoubtedly going to render some spores as passengers in the mucous on the foot. Sooner or later, these will be deposited in a new location.

The ability of snails and slugs to glide across bryophytes and to climb setae to capsules suggests that these animals may be important as dispersal agents. But how widespread are herbivory and dispersal among bryophytes that temporarily host these slow-moving animals?

Although we know that bryophyte spores reach the mollusc gut, experiments are needed to see if spores expelled in feces are able to colonize successfully. Davidson (1989) found that ***Brachythecium rutabulum*** (Figure 101) and ***Mnium hornum*** (Figure 80) spores eaten by ***Arion*** species actually germinated better than controls.

Manfred Türke sent me images of mosses in the feces of the slug ***Arion vulgaris*** (Figure 102). I was amazed at the size of the fragment of moss in the feces (Figure 103-Figure 104). This is a potential means for dispersal, but the various species of bryophytes must be tested for viability. Digestive enzymes and extreme *p*H could damage the moss cells. On the other hand, the pathogenic fungi ***Phytophora*** spp. (Figure 105) survive as both oospores and filaments and are viable after passing through the digestive system of this slug species (Telfer *et al*. 2015). This was demonstrated by culturing the feces on agar.

Figure 102. ***Arion vulgaris***, a slug that eats mosses, potentially dispersing them. Photo by Dilian Georgiev through Creative Commons.

Figure 103. ***Arion vulgaris*** feces with bryophytes and other material in it. Photo courtesy of Manfred Türke.

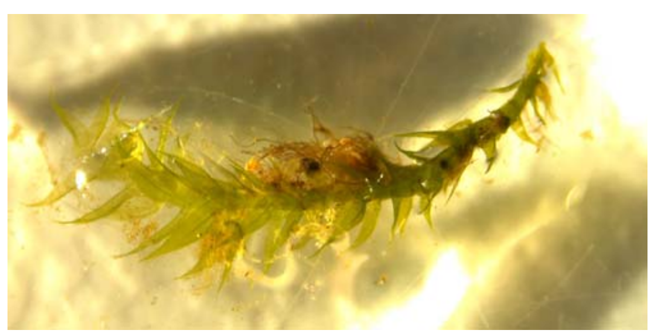

Figure 104. ***Arion vulgaris*** bryophyte from slug feces. Photo courtesy of Manfred Türke.

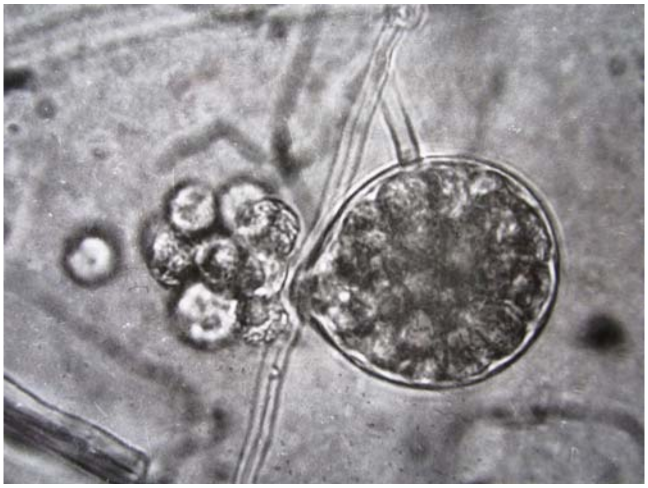

Figure 105. ***Phytophthora parasitica*** zoosporangia, a genus that survives passage through the gut of ***Arion vulgaris***. Photo by Tashkoskip, through Creative Commons.

Figure 107. ***Leptobryum pyriforme*** with capsules. Spores are able to pass through the guts of at least some slugs and remain viable. Photo by Michael Lüth, with permission.

To provide additional information on the potential dispersal ability of slug feces, Boch *et al*. (2013) fed capsules of four bryophyte species [***Bryum pallescens*** (Figure 106), ***Funaria hygrometrica*** (Figure 69), ***Leptobryum pyriforme*** (Figure 107), ***Pellia endiviifolia*** (Figure 108)] to three slug species [***Arion vulgaris*** (Figure 102), ***A. rufus***; Figure 3, Figure 70, Figure 73), ***Limax cinereoniger*** (Figure 109)]. Among the 117 bryophyte samples, 51.3 % of the spore cultures had germination following gut passage.

Figure 108. ***Pellia endiviifolia*** with sporophytes. The spores of this species are able to pass through the gut of several slug species and remain viable. Photo by Janice Glime.

Figure 106. ***Bryum pallescens*** with capsules. Spores of this species pass through the guts of several slugs and retain their viability. Photo by David T. Holyoak, with permission.

Figure 109. ***Limax cinereoniger*** on a mat of moss. Photo by Michal Maňas through Creative Commons.

Boch *et al*. (2013) found that germination rates did not differ among the bryophyte species, but the species of slug

had strong effects. Among these three slugs, ***Limax cinereoniger*** (Figure 109) ate the lowest percentage of the bryophytes provided, and even correcting for that, they had the lowest percentage of feces samples (12.9%) producing protonemata. On the other hand, 76% of those of ***Arion vulgaris*** (Figure 102) and 74% of those of ***Arion rufus*** (Figure 3, Figure 70, Figure 73) produced protonemata (Figure 110).

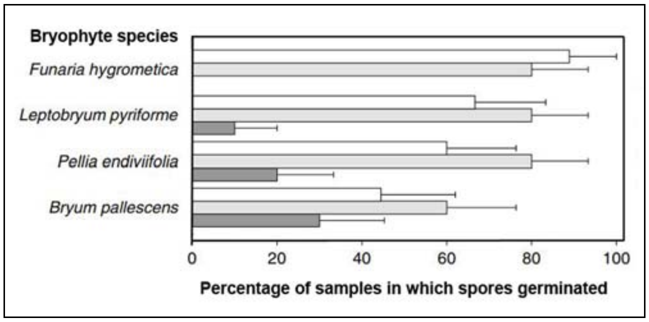

Figure 110. Comparison of spore germination from bryophytes cultured from the feces of three species of slugs. White bars = ***Arion rufus***; light grey bar = ***Arion vulgaris***, dark grey bar = ***Limax cinereoniger***. Redrawn from Boch *et al*. (2013).

Türke *et al*. (2013) provide evidence that slugs do indeed disperse fragments of mosses by consuming spores and fragments. For tracheophyte seeds, they suggested an average of 5 m dispersal distance, exceeding the typical less than 1 m in dispersal by ants. In some slugs, the seeds are destroyed in the digestive tract, but in other cases they remain viable propagules.

Boch *et al*. (2015) discussed several ways that slugs benefit bryophytes. Their herbivory on tracheophytes (lignified vascular plants) permits more light to reach the low-growing bryophytes. But they also crawl across bryophytes and some eat the bryophytes. This puts them in the position to disperse spores, fragments, and other propagules.

Nevertheless, documentation of the effect of the slugs on the bryophyte community is meager. Boch and coworkers (2015) designed a factorial common garden experiment to determine some of the effects of slugs on the bryophyte vegetation. They collected sporophytes of 11 native and 1 invasive bryophyte species [***Barbula convoluta*** (Figure 111), ***Brachythecium rutabulum*** (Figure 101), ***Brachythecium velutinum*** (Figure 112), ***Bryum*** sp. (Figure 106), ***Campylopus introflexus*** (Figure 113), ***Ceratodon purpureus*** (Figure 114), ***Funaria hygrometrica*** (Figure 69), ***Leptobryum pyriforme*** (Figure 115), ***Marchantia polymorpha*** (Figure 98), ***Phascum cuspidatum*** (Figure 116), ***Plagiomnium affine*** agg. (Figure 117), ***Pohlia*** sp. (Figure 118)], representing 8 families. They used three enclosure treatments: slugs previously fed with bryophyte sporophytes, slugs that had not been fed sporophytes, no slugs. The researchers demonstrated that bryophyte **cover** increased in 21 days from 1.4% to 3.9% in plots where slugs had been fed, an increase that was 2.8 times higher than in the other two treatments. After eight months, the **species richness** was 2.6X higher (5.8 vs 2.2) than in the other treatments. The researchers concluded that the slugs contributed to increasing bryophyte cover and diversity by reducing the dominance of tracheophytes. The early increase in cover in the enclosures with slugs fed sporophytes suggests that they also accomplish dispersal.

Figure 111. ***Barbula convoluta*** with capsules. Photo by Kristian Peters, with permission.

Figure 112. ***Brachythecium velutinum*** with unopened capsules. Photo by Michael Lüth, with permission.

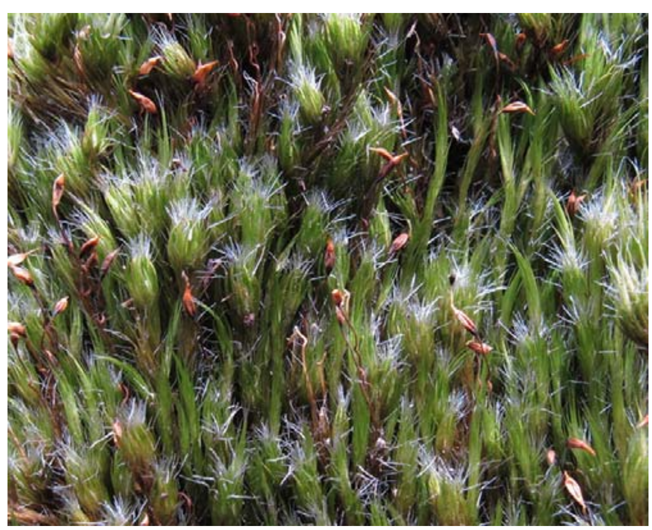

Figure 113. ***Campylopus introflexus*** with capsules. Photo by Michael Lüth, with permission.

Figure 114. ***Ceratodon purpureus*** with young capsules, showing the normal proliferation. Photo by Michael Lüth, with permission.

Figure 115. ***Leptobryum pyriforme*** with numerous immature capsules. Photo by Michael Lüth, with permission.

Figure 116. ***Phascum cuspidatum*** with unopened capsules. Photo by Michael Lüth, with permission.

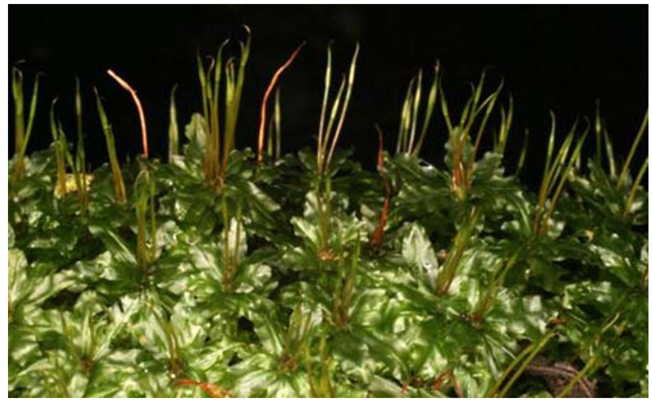

Figure 117. ***Plagiomnium affine*** with developing capsules. Photo by Jan-Peter Frahm, with permission.

Figure 118. ***Pohlia nutans*** with immature capsules. Photo by Michael Lüth, with permission.

When the question of bryophyte dispersal by slugs arose on Bryonet, Scott Redhead (Bryonet 26 August 2016) suggested that this might even occur in the **Splachnaceae**. To that suggestion, Michael Lüth posted an image of ***Tetraplodon mnioides*** (Figure 119) showing one uneaten capsule and one that had been removed by an animal, possibly a slug, documenting his own observations of capsule herbivory. Christian Schröck (Bryonet 26 August 2016) likewise observed grazed capsules in ***Voitia*** and ***Tetraplodon***. However, we need observations of feeding to determine the identity of the herbivores.

Figure 119. ***Tetraplodon mnioides*** with one capsule eaten by an unidentified herbivore. Photo by Michael Lüth, with permission.

Lüth (2010) suggested that the pre-dispersal stage of the capsules on **Splachnaceae** are likely to attract herbivores that differ from the flies that spread the spores. At this earlier stage, the capsules have a different odor from that during the dispersal stage. This odor lasts for only a short time and is therefore often missed by field biologists. On Bryonet (26 August 2016), Lüth explained that ***Splachnum ampullaceum*** smells like *Vaccinium oxycoccos* and occurs in the same habitats, often blending with these cranberries. And ***Tetraplodon mnioides*** (Figure 119) smells like ***Vaccinium myrtillus***. Although not all evolutionary successes are linked to adaptation, it makes one wonder if these early odors are adaptive to facilitate a longer dispersal and subsequent deposition in dung, although one might assume that would require a larger mammal, not a slug.

Figure 120. ***Splachnum ampullaceum*** sporophytes with a cranberry of similar color to the right. Photo by Michael Lüth, with permission.

I think most people would consider dispersal by snails and slugs to be distance-limited. But perhaps, with the help of birds, this is not so limited. Kawakami *et al*. (2003) demonstrated that the Japanese White-eyes (***Zosterops japonicus***; Figure 121) and the Brown-eared Bulbuls (***Hypsipetes amaurotis***; Figure 122) are birds that eat snails. In fact, five species of snails are able to remain in their shells and appear in the feces. If these snails had eaten moss spores, those spores might be transported a considerable distance, yet be viable in the gut of the snail. It is probably a rare event. Lots of questions remain in this relationship, but the scenario brings up interesting hypotheses.

Malone (1965) discovered another possibility, exemplified by the Killdeer (***Charadrius vociferus***; Figure 123). Malone found two species of freshwater snails attached to the feet of the Killdeer. These were able to remain attached and viable long enough to effect dispersal. The snail ***Galba obrussa*** was able to survive 14 hours on Killdeer feet out of water. But the likelihood that an aquatic snail is carrying bryophyte spores is small due the rarity of capsules. Nevertheless, if a wetland snail has similar behavior, it has a better chance of having consumed spores from wetland mosses.

Figure 121. ***Zosterops japonicus***, a bird that passes intact snails through the gut. Photo by Dick Daniels, through Creative Commons.

Figure 122. ***Hypsipetes amaurotis***, a bird that passes intact snails through the gut. Photo by Nubobo, through Creative Commons.

Figure 123. ***Charadrius vociferus***, a species that disperses snails on its feet. Photo by Andrew C, through Creative Commons.

One additional factor determining the suitability of a slug for spore (or fragment) dispersal is the habitat where feces are likely to be deposited. Researchers have made the first steps in understanding the role of slugs in bryophyte dispersal, but much remains to be explored.

Bryophytes as Home

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 & Symondson 2001). While some spiders can probably navigate the spaces within the moss mat, it seems unlikely that most 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.

Even snails are predators on slugs. The shell of the snail makes navigation among the bryophyte branches more difficult, potentially making the bryophytes a refuge for the smaller of vulnerable slugs.

In a study of bryophyte inhabitants in the Bükk Mountains of Hungary, Varga (2008) found the tiny gastropods ***Punctum pygmaeum*** (Figure 124) and ***Pupilla muscorum*** (Figure 154) among the terrestrial mosses ***Plagiobryum zieri*** (Figure 125), ***Hypnum cupressiforme*** (Figure 126), and ***Tortella tortuosa*** (Figure 127). Standen (1898) found ***Punctum pygmaeum*** from moss shakings. From my own observations, it appears that snails and slugs are common on and even in bryophyte clumps, but finding documentation on the use of bryophytes by these small species evades even the aggressive Google search.

Figure 124. The tiny ***Punctum pygmaeum*** on ***Ena montanum***, both on a moss. Photo by Stefan Haller, with permission.

Figure 125. ***Plagiobryum zieri***, a moss that supports the gastropods ***Punctum pygmaeum*** and ***Pupilla muscorum***. Photo by Michael Lüth, with permission.

Figure 126. Slug on ***Hypnum***. Photo by Janice Glime.

Figure 127. ***Tortella tortuosa*** in Europe. Photo by Michael Lüth, with permission.

The European snails ***Azeca goodalli*** (Figure 128), ***Euconulus fulvus*** (Figure 129), ***Columella edentula*** (Figure 130), ***Discus*** (subgen ***Goniodiscus***) ***rotundatus*** (Figure 131), ***Lauria cylindracea*** (Figure 132-Figure 133, ***Vertigo pusilla*** (Figure 134), and ***Vitrina pellucida*** (Figure

135) live among mosses, among other substrata (Cloudsley-Thompson & Sankey 1961). ***Carychium tridentatum*** (Figure 136), ***Discus rotundatus***, ***Cepaea hortensis*** (Figure 137), ***Oxychilus navarricus*** (formerly *O. helveticus*; Figure 138), and several rare species of ***Aegopinella*** (formerly in *Retinella*) [***A. pura*** (Figure 139), ***A. nitidula*** (Figure 140-Figure 141)] are known under mossy brick rubble (Verdcourt 1954). ***Clausilia bidentata*** (10-11 mm; Figure 142) is also rare, but can be found under moss. Standen (1898) reported on ***Clausilia rugosa*** (Figure 143) swarming on mossy walls in the UK and feeding on mosses and lichens. Standen (1898) found the snail ***Acme lineata*** on a patch of the thallose liverwort ***Marchantia*** sp. (Figure 98).

Figure 128. ***Azeca goodalli*** shell. Photo by Francisco Welter Schultes, through Creative Commons.

Figure 129. ***Euconulus fulvus***. Photo by Brian Eversham, with permission.

Figure 130. ***Columella edentula***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 131. ***Discus rotundatus*** on moss. Photo by Christophe Quintin, through Creative Commons.

Figure 132. ***Lauria cylindracea*** on bark. Photo by Christophe Quintin, through Creative Commons.

Figure 133. ***Lauria cylindracea***, whose small size can be seen in comparison to this seed. Photo by Christophe Quintin, through Creative Commons.

Figure 134. ***Vertigo pusilla*** on bark. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 135. ***Vetrina pellucida*** on bark. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 136. ***Carychium tridentatum*** on moss-covered branch. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 137. ***Cepaea hortensis*** venturing into one of the **Pottiaceae** mosses. Photo by Stefan Haller, with permission.

Figure 138. ***Oxychilus navarricus*** on the moss ***Rhytidiadelphus squarrosus***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 139. ***Aegopinella pura*** on leaf litter. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 140. ***Aegopinella nitidula*** on moss. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 141. ***Aegopinella nitidula*** showing shell coils. Photo by Brian Eversham, with permission.

Figure 142. ***Clausilia bidentata*** on moss. Photo by Christophe Quintin, through Creative Commons.

Figure 143. ***Clausilia rugosa*** on bark, a species that eats mosses and lichens. Photo by O. Gargominy, through Creative Commons.

Eucobresia diaphana (Figure 144) lives in humid, cool places on mountains and in forests of Europe, where it is likely to encounter mosses, as seen in Figure 144 (Welter Schultes 2012b), but other than this picture, I can't verify what use it might make of them.

Figure 144. ***Eucobresia diaphana*** on a species of the moss ***Tortula***. Photo by Stefan Haller, with permission.

On the South Pacific Kermadec Islands, Iredale (1913) remarked that in dry weather one must look for the snails among the mosses, where they hide from the dryness. He commented that they are quite variable in choice of trees, with one bole producing a dozen or more while the next half dozen adjoining trees disclose none.

Not surprisingly, new species still lurk amid the bryophytes. Efford (1998) found a new species of the carnivorous New Zealand endemic genus ***Rhytida*** (Figure 145), and reported observations by others of ***R. patula*** and ***R. meesoni perampla*** crawling on mosses and tree trunks at night. These and other New Zealand snails often fall prey to introduced predators. ***Wainuia urnula*** (Figure 146), another night-active snail on mosses, tree trunks, and rocks, was readily eaten by possums, rats, and hedgehogs in captivity. Efford (2000) found that 82% of the 315 ***W. urnula*** snails examined had an unusual food in the feces and gut – terrestrial amphipods. Its relative, ***W. edwardi*** (Figure 147), did not consume amphipods, and no other gastropod is known to consume them. The adaptation for consuming amphipods appeared to be largely behavioral, although there were some differences in the teeth.

Figure 145. ***Rhytida otagoensis***, member of a carnivorous genus that has some moss-dwellers. Image by James Atkinson, with permission.

Figure 146. ***Wainuia urnula***, a tiny night-active New Zealand endemic snail that traverses mosses, as shown here. Photo by Andrew Spurgeon, with permission.

Figure 147. ***Wainuia edwardi***, member of a genus that lives among mosses. Photo by James W. Atkinson, with permission.

Epiphytic

Wiesenborn (2003) observed snails in the Riverside Mountains of California and found that the active snails preferred epiphytic mosses (Figure 148) and lichens compared to plant detritus and four sizes of rocks as habitat. They suggested that the epiphytes could provide these snails with food or moisture. Tree bark soon becomes a desert after the rain dries up, but mosses remain moist much longer, permitting the snails to be active longer and to search there for food where other small invertebrates likewise take refuge from desiccation.

Figure 148. ***Monachoides incarnatus*** on bark where it often encounters bryophytes. Photo by Stefan Haller, with permission.

Tropical islands, especially Hawaii, are particularly vulnerable to invasive species. With all the visitor traffic and import/export business, hitchhikers easily reach the islands. Snails are among these, and may be one of the causes of the apparent extinction of the bird called Po'ouli (***Melamprosops phaeosoma***; Figure 149) (Mountainspring *et al*. 1990). This native Hawaiian bird is especially adapted to feeding on land snails and insects on branches and under mosses, lichens, and bark. Its toes are large and are used for prying up moss and bark to acquire tree snails. The bill is stout, withstanding the force needed for manipulating the snails. Its demise is due largely to increased activity and habitat modification by feral pigs, avian disease, and possible gene pool impoverishment due to low numbers. But it also suffers competition for food by the introduced garlic snail (***Oxychilus alliarius***; Figure 150), a native of northwestern Europe (Welter Schultes 2012a) that emits a garlic odor when it is disturbed. This species is likewise a moss-dweller of mountain slope forests. It feeds on living and dead plant tissue, but it also consumes small snails and the eggs of other snails and slugs (Oxychilus 2011).

Figure 149. Po‘ouli (***Melamprosops phaeosoma***) on a mossy branch. Note the sturdy beak used to pry loose bark or crush snails found under bryophytes. Photo through Wikimedia Commons.

Figure 150. ***Oxychilus alliarius*** on moss on bark. Photo © Roy Anderson <habitas.org.uk>, with permission.

The slug ***Prophysaon vanattae*** (scarletback taildropper; Figure 151) is one of those slugs 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 152).

Figure 151. ***Prophysaon vanattae***, the scarletback taildropper, can be found hiding under mosses. Photo by Kristiina Ovaska, with permission.

Figure 152. ***Prophysaon vanattae*** with eggs on a moss. Photo by Kristiina Ovaska, with permission.

Pilsbry (1948) suggested that the pupillid snail ***Bothriopupa variolosa*** in eastern North America might prefer mossy rocks and trees.

Figure 153. ***Bothriopupa tenuidens***; ***B. variolosa*** seems to prefer mossy tree trunks and rocks. Image copyright Gary Rosenberg, www.DiscoverLife.

Calcareous Areas

Because of the need for calcium to make the shell, many snails are dependent on limestone habitats to obtain this important resource. Hence, this is a good place to look for snails on mosses growing there.

Pupilla muscorum (Figure 154) is named for its occurrence among mosses in Great Britain, although it also occurs under stones and in leaf litter (Ehrmann 1956). This tiny (3-4 mm high shell) moss snail often prefers calciferous ground, but others describe it as indifferent to limestone content (Nordsieck 2012a). These snails are **ovoviviparous**. The eggs can survive over winter inside the female's body and are laid in the favorable conditions of spring. At that point, it is not the eggs that must survive because the juveniles usually hatch during oviposition. ***Pupilla triplicata*** (Figure 155) is likewise a moss dweller in Hungary and elsewhere (Deli *et al*. 2002).

Figure 154. ***Pupilla muscorum***. Photo by Malcolm Storey, through Creative Commons.

Figure 155. ***Pupilla triplicata***, a European moss dweller. Photo by O. Gargominy, through Creative Commons.

Another tiny conical snail (2-3 mm) of calcareous areas is ***Acicula fusca*** (Figure 156) in moss on chalk cliffs at Ballycastle, and on chalk underlying basalt at Black Head, Antrim, UK (Anderson 1996). And ***Pomatias elegans*** (Figure 157) occurs on mosses in limestone areas in the Burren, County Clare, UK (Platts *et al*. 2003).

Figure 156. ***Acicula fusca***, a tiny snail that lives among mosses on chalk cliffs. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 157. ***Pomatias elegans*** at Cheddar, Somerset, UK. Photo by Roger S. Key, with permission.

Trochulus (formerly ***Trichia***) ***plebeia*** (Figure 158) occurs in wet mossy areas by springs in limestone areas (Gilbert *et al*. 2005). ***Trochulus villosus*** (Figure 159) lives in the German Alps and requires high moisture (Welter Schultes 2010), making bryophytes useful for maintaining that moisture. This strange genus of snails has hairs on its shell that help to hold it against wet surfaces (Gilbert *et al*. 2005). I don't have any indication that these hairs offer any particular help for living among bryophytes, but if they have any tactile properties, they could help keep it from getting stuck between branches by warning that the passage was getting too narrow.

Figure 158. ***Trochulus plebeia***, a hairy snail, at Sugley Wood, UK. Photo by Brian Eversham, with permission.

Figure 159. ***Trochulus villosus*** on mosses in Germany. Photo by Stefan Haller, with permission.

The European family **Clausiliidae**, known as door snails, derive their name from the "sliding door" that covers the opening of the shell (Wikipedia 2012a). This calcareous door is known as a **clausilium**, hence the family name. It permits the snail to retreat into its shell and seal it off against predators. ***Cochlodina laminata*** (Figure 160), the plaited door snail, lives "between mosses" as well as leaf litter, but may also be found climbing trees in deciduous forests and montane pine forests (Welter Schultes 2012b). ***Clausilia dubia*** (Figure 161) is a calciphilic inhabitant of humid, shady rocks and old walls, but also lives on tree trunks "full of moss." Michael Proctor (pers. comm. 23 April 2016) informed me that this species is very common on Carboniferous limestone in Yorkshire Dales, UK, in the bryophyte and lichen habitats. ***Macrogastra ventricosa*** (Figure 162), the ventricose door snail, lives in places with plentiful mosses on the forest floor or on tree trunks, mostly in the mountains (Welter Schultes 2012b). ***Macrogastra attenuata*** (Figure 163) lives between moss-covered rocks as well as on stones, rocks, and leaf litter in montane forests.

Figure 160. ***Cochlodina laminata*** on bark where it appears to be grazing mosses. Photo by Andrew Dunn, through Creative Commons.

Figure 161. ***Clausilia dubia*** with moss. Photo by O. Gargominy, through Creative Commons.

Figure 162. ***Macrogastra ventricosa*** on moss. Photo by J. C. Schou, Biopix, through Creative Commons.

Figure 163. ***Macrogastra attenuata***, a species of moss-covered rocks in montane forests of Europe. Photo by Niels Sloth, with permission.

Vertigo meramecensis (Meramac River snail), unlike a number of other members of the genus, is a strict calciphile (Nekola & Coles 2010). It is a species of special concern that lives in Iowa and Missouri, USA, and dwells in decomposed leaf litter of moss-covered ledges and shaded carbonate cliffs, among other places.

Bogs and Mires

True bogs are acid, poor fens are acid, intermediate fens have intermediate *p*H levels, and rich fens are basic. For a snail, that *p*H range is an important consideration in choice of habitat because of the need for calcium in forming a shell. Because of this relationship, most malacologists have considered ***Sphagnum*** (Figure 164) peatlands, heathlands, and pine forests as unsuitable habitats for snails and consequently have poor snail biodiversity (Karlin 1961; Kerney & Cameron 1979; Horsák & Hájek 2003).

In fact, Nekola (2010) found that highly and even moderately acidic sites had significantly ($P<0.000000005$) lower richness and abundance than did neutral and calcareous habitats. Nevertheless, the typical acid site supported 5-10 species.

But some snails actually thrive in the low *p*H of bogs and other acid habitats. One such snail is ***Vertigo malleata*** (Figure 165), an extreme **calcifuge**. The degree to which snails have been overlooked in these habitats is exemplified by finding this new species in 60 sites out of 100 acid sites investigated from Maine to Florida, USA (Coles & Nekola 2007). In the bogs it was found primarily in leaf litter on top of the ***Sphagnum*** (Figure 164). Nekola (Jeff Nekola, pers. comm. 16 April 2012) informed me that ***Vertigo malleata*** was virtually absent in the ***Sphagnum*** itself, occurring only where there was leaf litter on top of the ***Sphagnum***. It would be interesting to watch its behavior if it is placed amid the ***Sphagnum***. Is it avoiding ***Sphagnum***, or seeking food only found among the litter? In more northern locations, ***V. cristata*** (Figure 166) or ***V. perryi*** may be present in bogs, but again, they only occur in the leaf litter, not among the ***Sphagnum*** (Jeff Nekola, pers comm. 16 April 2012). ***Vertigo cristata*** is likewise common in pine and spruce forests, heaths, and ***Sphagnum*** peatlands (Nekola & Coles 2010).

Figure 164. ***Sphagnum*** blanket bog, a habitat that does not provide enough calcium for snails. Photo from Creative Commons.

Figure 165. ***Vertigo malleata*** from Lewis Ocean Bay, South Carolina, USA. This snail lives in ***Sphagnum*** peatlands, but avoids the ***Sphagnum***, living in patches of leaf litter on top of it. Photo by Jeff Nekola, with permission.

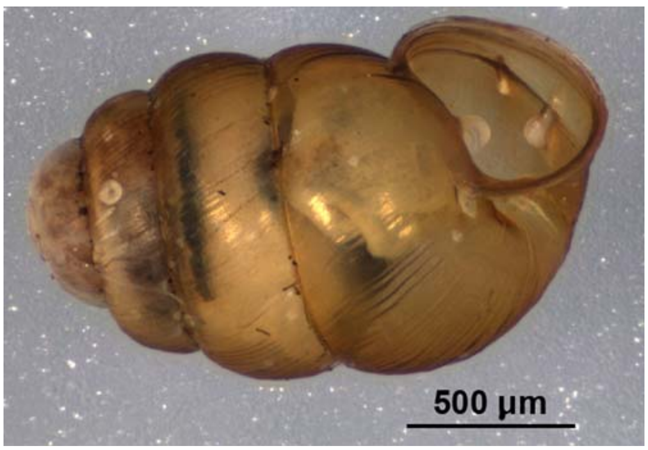

Figure 166. ***Vertigo cristata***, a species that lives on leaf litter, but not ***Sphagnum***, in bogs. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

It appears that other snails that live in bogs and poor fens likewise typically avoid the ***Sphagnum*** (Figure 164). Like ***Vertigo malleata*** (Figure 165), ***Gastrocopta tappaniana*** occurs in decomposing leaf litter of fens, pocosins, and ***Sphagnum*** bogs (Nekola & Coles 2010). Even ***Vertigo perryi***, a resident on the sides of ***Sphagnum*** hummocks, occurs on sedge leaf litter there. And ***Vertigo ventricosa*** (Figure 167) occurs in well-decomposed graminoid and broadleaf plant litter in the ***Sphagnum*** peatlands and poor fens.

Slugs have much less need for that important element – calcium (Ca). In boggy habitats, these gastropods would seem to have little choice but to travel across bryophytes (Stanisic 1996). ***Deroceras laeve*** (Figure 168) is among the slugs that traverse the complicated topography of bogs and mires. But their specific relationships to the bryophytes seems unknown. On the other hand, another member of the genus, ***Deroceras reticulatum*** (Figure 169), is a ubiquitous slug, but Anderson (2010) points out that raised and blanket peat or exposed ground above 300 m are the only habitats where it is not likely to be found. Hence, it appears that physiological differences are important in separating these slugs.

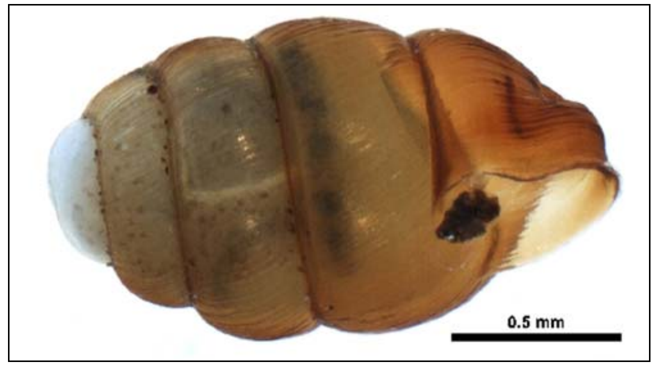

Figure 167. ***Vertigo ventricosa***, a species of litter in peatlands. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 168. ***Deroceras laeve*** (marsh slug) at Flitwick Moor, Bedfordshire, UK. Photo by Brian Eversham, with permission.

Figure 169. ***Deroceras reticulatum*** on a bed of mosses (not ***Sphagnum***). Photo © Roy Anderson <habitas.org.uk>, with permission.

Aquatic

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).

Frost (1942) found a strong difference in gastropod inhabitants among bryophytes between an acid and an alkaline stream in her River Liffey survey in Ireland. In the limestone stream, she found 17 snails among the bryophytes, but she found none in the acid stream. Moss inhabitants in the limestone stream included ***Ancylus fluviatilis*** (Figure 170) and a species of ***Planorbis*** (Figure 171). She pointed out that these molluscs were only occasionally found among the mosses.

Figure 170. ***Ancylus fluviatilis*** showing its close adherence to the substrate. Photo by Mauro Mariani, through Wikimedia Commons.

Figure 171. ***Planorbarius corneus***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Invasive species such as the carnivorous ***Euglandina rosea*** (Figure 172), a native of tropical North America, can have severe effects on native snail species elsewhere (Kinzie 1992). In Hawaii, this species has endangered the aquatic **endemic** (Hawaii only) lymnaeid snails due to its seek and capture behavior. The few surviving individuals are primarily restricted to streamside seeps or damp mosses and liverworts covering rocks near waterfalls.

Figure 172. ***Euglandina rosea***, an invasive carnivore. Photo through Wikimedia Commons.

Plant Protectors

Not all slugs and snails seem to share a love of bryophyte habitats. As already noted, some seem to avoid them. Heinjo During has shared with me a story that unravelled in the Netherlands, published by Bart van Tooren (1990). To quote van Tooren, an increasing number of *Linum* (flax) seedlings correlates with an increasing number of bryophytes and other plants. Presumably, the slugs that were eating the seedlings would not traverse the bryophytes to get to these vulnerable young plants. They experimented by comparing plots with >70% cover of bryophytes with those having <20% cover. Their results were complicated by superimposing treatments of added water and/or NPK nutrients. In the control plots (no additions), the survival of *Linum* (flax) seedlings was greatest in plots with low bryophyte cover. However, in all three treatments at Vrakelberg the survival was greatest in plots with >70% bryophyte cover, whereas at Laamhel the addition of water plus nutrients was the only treatment that resulted in a large shift to greater survival with high bryophyte cover.

Although van Tooren (1990) was unable to demonstrate significant effects of bryophytes in his 1990 study, he and his coworkers did find them on the same slope in the 1981 study (Keizer *et al*. 1985). Bryophytes under the growing conditions of that year significantly reduced mortality of the tracheophytes *Linum catharticum* and *Carlina vulgaris*. Apparently, bryophytes may serve as deterrents to slugs in some years when weather conditions might otherwise encourage herbivory, but provide little support for them in years when nutrients and/or water availability are different. Such interactions between species that change with the weather require further investigation.

Getting and Staying Connected

Snails require calcium for their shells (Hotopp 2002). Hence, acidic bogs and poor fens with acidic ***Sphagnum*** species are inadequate habitats for them (Peterka *et al*. 2021). Those that are able to find enough calcium to

survive there are further endangered by birds that are unable to find enough calcium for their eggshells, forcing those that are able to do so to seek out snails for food so they can fortify their calcium intake (Mänd *et al*. 2000).

It is therefore not surprising that snails are scarce in acidic bogs and are negatively related to the ***Sphagnum*** (Figure 173) species (Horsák & Hájek 2003; Peterka *et al*. 2021). But when Peterka *et al*. (2021) examined the relationship of snails to age of rich fens, they found no correlation, whereas there was a correlation with tracheophytes. Nevertheless, fen age had a significant effect of snail diversity, and particularly on two dominant snails. These two snails [***Euconulus alderi*** (Figure 174), ***Vertigo geyeri*** (Figure 175)] displayed significant ($P<0.05$) non-random affinity to older fens than would be expected by chance. Peterka and coworkers suggested that the lack of correlation of bryophytes with fen age was due to the ability of their spores to disperse (Frahm 2012; Sundberg 2013) and the ability to establish more quickly through fragments (Mälson and Rydin 2007; Wilkinson et al. 2017) than the seeds of flowering plants and conifers.

Figure 173. ***Sphagnum angustifolium***, a poor fen species that helps to create an acidic habitat that is detrimental to snails. Photo by Hermann Schachner, through Creative Commons.

Figure 174. ***Euconulus alderi***, a snail species for which abundance is significantly affected by rich fen age. Photo by Pekka Malinen, through Creative Commons.

Figure 175. ***Vertigo geyeri*** on moss, a snail species for which abundance is significantly affected by rich fen age. Photo by Roy Anderson, through Creative Commons.

Mussels (Bivalve Molluscs)

Mussels are not common bryophyte inhabitants, but can occasionally occur there in aquatic environs. Frost (1942) found ***Sphaerium corneum*** (Figure 176) and four species of ***Pisidium*** (Figure 177) among the mosses in the limestone stream in her River Liffey, UK, survey, but their typical niches were elsewhere in the stream.

Some bivalve molluscs 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 92) and ***Leptodictyum riparium*** (Figure 178) growing on freshwater mussel shells.

Figure 176. ***Sphaerium corneum*** on an aquatic plant. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 177. ***Pisidium amnicum***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 178. ***Leptodictyum riparium***, a moss known to grow on freshwater mussels**.** Photo by Michael Lüth, with permission.

ECHINODERMATA

I refuse to create a chapter for this marine phylum, but one observation is interesting enough to note here. Claudio Delgadillo-Moya (pers. comm. 30 March 2016) reported to me that a student who is working on sea urchins has found moss tissue in the gut of one and leafy liverwort fragments in another! There is no bryophyte known to be marine, but some do tolerate sea spray and live near the water. Most likely one of these, no, two of these, fell into the water or washed in from a stream or river. Resourceful urchin!

Summary

Snails and slugs (gastropods) have often been observed on bryophytes. They are adapted to land with a calcified slime **epiphragm** to cover the shell opening and **respiratory pore** in the body. A **radula** of many teeth permits them to scrape their food. Reproduction is mostly by **simultaneous hermaphroditism**. This may be facilitated by a **love dart** that facilitates movement of sperm cells to the sperm pouch by injecting hormones. Larvae develop within the egg in most so that the gastropods are typically **oviparous**. A few are known to deposit eggs in mosses.

The white desert snail, ***Eremarionta immaculata***, is common on bryophytes and seems to prefer them as a habitat. The copse snail, ***Arianta arbustorum*** is a night-active 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.

Adaptations include "jumping" (***Hemphillia***), small size, conical snail, hibernation/estimation, and no shell (slugs). 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 molluscs seem to avoid leaves with **awns**. Nutritional quality may be poor in some, and some have antiherbivore compounds that interfere with development, digestion, and palatability. In some cases the moss structure is such that the snails actually lose weight, whereas moss paste fosters a weight gain. But the gastropods 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. And some leafy mosses are palatable.

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.

Gastropods can be common among epiphytes, avoid acid habitats, and abound in limestone habitats. The acidity produced by poor fen species can exclude them because of inability to produce a hard shell.

Tiny mussels are able to live among bryophytes in aquatic habitats. ***Fissidens fontanus*** and ***Leptodictyum riparium*** can live on the shells.

Echinoderms generally have no association with bryophytes, but if a bryophyte falls into the marine water it may occasionally be eaten.

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