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CHAPTER 10-3
ARTHROPODS: CRUSTACEA – ISOPODA, MYSIDA, AND DECAPODA

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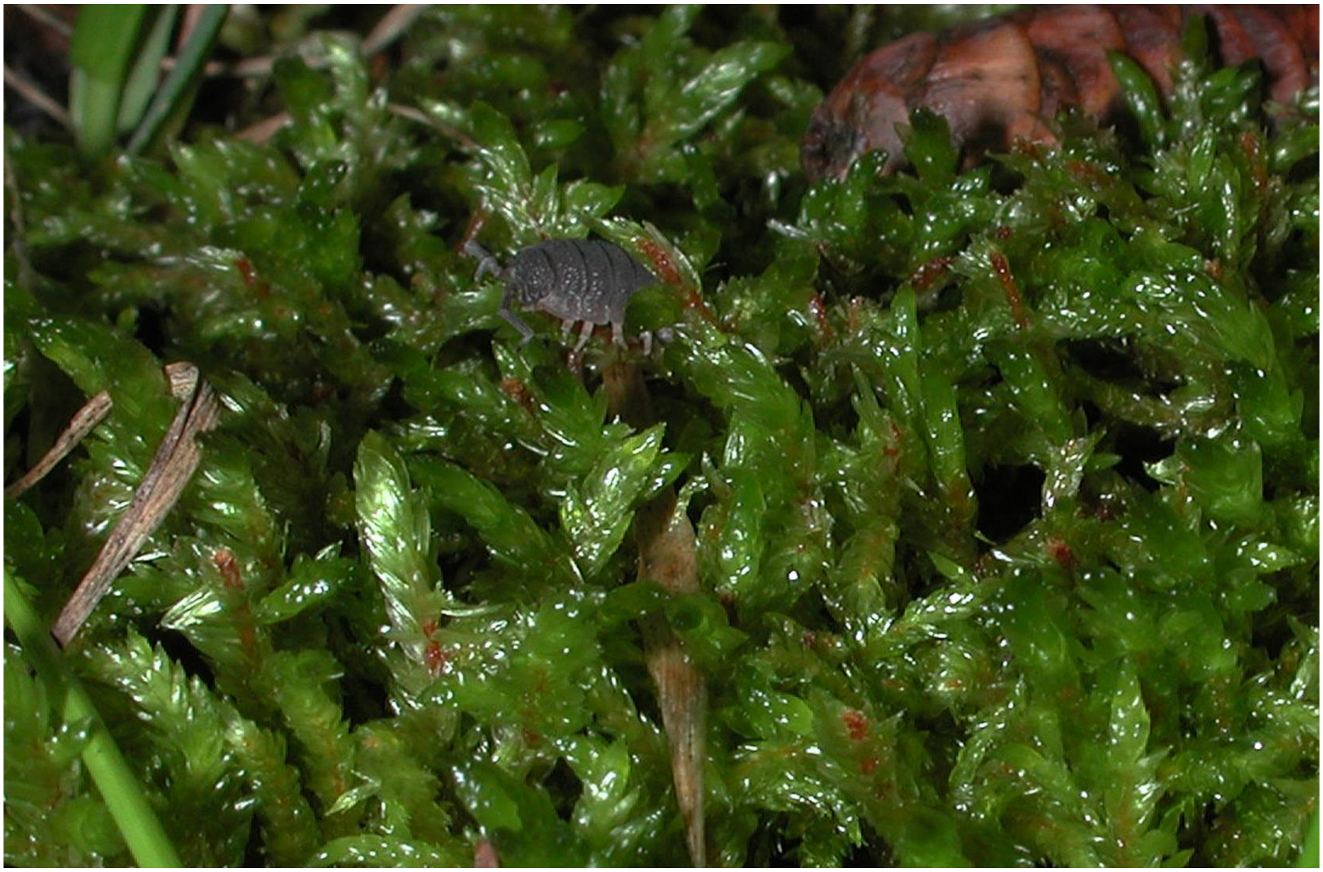

Figure 1. ***Porcellio scaber*** eating ***Pleurozium schreberi*** at midnight in Houghton, Michigan, USA. Photo by John Hribljan, with permission.

CLASS MALACOSTRACA, ORDER ISOPODA

Then there are the Isopoda (Figure 1), the well-known pillbugs, woodlice, roly polies, potato bugs, or sowbugs (but they aren't bugs!). These aren't insects at all, but are arthropods with legs on each segment, sometimes included among the **multipedes**, which is an unofficial classification referring to arthropods with many legs. And at least some of them seem to love mosses.

As a teacher, these were my favorite creatures. They have wonderful behavior responses to all sorts of things, especially light, moisture, and contact. Hence, they were excellent experimental organisms for behavior experiments for beginning students. They were easy to collect (just put out potatoes, with holes drilled through them, in a deciduous forest and give them 2-3 days to colonize). And they responded quickly and predictably.

But for research on herbivory on bryophytes, these organisms are unparalleled. Both aquatic and terrestrial species eat mosses, are abundant, and can be used to test for preferences. Nevertheless, they should not be considered as models for the feeding preferences of other invertebrates, as you will see when we discuss digestion.

I have a small moss garden, and it is occasionally the site of my experiments, planned or otherwise! I had inherited a mat of mosses that had made themselves unwelcome on an asphalt parking lot. Some of these I had draped over a large rock in hopes that they would find it similar to their past home. In an attempt to keep them in place, I had used a mix of raw egg to act as glue. All seemed well for 2-3 weeks. Then one day when I went to look at them the mat looked like Swiss cheese! This carpet of a half-meter diameter had numerous relatively large holes in it! I found the carpet was loose, so I lifted it from the rock. As I did that, woodlice (mostly ***Porcellio scaber***, Figure 2) fell to the ground and scrambled for cover. There were at least 20 of them! And many still remained on or within the mat.

Figure 2. ***Porcellio scaber***, a common moss inhabitant. Photo from <www.aphotofauna.com>, with permission.

Compared to other arthropods, the isopods, at least on land, probably have the most interaction with the bryophyte community. Božanić (2008) sampled 66 mosses and extracted their inhabitants using heat with a Tullgren apparatus. She recorded multiple factors to determine the niche requirements of the faunal species. The mosses represented 15 species. The **Isopoda** were the most abundant taxa (439 individuals); others included **Chilopoda** (centipedes), **Diplopoda** (millipedes), **Araneae** (spiders), **Pseudoscorpionida** (pseudoscorpions), **Opilionida** (daddy-long-legs), **Lumbricidae** (earthworms), and **Formicidae** (ants). The diplopods (another multipede) were second in abundance (240 individuals). The most important environmental factors in determining the faunal higher taxa were type of substrate, height above ground, and moss/sample area. The species factors, like those of the higher taxa, were substrate type and height above the ground, but in addition to these the tree diameter was important, possibly indicating colonization time. Farkas (2007) likewise found tree diameter to be important for the isopods ***Porcellium collicola*** (Figure 3), ***P. conspersum***, and ***Trachelipus rathkii*** (Figure 4), all rather common among epiphytic mosses in Hungary.

Figure 3. ***Porcellium collicola***, an isopod that lives among epiphytic mosses. Photo by Dragiša Savić, with permission.

Figure 4. ***Trachelipus rathkii***, an isopod that lives among epiphytic mosses in Hungary. Photo by Dragiša Savić, with permission.

External Anatomy

Isopods have two compound eyes (Figure 5) that permit them to detect motion easily. They have a very small head, long thorax, and short abdomen (Figure 6). There are two pairs of antennae, but the first is short and not always visible (Figure 5). That pair may have a chemosensory function to detect odors and tastes (Massey University 2014). The second pair of antennae is large and easily seen; the function is **tactile** (touch sensation).

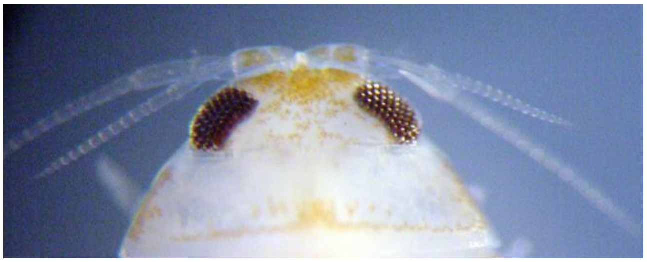

Figure 5. Isopod head showing compound eyes. Note the multiple small sections in each eye. Photo from NOAA, through public domain.

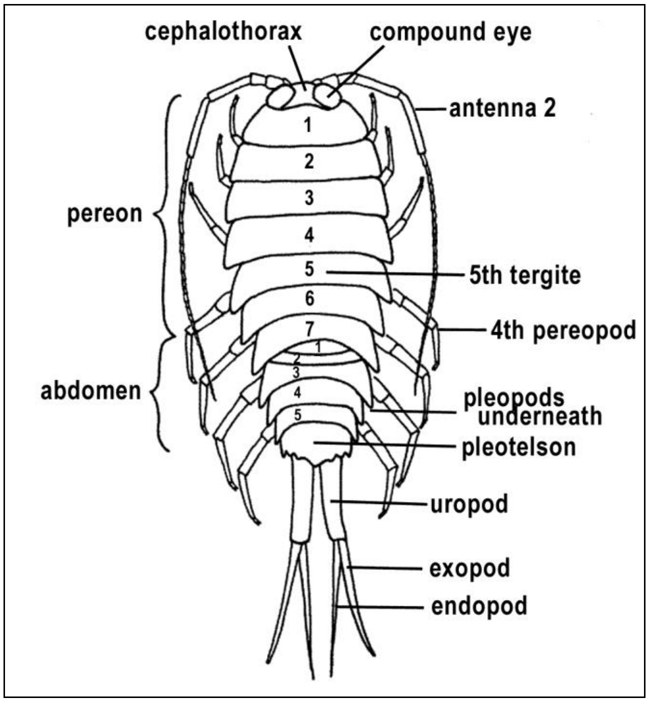

Figure 6. ***Ligia***, a genus that sometimes inhabits bryophytes, showing typical isopod external anatomy. Redrawn from Richard Fox.

Adaptations to Terrestrial Life and to Bryophytes

Isopods are predominately aquatic and marine. Life on land requires special adaptations. Even so, some isopod taxa have rather broad niches. ***Porcellio laevis*** (Figure 7), a cosmopolitan species and largest member of the genus, at least in the UK (Harding & Sutton 1985), is known for its plasticity in response to the environment (Lardies & Bozinovic 2008), and this plasticity may be the most important adaptation of all. There seem to be few morphological adaptations specific to land dwelling, although one could argue there are no really large species like some of the marine species.

Figure 7. ***Porcellio laevis***, an isopod from which we have learned many terrestrial adaptations. Photo by Roger S. Key, with permission.

Bryophytes make good homes for isopods. These organisms hide from light and require a moist environment, conditions which can be provided by bryophytes. There are probably many species still to be discovered on land, especially among bryophytes, because of the sheltering behavior of isopods in daylight.

Water Relations

For any organisms evolving from water to land, maintenance of hydration is a critical adaptation. Dias *et al*. (2013) experimented with 22 species of terrestrial northwestern European isopods to determine the importance of three traits related to desiccation resistance. They found that 90% of the interspecific variation could be explained by water loss rate and fatal water loss. Body surface area affects desiccation resistance through modification of water loss rate. Soil moisture affects species distributions, and by extension, it is likely that bryophyte moisture does as well.

Edney (1951a) examined the evaporation of water from woodland isopods and found that in ***Armadillidium*** (Figure 8-Figure 9) and ***Porcellio*** (Figure 7) it was the **pleopods** (abdominal appendages also known as swimmerets, Figure 6, Figure 10) that lost water most rapidly, ranging 10-20 times as fast per unit area as the dorsal or ventral surfaces. However, the most water was actually lost from the dorsal and ventral surfaces because of the much greater area. Water loss rates differed among the terrestrial genera tested, in the order from greatest loss to least as ***Ligia*** (Figure 11), ***Philoscia*** (Figure 12), [***Oniscus*** (Figure 13), ***Porcellio*** (Figure 7), *Cylisticus*], and ***Armadillidium nasatum*** (Figure 9) to ***A. vulgare*** (Figure 8). This order also reflects the progression from most moist to least moist habitat preferences. ***Armadillidium*** species further conserve water by curling (Figure 9), a behavioral adaptation that earned it the name of roly poly.

Figure 8. ***Armadillidium vulgare***, the common roly poly that rolls into a ball. Photo from <www.aphotofauna.com>, with permission.

Figure 9. ***Armadillidium nasatum*** curled into a ball, permitting it to reduce water loss. Photo by Lynette Schimming, through Creative Commons.

Figure 10. ***Oniscus asellus*** lying on its back and exposing its **pereopods** (see Figure 6). The **pleopods** are on the white abdomen behind these 7 pairs of legs and cannot be discerned in this picture. Note that the head is to the right where you can see two of the antennae. Photo by Brian Eversham, with permission.

Figure 11. ***Ligia oceanica***, member of a coastal genus that readily loses water. Photo by Gilles San Martin, through Wikimedia Commons.

Figure 12. ***Philoscia muscorum*** in bark crevice in the forest. Photo by Brian Eversham, with permission.

Figure 13. ***Oniscus asellus***, a frequent moss-dweller in western and northern Europe. Photo by Brian Eversham, with permission.

When terrestrial isopods become desiccated, they can restore their original weight by absorption of moisture through the mouth and anus by contact with free water surfaces, and by mouth from moist surfaces (Edney 1954). This suggests a possible role for the bryophytes as pillbugs traverse such dry habitats as tree bark, rocks, or even soil. They could run from clump to clump of moss, rehydrating when they visit the mosses (or liverworts). Edney (1954) suggests that they are most susceptible to mortality during their wandering rather than while in their selected permanent shelter habitat. Interestingly, living isopods could rehydrate by absorption of water vapor or liquid water, but dead ones could not (Edney 1951a).

Waste Elimination

Even the elimination of waste products must be modified to conserve water on land. Digestive and bodily processes accumulate nitrogenous wastes, and these are toxic, requiring a means of efficient elimination. In aquatic animals, these are usually eliminated as toxic ammonia that is diluted in water (Dresel & Moyle 1950). But terrestrial animals cannot afford the large quantity of water needed to dilute ammonia to safe levels. Nevertheless, like aquatic isopods, most terrestrial isopods still excrete ammonia, but with a twist. They lack any organ homologous to the kidney or liver to detoxify or facilitate excretion of ammonia (Hartenstein 1968). Hartenstein studied this ammonia elimination mystery in ***Oniscus asellus*** (Figure 13) and concluded that rather than excreting liquid ammonia like most aquatic animals, the terrestrial isopods eliminate their ammonia as a gas. In addition, some of the nitrogen waste is stored in the body wall as uric acid and is eliminated during molting. Wieser and Schweizer (1970) likewise found that the terrestrial isopods ***Oniscus asellus*** and ***Porcellio scaber*** (Figure 1-Figure 2) eliminate their ammonia as gas. Their data refute earlier ideas that nitrogen metabolism is suppressed; instead, they accounted for loss of all the excess nitrogen intake through body wall storage and mostly through the body wall as ammonia gas, thus eliminating the need for large water losses – or kidneys.

Osmotic Balance

The osmotic pressure of the blood of terrestrial species is somewhat lower than that of sea water and adaptation to land seems to be achieved by osmotic tolerance rather than regulation (Edney 1954). Nevertheless, ***Porcellio scaber*** does not change its body fluid concentration as rapidly as it loses weight during desiccation (Horowitz 1970), implying it could have a limited balancing mechanism. Lindqvist and Fitzgerald (1976) explored this further and determined that initially the blood osmotic concentration remains essentially unchanged until about a 10% loss of body weight. Meanwhile, the oral fluid increases its osmotic concentration rapidly during about 90 minutes of drying. When severe desiccation occurs, these two compartments progress to an osmotic equilibrium, presumably due mostly to withdrawal of water from the gut lumen into the blood.

Molting has the potential to affect the osmotic balance. Calcium is an important element in the exoskeleton. Before the animal molts, the calcium is resorbed and stored in the body of terrestrial isopods and little is lost, whereas in aquatic taxa, little is resorbed and most of the exoskeleton calcium is lost (Greenaway 1985). When needed, additional calcium is gained from food and **exuviae** (shed exoskeleton). Despite this resorption of high amounts of calcium in terrestrial species, most of it is not stored in ionic form and thus has little effect on the osmotic balance.

Respiration

Terrestrial isopods have **pseudotracheae**, assisting them with respiration in dry air (Edney 1954), whereas the importance of integumental oxygen absorption decreases in terrestrial species compared to aquatic species. The inner branch of each **pleopod** (Figure 6, Figure 10) is modified into a gill-like structure (Figure 14) with a thin, permeable cuticle where gas exchange occurs (Schotte *et al*. 2008-2014). These even somewhat resemble lungs in the terrestrial isopods.

Figure 14. *Porcellio siculoccidentalis* pleopods modified to function in gas exchange and resembling lungs. Photo by Giuseppi Montesanto, with permission.

Temperature Tolerance

The temperature tolerance follows the same sequence of genera as for water loss rates above [least in ***Ligia*** - Figure 11 < ***Philoscia*** - Figure 12 < (***Oniscus*** - Figure 13, ***Porcellio*** - Figure 7, *Cylisticus*) < ***Armadillidium*** (Figure 8)], with ***Armadillidium*** having the highest temperature tolerance (Edney 1951b). There was no difference in body temperature between living and dead woodlice, and once the animals reached equilibrium their temperatures differed from that of the air by no more than 0.1°C in moist air. However, in dry air the isopod temperatures were depressed relative to air temperature, apparently due to evaporative cooling.

Moisture and Temperature Interaction

Temperature and moisture rarely act alone in ecosystems, and responses by isopods to one of these typically depends on the other. In experiments with the isopods discussed above, Edney (1951b) found that after 30 minutes in dry air at 20° and 37°C, mean temperature depressions were for ***Ligia*** (Figure 11), 2.6°C and 6.8°C; ***Oniscus*** (Figure 13), 1.5 and 2.7°C; ***Porcellio*** (Figure 7), 0.4 and 1.3°C; ***Armadillidium*** (Figure 8), 0.5 and 1.8°C, respectively. ***Ligia*** differed from the others, with its body temperature rising for at least 2 hours, whereas the others reached equilibrium at a temperature lower than ambient air temperature after 25 minutes. It is the ability to evaporate water rapidly that permits these isopods to maintain a safe temperature for short intervals, and this at least partly explains their need for moist environments. On the other hand, if the air is saturated, they are unable to use evaporative cooling, and higher temperatures become lethal. Both temperature and moisture needs explain the migration of the isopods to deeper moss layers or even into the soil in the daytime, returning to the surface for feeding at night.

Behavior

The best adaptations of this group seem to be behavioral (Edney 1954), and these behaviors are what make them so interesting to watch. Pick up a rock and pillbugs scramble in all directions, soon disappearing under leaves or into the soil. They run from light, which might be an indicator of drying conditions. They seem to lack a well-developed cuticle, although both endocuticular and epicuticular layers are known from some species (Edney 1968), and thus they are able to use evaporative cooling, but this only works for a short time, hence making a behavioral solution essential.

Edney (1968) suggests that the nightly activity of ***Porcellio scaber*** (Figure 1-Figure 2) on trees may permit them to transpire excess water. ***Armadillidium vulgare*** (Figure 8) also has greater activity at night when the air is more moist. It appears that males of ***Porcellio scaber*** and ***Armadillidium vulgare*** use surface shelters, including bryophytes, between foraging events (Dangerfield & Hassall 1994), sometimes providing them with a location to gain or reduce water content.

Congregating Behavior

Aggregating or congregating (Figure 15) in large numbers in a suitable habitat, as is easily observed under a log, board, or small rock, is generally accepted as a means to reduce their water loss to the atmosphere (Broly *et al*. 2013). This behavior is mostly **thigmotactic** (a contact response), and possibly **olfactic** (an odor response) (Edney 1968). Olfaction seems to play a role in seeking shelter. But the role of aggregation in preventing water loss may be misleading. Broly and coworkers suggest other potential benefits, including reduction of oxygen consumption, increase in body growth, stimuli for reproduction, better access to mates, shared predator defense, promotion of coprophagy, sheltering, and acquisition of internal symbionts. They suggest that congregating behavior provides terrestrial isopods with a non-physiological alternative to coping with climate constraints.

Figure 15. Isopod congregation. Photo by William Leonard, with permission.

But crowding does not seem to have the same benefit for all terrestrial isopods. ***Armadillidium nasatum*** (Figure 16) and ***A. vulgare*** (Figure 8), members of the most xeric genus, had reduced growth rate, survivorship, and size at first reproduction as density increased in laboratory experiments (Ganter 1984). Since limited food reduced both growth rate and mortality in these experiments, these same detrimental factors might not exist in nature where foraging might be unlimited.

Figure 16. ***Armadillidium nasatum*** showing two color variants. Photo by Stan Gilliam, through Creative Commons.

To put this in perspective, Hassall *et al*. (2010) experimented with aggregation behavior in ***Philoscia muscorum*** (Figure 17), ***Oniscus asellus*** (Figure 13), ***Porcellio scaber*** (Figure 1-Figure 2), and ***Armadillidium vulgare*** (Figure 8) from Norwich, UK. The first three are isopods known from terrestrial bryophytes, whereas ***Armadillidium vulgare*** tends to occur in drier habitats. The first three species clump more at lower levels of relative humidity and at higher temperature, whereas changing the humidity has little effect on clumping in ***A. vulgare***.

Figure 17. ***Philoscia muscorum*** on moss. Photo by Dick Jones, with permission.

Sheltering

Sheltering (staying in one place that is protected) is common among some isopods, but not others (Hassall & Tuck 2007). ***Porcellio scaber*** (Figure 1-Figure 2), a common moss dweller, sheltered significantly more than either ***Platyarthrus hoffmannseggi*** (Figure 18) or ***Armadillidium vulgare*** (Figure 8), and ***Philoscia muscorum*** (Figure 17) sheltered the least, despite some individuals spending at least winter under mosses. Sheltering declined in all four species after the breeding season, continuing through winter. ***Porcellio scaber*** sheltered more where the soil was more **calcareous** (occurring on chalk or limestone), ***Philoscia muscorum*** more under the shade of trees, and both ***P. muscorum*** and ***Armadillidium vulgare*** more in grazed than in ungrazed areas. For ***A. vulgare*** sheltering was positively correlated with both rainfall and temperature of the day before sampling, whereas for ***Philoscia muscorum*** it was negatively correlated with rainfall.

Figure 18. ***Platyarthrus hoffmannseggi***, an isopod that shelters under mosses. Photo by Jan van Duinen <http://www.janvanduinen.nl/>, with permission.

Dias *et al*. (2012) examined the influence of microclimate on sheltering in three terrestrial isopods: ***Porcellio scaber*** (Figure 1-Figure 2), ***Oniscus asellus*** (Figure 13), and ***Armadillidium vulgare*** (Figure 8, Figure 23). The first two are common among mosses, whereas ***A. vulgare*** typically lives in drier habitats. All three species spent more time sheltering and less in activities when the environment was drier (50% relative humidity) compared to more moist conditions (90% relative humidity). ***Oniscus asellus*** is the least terrestrialized of these three and thus the most susceptible to desiccation. Sheltering can also reduce the quality of food consumed because less time is spent on foraging.

Reproduction

Reproduction among terrestrial invertebrates usually requires modifications from that of aquatic taxa. Terrestrial isopods carry their young in a **marsupium** (brood pouch, Figure 19). The marsupium is filled with fluid and the eggs and embryos are surrounded by mucous. Warburg (1987) considers this to be one of the most important innovations for successful living on land. The mucous may contribute to nourishment of the young, possibly explaining their ability to survive when the mother doesn't eat.

Figure 19. ***Armadillidium vulgare*** lying on its back, showing young (cream-colored) isopods in a brood pouch on the ventral side. Photo by Malcolm Storey, through Creative Commons.

In the isopods, gonadal development is stimulated by a long photoperiod and high temperatures (Edney 1968). Temperature seems to play a role in controlling reproductive output and consequent water loss.

Females are dominant throughout most of the year in ***Porcellio scaber*** (Figure 1-Figure 2) (Nair 1998), and this is likely true in other species as well, sometimes indicating **parthenogenesis** (reproduction from an egg without fertilization). Some species that exhibit parthenogenesis do not necessarily do so in their populations everywhere (Christensen 1979; Fussey & Sutton 1981; Fussey 1984). For example, in the British Isles some populations of an isopod that often lives among bryophytes, ***Trichoniscus pusillus*** (Figure 25), are parthenogenetic and others are not. Christensen (1979) demonstrated that the parthenogenetic populations represented different genotypes in this species. Fussey (1984) was unable to find a relationship between this parthenogenetic expression and latitude, longitude, altitude, or seven climatic variables, but it did correspond with calcareous habitats.

But genes are not the only causes of alteration in the reproductive type. The bacterium *Wolbachia pipientis* is able to infect the isopods ***Hyloniscus riparius*** (Figure 20), ***Trachelipus rathkii*** (Figure 26), and ***Trachelipus ratzeburgii*** (Figure 21) (Nyirő *et al*. 2002), all species known to inhabit mosses (Božanić 2011). The bacterium lives in the ovaries and can cause such changes as loss of maleness and shift to parthenogenesis in these isopods. The bacterium also infects the eggs and thus is transferred from mother to offspring. Could the antibiotic properties of bryophytes protect the isopods from this population-altering bacterium?

Figure 20. ***Hyloniscus riparius***, whose gender is altered by the bacterium *Wolbachia pipientis*. Photo by Dragiša Savić, with permission.

Figure 21. ***Trachelipus ratzeburgii***, an isopod whose gender is altered by the bacterium *Wolbachia pipientis*. Photo by Dragiša Savić, with permission.

Food quality can have a strong effect on the success of both reproduction and survival of the offspring. For example, Kautz *et al*. (2000) were only able to maintain a stable population of ***Trichoniscus pusillus*** (Figure 25) on a diet of *Alnus* litter with high microbial activity. Such needs may explain changes in the diet of isopods throughout the year. It would be interesting to test the effect of a bryophyte diet on reproductive success.

On the other hand, Lavy *et al*. (2001) found that in ***Porcellio scaber*** (Figure 1-Figure 2) and ***Oniscus asellus*** (Figure 13) diet had no effect on the number of juveniles or their weight. Rather, the weight of the offspring was correlated with the weight of the female. Nair (1998) found that for ***Porcellio scaber*** in Benghazi, Libya, the total number of eggs correlated with body length of the female.

High temperatures can be lethal or detrimental to developing isopods. In the terrestrial *Porcellio ficulneus*, at 25°C, oocytes matured sooner, and many were resorbed (Hornung & Warburg 1993). The Mediterranean population compensated for these losses by breeding earlier. Females must balance the advantages of faster brood development in higher temperatures with the risk of excessive water loss (Dangerfield & Hassall 1994).

Incubation periods for ***Porcellio scaber*** (Figure 1-Figure 2) in Benghazi were 18 days in summer and autumn but extended to 32 in late winter and spring (Nair 1998). Spring embryo production was higher in spring compared to summer and autumn. In ***Armadillidium vulgare*** (Figure 8), if females are dehydrated, they reproduce instead of growing (Warburg 1987).

Terrestrial isopods care for their young, an uncommon feature in the aquatic habitat (Lardies *et al*. 2004). Such care can be costly energetically, but it increases the survival of the young in the terrestrial environment, and it might even reduce water loss of the adult, much like the congregating behavior. But there is a downside. Lardies and coworkers found that in ***Porcellio laevis*** (Figure 7) not only was the carrying of developing eggs energetically costly, the females carrying them had a lower ingestion rate and lower ability to digest food than non-carrying females. The net result was that egg-carrying females stored only about 20% as much energy as females with no eggs.

Carrying eggs and young creates other problems for these woodlice. Females carrying broods were slower and moved shorter distances to avoid light than non-brooding females of ***Porcellio laevis*** (Figure 7) (Kight & Nevo 2004). Physical stress causes a reduction in both distance travelled and velocity in brooding females. Many eggs and embryos die before reaching their swimming stage. These are typically eaten by their siblings in the marsupium and larger larvae often eat the smaller ones (Warburg 1987). Once the young leave the marsupium they begin a life free of their mother.

Predators

Bryophytes can serve as a refuge for hiding from large predators like birds, but they may not be so safe from insect predators. Ants such as ***Tetramorium caespitum*** (Figure 22) influence the behavior of the isopods ***Armadillidium vulgare*** (Figure 8) and ***Porcellio laevis*** (Figure 7) (Castillo & Kight 2005). ***Armadillidium vulgare*** females were hidden better than those of ***P. laevis*** whether ants were present or not. But some of their behavior was rather strange. Isopods that had no experience with ants remained further from them than those with previous exposure, with ***P. laevis*** keeping a significantly greater distance than that of ***A. vulgare***. This difference in behavior of the two species may be explained by the ability of ***A. vulgare*** to roll into a ball (Figure 23), whereas ***P. laevis*** is endowed with the ability of rapid locomotion.

Figure 22. Ant ***Tetramorium caespitum*** eating larva, most likely of an insect. This ant causes soil isopods to stay hidden. Photo from Antwiki, through Creative Commons.

Figure 23. ***Armadillidium vulgare*** in a ball, a protection against predators. Photo from <www.aphotofauna.com>, with permission.

The brooding period of ***Armadillidium vulgare*** (Figure 8) was shortened when it was exposed to ants, whereas such exposure had no effect on brood time for ***Porcellio laevis*** (Figure 7) (Castillo & Kight 2005). This is a greater advantage for ***A. vulgare*** because it is unable to roll into a sealed ball when it is carrying its brood. Nevertheless, ***P. laevis*** is slowed down when carrying a brood (Kight & Ozga 2001; Kight & Nevo 2004).

Overwintering

It is difficult to find information on the use of bryophytes for overwintering of crustaceans. Samouelle (1819) reported that one could find ***Philoscia muscorum*** (Figure 17) under mosses in January in Great Britain. Le Gay Brereton (1957) reported that the isopod ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) overwintered "in large numbers" in the moss layers at the bases of oaks (*Quercus*) and ash (*Fraxinus*). These same aggregations did not occur at eye level, suggesting that the larger moss clumps at the tree bases were more suitable than the small clumps or shallow mats of the bole. One would presume that the tree base had both warmer and less desiccating conditions than any position on the bole.

Figure 24. ***Porcellio scaber***, a common moss dweller and consumer that eats its own feces to assimilate more nutrients. Photo by Eric Schneider, with permission.

Terrestrial isopods are not well adapted to cold temperatures and must seek locations where they are insulated from the cold. ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24), a common species that is known from bryophytes and under many other objects, is able to adjust somewhat by acclimation, but is nevertheless susceptible to both freezing and chilling (Tanaka & Udagawa 1993). The temperature causing 50% mortality was -1.37°C in August but dropped to -4.58°C in December. At -7°C, the animal was unable to avoid freezing of its tissues, a temperature limit that was the same throughout the year.

The winterization in ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) corresponded to the presence of low molecular weight carbohydrates that may have protected it against chilling injury (Tanaka & Udagawa 1993). The supercooling temperature of -7°C seemed to be associated with the year-round gut content. We know that at least in the autumn this species can live among mosses and deciduous and conifer leaf litter where it prefers mosses as food (Hribljan 2009; Hribljan & Glime in prep). Could the mosses help to prepare it for winter by contributing arachidonic acids that have lower freezing points (see Prins 1982)? Hansen and Rossi (1991) showed that ***Rhytidiadelphus triquetrus*** (Figure 49), a food of ***Porcellio scaber*** in autumn (Figure 53; Hribljan 2009; Hribljan &

Glime in prep), contains 30% arachidonic acid at 20°C, which slightly decreases at lower temperatures. Tanaka and Udagawa (1993) also suggest that food derivatives could serve as ice nucleation centers that could reduce freezing of tissues.

Bryophytes as Food

In the other crustaceans, we have seen that bryophytes serve mostly as trapping devices, collecting detritus and growing periphyton that can serve as food for the crustaceans. The crustaceans have carried their aquatic habit of eating detritus into the terrestrial environment. Isopods are also litter-dwelling organisms that eat litter, but they eat bryophytes too.

Digestion

Generally bryologists might not care much about the digestive process of a bryophyte dweller, but understanding isopod digestion helps us explain bryophyte herbivory and why isopods can be such good bryovores whereas other invertebrates generally are not. As organisms derived from aquatic ancestry, isopods required adaptations to digest terrestrial food. They are among the few organisms known to readily eat bryophytes. Food sources on land can differ somewhat for isopods, although leaf litter, a common food for them, is available in streams and lakes as well as on land.

Hames and Hopkin (1989) observed the digestive tracts of two terrestrial isopods known from mosses, ***Oniscus asellus*** (Figure 13) and ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24), and determined that their digestive tracts are divided into five regions: foregut, anterior chamber, papillate region, rectum, and hepatopancreas. The latter opens into the foregut. There is a powerful muscular sphincter between the papillate region and the rectum.

As food passes from the foregut to the hindgut it is mixed with secretions from the hepatopancreas (Hames & Hopkin 1989). When the hindgut is full, muscles contract to force the liquids and fine food particles back to the foregut through special channels. This re-entry can occur several times, each time being subject to further degradation by the microbial gut flora. Material left in the hindgut passes to the rectum where the fecal pellets are compacted for expulsion. And like a rabbit, ***Armadillidium vulgare*** (Figure 8) and ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) eat their own fecal pellets, preferring fresh ones to decaying ones (Hassall & Rushton 1982). Hames and Hopkin (1989) suggest that the ability to recycle the food, each time extracting more liquid, may be one of the major changes making their life on land successful.

Isopods are good at digesting their food but poor at assimilating it. This may also help explain their ingestion of feces, to gain more nutrients from it (Warburg 1987). Food quality is important for growth (Merriam 1971), and fresh leaves are better for growth than decayed leaves (Beck & Bretowsky 1980).

But we are left with the question of circumventing the high **phenolic** content of bryophytes and some types of leaf litter. **Phenolic** compounds are known for their production as a stress response in bryophytes (Graham *et al.* 2004). There is ample evidence that they deter herbivory in both terrestrial and aquatic bryophytes, as discussed below. But it appears that not all isopods are created equal in their tolerance of phenolic compounds. And not all bryophytes are equal in making them.

Zimmer (1997) showed that the common moss dweller ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) has significant ability to reduce gut surface tension. Phenolic compounds, well known to prevent digestion in other invertebrates due to the ability of the phenolics to increase the surface tension, seem to have a less negative effect on this species. These surfactants may be the key to the ability of ***Porcellio scaber*** to eat mosses without suffering from the typical binding of proteins suffered by many other kinds of organisms that eat phenolics. In insects, the phenolics precipitate proteins in the diet, preventing the insects from assimilating these essential nutrients, but in the isopods the surfactants bind the phenolics, leaving the proteins free for assimilation by the isopods. The concentration of surfactants in ***Porcellio scaber*** was 80 times as high as the "critical micelle concentration" needed to permit binding of the phenolics.

Further research on ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24) indicated that endosymbiotic bacteria residing in the hepatopancreas were able to oxidize the phenolics, disabling their adverse properties (Zimmer 1999). When the gut flora of ***Porcellio scaber*** was reduced, Zimmer demonstrated that bacteria in the gut apparently had an important role in hydrolyzing gallotannins. When galloylglucose esters were ingested, they greatly reduced the microbial component of the hindgut. Ingestion of gallic acid reduced both palatable fungi and bacteria, but not as strongly, and increased the gut microflora. Zimmer's study suggests that the ingestion of hydrolyzable tannins, as found in some mosses, can inhibit the digestion of other foods in the diet of this species. The gut differences among the isopod species can account for their preferences among bryophytes, and possibly account for those taxa that don't eat bryophytes at all. Similarly, differences in hydrolyzable tannin concentrations among bryophyte species can account for preferences for some bryophytes over others.

Zimmer and Brune (2005) examined the physiological properties of the gut of four species of terrestrial isopods [***Oniscus asellus*** (Figure 13), ***Porcellio scaber*** (Figure 1-Figure 2, Figure 24), ***Trichoniscus pusillus*** (Figure 25), and ***Trachelipus rathkii*** (Figure 26)]. These adaptations were manifest as a steep gradient of oxygen, high at the periphery and low at the center of the gut transection. This gradient provides suitable habitat for both aerobic and anaerobic symbionts that can contribute to digestion. The *p*H gradient ran from acidic in the anterior hindgut to neutral in the posterior hindgut of ***O. asellus***, ***P. scaber***, and ***T. rathkii***. In ***Trichoniscus pusillus***, the *p*H in the hindgut lumen was nearly constant. Zimmer and Brune (2005) suggested that the *p*H gradient differences may be adaptive in providing differences in the digestion of lignocellulose from their food sources. Bryophytes lack true lignin, so the expenditure of resources to create the conditions suitable for digesting lignin could be spared in those isopods that eat mosses. These differences in gut physiology could also account for some of the differences in food preferences and survival of isopods on bryophytes vs other foods.

Figure 25. ***Trichoniscus pusillus***, a terrestrial isopod. From <www.aphotofauna.com>, with permission.

Figure 26. ***Trachelipus rathkii***, a terrestrial isopod. Photo by R. E. Jones, with permission.

Terrestrial Consumers

Terrestrial isopods seem to prefer a varied diet and exhibit food preferences (Dudgeon *et al*. 1990). Dudgeon and coworkers found that four species of isopods from a Hong Kong forest ate more food when given a mixture of leaves than when only one type was available. Their preferences did not seem to relate to ash, calcium, copper, soluble tannin, or energy content. Dudgeon and coworkers suggested that the isopods satisfied their nutrient requirements by consuming certain foods, then switching to others to avoid excessive tannins or other allelochemicals.

Rushton and Hassall (1983a, b) examined the feeding preferences and rates of ***Armadillidium vulgare*** (Figure 8) among dicotyledonous and monocotyledonous plants and bryophytes (***Calliergonella cuspidata***, Figure 27). This pillbug, known as a roly poly due to its ability to roll into a ball, can live in drier habitats than ***Porcellio*** and is much less likely to be associated with mosses. These isopods initially preferred the dicotyledonous plants to the other two choices. But after the monocotyledonous plants began to decay, these were preferred. Nevertheless, eating monocots increased mortality and drastically reduced growth rates and reproductive output, even when it was in a later decay state. Defenses in the food become more concentrated as the food decays and carbon sources are removed. Chemical defenses in mosses may play a role in the isopod choice of leaf litter over mosses in ***Armadillidium vulgare***.

Figure 27. ***Calliergonella cuspidata***, a moss that seems to deter feeding by ***Armadillidium vulgare***. Photo by J. C. Schou, through Creative Commons.

Rushton and Hassall (1983a) suggested that ***Armadillidium vulgare*** (Figure 8) compensates for low quality food by eating more, but that plant defenses can interfere with this compensation. Even though the moss is likely to provide a suitable moist habitat, and ***Armadillidium vulgare*** may be able to absorb at a high rate on low quality food by increasing its rate of consumption, it appears that plant defenses of ***Calliergonella cuspidata*** (Figure 27) might outweigh its habitat desirability (Rushton & Hassall 1983a).

Dead mosses may be less desirable than dead tree leaves or even monocot leaves, particularly after the tracheophyte leaves begin to decay. It is likely that very little nutritional material is available relative to cell wall material in dead mosses (see Pakarinen & Vitt 1974 for lower N content), especially if nutrients are moved from dead portions to living portions, but that relationship requires further testing.

Figure 28. ***Hypopterygium didictyon*** from Chile, a moss in the same genus as one grazed in Costa Rica. Photo by Juan Larrain, with permission.

Nevertheless, at times isopods can be voracious consumers of bryophytes. Angela Newton (Bryonet, 20 November 2006) reported seeing extensive grazing on ***Hypopterygium*** sp. (Figure 28) in the montane rainforest of Costa Rica. The isopods sheared off the green lamina and left the branches and costa, much like the feeding behavior of insects on tracheophyte leaves. However, grazing of isopods and silverfish on damp herbarium labels and plants in packets made her question whether they were simply feeding on the associated fungi and consumed the mosses in the process.

Isopods can be downright pests on garden mosses. Henk Greven, in a communication to Bryonet (23 October 2003) writes: "Apart from mammals, birds and slugs, sow-bugs (***Oniscus asellus*** L.; Figure 13) are fervent bryophyte eaters. In my garden, I keep several ***Grimmia*** species on pieces of rock. When I put these on the ground, sow-bugs are hiding during the day under these rocks. In the evening they climb above and start eating my ***Grimmias***. They have a special preference for ***Grimmias*** growing on limestone, basic sandstone, and basic basalt. In no time, they have eaten all my ***Grimmia plagiopoda*** (Figure 29), ***G. crinita*** (Figure 30), and ***G. orbicularis*** (Figure 31). Species on acidic rock, however, are not safe either. The only species they don't like is ***Ptychomitrium polyphyllum*** (Figure 32). I had this species nearly ten years on a piece of rock on my garden floor. I learnt my lesson and now I keep pieces of rock on a table where they are safe from sow-bugs."

Figure 29. ***Grimmia plagiopoda***, a species that seems to be preferred food for ***Oniscus asellus*** on limestone rocks. Photo by Michael Lüth, with permission.

Figure 30. ***Grimmia crinita***, a species that seems to be preferred food for ***Oniscus asellus***. Photo by Michael Lüth, with permission.

Figure 31. ***Grimmia orbicularis*** with capsules, growing on rock. This seems to be a preferred food for ***Oniscus asellus*** in limestone habitats. Photo by Michael Lüth, with permission.

Figure 32. ***Ptychomitrium polyphyllum***, a moss that is not eaten by ***Oniscus asellus***. Photo by David T. Holyoak, with permission.

Likewise, I have already reported above on my own sad experience with ***Porcellio scaber*** (Figure 24) eating my carpet of mosses so that it looked like Swiss cheese. And Daniel Marsh (Bryonet, 18 November 2006) reported that wood lice (isopods) have usually consumed any liverwort he tried to cultivate in his garden or greenhouse. "The attraction seems to be immediate." In contrast, he reports that he has not noticed such consumption of liverworts by isopods in wild communities.

We (Weston 1995; Liao & Glime unpubl) attempted to find out what sorts of things might deter pillbugs (***Porcellio scaber*** (Figure 24). Using ***Polytrichum juniperinum*** (Figure 33) and ***P. commune*** (Figure 34) from Houghton, MI, USA, we compared consumption of stems and leaves. ***Polytrichum juniperinum*** leaves were consumed 3:1 over stems; ***P. commune*** leaves were consumed 5.5:1 over stems (Figure 35). It made no difference whether the leaves were still connected to the stems or not.

Figure 33. ***Polytrichum juniperinum***, a species in which ***Porcellio scaber*** prefers eating leaves over stems. Photo by Li Zhang, with permission.

Figure 34. ***Polytrichum commune***, a species in which ***Porcellio scaber*** prefers eating leaves over stems. Photo by David T. Holyoak, with permission.

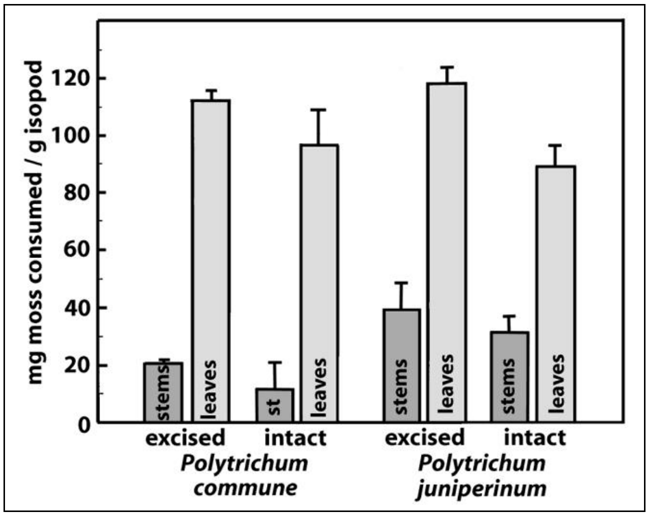

Figure 35. Comparison of mean isopod (***Porcellio***) consumption ± 95% CI of excised leaves and stems vs intact leaves and stems in two species of moss. Data based on unpublished laboratory data of Weston 1995; Liao & Glime unpublished data; n = 3.

In both ***Polytrichum juniperinum*** (Figure 33) and ***P. commune*** (Figure 34), the leaves had roughly double the protein content per dry weight compared to the stems (Figure 36) (Weston 1995; Liao & Glime unpubl), suggesting that the isopod ***Porcellio scaber*** (Figure 24) could gain more protein nutrition from eating leaves. And structurally leaves would seem to be easier to chew than the tough stems endowed with thickened walls and coloration suggesting phenolic compounds. But it is surprising to find that the leaves of at least ***P. commune*** seem to have a higher concentration of phenolic compounds than do their stems (Figure 37), yet that species had the higher consumption ratio of leaves to stems. Perhaps the presence of folded-over leaf edges in ***Polytrichum juniperinum*** (Figure 38), absent in ***P. commune*** (Figure 39), makes it easier to obtain the nutritious photosynthetic lamellae in ***P. commune*** (Figure 39).

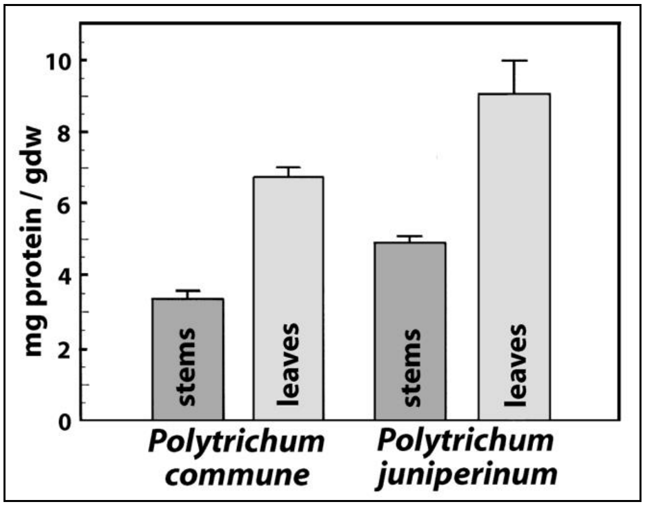

Figure 36. Comparison of mean protein ± 95% CI in stems and leaves of two ***Polytrichum*** species. Based on Weston 1995; Liao & Glime unpublished data; Bradford's (1976) test, n = 3.

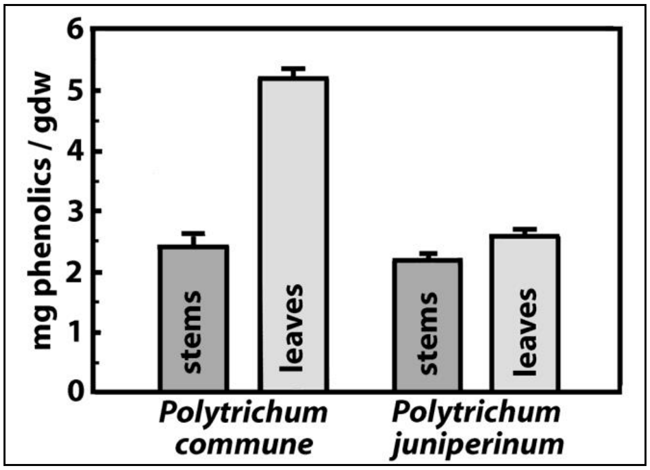

Figure 37. Comparison of mean phenolic content ± 95% CI in stems and leaves of two ***Polytrichum*** species. Based on Weston 1995; Liao & Glime unpublished data; Folin-Denis test (Swain & Hillis 1959) and Prussian Blue test for tannin; n = 3.

Figure 38. ***Polytrichum juniperinum*** leaf cross section showing margin of leaf rolled over the lamellae, partially covering them. Photo by John Hribljan, with permission.

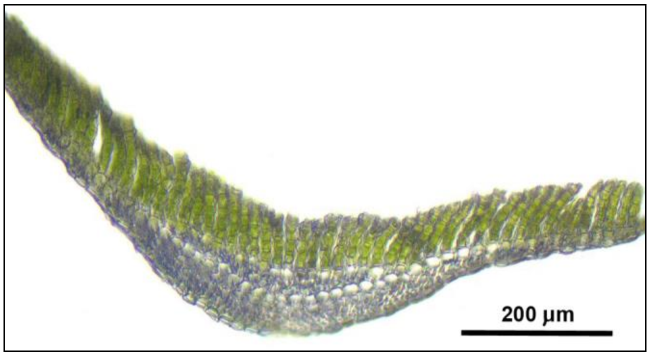

Figure 39. ***Polytrichum commune*** leaf cross section showing absence of rolled over leaf margin, thus giving exposure to all the lamellae. Photo by Kristian Peters, through Creative Commons.

Isopods can be a major inhabitant of bryophytes, becoming especially obvious at night when they migrate to the surface to feed (Hribljan & Glime in prep.). But even the isopods are fussy about which bryophytes they eat. Phenolic content seems to deter isopod consumption of various leaves (Warburg 1987). But deterrents may not be the only answer to these food preferences. ***Porcellio scaber*** (Figure 24) will eat ***Thuidium delicatulum*** (Figure 40-Figure 41) ravenously, but ignore ***Dicranum polysetum*** (Figure 42) and sometimes ignore ***Pleurozium schreberi*** (Figure 43) (Liao 1993; Glime 2006). When faced with ***Polytrichum*** (Figure 33), they eat the leaves, but little of the stems (Liao 1993, unpublished data; Hribljan 2009). This suggests that chemistry might be more important than structure, as ***Thuidium delicatulum*** is a crunchy moss with papillae (but small leaves, Figure 41) whereas ***P. schreberi*** and ***D. polysetum*** are softer and more flexible, lacking papillae (but with large leaves). But it appears that we may not have examined enough potential deterrents in ***Thuidium***. And we need to beware of differences between populations and seasons. Fatoba *et al*. (2003) found that whereas ***Thuidium gratum*** from the Nigerian tropics lacked detectable phenolics, it had tannins, alkaloids, and cardiac glycosides. In a different location in tropical Nigeria (and a different date), Adebiyi *et al*. (2012) found that this same species had a high content of saponins (absent in the Fatoba *et al*. 2003 study) and flavonoids, but also had a very low content of phenolics. Perhaps isopods, like many humans, just prefer a crunchy snack.

Figure 40. ***Thuidium delicatulum***, a moss readily eaten by ***Porcellio scaber***. Photo by Bob Klips, with permission.

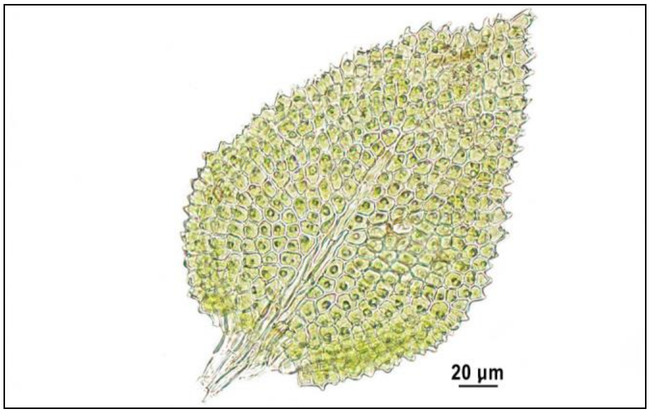

Figure 41. ***Thuidium delicatulum*** branch leaf showing small cells and papillae (note bumps on cells). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 42. ***Dicranum polysetum***, a moss that is ignored, not eaten, by ***Porcellio scaber***. Photo by Bob Klips, with permission.

Figure 43. ***Pleurozium schreberi***, a moss that is sometimes eaten and sometimes ignored by the wood louse ***Porcellio scaber***. Photo by Janice Glime.

Hribljan and Glime (in prep) explored the food preferences of populations of ***Porcellio scaber*** (Figure 24) in the Keweenaw Peninsula of Michigan, USA. In food preference experiments, these isopods preferred the moss ***Pleurozium schreberi*** (Figure 44) over leaf litter from ***Acer saccharum*** (Figure 45) and ***Pinus strobus*** (Figure 46) in each of three study months of September – November (Figure 47). They compared the carbohydrates, proteins, and phenolics in these three species for the three months of the feeding trials and found that ***Pleurozium schreberi*** had the lowest levels of phenolics and highest levels of carbohydrates of the three choices of food (Figure 48). This is interesting because some studies (*e.g.* Pakarinen & Vitt 1974) have suggested that mosses were unable to provide enough energy for herbivores, but it appears that compared to leaf litter the mosses may, at least at times, have more carbohydrates than litter and be preferred food for isopods. Furthermore, all five mosses tested [***Pleurozium schreberi***, ***Thuidium delicatulum*** (Figure 40-Figure 41), ***Polytrichum juniperinum*** (Figure 33), ***Rhytidiadelphus triquetrus*** (Figure 49), and ***Dicranum polysetum*** (Figure 42)] had higher carbohydrate contents than the leaf litter of the trees tested (Figure 50-Figure 51). However, protein was higher in both types of tree leaf litter tested compared to that of ***Pleurozium schreberi*** (Figure 48).

Figure 44. ***Pleurozium schreberi*** showing damage from ***Porcellio scaber*** that feeds on it at night. Note the less green plants on left that have suffered considerable damage. On the right you can see naked red stem tips where leaves and buds have been eaten. Photo by John Hribljan, with permission.

Figure 45. Freshly fallen *Acer saccharum* (sugar maple) leaves, a food source less preferred by ***Porcellio scaber*** than the moss ***Pleurozium schreberi*** in September to November. Photo by Janice Glime.

Figure 46. A common sight of needles of *Pinus strobus* (white pine) mixed with the moss ***Pleurozium schreberi***. The needles are a food less preferred in September to November by ***Porcellio scaber*** than the moss ***Pleurozium schreberi***. Photo by Janice Glime.

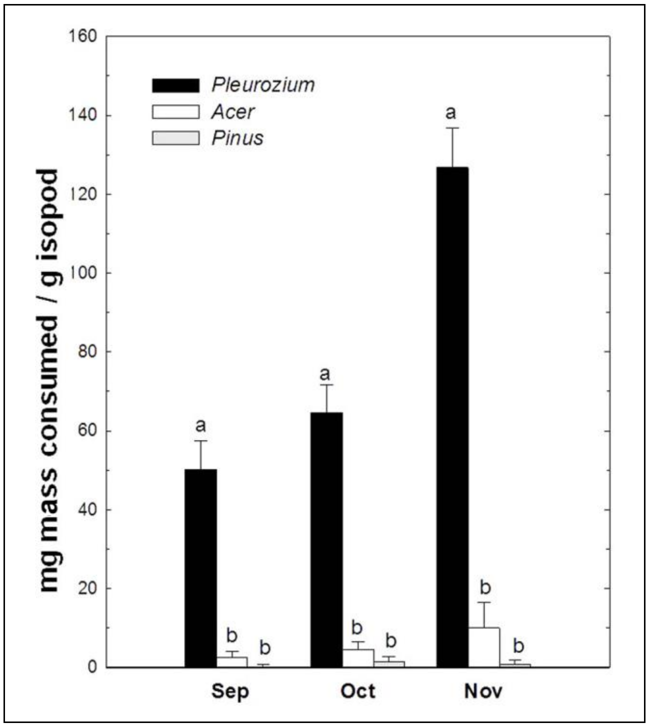

Figure 47. Comparison of mean air-dried mass (±95% CI) consumed by isopods in 24 hours when given the choice of the moss ***Pleurozium schreberi*** and the tree leaves of ***Acer saccharum*** and ***Pinus strobus***. The same letters signify means that are not significantly different from each other ($\alpha = 0.05$ post two-way ANOVA & Tukey test, n = 10). Hribljan 2009; Hribljan & Glime in prep.

Based on these experiments, Hribljan and Glime (in prep) compared the preferences among five species of mosses that occurred within the foraging distance of the isopods. ***Porcellio scaber*** (Figure 24) significantly preferred the moss ***Pleurozium schreberi*** (Figure 44) to the mosses ***Rhytidiadelphus triquetrus*** (Figure 49), ***Thuidium delicatulum*** (Figure 40), ***Dicranum polysetum*** (Figure 42), and ***Polytrichum juniperinum*** (Figure 50), with ***Pleurozium schreberi*** and ***Rhytidiadelphus triquetrus*** having lower phenolic concentrations than ***Dicranum polysetum*** and ***Polytrichum juniperinum*** (Figure 51). The

Thuidium delicatulum, preferred in earlier experiments over ***Pleurozium schreberi*** (Liao 1993; Glime 2006), was not among the top preferences, perhaps due to its lower carbohydrate content at a time of year when the isopods were preparing for winter.

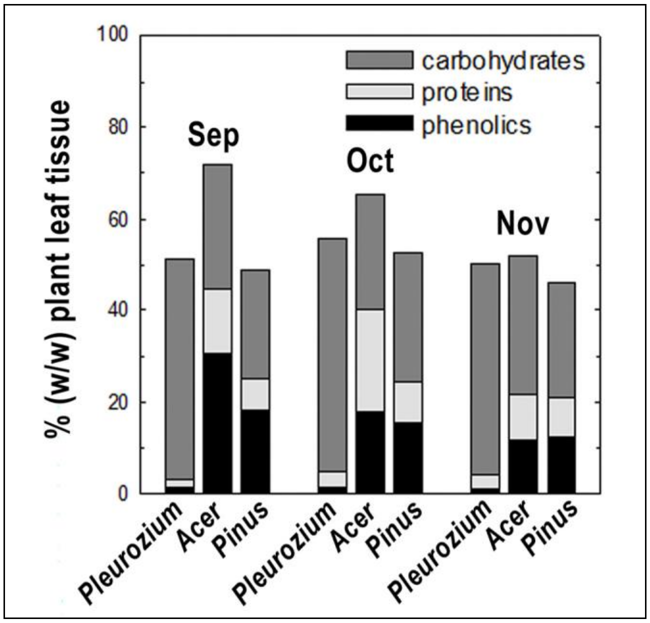

Figure 48. Comparison of percent of carbohydrates, proteins, and phenolics in freeze-dried leaves of the moss ***Pleurozium schreberi***, sugar maple tree ***Acer saccharum***, and white pine ***Pinus strobus***. Samples were taken once each month during to compare stages of decay in the tree leaves. Values are means of 10 samples. Redrawn from Hribljan & Glime (in prep).

Chemical analysis revealed that ***P. schreberi*** contains a high protein:phenolic ratio (Figure 55) (Hribljan & Glime in prep). Despite the high phenolic content and low protein content of ***Rhytidiadelphus triquetrus*** (Figure 49), these isopods would still consume it (Figure 52-Figure 53), perhaps for its high carbohydrate content, but it was not a preferred food (Figure 50-Figure 51). On the other hand, the feces indicated that this moss had not been well digested (Figure 54). As a terrestrial moss, it collects only minimal detritus, suggesting that it could have limited food value. ***Dicranum polysetum*** was least preferred despite a relatively high carbohydrate content (Figure 50-Figure 51).

Figure 49. ***Rhytidiadelphus triquetrus***, a less preferred bryophyte as autumn food for ***Porcellio scaber***, growing as it typically does amid leaf litter. Photo by Michael Lüth, with permission.

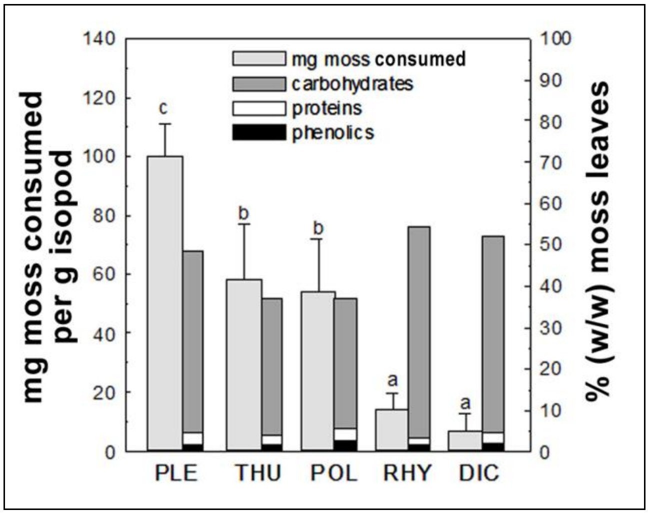

Figure 50. Comparison of moss consumed (mean ±95% CI) with mean percent by weight of phenolics, proteins, and carbohydrates in leaves of the mosses ***Pleurozium schreberi*** (PLE), ***Thuidium delicatulum*** (THU), ***Polytrichum juniperinum*** (POL), ***Rhytidiadelphus triquetrus*** (RHY), and ***Dicranum polysetum*** (DIC). n = 10. Hribljan 2009; Hribljan & Glime in prep.

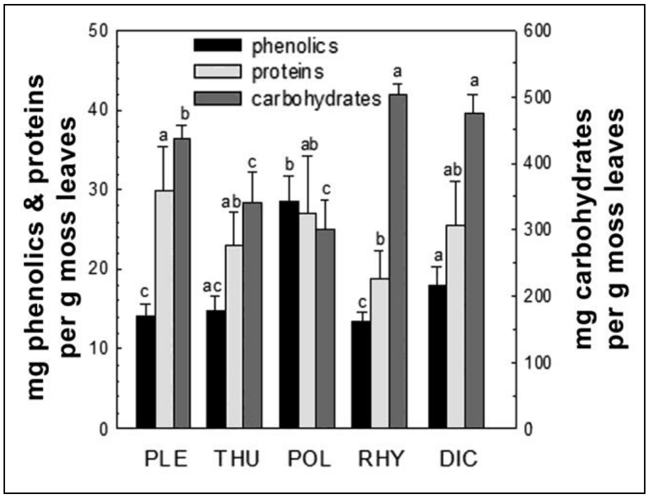

Figure 51. Comparison of means ±95% CI of phenolics, proteins, and carbohydrates in leaves of the mosses (arranged from most to least eaten) ***Pleurozium schreberi*** (PLE), ***Thuidium delicatulum*** (THU), ***Polytrichum juniperinum*** (POL), ***Rhytidiadelphus triquetrus*** (RHY), and ***Dicranum polysetum*** (DIC). n = 10. Bars with the same letters are not significantly different (α=0.05, n=10).

Figure 52. Branches of ***Rhytidiadelphus triquetrus*** that have been nibbled by ***Porcellio scaber***. Photo by John Hribljan, with permission.

Figure 53. Moss branches of ***Rhytidiadelphus triquetrus*** being eaten by ***Porcellio scaber***. Photos by John Hribljan, with permission.

Figure 54. Moss leaf fragments extracted from feces of ***Porcellio scaber*** fed only ***Rhytidiadelphus triquetrus***. Photo by John Hribljan, with permission.

Hribljan (2009) suggested that the protein:phenolic ratio might be more important in determining isopod herbivory than concentration of phenolic compounds alone. In this case, ***Pleurozium schreberi*** (Figure 44) had the highest ratio of proteins:phenolics (Figure 55), but it was not significantly different from that of ***Dicranum polysetum*** (Figure 42), which had the lowest mass eaten, suggesting that this ratio alone did not account for the preference (Hribljan & Glime in prep). With their unusual digestive tracts (see Digestion above), the terrestrial isopods may be able to gain sufficient nutrition from mosses despite phenolics, whereas other arthropods like the cranefly ***Tipula montana***, a moss-food-avoider, cannot (Smith *et al*. 2001).

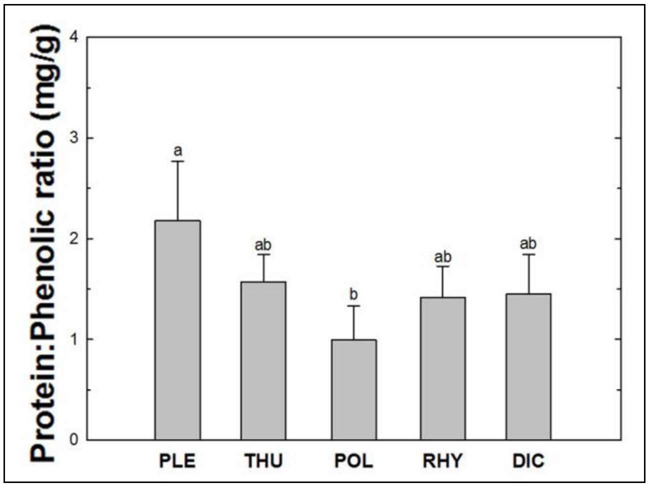

Figure 55. The mean protein:phenolic ratio of leaves (± 95% CI), arranged in order from most to least consumption, of freeze-dried mosses ***Pleurozium schreberi*** (PLE), ***Thuidium delicatulum*** (THU), ***Polytrichum juniperinum*** (POL), ***Rhytidiadelphus triquetrus*** (RHY), and ***Dicranum polysetum*** (DIC). n = 10; bars with the same letter are not significantly different, post ANOVA Tukey test, α = 0.05).

We cannot rule out the possible importance of carbohydrates, and Forman (1968) provides evidence that caloric content is highest in two of the mosses that seem to be preferred in our experiments (Hribljan & Glime in prep). Forman showed that ***Thuidium delicatulum*** (Figure 40) had the highest caloric value (4305 cal/gdw) among the ten mosses he tested; ***Pleurozium schreberi*** (Figure 43) had the second highest caloric content (4240 cal/gdw), fitting with our data on carbohydrates. On the other hand, the lowest content was that of ***Dicranella heteromalla*** (Figure 56) (3749 cal/gdw), a moss in the same family as ***Dicranum polysetum*** (Figure 42), the latter being least preferred in our experiments. Furthermore, Sveinbjörnsson and Oechel (1991) found that the carbohydrate concentration varied with season in ***Polytrichum commune*** (Figure 34), but not in ***Polytrichastrum alpinum*** (Figure 57). Could it be that some bryophytes become more desirable in autumn due to higher carbohydrate concentrations?

Figure 56. ***Dicranella heteromalla*** in its typical soil bank habitat. This moss has a relatively low caloric content. Photo by Janice Glime.

Figure 57. ***Polytrichastrum alpinum*** with capsules. Photo by Michael Lüth, with permission.

Several other factors could account for the preferences. First, we know that other deterrents such as saponins, alkaloids, and steroids are present in some mosses and were not tested here (Adebiyi *et al*. 2012). Leaf structure could make it difficult to obtain energy from the leaves or they might be harder to chew and break off (**toughness**). We have no measures of such toughness differences for these species, so we must keep an open mind about that possibility. The structure of the cell wall might make it difficult to obtain the cell contents easily (Figure 58-Figure 59). As seen in Figure 58, ***Pleurozium schreberi*** has much thinner cell walls than the much less preferred ***Dicranum polysetum*** (Figure 42, Figure 59). But does this really translate to toughness? Or edibility? And the leaves might differ from the stems in their phenolic content, making measurements of whole plants meaningless if only leaves are eaten. However, Hribljan and Glime (in prep) used only leaves for their analyses of proteins, carbohydrates, and phenolics. They did compare the chemistry of stems and leaves in ***Pleurozium schreberi***; for all three chemical groups (phenolics, protein, carbohydrates), leaves had the higher content (Figure 60).

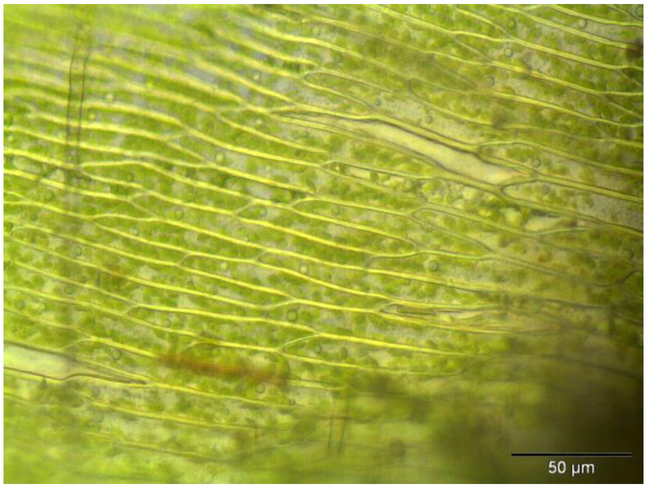

Figure 58. Leaf cell structure of ***Pleurozium schreberi*** showing thin cell wall and high ratio of cell contents to cell wall. This species was most consumed among the five moss species in the study by Hribljan and Glime (in prep.). Photo from Wikimedia Commons.

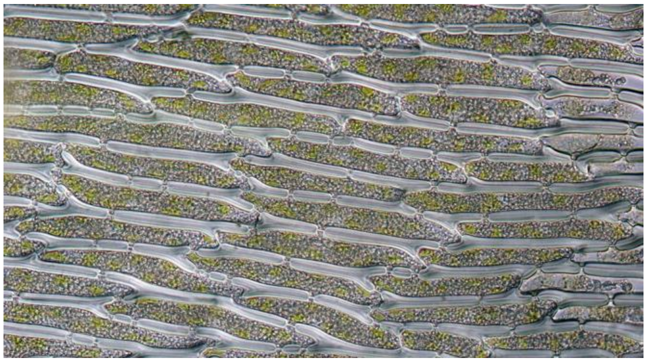

Figure 59. Leaf cell structure of ***Dicranum polysetum*** showing thick cell wall and low ratio of cell contents to cell wall. This species was least consumed among the five moss species in the study by Hribljan and Glime (in prep.). Photo by Walter Obermayer, with permission.

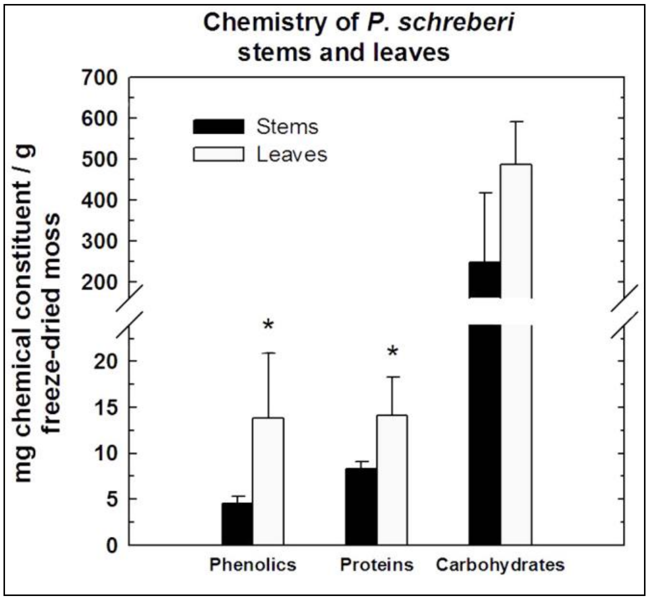

Figure 60. Comparison of mean phenolic, protein, and carbohydrate content (± 95% CI) of ***Pleurozium schreberi*** between freeze-dried leaves and stems (paired t-test, an asterisk indicates a significant difference between the two bars, $\alpha = 0.05$, n = 3).

These studies leave many questions unanswered, especially regarding season. Do the concentrations in the bryophytes change with season? Do the isopod needs change with season? Does the tree litter change in such a way that bryophytes are preferable at some times and not others without requiring any change in the bryophytes? And are the relationships the same if liverworts are presented instead of mosses? Finally, what evolutionary patterns can we observe and how do they relate to habitat and dominant herbivores?

Defenses and Apparency Theory

Plant defenses can be grouped into **physical** and **chemical defenses**. **Physical defenses** include structural modifications into such deterrents as thorns and spines or tissue modifications that include hard cell walls (Cooper & Owen-Smith 1986). The small bryophyte structure does not permit the large thorns found in some tracheophytes, but hard cell walls and hard papillae as extensions of the cell wall do fall into this category.

Chemical defenses can be divided into **quantitative** and **qualitative defenses** (Feeney 1975, 1976; Rhoades & Cates 1976; Yamamura & Tsuji 1995). **Qualitative defenses** include toxic substances like the milky juices of milkweed plants. Few bryophytes have been tested for such substances as those found in the milkweed, but as mentioned above, similar compounds do exist in the few that were tested (Fatoba *et al*. 2003; Adebiyi *et al*. 2012). **Quantitative defenses**, on the other hand, are quite common in bryophytes and typically interfere with digestion (Yamamura & Tsuji 1995), creating malnutrition in the herbivore. Phenolics typically fall in this category.

The **apparency theory** (Feeney 1976) was developed to explain the production of secondary compounds such as **phenolics** among some plants and not others (Coley *et al*. 1985). Coley and coworkers contended that resource availability in the environment was a primary determinant of both the amount and type of plant defense. Under resource limitation, slow-growing plants are favored by the environment over fast-growing plants because the former use lower levels of resources. At the same time, slow growth rates favor larger investments in **antiherbivore** defenses because growth is not fast enough to replace effects of herbivory. Since bryophytes are slow-growing, they are often able to inhabit locations with low levels of resources, including sunlight, where few other plants grow robustly, making the bryophytes one of the obvious, or **apparent**, plants in the area. Hence, bryophytes could benefit in these situations by the production of antiherbivore compounds. In fact, development of such compounds may have been essential to their success on land as the arthropods likewise became terrestrialized (Graham *et al*. 2004). Phenolic compounds, occurring in varying concentrations from the bryophytes tested, are useful as antiherbivore compounds. And it appears that bryophytes are not eaten by many kinds of organisms. Isopods are a notable exception to that avoidance. But even they have preferences.

We have seen above that for the isopod ***Porcellio scaber*** (Figure 1-Figure 2), ***Dicranum polysetum*** (Figure 42, Figure 59) is a less-preferred moss compared to ***Thuidium delicatulum*** (Figure 50) (Hribljan & Glime in prep). The former is an **apparent** moss (one with high visibility in its habitat) with high concentrations of secondary compounds (phenolic compounds), whereas ***Thuidium delicatulum*** is **unapparent** (grows with other potential food plants) and is low in secondary compounds (Liao 1993). Furthermore, ***Thuidium delicatulum*** tends to grow where there is more sun and often more nutrients, thus supporting the concept that production of phenolic compounds may be related to resource limitation (see Coley *et al*. 1985).

But it is not so simple. ***Pleurozium schreberi*** (Figure 43) is a very apparent moss, sometimes covering hectares with 100% cover, yet had the highest consumption. The study by Liao (unpublished) and the discussion here related to the study by Hribljan and Glime (in prep) seem to be the only studies that have tested the apparency theory in bryophytes. This should be an interesting topic for study.

Aquatic Consumers

Among the aquatic isopods, some consume bryophytes, but others apparently do not. Torres-Ruiz *et al*. (2007) traced food and fatty acids in macroinvertebrates and determined that the isopods in a stream food web fed on terrestrial food sources and on algae. ***Asellus*** species consume a variety of aquatic vegetation. Marcus *et al*. (1978) experimented with a sometimes moss dweller, ***Asellus aquaticus*** (Figure 61), and demonstrated that it ate both *Elodea canadensis* and **periphyton** (adhering algae), being able to survive on either. They found fragments of *Elodea* leaves and pieces of oak (*Quercus*), as well as the alga *Oedogonium* in the guts of some individuals of this species from Lake Windermere, England.

Figure 61. ***Asellus aquaticus***, an aquatic isopod that dines on ***Fontinalis novae-angliae***. Photo from Wikimedia Commons.

Parker *et al.* (2007) found that ***Asellus aquaticus*** (Figure 61) consumed large quantities of the brook moss ***Fontinalis novae-angliae*** (Figure 62) but rejected the riverweed *Podostemum ceratophyllum* (Figure 63), despite having similar protein content in both. The isopods continued to eat the ***F. novae-angliae*** even when the organic matter was removed from the plants, demonstrating that the moss itself was most likely a food source. They suggested that the mosses served as a refuge against larger predators that could eat the ***A. aquaticus***, largely because such predators as crayfish (*Procambarus spiculifer*, Figure 64; Figure 95) and Canada geese (*Branta canadensis*; Figure 65) avoided the mosses despite its comprising 89% of the plant cover in the stream. It seems that the chemical deterrents to the geese and crayfish served to protect the many macroinvertebrates living there. And to the advantage of the ***A. aquaticus***, these isopods rejected the riverweed. On the other hand, this species was not deterred by the chemical defenses of the mosses.

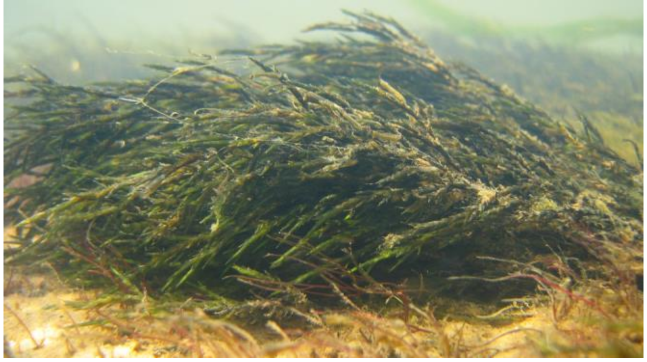

Figure 62. ***Fontinalis novae-angliae***, a habitat and a food source for species of ***Asellus***. Photo by John Parker, with permission.

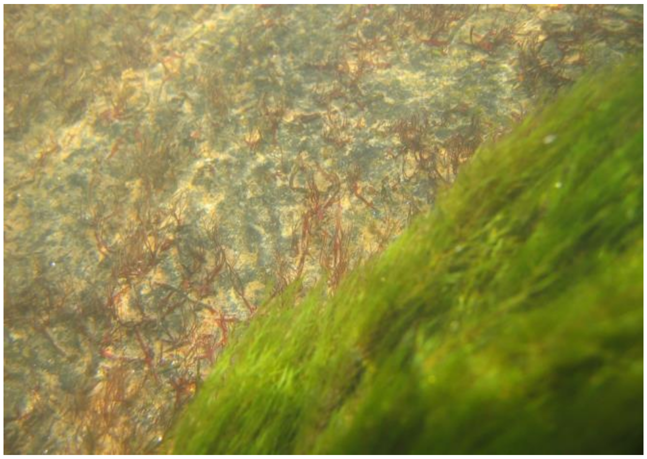

Figure 63. *Podostemum ceratophyllum* (riverweed) in upper left, appearing as fine red threads here. This plant has been heavily grazed, whereas the ***Fontinalis novae-angliae*** on the right has not. Photo by John Parker, with permission.

Figure 64. *Procambarus spiculifer*, a crayfish that avoids mosses, thus making the mosses a protected site for the isopods dwelling there. Photo by Chris Lukhaup, with permission.

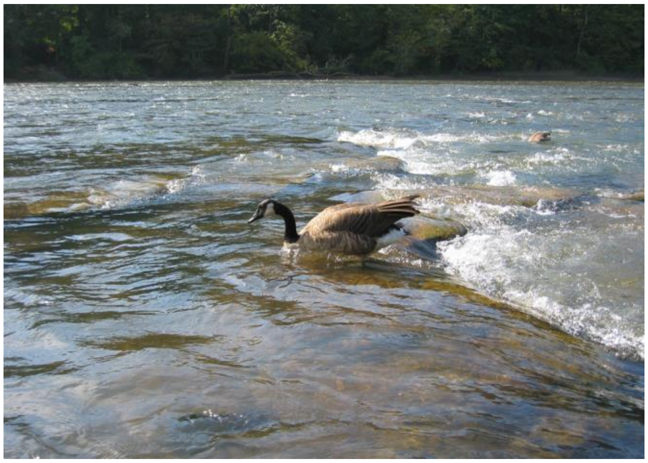

Figure 65. ***Branta canadensis*** (Canada Goose), a large bird that avoids mosses, thus permitting the mosses to protect would-be food items that hide there. This one is feeding on riverweed (*Podostemum ceratophyllum*). Photo by John Parker, with permission.

Asellus *cf.* ***militaris*** (Figure 66) eats ***Fontinalis antipyretica*** (Figure 66) in lab experiments and in the field (LaCroix 1996a). Likewise, ***A.*** cf. ***militaris*** feeds on ***Fontinalis novae-angliae*** (Figure 62) in its native aquatic habitat (LaCroix 1996a; Parker *et al.* 2007). Fragments of ***F. antipyretica*** were found in the feces of freshly collected ***A.*** *cf.* ***militaris*** (Figure 67), and when ***A.*** *cf.* ***militaris*** was cultured in the lab with the moss as a substrate it produced fecal pellets containing the moss. Gut analysis revealed diatoms and detrital matter along with small fragments of ***Fontinalis*** (Figure 68). LaCroix found that even terrestrial isopods would eat ***F. antipyretica***.

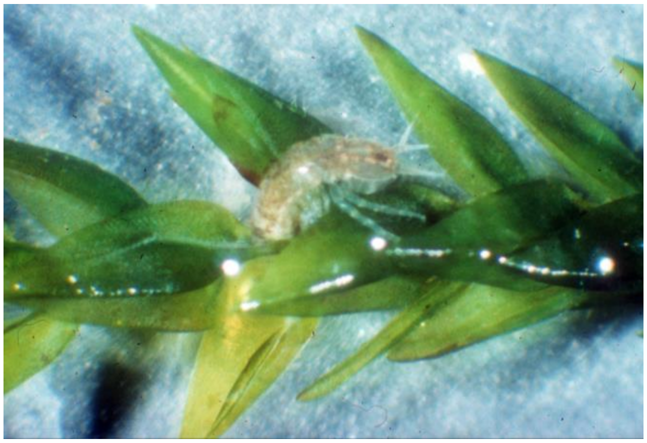

Figure 66. ***Asellus*** *cf.* ***militaris*** on a branch of ***Fontinalis antipyretica***, where it lives in slow-moving streams and uses the moss as a food source. Photo by Jacob LaCroix, with permission.

Figure 67. ***Asellus*** *cf.* ***militaris*** feces containing ***Fontinalis antipyretica*** and detrital matter. Photo by Jacob LaCroix, with permission.

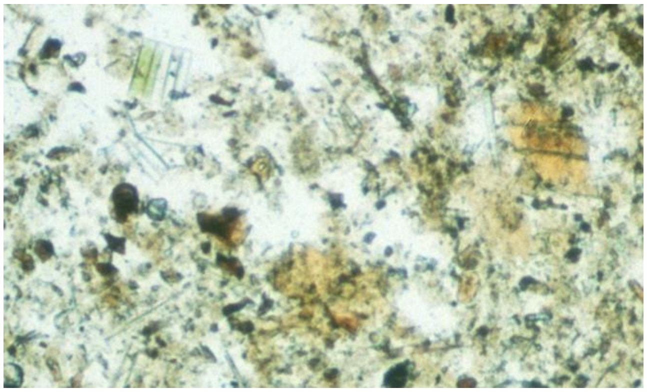

Figure 68. ***Fontinalis antipyretica*** and diatoms in gut of ***Asellus*** *cf.* ***militaris***. Photo by Jacob LaCroix, with permission.

Stern and Stern (1969) determined the greatest abundance in February and the lowest in July in a cold springbrook in Putnam County, Tennessee, USA. ***Asellus***

militaris occurs on ***Fontinalis antipyretica*** for the first few instars, then moves to the leaf litter.

Observations by LaCroix and Glime (unpublished) suggest that this species can live among the mosses for a much greater part of the life cycle in northern Michigan, USA. Like terrestrial isopods, ***Asellus** cf.* ***militaris*** (Figure 66) avoids the light. Hence, more of these isopods were on the mosses in the shade in the stream than in the sun (LaCroix 1996a; Glime 2006). When both sun and shade mosses were brought to the lab and placed under the same light conditions, the isopods preferred those that had grown in the sun. Furthermore, the isopods chose to go to the mosses collected from the sunny location under both light and dark conditions (LaCroix 1996a). Surprisingly, the shade populations had higher concentrations of phenolic compounds (LaCroix 1996a), a phenomenon contrary to the use of phenolic compounds as light protectants in tracheophytes (Swain & Hillis 1959; Martin & Martin 1982; Mole *et al.* 1988; Vergeer *et al*. 1995), but consistent with the preference for those grown in the sun when light was no longer a factor. Bryophytes often take advantage of phenolic compounds as protection against UV radiation (Jorgensen 1994; Clarke & Robinson 2008; Wolf *et al*. 2010), suggesting that herbivory was a stronger factor in this case than light. This combination of circumstances raises several questions.

First, how can we explain isopod preference for high phenolic shade bryophytes in the field but preference for lower phenolic sun bryophytes in the lab (Figure 69)? Parker *et al*. (2007) showed ***Asellus aquaticus*** (Figure 61) was not deterred by extracts from ***Fontinalis novae-angliae*** (Figure 62). Parker *et al*. suggested these isopods have some means to render the deterrent compounds ineffective, as suggested above in the discussion of the digestive system. LaCroix (1996a, b) concluded that food quality of the moss determined what isopods ate, but that shade was a more important determining factor controlling their location (and hence available food) in the field. This combination can structure communities in which small invertebrates live among unpalatable hosts that provide enemy-free space, and isopods have the benefit of avoiding their own predators while being able to eat the substrate.

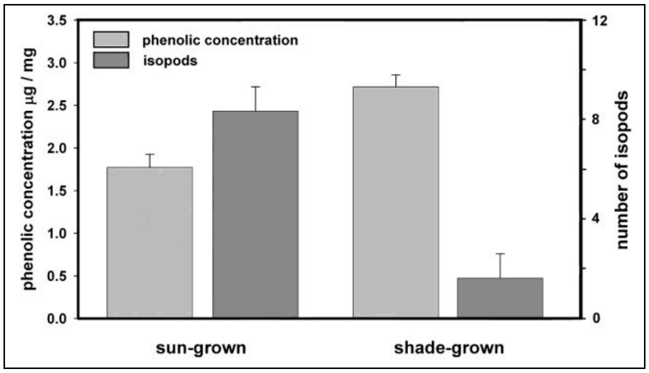

Figure 69. Comparison of moss ***Fontinalis antipyretica*** mean phenolic content (± 95% CI) and number of moss-dwelling isopods ***Asellus** cf.* ***militaris*** (± 95% CI) choosing to inhabit it. Most of the isopods in the lab chose to go to the sun-grown ***Fontinalis antipyretica*** that had a lower phenolic content than that in the shade plants. Based on LaCroix 1996b.

Apparency or UV Protection?

Having suggested an explanation for the behavior of the isopods, we are left with the question of the higher production of phenolic compounds by the bryophytes in the shade compared to those in the sun. As suggested above for terrestrial bryophytes, it is possible that the production of phenolic compounds by mosses in the shade is an evolutionary response to **apparency**. In shady locations of streams, mosses are likely to be the dominant macrophyte vegetation, with aquatic tracheophytes preferring sun LaCroix 1996a). As the dominant (most apparent) organism, probability would make the bryophytes the most likely to be eaten. Furthermore, the ***Fontinalis*** had phenolic compounds in both locations, so it is likely that they had sufficient levels in the sun to provide the needed protection against UV radiation.

Could it be that the ***Fontinalis*** produces phenolic compounds in response to herbivory? If so, are they able to signal (chemically) to the nearby mosses to do likewise? Or might this moss have evolved to produce more phenolic compounds in the shade under the selective pressure of one of its primary herbivores, aquatic isopods, that spends most of its time in the shade?

Habitat

You know where isopods hang out. Look under anything with a tiny bit of space to give access and you will find them. They go scurrying away in seek of shelter when you lift their cover. But look out at night. They come out in force to eat your vegetables – and your mosses.

Bryophytes seem to play multiple roles in the niches of isopods. For terrestrial species, bryophytes provide refuge against some predators, but even for litter-dwelling species they may represent islands for rehydration amid a dry food area. But the bryophytes can also serve as food, especially at night when desiccation is less of a problem. Aquatic bryophytes likewise serve as a refuge against predators and can also serve as food or a food substrate for periphyton and detritus. Zimmer and Topp (1997) found that ***Porcellio scaber*** (Figure 1-Figure 2) populations decreased in response to acidification, and that microorganisms, often reduced by acid conditions, were important in the maintenance of juveniles.

It seems logical that the first consideration for a habitat for isopods is a moist place with good aeration that provides shelter and darkness, but that also has a food source. In the water, detritus and periphyton can serve as the food source, but on land periphyton is too minor and detritus is more likely to be in the soil. Hence, bryophytes that provide these physical characteristics and are also palatable and chewable become a food source and provide a suitable habitat.

Terrestrial

Terrestrial habitats require special adaptations for these groups, as discussed above. Edney (1954) found that terrestrialization increased in the order of **Ligiidae**, **Trichoniscidae**, **Oniscidae**, **Porcellionidae**, to **Armadillidiidae**. This order can be interpreted as their order for tolerating drought. And each of these families has members known from bryophytes.

Božanić (2011) sampled the moss invertebrate fauna in a forest in the Vrapač National Nature Reserve, Czech Republic. The most abundant groups were **Acarina** (mites – 2946 individuals), **Collembola** (springtails – 1341 individuals), and **Isopoda** (320 individuals). Within moss colonies on the forest floor and tree trunks they found the isopods ***Androniscus roseus***, ***Hyloniscus riparius*** (Figure 86), ***Hyloniscus*** spp., ***Lepidoniscus minutus***, ***Ligidium hypnorum***, ***Porcellium collicola*** (Figure 3), ***Porcellium conspersum***, ***Trachelipus rathkii*** (Figure 26), ***Trachelipus ratzeburgii*** (Figure 85), ***Trachelipus*** spp., and ***Trichoniscus pusillus*** (Figure 25). In the adjoining forest floor, the isopods were not among the most numerous groups sampled. Sample size was important in determining abundance, with more isopods occurring in larger sample sizes of ~400 sq cm. ***Trichoniscus pusillus*** and ***Hyloniscus riparius*** in particular preferred thicker mosses, especially in ***Plagiomnium undulatum*** (Figure 70) with a 50-mm thickness. These two species are known to be **hygrophilous** (water-loving) (Tajovský 2000), perhaps explaining their preference for thicker mats that could retain moisture longer. This preference could create danger as this thicker moss was also in the range of preference of a predator ant, ***Myrmica ruginodis*** (Figure 71), that occurred primarily in mosses having 40-50 mm thickness (Božanić 2011). In poplar forests of Hungary, ***Hyloniscus riparius*** (Figure 86) occurs primarily in wet, decaying trees that are covered with mosses (Farkas 1998).

Figure 70. ***Plagiomnium undulatum***, a moss that forms 50 mm deep mats where the isopods ***Trichoniscus pusillus*** (Figure 25) and ***Hyloniscus riparius*** (Figure 86) take shelter. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Philoscia muscorum (Figure 17), an isopod with a mossy name, is common and widespread in the UK among mosses and other substrata (Stenhouse 2007). ***Porcellio*** is perhaps the most common genus in the Northern Hemisphere, occurring with mosses in Europe and North America. ***Porcellio scaber*** (Figure 1-Figure 2) is often found among mosses and is one of the commonest of the woodlice in the UK (Stenhouse 2007). Its ability to feed on bryophytes is discussed above.

Diver (1938) examined the common woodlouse (***Porcellio scaber***, Figure 24) in five coastal animal successional zones in the British Isles where the plant carpet played a major role in characterizing the habitat. In the *Calluna-Psamma* zone, there was a well-developed lichen-moss carpet that replaced the grass turf. Nevertheless, only one species of isopod occurred there, whereas two more were added in the *Calluna* zone where the ground cover was nearly 100% *Calluna*. In a separate study that compiled many records, Harding and Sutton (1985) reported ***Trichoniscus pusillus*** (Figure 25) from all five dune zones, but primarily in dune slacks, where it was associated with mossy areas as well as damp hollows, large pieces of concrete, or decaying wood.

Figure 71. ***Myrmica ruginodis***, an ant that lives among the same mosses as the isopods ***Trichoniscus pusillus*** and ***Hyloniscus riparius***, and is a known arthropod predator. Photo by Boris Ginestet and Nicolas Calmejane, through Creative Commons.

Božanić and coworkers (Božanić 2008; Božanić *et al*. 2013) used heat to extract invertebrates from 61 terrestrial bryophyte samples from forests of the Czech Republic. They found 45 invertebrate species (13 higher taxonomic groups) from among 15 bryophyte species. The moss ***Brachythecium oedipodium*** (Figure 72) seems to be a preferred habitat, exhibiting the highest invertebrate diversity on decaying wood, where **Isopoda** were the most abundant (439 specimens), but diversity was also high in ***B. salebrosum*** (Figure 73) (mean 4 spp. per sample) and ***B. rutabulum*** (Figure 74) (mean 5.5 spp. per sample).

Atrichum undulatum (Figure 75), ***B. rutabulum***, and ***Hypnum cupressiforme*** (Figure 76) were the most frequent mosses and presented a high number of invertebrate taxa. This abundance is despite the content of hydroxycinnamic and phenolic acids present in ***B. rutabulum*** (Davidson *et al*. 1989).

Figure 72. ***Brachythecium oedipodium***, a preferred habitat for invertebrates, including **Isopoda**. Photo by Michael Lüth, with permission.

Figure 73. ***Brachythecium salebrosum***, a bryophyte with a high diversity of invertebrates. Isopods were most abundant in small cushions. Photo by Michael Lüth, with permission.

Figure 74. ***Brachythecium rutabulum*** capsules, a moss with high invertebrate diversity, including isopods. Photo by Martin Cooper, through Creative Commons.

Figure 75. ***Atrichum undulatum***, mosses where clump size is important in determining isopods (smaller clumps) vs annelids (larger clumps). Photo by Michael Lüth, with permission.

Figure 76. ***Hypnum cupressiforme***, a bryophyte with a high diversity of invertebrates. Isopods were most abundant in small cushions. Photo by Michael Lüth, with permission.

Type of substrate, size of cushion, and height above the ground were important determinants of the invertebrate species in these Czech forests (Božanić 2008; Božanić *et al*. 2013). **Isopoda** were numerous in small cushions, in contrast to the **Enchytraeidae** (Annelida) that were abundant in larger moss carpets. The woodlice (isopods) were most abundant among the moss ***Plagiomnium*** (Figure 77) on the ground. Tree size also played a role, with isopods ***Trichoniscus pusillus*** (Figure 78) and ***Porcellium collicola*** (Figure 3) living among mosses on smaller trees, whereas the isopod ***Trachelipus rathkii*** (Figure 26) occurred among mosses growing on larger trees. It is possible that correlation with tree diameter resulted from colonization rates and succession of the community. Nevertheless, ***T. pusillus*** also occurred among mosses on volcanic rock in the Azores (Vandel 1968). Because the bryophyte habitat was one of the earliest ones available to invasion of land, Božanić and coworkers (2013) suggest that the bryophytes may serve as refugia in expected future climate change.

Figure 77. ***Plagiomnium drummondii*** on rocks in forest, a moss where isopods are abundant. Photo by Janice Glime.

Figure 78. ***Trichoniscus pusillus***, an isopod that lives among mosses on small trees and among mosses on exposed lava rocks. Photo by Graham Montgomery, with permission.

While pillbugs require moisture, a boggy habitat can be too moist. Although ***Armadillidium*** is among the best adapted of isopods to terrestrial life, surviving in relatively dry habitats, some species do use mosses as a habitat. Dale and Dale (1986) report ***Armadillidium pulchellum*** (Figure 79) in moss mats of the coastal cliff slopes in the UK. They were surprised to find this species also inland in abundance under mosses on a wall. Harding and Sutton (1985) likewise report them under mats of mosses as well as under stones and mats of the flowering plants *Thymus* spp. and *Sedum anglicum* in the UK. In the daytime, one can also find ***Armadillidium pictum*** (Figure 80) under stones and among mosses in the UK (Harding & Sutton 1985).

Figure 79. ***Armadillidium pulchellum***, a coastal isopod found among coastal mosses in the UK. Photo by Jan van Duinen <http://www.janvanduinen.nl/>, with permission.

Figure 80. ***Armadillidium pictum***, an isopod that lives under stones and among mosses in the UK. Photo by Jan van Duinen <http://www.janvanduinen.nl/>, with permission.

The genus ***Ligia*** (Figure 81) is one of the less terrestrialized isopods, requiring more moisture than other terrestrial genera that have been studied, often living in tidal zone cliffs and rocky beaches. But on the Hawaiian Island of Kauai, ***L. perkinsi*** commonly occurs among wet mosses of indigenous trees in the montane rainforests above 600 m, whereas on Oahu it is known instead from a windward wet rocky cliff at only 300 m (Taiti *et al*. 2003).

Figure 81. ***Ligia*** sp., related to the moss dweller ***Ligia perkinsi*** that occurs among wet mosses on trees in Hawaiian rainforests. Photo by Steve Nanz, through Creative Commons.

Isopods even live in the exposed higher parts of trees. In the neotropical montane forests of Costa Rica, isopods dwell in both the ground litter and canopy litter, which includes bryophytes (Nadkarni & Longino 1990). But in the montane forests, the isopods had higher densities on the ground.

In the Polynesian islands, ***Philoscia truncata*** occurs both under stones and among mosses at 500 m on the Society Islands (Jackson 1938). On the Mangareva Islands ***Spherillo marquesarum*** occurs under mosses and rocks. In the Tasmanian temperate rainforests, isopods and other invertebrates often occur among mosses in places where they are not common on other substrates (Greenslade 2008). The higher moisture content of the mosses most likely accounts for the higher species richness, with 28 species of isopods among the mosses there. ***Stylonischus nichollsi*** is common in Tasmania and can occur among ***Sphagnum*** (Figure 83) at 1600 m at Point Lookout (Green

1974). In the Antarctic, several species of ***Styloniscus*** occur among mosses: ***S. otakensis*** (Figure 88), ***S. pallidus***, ***S. thompsoni***, ***S. verrucosus*** (Pugh *et al*. 2002).

Working in the Azores and Madeira, Vandel (1968) found a number of bryophyte-dwelling species not mentioned in other locations cited here, including ***Trichoniscus pygmaeus*** among mosses, ***Miktoniscus chavesi*** among mosses in a lava field and the bottom of a crater, but also among liverworts in *Erica* bush, ***Chaetophiloscia guernei*** among mosses in the *Erica* forest and other indigenous vegetation, and ***Eluma purpurascens*** among mosses at snowline, under mosses at the roadside of an old lava field, and among mosses in the *Erica* forest and heath. ***Androniscus dentiger*** (Figure 82) occurred on exposed lava rocks covered with mosses and lichens

Figure 82. ***Androniscus dentiger***, an inhabitant of mosses and lichens on lava rock in the Azores. Photo by Gilles San Martin, through Creative Commons.

Peatlands

Sphagnum (Figure 83) in peatlands often has its own unique fauna, in part due to the unique assemblage of plants. The *p*H can influence some species. The surface can get quite hot, thus being inhospitable to isopods. But within the peat mats, the gradient of temperature and moisture often provides suitable habitat with the possibility for vertical migration as conditions fluctuate.

Figure 83. ***Sphagnum cristatum***, a moss from boggy habitats where the isopod ***Trachelipus rathkii*** (Figure 26) lives in New Zealand. Photo by Jan-Peter Frahm, with permission.

Antonović *et al*. (2012) used pitfall traps to study the isopods living in the Dubravica peat bog and surrounding forest in Croatia. They found eight species of isopods, comprising 389 individuals, during their two-year study, with little difference in species richness between the bog and forest. They considered the small size of the bog peatland, progressive succession of plant life, and interactions among species to account for the high species richness there. Where the grass *Molinia* spread into the bog, the ***Sphagnum*** (Figure 83) was less humid and provided habitats for forest isopod species. The edge (**ecotone**) had the highest diversity, probably due to multiple factors: greater variety of niches, seasonal immigration, and less predator abundance relative to the open bog. Within the bog, cohabiting lycosid spiders (see Chapter 7-4 on Peatland Spiders) and ***Myrmica*** ants (Figure 84) were a threat to the isopods. In the bog ***Trachelipus rathkii*** (Figure 26), a known bryophyte dweller, was the most common isopod, whereas in the forest it was ***Protracheoniscus politus*** (Figure 85). Bog-specific species were absent. Instead the isopod fauna was dominated by widespread species with wide niche requirements, which Antonović *et al*. attributed to the degradation process on the bog. Antonović and coworkers considered one bog inhabitant here, ***Hyloniscus adonis*** (see Figure 86), to be **tyrphoxenous**, *i.e.*, a vagrant not reproducing in the bog.

Figure 84. ***Myrmica*** sp, an ant predator genus to isopods in bogs. Photo by Alex Wild <www.alexanderwild.com>, with permission.

Figure 85. ***Protracheoniscus politus*** (top) and ***Trachelipus ratzeburgii*** (bottom), the upper being the most common moss dweller in a forest surrounding a bog in Croatia. Photo by Walter Pfliegler, with permission.

Figure 86. ***Hyloniscus riparius***, relative of the vagrant isopod ***Hyloniscus adonis*** in bogs. Photo by Tom Murray, through Creative Commons.

Springs

I expected to find a number of records of isopods among mosses in springs and was surprised to find relatively few. In some of these, although mosses were abundant, the isopods were in the open water and bottom sediments, but not among the mosses (Gooch & Glazier 1991; Erman 2002). Erman (2002) could find no relationship between moss mats and invertebrate diversity, including that of isopods. The only relationship he found was that the mosses indicated that the spring had constancy and persistence.

In his study of isopods in habitats of the Azores and Madeira, Vandel (1968) found ***Trichoniscus pusillus*** (Figure 25) among mosses in a spring on the mountain slope and among ***Sphagnum*** at another spring. But the other spring species were less familiar among moss dwellers, including ***Miktoniscus chavesi***, ***Chaetophiloscia guernei***, and ***Eluma purpurascens*** among mosses. ***Oniscus asellus*** occurred among mosses in sheltered ravines and under wet moss in the ravine.

Waterfalls

Waterfalls provide a variety of niches from very aquatic to damp terrestrial. These microhabitat niches change as water levels recede and may be quite dry in summer when the waterfall recedes or disappears altogether. Stephensen (1935) found terrestrial Talitridae in such habitats in Java in the Marquesas where ***Orchestia floresiana*** occurred among mosses of rivulets, fountains, and waterfalls.

Aquatic

Aquatic isopods can also be moss inhabitants. Fontaine and Nigh (1983) suggest that aquatic isopods like ***Asellus*** (Figure 61) may be limited by their slow colonization rate. When such host plants as ***Nitellopsis*** (Figure 87) die off, the isopods need an alternative substrate with sufficient food available (Hargeby 1990). In habitats where bryophytes occur, these bryophytes could provide the permanence needed by the slow isopod colonizers.

Figure 87. ***Nitellopsis obtusa***, an alga that provides habitat for isopods like ***Asellus*** but that can disappear in some habitats for part of the year, causing the isopods to seek other shelter. Photo through Public Domain.

Although ***Asellus aquaticus*** (Figure 61) is well known from bryophytes, it is the juveniles that are most abundant in algal and bryophyte mats, whereas the larger adults are typically associated with large-sized substratum particles (Graca *et al*. 1994). As already noted in discussing bryophytes as food, ***Asellus*** *cf.* ***militaris*** (Figure 66) occurs in mats of ***Fontinalis*** spp. in streams where it feeds on both the mosses and associated detritus and periphyton.

On Macquarie Island in the sub-Antarctic, ***Styloniscus otakensis*** (Figure 88) lives among mosses on margins of streams, among other places (Greenslade 2008). Cowie and Winterbourn (1979) found that the isopod ***Styloniscus otakensis*** was the only common invertebrate on the moss ***Cratoneuropsis relaxa*** (Figure 89) in the outer spray zone of a spring brook in the Southern Alps of New Zealand. They attributed differences in fauna among the moss species to differences in flow rates, availability of detritus, and differences in water saturation.

Figure 88. ***Styloniscus otakensis***, an aquatic species in a genus with a number of terrestrial moss-dwelling members in forests and bogs of Tasmania, New Zealand, and nearby islands. Photo by Mark Stevens. PERMISSION PENDING.

Figure 89. ***Cratoneuropsis relaxa***, genus of mosses that occur in springbrooks in the Southern Alps of New Zealand and home to ***Styloniscus otakensis***. Photo by Tom Thekathyil, with permission.

South Africa may have species unfamiliar to most of us in the Northern Hemisphere. Enckell (1970) found ***Protojanira prenticei*** among mosses in the upper part of a streamlet there.

Pollution

Pollution in the form of heavy metals can quickly move up the food chain in streams. Detrital feeders like ***Asellus*** species can concentrate the metals from the detritus on the streambed or among mosses, then get eaten by larger invertebrates or fish, further concentrating the pollutants (Eimers *et al*. 2001). However, Eimers and coworkers found that when the sediment organic content was increased (20% peatmoss), the cadmium concentration in ***Asellus racovitzai*** decreased compared to that of mineral sediment treatments, indicating that bryophytes, especially ***Sphagnum*** (Figure 83), might be able to protect the isopods and organisms higher up the food chain by sequestering the heavy metals and keeping them out of the water column. Other mosses, for example ***Fontinalis antipyretica*** (Figure 66), occurring in the same waters with ***Asellus aquaticus*** (Figure 61), also accumulate heavy metals. Lithner *et al*. (1995) found that when the *p*H decreased, the bioconcentration factors decreased in the bryophytes while several of the metals simultaneously increased in fish. Hence, using aquatic bryophytes as bioaccumulators to protect the organisms is complicated, but they could be a useful tool to predict imminent fish die-off.

CLASS MALACOSTRACA, ORDER MYSIDA

The **Mysida** are known as oppossum shrimps because of the brood pouch where females carry their larvae. Mysids are not common on bryophytes, but they can use them as a restaurant in aquatic habitats. ***Mysis relicta*** (Figure 90) in Char Lake, Northwest Territories, Canada, feeds primarily on diatoms and inorganic particles on moss substrata (Lasenby & Langford 1973). It is known as an opportunistic feeder, permitting it to survive on a variety of resources (Grossnickle 1982).

Figure 90. ***Mysis relicta***, a species that feeds on diatoms and detritus among mosses in some habitats. Photo by Perhols, through Creative Commons.

CLASS MALACOSTRACA, ORDER DECAPODA

Decapods include such animals as crayfish, lobsters, crabs, and hermit crabs. For such large invertebrates to succeed on land they have developed morphological, physiological, biochemical, and behavioral adaptations (Bliss & Mantel 1968). Adult land crabs maintain water balance through the coordinated action of gills, pericardial sacs, and the gut, taking up, storing, and redistributing both salts and water to maintain an osmotic and water balance. In larvae, on the other hand, this suite of responses is not practiced. As is known for the isopods, there is evidence that at least some decapods excrete some of their ammonia as a gas (Weihrauch *et al*. 2004). Adult land crabs use both gills and the highly vascularized lining of the branchial chambers for gas exchange (Bliss & Mantel 1968). They generally cannot survive low temperatures, but their cytochrome C seems to help in their survival of high temperatures. Finding a mate is typically accomplished by both visual and acoustic signals, coupled with ritualistic behavior.

Decapods generally are too large to live among most bryophytes, but they are not without interesting bryological interactions. The decapod ***Thalassina anomala*** (Figure 91-Figure 93), a mud lobster, forms soil mounds (Figure 92-Figure 93) when it builds its nest (Yamaguchi *et al*. 1987). It is on these soil mounds in the mangrove forests of Japan that ***Fissidens microcladus*** dwells. By living on the soil mounds, the moss is never submerged at high tide and most likely benefits from the moist air.

Figure 91. ***Thalassina anomala***, a mud lobster that makes mounds in mangrove forests – mounds that have somewhat unique flora including ***Fissidens microcladus***. Photo by Ariff Aziz, through Creative Commons.

Figure 92. Mound of the mud lobster, ***Thalassina anomala***, in a mangrove forest. Photo by Ariff Aziz, through Creative Commons.

Figure 93. Close view of a mound of the mud lobster, ***Thalassina anomala***, showing greenish patches that could be protonemata of the moss ***Fissidens microcladus***. Photo by Ariff Aziz, through Creative Commons.

Coffey and Clayton (1988) have suggested that deep water bryophytes in New Zealand lakes do not occur in the presence of freshwater crayfish. It appears that in the presence of the crayfish ***Paranephrops*** spp. (Figure 94), the bryophytes suffer both mechanical damage and browsing. In Lake Wanaka, there is a deep water (down to 50 m) community of bryophytes (Coffey & Clayton 1988). But in other New Zealand lakes the mosses were absent. This absence correlated with the presence of large crayfish (***Paranephrops*** spp.) populations. Coffey and Clayton suggest that the mosses are absent not due to different habitat needs from the crayfish, but from the browsing and mechanical damage caused by the crayfish.

Figure 94. ***Paranephrops planifrons***, member of a genus of crayfish that inflicts mechanical damage on bryophytes. Photo by David Wilson, through Creative Commons.

The relationship of the ***Parenephrops*** species with stream mosses contrasts with the avoidance of mosses by the crayfish ***Procambarus spiculifer*** (Figure 64, Figure 95; see also discussion under Isopoda – Aquatic Consumers) reported by Parker *et al*. (2007). The latter crayfish is selective in its plant habitat, choosing the flowering plant *Podostemum ceratophyllum* (riverweed; Figure 96) over ***Fontinalis novae-angliae*** (Figure 62; Figure 96), despite the greater abundance of the moss (89% of total biomass) (Parker *et al*. 2007). Furthermore, the mosses supported twice as many macroinvertebrates as did the riverweed. This revelation suggests that the mosses might provide a safe refuge for macroinvertebrates, allowing them to escape from larger predators, perhaps due to their chemical defenses. This hypothesis is supported by the presence in the moss of C_{18} acetylenic acid, octadeca-9,12-dien-6-ynoic acid, a defense compound that inhibits crayfish feeding. A similar avoidance was absent in the amphipods and isopods in the stream, permitting them to find safe refuge there. This discriminatory behavior of the antifeedant against crayfish but not microcrustacea permits these small arthropods to live where they can avoid the predation of larger arthropods.

Figure 95. ***Procambarus spiculifer*** eating *Egeria densa*. This crayfish avoids eating the moss ***Fontinalis novae-angliae***, thus protecting its invertebrates as well. Photo by John Parker, with permission.

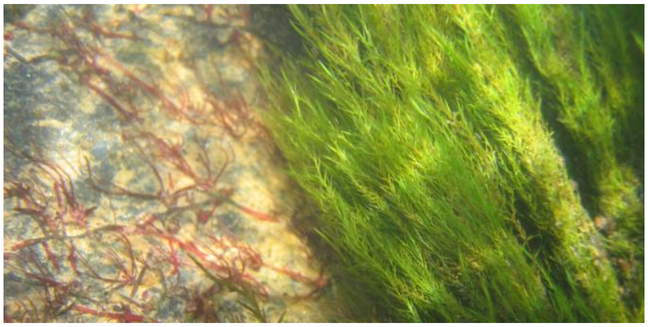

Figure 96. ***Podostemum ceratophyllum*** (**left**) and ***Fontinalis novae-angliae*** (**right**) showing effects of grazing by the crayfish ***Procambarus spiculifer*** on the ***P. ceratophyllum***. The moss remains untouched. Photo by John Parker, with permission.

Summary

Isopods include a number of terrestrial genera, many of which include bryophyte dwellers, including the families **Ligiidae**, **Trichoniscidae**, **Oniscidae**, **Porcellionidae**, and **Armadillidiidae**. *Asellus* seems to be the most common genus in streams. Springs seem to have few isopods inhabiting mosses. Other taxa benefit from the moisture of bogs, migrating vertically to achieve optimum moisture and temperature.

As descendents of aquatic and marine organisms, isopods benefit from the moisture and protection of bryophytes, finding food among them as detritus, periphyton, and the bryophytes themselves. Their digestive system is modified by reducing gut surface tension and culturing gut flora to render the phenolic compounds safe in their diet. They are known to eat a wide range of bryophytes, but they do have preferences, and some taxa are ignored.

In addition to sheltering, the isopods use the bryophytes as a place to remove excess water or gain needed water. They conserve water by releasing their nitrogenous waste as ammonia gas. Isopods are sensitive to temperature, and bryophytes can provide shade and evaporative cooling.

Isopods often go into the soil in the daytime, emerging and climbing to the tips of the bryophytes to dine at night. They congregate under bryophytes, as well as rocks, logs, and boards, reducing water loss and oxygen consumption, stimulating reproduction, increasing predator defense, promoting coprophagy, and acquiring internal symbionts. Reproduction is typically sexual, but parthenogenesis is possible in some taxa. The eggs and young are carried by the mother.

Some isopods overwinter under bryophytes or in the soil under bryophytes. They generally cannot survive temperatures below -7°C.

At least some bryophytes exemplify the **apparency theory**. The bryophytes are small and slow-growing. They contain a wide range of antiherbivore compounds that deter most herbivores. Isopods, on the other hand, circumvent the antiherbivore compounds through their digestive system, permitting them to gain a food source (bryophytes) where they are protected from a number of would-be predators. However, ants are a predatory threat even among the bryophytes.

Members of the order **Mysida** are rarely reported from bryophytes, but in Char Lake they feed on diatoms and inorganic particles among mosses.

The Decapoda (crayfish) generally do not live among mosses, in some cases actually avoiding them, apparently due to the presence of C_{18} acetylenic acid, octadeca-9,12-dien-6-ynoic acid in the mosses (and possibly other compounds). Others damage the bryophytes by moving their heavy bodies across them. Invertebrates are able to avoid predation by crayfish by living among the mosses.

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