

CHAPTER 10-1

ARTHROPODS: CRUSTACEA – COPEPODA AND CLADOCERA

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Figure 1. *Simocephalus* sp. with eggs in the carapace. Note the white *Vorticella* on the lower left edge of the carapace and near the base of the antennae. Photo by Jasper Nance through Creative Commons.

SUBPHYLUM CRUSTACEA

Crustaceans (Figure 1) are those tiny arthropods that most of us have never noticed on the bryophytes. But in some habitats, and some parts of the world, the bryophytes – invaders of land – are home for such terrestrialized arthropods.

This large subphylum is mostly marine or aquatic, including such familiar animals as barnacles, crabs, crayfish, krill, lobsters, and shrimp (Wikipedia: Crustacean 2011). But it is mostly the smaller animals, the microcrustacea, that inhabit the bryophytes. The Crustacea are distinguished from other arthropods by their two-part limbs (**biramous**; e.g. the pincers on the end of a crab claw or divided antenna of *Daphnia* or *Simocephalus* – Figure 13) and a life cycle that includes a **nauplius** larva stage (first larval stage of many crustaceans, having an unsegmented body and usually a single eye, Figure 2), although most have additional larval stages after that. Almost all of them have a chitinous exoskeleton.



Figure 2. Nauplius of copepod. Photo from Wikipedia Creative Commons.

Reproduction

Most crustaceans have separate sexes, but some change sex and many are **parthenogenetic**, with females producing viable eggs that develop into new organisms in the absence of fertilization (Wikipedia: Crustacean 2011). Eggs are generally released into the water column, but some **isopods** form a brood pouch and carry their eggs and young around with them. Many **copepods** form egg sacs that hang from the body until the young hatch. **Decapods** typically carry their eggs attached to their swimmerets. The **meiofauna** [small metazoans that pass through 500µm or greater sieves, but are retained on 40 or 62 or 40 µm sieves (Dražina *et al.* 2011)] of springs typically have shorter life cycles, permitting such groups as cyclopid copepods to have a rapid recruitment ability (Robertson 2002) and other copepods and ostracods to develop rapidly compared to insects, completing their development in only a few months (Dole-Olivier *et al.* 2000).

Dispersal

As with mites and other bryophyte dwellers, microcrustacea might be dispersed on a "magic carpet" – bryophyte fragments on which they are living. Sudzuki (1972) tested this hypothesis by exposing moss-soil samples to wind velocities of 2.9 m s⁻¹. Sampling at distances of 100-400 cm from the "wind" source, they determined that even after 2 months, wind velocities up to 2 m s⁻¹ failed to disperse the Crustacea. Those animals dispersed were primarily protozoa. Nevertheless, encysted animals could get dispersed with bryophyte fragments or even with moss clumps that get carried by small mammals or wind.

Habitat Fragmentation

Microarthropods must move from one leaf patch to another, or from hiding places to food sources. During this time, especially if disturbed during the daytime, they are vulnerable to desiccation. Gonzalez *et al.* (1998) experimented with such fragmented microcosms to determine parameters that led to success of the inhabitants. They found that when microecosystems were fragmented, species declines occurred. But when the patches were connected by habitat corridors, much as has been shown for large mammals, both abundance and distribution of the fauna experienced a rescue effect through immigration. Bryophytes can often serve as such corridors, providing places to replenish lost moisture and to hide from predators.

Gonzalez and Chaneton (2002) used bryophyte habitats for experimentation. They fragmented the bryophyte communities and found that this system likewise experienced loss of both faunal species richness and community biomass. Rare species were more likely to become extinct. Moss habitat corridors that connected fragments to a larger "mainland" of bryophytes permitted immigration and maintained microarthropod richness, abundance, and biomass in the fragments.

While we tend to view corridors as continuous suitable habitats, such continuity is probably not necessary for the larger arthropods like isopods. They can use the bryophyte clumps as islands of safety between larger suitable habitats such as leaf litter.

Habitat Importance

Krebs (2001) reminded us that habitat heterogeneity is related to the creation of more ecological niches. Bryophytes can create many niches, providing protected space for the small microcrustaceans. Srivastava *et al.* (2004) contend that moss-arthropod ecosystems form natural microcosms that are useful for testing such concepts as fragmentation, metacommunity theory, and connections between biodiversity and ecosystem processes. Their small size, short generation times, hierarchical spatial structure, and contained, definable systems provide advantages in conducting field experiments that are subject to natural conditions and interactions with neighboring communities. The authors argue that "natural microcosms are as versatile as artificial microcosms, but as complex and biologically realistic as other [larger] natural systems."

Terrestrial

Acosta-Mercado *et al.* (2012) found strong support for the hypothesis that abiotic factors (especially water chemistry of the bryophytes and pH) are important determinants of terrestrial microcrustacean diversity. They added that water-holding capacity is correlated with the morphology and canopy structure of the bryophytes. Roughness of the bryophyte canopy in the Bahoruco Cloud Forest, Cachote, Dominican Republic, was important in determining differences in species composition. For amoebae, the lowest species richness was on *Acroporium pungens* (Figure 3), a species with low roughness and faunal density, whereas *Thuidium urceolatum* had the highest roughness index, highest faunal richness, and highest species density. But for the 26 microcrustacean morphospecies among 11 bryophyte species, there was no detectable canopy effect on faunal richness or density. The lowest density of 1 individual per 50 cm² was on the cushions of *Leucobryum* (Figure 4) with a maximum of 6±3.37 on the same area of the thallose liverwort *Monoclea* (Figure 5), suggesting that openness of the community might play a role in diversity.



Figure 3. *Acroporium pungens* in the Neotropics, a species with low roughness and low faunal density. Photo by Michael Lüth, with permission.



Figure 4. *Leucobryum glaucum* cushion, a species with low faunal density. Photo by Janice Glime.



Figure 5. *Monoclea forsteri*, a liverwort that harbors a relatively high microcrustacean diversity. Photo by Jan-Peter Frahm, with permission.

Peatlands

Peatlands, for our purposes those habitats dominated by *Sphagnum* and not including other types of peatlands (Figure 6), provide a mix of moist and dry mosses and pools influenced by those mosses. The "terrestrial plankton" are often sensitive to high CO₂ concentrations and low O₂ tensions such as those found among rotting leaves and other areas with high rates of decomposition (Stout 1963). For these organisms with good tolerance for low pH (sometimes below 4.0), *Sphagnum* provides a suitable habitat. Krebs (2001) found that the center of the *Sphagnum* moss mat had a higher species diversity than the edges, perhaps due to additional niches (habitat heterogeneity) resulting from the plant-associated species dwelling there.

On the other hand, the low pH created through cation exchange and organic acids produced by mosses in the genus *Sphagnum* (Figure 6) is detrimental to many organisms. Hillbricht-Ilkowska *et al.* (1998) examined the role of pH on Crustacea and other organisms by providing powdered lime to the system. Measurements after 1-4 years and 20-23 years indicated that both the water Ca and that of the sediment were permanently raised. This change coincided with a significantly increased rate of decomposition and an increase in species richness and diversity of crustaceans, among others. Overall diversity was doubled. The treatment eliminated peatmosses from encroaching on the lake but had no effect on those of the surrounding area.



Figure 6. Bohemia bog with *Sphagnum cuspidatum*, *S. denticulatum*, and others, showing the varied habitats of hummocks, hollows, and small pools available to bog fauna. Photo by Jonathan Sleath, with permission.

To add to this image of *Sphagnum* (Figure 6) as an unfriendly substrate, Smirnov (1961) stated that few animals were specialized to gain their nutrition by consuming emerged *Sphagnum*. He cited only one species of flies whose larvae are known to feed directly on *Sphagnum*. On the other hand, in such *Sphagnum* lakes the bladderwort, an insectivorous plant, traps and digests Crustacea such as *Daphnia* (Cladocera) – a not so friendly place for many.

But *Sphagnum* (Figure 6) may play a more positive role in the lives of these fauna. *Sphagnum* has long been known for its antibiotic properties; it was used as a wound dressing in WWI. Could it protect the crustaceans from fungal or bacterial attacks? Furthermore, for these invertebrates it may serve as a refugium – a place to escape predators (Kuczyńska-Kippen 2008), possibly due to its antifeedant properties as well as small hiding places.

Springs

Among the favored habitats of limnoterrestrial (living in wet films on land) Crustacea are mosses of springs, *i.e.* these Crustacea are **crenophilous**, where temperature and pH were important determinants of community composition in four Northern Apennine springs (Bottazzi *et al.* 2011). Mosses in these springs usually had harpacticoid copepods and ostracods representing the Crustacea. The moss inhabitants had a seasonality, whereas drift assemblages did not. Bottazzi *et al.* suggest that the mosses were important in increasing the species diversity in these springs.

Springs are often a transitional habitat between aquatic and terrestrial systems. Even within the spring habitat, such a transition is typical, and moisture zones within the habitat can change as the seasons and weather change. Thus, the bryophytes of this habitat provide not only a refuge, but an avenue (more like a labyrinth) where macroinvertebrates can travel to escape the receding preferred moisture level.

Crustacea are not usually seen among bryophytes, but in some areas they can be quite abundant. For example, Michaelis (1977) reported that at Pupu Springs in New Zealand, there were ten species of bryophytes. The fauna included Crustacea among the most abundant groups. Suren (1993) suggests that the abundance of crustaceans in the New Zealand bryofauna may be due to the absence of some of the bryophyte dwellers found elsewhere, *i.e.* some families of Trichoptera (caddisflies), Plecoptera (stoneflies), and Ephemeroptera (mayflies).

Bottazzi *et al.* (2011) reported the **ostracods** and **Harpacticoida** (an order of copepods) among the three most abundant taxon groups among mosses in northern Apennine **rheocrene springs** (springs that become streams immediately upon emerging from the ground). Like Michaelis (1977) and Suren (1993), they suggested that favorable habitats, including mosses, accounted for the high diversity and the large numbers of these two crustacean groups.

Bottazzi *et al.* (2011) concluded that emergent mosses were important in increasing species diversity of these springs (see also Barquín & Death 2009; Ilmonen & Paasivirta 2005). Bryophytes act as an ecotone between the aquatic and terrestrial habitat by creating a range of microhabitats that vary both horizontally and vertically (Lindgaard *et al.* 1975; Thorup & Lindgaard 1977), including the **madicolous** zone (having thin sheets of water flowing over rock surfaces). These provide a range of moisture conditions that permit the meiofauna to migrate to a more suitable location as moisture conditions change. While providing a refuge from rapid flow (Madaliński 1961; Elliot 1967; Gurtz & Wallace 1984; Suren 1992; Glime 1994), bryophytes provide a variety of food sizes in trapped particulate matter (Habdija *et al.* 2004). Linhart *et al.* (2002c) demonstrated a direct association between harpacticoid copepods, including nauplii, and trapped organic and mineral matter among the mosses.

Lindgaard *et al.* (1975) found that in the Danish spring at Ravnkilde these vertical and horizontal differences among the bryophytes provided a source of diversity among the macroinvertebrates. They found that whereas the horizontal zonation sported different assemblages of species, the fauna of the neighboring stones had little influence on the moss fauna. More importantly, the flow rate and available detritus as a food source could account for the horizontal differences.

Lindgaard *et al.* (1975) found that the numbers of individuals fluctuated throughout the year, corresponding with changes in the life cycle stages of the dominate species. Bryophyte habitation is also seasonal in Northern Apennine springs, with a maximum in the spring and minimum in winter, whereas seasonal habitation is nearly constant in non-bryophyte areas sampled by the traps Bottazzi *et al.* (2011). On the other hand, permanent meiofauna had its minimum in autumn; temporary meiofauna of the mosses peaked in spring, then decreased thereafter.

Streams

Bryophytes in streams create a rich source of invertebrate fauna, so much so that the aquatic moss *Fontinalis antipyretica* (Figure 7) was transplanted to streams in South Africa to increase the food source for

trout (Richards 1947). The bryophytes are able to provide a refuge from fast-flowing water and to increase stream heterogeneity (Tada & Satake 1994; Wulfhorst 1994; Dražina *et al.* 2011).



Figure 7. *Fontinalis antipyretica*. Photo by Jan-Peter Frahm, with permission.

Despite their seeming rarity among bryophytes, Amos (1999) included ostracods, cladocerans, copepods, and amphipods as "life in the torrent" in the UK – a description of the inhabitants of *Fontinalis* (Figure 7). His point was that "all was quiet" at the bottom of the moss clump despite the torrent occurring at the surface.

Linhart *et al.* (2002a), in Europe, found that regulated channels had a much greater meiofauna, including **Cladocera** and **Harpacticoida** (copepods), when the channel was overgrown by aquatic bryophytes, in this case *Fontinalis antipyretica* (Figure 7). In a different stream, the meiofauna of mosses was an order of magnitude higher than that in the surrounding mineral substrate (Linhart *et al.* 2000), but the crustaceans were not a significant part of this fauna. Rather, the density of the **Harpacticoida** was the second most abundant group in the gravel, where the fine particulate matter was also highest compared to that among the mosses. They further determined that high flow rates approaching the mosses had a negative impact on the crustaceans [**Cladocera**, **Ostracoda**, and **Cyclopoida** (an order of copepods)], although the velocity seemed to have no effect on the **Harpacticoida** (Linhart *et al.* 2002b, c). They suggested that fine detritus trapped by the *F. antipyretica* provided food for the **harpacticoid copepods**. It is interesting that in their 2000 study Linhart *et al.* suggested that it is "questionable whether *F. antipyretica* can serve as a refuge from the current for stream meiobenthos," a seeming contradiction to their conclusions in a different stream. It appears that food is the primary factor in distribution of the microcrustacea, but that does not rule out the role of the mosses as a refuge when sufficient food is present.

Collection Methods

Methods of collection can have a biasing effect on the relative numbers of taxa collected. Copepods and other **Crustacea** in aquatic habitats can be collected by squeezing mosses into a collection bottle or squeezing the mosses in place and collecting the crustaceans downstream from the mosses with a plankton net (Gerecke *et al.* 1998; Reid 2001; Stoch 2007). Copepods, ostracods, and

amphipods may all be extracted from forest litter by the Berlese funnel, but as the litter dries out many will perish before they can escape (Stout 1963). Heat extraction can present the same problem. Chapman (1960) was successful in extracting terrestrial ostracods alive by slowly drying out the leaf litter (but it would work for bryophytes as well) in a Berlese funnel, using a water-jacket at 40° C to avoid overheating, in which case the ostracods close their valves and stop moving. The end of the funnel led to water rather than alcohol.

CLASS BRANCHIOPODA, ORDER CLADOCERA

The class name of **Branchiopoda** literally means gill feet and refers to the **pereiopods** by which the aquatic species can swim. The order name **Cladocera** derives from the Ancient Greek κλάδος (kládos, "branch") and κέρας (kéras, "horn").

Adaptations

Structural

Cladocera are a predominately aquatic group of small individuals known as water fleas (no relationship to the insect group of fleas). They swim using their antennae, using a series of jerks similar to the hops of a flea. Some have adapted to terrestrial habitats with free water, such as bromeliad basins. Others are able to use the film of water from the capillary spaces and leaf surfaces of bryophytes. Not only are the antennae important for swimming, but they are also powerful chemical sensory organs (Ecomare 2014). They can use these not only to find food, but also to detect the presence of enemies. The body of a cladoceran is a valve-like carapace that covers an unsegmented thorax and abdomen. Adults have a single compound eye.

Life Cycle Strategies

Cladocerans spend most of their lives as a female population that reproduces multiple times asexually by **cyclical parthenogenesis**. When conditions become unfavorable, they produce male offspring and subsequently reproduce sexually, producing resting eggs that remain within the carapace (*Daphnia*; Figure 8). In this state, they can dry out and travel long distances on wind currents or as hitch hikers on other travelling animals or even moss fragments. In fact, some of these dormant eggs are known to remain viable for 70-80 years in Lake Superior sediments (Kerfoot & Weider 2004) and can even survive the digestive tracts of birds (Figuerola & Green 2002).

Habitats

Cladocera are primarily aquatic and marine, but a few are adapted to terrestrial living, taking advantage of films of water, pools in bromeliads, and other surfaces where they have easy access to water when they are active.

Terrestrial

Since Cladocera live primarily in fresh or marine water, living on land requires special adaptations for both water conservation and locomotion. It seems that few cladoceran species have accomplished this, or we simply

haven't found them yet. There are indications that appendage reduction is a terrestrial adaptation in this group. After all, why waste energy to make appendages that are not useful. Frey (1980) describes the non-swimming chydorid *Bryospilus* (Figure 9) from wet cloud forests as lacking a compound eye, a change that still requires explanation. The genus resembles the limnoterrestrial genus *Monospilus*, possibly through convergence. They exhibit reduced setation on their antennae and trunk limb, perhaps facilitating their slow crawl among wet bryophytes as high as 3-5 m above the forest floor.



Figure 8. *Daphnia pulex* with three eggs shown here to the right of the digestive tract. Photo by Paul Hebert, through Wikimedia Commons.

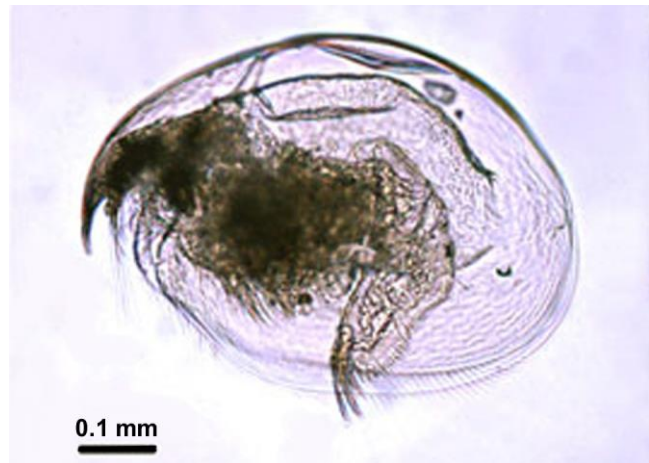


Figure 9. *Bryospilus repens*, a chydorid cladoceran that lives mostly in wet moss.. Photo by Francisco D. R. Sousa <Cladocera.wordpress.com>, with permission.

Existing 3-5 meters above the rainforest floor are Cladocera that crawl from place to place, unable to swim. Frey (1980) reported the cladoceran *Bryospilus repens* (Figure 9), a semiterrestrial species known from wet mosses in Puerto Rico, Venezuela, and New Zealand, and

Bryospilus bifidus from New Zealand, both in the same subfamily of Chydoridae as *Alona* (Figure 10-Figure 11), a common cladoceran from springs. Resting eggs are often buried in deep masses of vegetation (Powers & Bliss 1983) where they are protected from water loss. Dispersal of fragments of mosses they inhabit can aid in dispersal of both eggs and adults to new sites. Frey suggested that the mossy habitat in the rainforest exhibited the same continuity through time as ancient lakes, thus being a likely site for even more endemic species. Van Damme *et al.* (2011) consider *B. repens* (Figure 9) to be a "well known" species that lives in wet moss. They consider its occasional presence in river samples to be the result of individuals that got washed into the river from these mossy homes.

There may be more species of these tiny cladocerans hiding among bryophytes in terrestrial habitats. These organisms are typically studied by aquatic biologists who spend their time looking at plankton. Terrestrial bryophyte habitats are rarely studied with the aim of locating **Cladocera**. I have to wonder if somewhere there might be some Cladoceran species living in liverwort lobules.

Peat Bogs

Living among *Sphagnum* (Figure 6) or in the bog pools requires a tolerance of low pH. Nevertheless, *Sphagnum* can increase the abundance of **Cladocera** by as much as tenfold in Swedish peatlands (Henrickson 1993). The heterogeneity of the *Sphagnum* habitat illustrated in Figure 6 provides shelter and refuge against predation while being a suitable foraging site. The bryophytes further contribute to this habitat through their production of antibiotics, organic acids, and cation exchange.

Bog lakes can support a number of species of Cladocera. Minelli (2004) listed *Alona quadrangularis* (Figure 10), *Alona affinis* (Figure 11), *Simocephalus exspinosus* (Figure 12), *S. vetulus* (Figure 13), and *Ceriodaphnia pulchella* as being among the common species in bog lakes in Italy. Hingley (1993) reported *Streblocerus serricaudatus* (Figure 14) and *Acantholeberis curvirostris* (Figure 15) swimming in UK peat pools. Macan (1974) likewise reported the latter species in *Sphagnum* (Figure 6). *Chydorus piger* (Figure 16) is typical of bare substrates such as rock or sand, but including *Sphagnum*, and is known from acidic pools in peatlands in Europe (Duigan & Birks 2000).

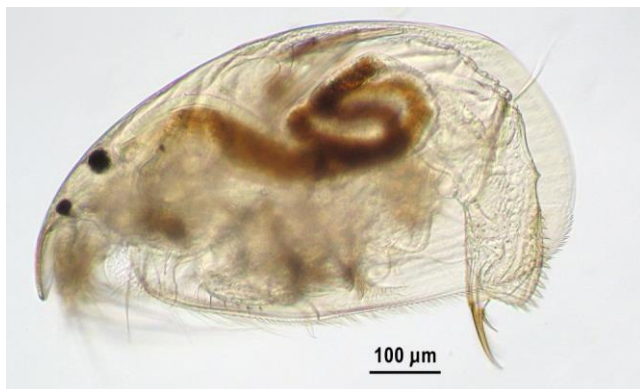


Figure 10. *Alona quadrangularis*, a common species in bog lakes. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 11. *Alona cf affinis*, a common species in bog lakes. Photo by Yuuji Tsukii, with permission.



Figure 12. *Simocephalus exspinosus*, a common species in bog lakes. Photo by Malcolm Storey through <<http://www.discoverlife.org/>>, through online license.

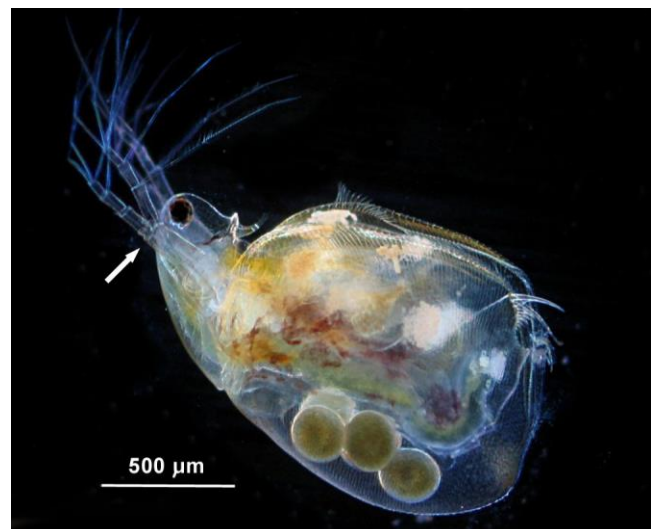


Figure 13. *Simocephalus vetulus*, a common species in bog lakes. Note the divided (biramous) antenna (**arrow**). Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

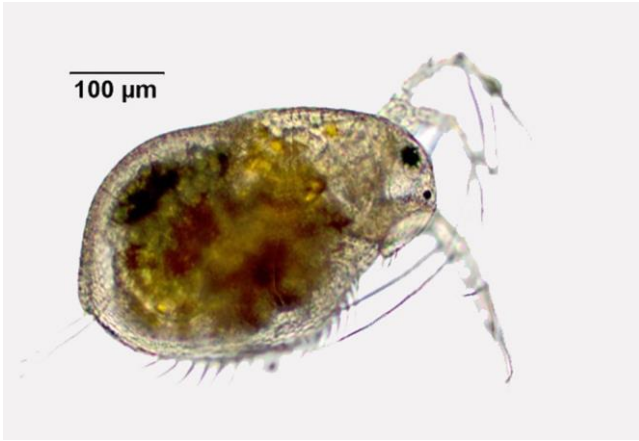


Figure 14. *Streblancerus serricaudatus*, a cladoceran that inhabits peatland pools. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.



Figure 15. *Acantholeberis curvirostris*, a cladoceran of peatland pools. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.



Figure 16. *Chydorus piger*, a cladoceran from peatland pools. Photo by Angie Opitz, through online permission.

Kairesalo *et al.* (1992) considers the peatland habitat to be unsuitable for *Daphnia* (Figure 17) because the available food is "recalcitrant." In a lake in southern Finland that was bordered by the mosses *Warnstorfia* (Figure 18) and *Sphagnum* (Figure 6), the organic carbon excreted by *Warnstorfia* suppressed the growth of planktonic algae and provided little contribution to bacterial productivity. This meant that bacterial productivity was necessarily dependent on humic acids for their carbon source, resulting in decreased availability of this food source for the *Daphnia*. The predominantly particulate matter in the water was largely useless for the *Daphnia* as a food source.



Figure 17. *Daphnia*. Photo by Gerard Visser through Creative Commons.



Figure 18. *Warnstorfia exannulata*, a peatland moss that seems to be "recalcitrant," unable to provide food for the Cladocera living there. Photo from Biopix through Creative Commons.

Cladocera have played a role in reconstructing the history of some peatlands. Duigan and Birks (2000) report on *Sphagnum* (Figure 6) and other bryophytes from 9200 BP microfossils in western Norway with *Alonella nana* (Figure 19), *Alonella excisa* (Figure 20), and *Alona rustica* (Figure 21). *Alona rustica* is also known in peat bogs among mosses in Italy (Minelli 2004).

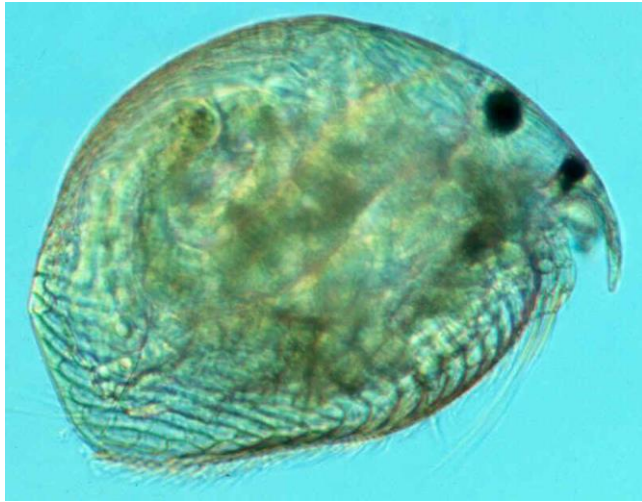


Figure 19. *Alonella nana*, a cladoceran from peat deposits in ~9200 BP. Photo from Great Lakes Research Laboratory, through public domain.



Figure 20. *Alonella excisa*, a cladoceran that occurs in peat deposits in ~9200 BP. Photo by Manuel Elias, ECOSUR, through Creative Commons.

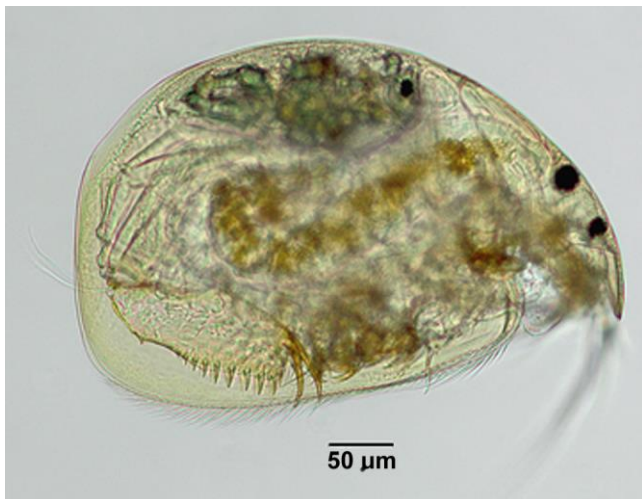


Figure 21. *Alona rustica*, a cladoceran that lives among bryophytes on stream banks. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

Aquatic

Lakes

Typically, cladocerans are rare among aquatic mosses, being adapted for planktonic life. However, in the subAntarctic lakes of South Georgia, the most common invertebrate was the cladoceran genus *Alona* (Figure 22), with 2544 individuals in a liter of water (Hansson *et al.* 1996). Several species in this genus were present, with the greatest numbers among mosses that extended into shallow lakes. In fact, the littoral mosses had the highest number of invertebrate species (20) and abundance (1539 individuals) of invertebrates in those lakes. With increasing UV levels reaching the shallow Antarctic lakes, mosses may provide refugia that protect these invertebrates from UV damage.



Figure 22. *Alona* sp., a genus with a number of terrestrial bryophyte-dwelling species. Photo by Yuuji Tsukii, with permission.

Van Damme *et al.* (2011) explain the absence of *Alona karelica* in littoral samples of European lakes by suggesting that it may actually be a terrestrial cladoceran that is normally associated with moss. This species has been reported twice from *Sphagnum* (Figure 6) in Europe (Flößner 2000; Kuczyńska-Kippen 2008) and its European distribution coincides with that of regions of high *Sphagnum* diversity (see Séneca & Söderström 2008; Van Damme *et al.* 2011). Another species of *Alona*, *A. bromelicola*, is from Nicaragua and lives in the basins of bromeliads (Van Damme *et al.* 2011). Yet another species, *Alona rustica* (Figure 21), is present in collections of bryophytes from stream banks in Italy (Margaritora *et al.* 2002), another transitional habitat. Such transitional habitats often have both higher diversity and density of organisms, a phenomenon known as the **edge effect** (Leopold 1933; Lay 1938; Good & Dambach 1943; Bider 1968; Wiens 1976).

Kuczyńska-Kippen (2008) examined the role of *Sphagnum* (Figure 6) compared to open water for zooplankton in a lake in Poland. The highest species diversity values occurred in the peat mat (mean = 0.67 for crustaceans compared to 1.76 for rotifers), whereas the

lowest values occurred in open water (0.36 and 0.99 respectively). The cladocerans present in the transition zone between the peat mat and the open water seem to relate to the presence of both invertebrate and vertebrate predators, and competition between the large cladocerans and smaller rotifers. For the cladocerans, *Sphagnum* (Figure 23) can serve as a refugium to protect them from other invertebrate predators.



Figure 23. *Sphagnum cuspidatum* mat (foreground) and nearby hummock (upper left), habitats where one can find more Cladocera than in the open water (upper left). Photo by Michael Lüth, with permission.

Cammaerts and Mertens (1999) discovered *Bryospilus repens* (Figure 9) in the **Palaeotropics** (tropical areas of Africa, Asia, and Oceania, excluding Australia) of western Africa, where it occurred in vernal pools of forests. This dispels the notion that this genus is strictly a moss dweller.

One problem in sorting out the Cladocera-bryophyte relationship is that species descriptions frequently fail to include the substrate, reporting only the general habitat, if even that.

Streams

Stream drift, a popular topic in the 60's and 70's, is generally a phenomenon we relate to the insects and other macroinvertebrates. But microcrustacea can be part of this as well. For moss-dwelling Cladocera, this is a means to get from one moss clump to another in an unfriendly moving environment. Peric *et al.* (2014) found that of 60 invertebrate taxa in a moss-rich karst system in Croatia, six were annelids and arthropods from the meiofauna, representing 35% of the total drift, but among the most abundant drift organisms were several species of *Alona* (26.7%) (Figure 22), a cladoceran known for being a moss-dweller (Hansson *et al.* 1996; Van Damme *et al.* 2011). The drift was lowest in winter and highest in autumn and late spring to early summer.

CLASS MAXILLOPODA, SUBCLASS COPEPODA

The name **Copepoda** comes from the Greek word *κοοπίπιδ*, which literally means oar-feet (Wikipedia: Copepod 2014). Copepods are microcrustacea, mostly 0.5-2 mm (Encyclopaedia Britannica 2012), usually occurring as planktonic or benthic organisms and not ones we would

expect to be frequent in moss communities. The entire group comprises about 13,000 species with three of its ten orders being the most common (**Harpacticoida**, **Cyclopoida**, **Calanoida**) and containing the ones known from bryophytes (Wikipedia: Copepod 2014). Copepods have two pairs of antennae and a single red compound eye (in most). They are perhaps the fastest organisms alive, swimming in irregular spurts (Kjørboe *et al.* 2010). Some of the meiofauna taxa have switched to **direct development** (lacking the larval stage) and care of their young (Dahms & Qian 2004), traits that are absent in most copepods but that are beneficial in a terrestrial environment.

The **Harpacticoida** (Figure 24) have a short pair of first antennae (Figure 25), often a somewhat wormlike body, and are mostly benthic (living on the bottom) (Wikipedia: Harpacticoida 2013). Nevertheless, Dumont and Maas (1988) consider the harpacticoid copepods to be widespread in wet habitats such as wet mosses. The harpacticoid copepods include crawlers, walkers, and burrowers (Dole-Olivier *et al.* 2000), pre-adapting the crawlers and walkers to mobility in the water film of bryophytes.



Figure 24. Terrestrial **Canthocamptidae** male, a harpacticoid copepod. Photo by Walter Pfliegler, with permission.



Figure 25. *Canthocamptus*, a harpacticoid copepod showing antennae. Photo by Yuuji Tsukii, with permission.

The **Cyclopoida** (Figure 26) are mostly **planktonic** (live in water column and float or drift – can't swim against a current) (Wikipedia: Cyclopoida 2013). Their antennae are longer than those of Harpacticoida but shorter than those of Calanoida, reaching no farther than the thorax. They are capable of rapid movement.



Figure 26. *Cyclops vicinus*, a cyclopoid copepod carrying egg sacs. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

The **Calanoida** (Figure 27) are also mostly planktonic species (Wikipedia: Calanoida 2013). Unlike the short antennae of the Harpacticoida, the first antennae of the Calanoida extend about half the length of the body or more.

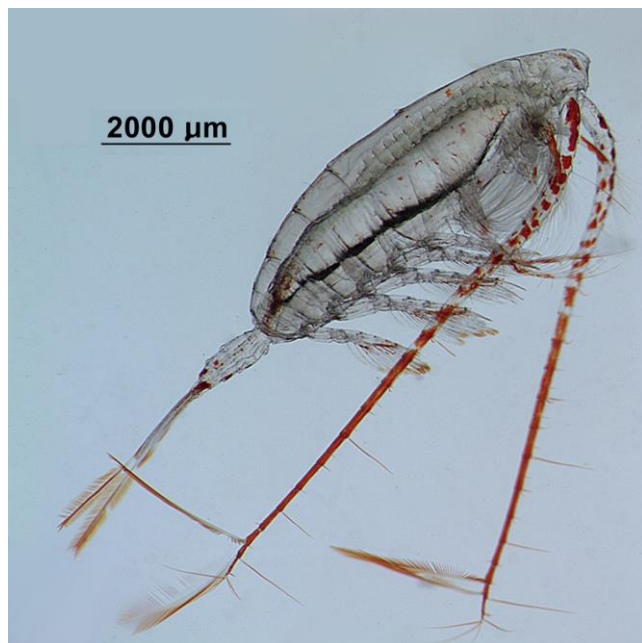


Figure 27. *Neocalanus cristatus*, a calanoid copepod showing the long antennae. Photo by Seward Line <www.sfos.uaf.edu>, with online permission for educational use.

Copepods are known for their egg longevity, with some surviving as much as 322 years (Hairston *et al.* 1995).

Adaptations

Copepods, like several other crustacean groups, have evolved to a terrestrial life style, but still live where water is generally available (Stout 1963). Bryophytes provide such a habitat. Stout suggests that through evolutionary time both copepods and ostracods moved from streams to adjoining moss carpets and currently are able to live among *Sphagnum* (Figure 23) as well as forest litter (Harding 1953, 1955).

Bryophyte-dwelling copepods are not very numerous, which probably explains, in part, the absence of descriptions of adaptations to the bryophytic habitat. Nevertheless, one might consider the adaptations to a terrestrial life style as exemplary of bryophytic adaptations. One such adaptation is the absence of hemoglobin (Green 1959). This is a stretch, because it appears that this pigment has evolved primarily in those species with a parasitic life style and a limited number of mud-dwelling taxa. Nevertheless, it suggests that oxygen is in adequate supply in the bryophytic habitat, so energy-requiring pigment development is not necessary.

Structure

The moss-dwelling **nauplius** (larval stage; Figure 28) of the copepod uses its antennae for swimming and possesses a single eye that can disappear in some species in later developmental stages. The copepod eye, in at least some species, senses the direction of light and permits the copepod, by moving its tail, to keep its back oriented toward the light (Land 1988). This behavior furthermore permits the copepod to distinguish its own species from other species by the movement patterns. Directed movement in response to light seems to be useful in minimizing exposure to UV light in tidal areas (Martin *et al.* 2000). These light avoidance behaviors are probably less useful among bryophytes.

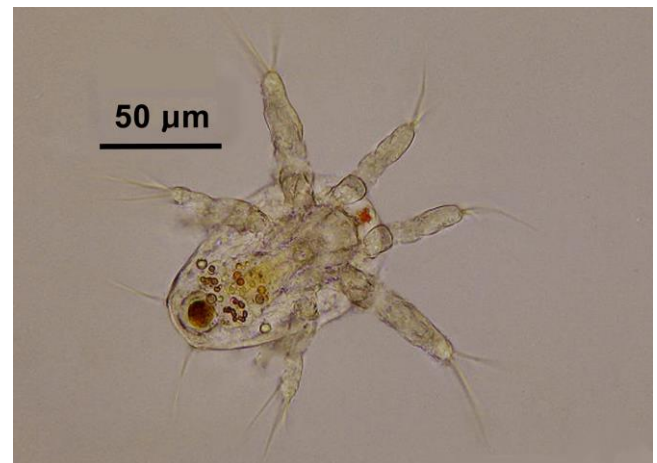


Figure 28. Copepoda nauplius, the immature state. Photo by Graham Matthews <http://www.micromagus.net/microscopes/pondlife_copepoda.html>, with permission.

Life Cycle Strategies

Whether living in water that freezes, pools that dry up, or among mosses and other terrestrial habitats, life cycle strategies are important in enduring unfavorable seasons

(Santer 1998). Terrestrial habitats are all unstable. Evolution favors traits that help the copepods sense and prepare for these potentially deadly periods. These strategies include dormancy and migration as escape mechanisms, but also include synchronizing growth and reproduction with favorable periods.

Dormancy is a common trait among copepods, particularly in higher and temperate latitudes (Dahms 1995; Williams-Howze 1997). It permits them to survive periods of desiccation and other unfavorable conditions. The timing of dormancy varies with the species and can occur in different forms in multiple life cycle stages, including desiccation-resistant resting eggs, arrested larval development, **encystment** of juveniles and adults (Deevey 1941; Dahms 1995), and arrested development of adults (Dahms 1995; Williams-Howze 1997). Dormancy saves energy during a time when living conditions are unfavorable. In addition to facilitating copepod survival during desiccation, dormancy helps copepods escape unfavorable temperatures, insufficient oxygen availability, limited food availability, and predation.

Among these dormancy strategies, one potential adaptation is encystment. *Canthocamptus staphylinoides* (Figure 29) is a harpacticoid copepod that encysts (Deevey 1941). Some members of this genus are known from mosses in the aquatic environment and peat bogs, where encystment can permit them to survive not only desiccation but also unfavorable temperatures.



Figure 29. *Canthocamptus staphylinoides*. Photo from US Geological Survey, through public domain.

Diapause can be defined as a delay in development in response to regular and recurring periods of adverse environmental conditions. In its narrow sense, it is initiated and terminated by triggers such as photoperiod, temperature, chemical cues, population density, and physiological factors (Dahms 1995).

Feeding

Fryer (1957a, b) considered chance encounter to be a primary mechanism in finding food for the mostly planktonic copepods. Nevertheless, chemoreceptors help them to distinguish edible from inedible food particles and thus may help somewhat in locating food. The carnivorous diet appears to be the primitive condition, with the change to an algal diet facilitating adaptive radiation.

Habitats

Reid (1986, 1987, 1999, 2011) has contributed considerably to our knowledge of bryophyte-dwelling

copepods. She reported them from such overlooked habitats as mosses (including *Sphagnum* – Figure 23) and liverworts, as well as from tree holes (Reid 1986). She described the new species *Muscocyclops thersasiae* from Brazil, primarily from soils, but also from mosses. Reid (2001) considered the publications on the harpacticoids and small cyclopoids from mosses in humid climates to be so numerous that they were almost impossible to review. She found that such "aquatic" mosses as *Sphagnum* (Figure 23) and *Hypnum* (Figure 30) as well as those bryophytes from more humid habitats provide homes for their own unique communities of copepods. Stoch (2007) attributes the copepod abundance to the complex spatial structure and high availability of food resources among bryophytes. In their study on *Fontinalis antipyretica* (Figure 7) meiofauna in Central Europe, Vlčková *et al.* (2002) found that harpacticoid copepods were able to feed on organic matter in the size range of 30-100 μm trapped within the moss clumps.



Figure 30. *Calliergonella lindbergii* (= *Hypnum lindbergii*), a moss genus where copepods are known to live. Photo by Jan-Peter Frahm, with permission.

Terrestrial

One would not expect a plankton organism like the copepods to occur on mosses on land, but a few have managed to venture into that habitat. Paul Davison (pers. comm. 9 November 2011) reported to me that harpacticoid copepods are well known from terrestrial mosses, but finding documentation of that has been challenging. Menzel (1921, 1925) reported both cyclopoid and harpacticoid copepods as moss dwellers. Bryophytes do not harbor a rich fauna, so they have not attracted much attention from the copepodologists. Nevertheless, those copepods that live among mosses can, at times, be important to ecosystem functioning. For example, the harpacticoid copepods are a first food source for the young salamanders living near and among the mosses (Paul Davison, pers. comm. 9 November 2011) (See Epiphytes below).

Scattered reports of terrestrial bryophyte-dwelling copepods, especially harpacticoids, occur in the literature (e.g. Olofsson 1918; Lang 1931), including mosses

(including *Sphagnum* – Figure 23) and liverworts as habitat.

The genus *Bryocamptus* seems to be among the more common taxa in the Eastern Hemisphere. *Bryocamptus pygmaeus* and *B. zschokkei* (Figure 31) occur primarily among mosses in Central Europe (Illies 1952). Harding (1958) reported *Bryocamptus stouti* from mosses in New Zealand.

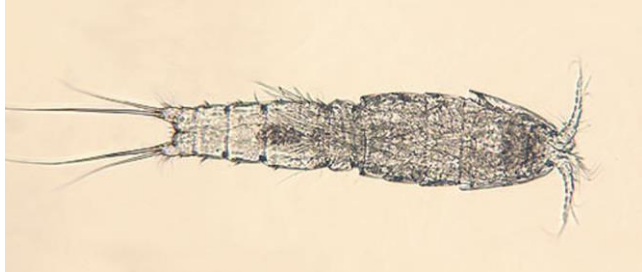


Figure 31. *Bryocamptus zschokkei* female, a moss dweller. Photo from US Geological Survey, through public domain.

Lewis (1984) reported twelve species of harpacticoid copepods from terrestrial mosses in forests and open areas in New Zealand. Lewis (1972a) found copepods in New Zealand among forest mosses that remained moist most of the year. These included *Elaphoidella silvestris* (see Figure 32), a copepod among damp mosses on the forest floor or nearby, but this species is limited to the damp conditions of higher altitude bush areas of North Island and dripping wet forests of the West Coast of South Island.



Figure 32. *Elaphoidella bidens*. Members of this genus live among damp mosses on the forest floor of New Zealand. Photo through Creative Commons.

Mrázek (1893) found the harpacticoid copepod *Maraenobiotus vejdoski* among mosses in Bohemia, and Harding (1953) reported them from woodland mosses in Scotland. These copepods are small and slender, permitting them to live an aquatic life in the water film among mosses (Harding 1953).

Scourfield (1939) reported *Bryocyclops* and *Muscocyclops* as living among mosses in Wales. With a name like *Bryocyclops muscicola*, one expects to find a moss-dweller. Reid (1999) reported this species, originally described from Indonesia, from a plant nursery in Florida, USA, apparently introduced with some of the plants, perhaps mosses. This is the only species of *Bryocyclops* known from continental US, although *Bryocyclops caroli* is known from Puerto Rico. In the Eastern Hemisphere the genus seems to be more common than in the Western Hemisphere, or perhaps just better known.

Menzel (1926) described the new species *Bryocyclops anninae* from moist mosses in Java and reported

Bryocyclops bogoriensis from the Fiji Islands among mosses and in tree holes. More recently, Watiroyram *et al.* (2012) listed ten additional wet moss dwellers in the genus *Bryocyclops* in Thailand, mostly near springs and waterfalls.

Harding (1953) reported that *Epactophanes* (Figure 54) and *Maraenobiotus* live in damp mosses in Europe. *Epactophanes muscicola* (in UK) avoids mosses that are very wet. Michailova-Neikova (1973) found that of the nine harpacticoid copepods living among wet mosses near water bodies on a mountain in Bulgaria, eight also lived among leaf litter.

In an apparently rare Western Hemisphere record of bryophyte dwellers, Rocha (1994) described *Metacyclops oraemaris* as a new species from moist moss in São Paulo, Brazil. In neighboring Suriname, Menzel (1916) found *Parastenocaris staheli* (see Figure 33) among mosses in the old leaf axils of the palm *Livingstonia*.



Figure 33. *Parastenocaris lacustris* female, member of a genus with species that live among epiphytic mosses. Photo from US Geological Survey, through public domain.

North American records seem to be almost non-existent. Nevertheless, Margaret (Maggie) Ray (pers. comm. 9 November 2011) told me that she found copepods in many of her bryophyte samples across North Carolina, USA. Paul Davison (pers. comm. 9 November 2011) likewise has often found them among bryophytic epiphytes in Alabama. Others have reported on them as a group (Camann 2011; Camann *et al.* 2011).

Seepage Areas – Seepage areas, typically with bryophytes, seem like a logical place to look for limnoterrestrial copepods. Scourfield (1932) found *Bryocyclops pygmaeus*, a common species, and *Speocyclops dimentiensis* among mosses of seeps on rock outcrops at Tenby in Wales. In New Caledonia, Hamond (1987) found *Fibulacamptus* among wet mosses as well as other wet terrestrial substrata.

Fiers and Ghenne (2000) suggested an interesting role for mosses in forests. They provide epigeal highways, especially for the tiny (~0.5 mm long) species, that help to connect the various patches of leaf litter and moist soils while also serving as a temporary or permanent habitat.

Epiphytes – It is interesting that one can see canopy food webs similar to those in the water, with bryophytes forming the habitat structure. In a (regrettably) rare North American study, Camann and coworkers (Camann 2011; Camann *et al.* 2011) report communities at 84 m above the forest floor in the redwood forest of California, USA. In these humus moss patches harpacticoid copepods dwell, encysting when conditions get dry. And further up the food web are Wandering Salamanders (*Aneides vagrans*; Figure 34), likewise bryophyte dwellers, that use the copepods as food. Most likely there are birds or other vertebrates that prey on the salamanders.



Figure 34. *Aneides vagrans*, a salamander whose larvae feed on terrestrial copepods. Photo by John P. Clare, through Creative Commons..

Antarctic

Pesta (1928) described the harpacticoid copepod *Attheyella koenigi* (Harpacticoida: Canthocamptidae; see Figure 35) from mosses in a stream on the island of South Georgia in the Antarctic. Also on the island of South Georgia, it is likewise the family Canthocamptidae that has the only known copepod species living among mosses at the edges of shallow lakes (Hansson *et al.* 1996). Although only three larval forms were found, the mosses were the only location where these copepods appeared in that study of Antarctic lakes. Also among these Antarctic dwellers is the harpacticoid copepod *Marionobiotus jeanneli* (family Thalestridae) living among wet mosses (Pugh *et al.* 2002).



Figure 35. *Attheyella americana* immature. This genus has several bryophyte-dwelling species. Photo by US Geological Survey, through public domain.

Peat Bogs and Sphagnum

Bog lakes and pools in peat bogs are often rich in copepod species (Minelli 2004). In the Italian bog pools and lakes (and likely throughout most of Europe as well), the copepods are represented by the orders Cyclopoida and Harpacticoida. The most abundant species are typically widespread predators, including *Megacyclops viridis* (Figure 36), *Macrocyclus albidus* (Figure 37-Figure 38), and *Diacyclops bicuspidatus* (Figure 39), and algal or detritus feeders including *Paracyclops fimbriatus* (see Figure 48), *Eucyclops serrulatus* (Figure 55), *Thermocyclops dybowskii* (see Figure 40), and *Tropocyclops prasinus* (Figure 41). *Megacyclops viridis* seems to have been introduced to the Great Lakes of North

America; in Austria it is commonly associated with salt pools (Kipp *et al.* 2012). The most common species in high-altitude peat bogs of Europe is *Acanthocyclops vernalis* (Figure 42), reaching an altitude of 2800 m in the Alps.



Figure 36. *Megacyclops viridis*, a widespread species whose habitats include peatlands. Photo by R. M. Kipp *et al.* at USGS, with permission.



Figure 37. *Macrocyclus albidus* female with egg sacs. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 38. *Macrocyclus albidus* nauplius. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 39. *Diacyclops bicuspidatus* with egg sacs, a widespread predator that can be found on Antarctic bryophytes. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.



Figure 42. *Acanthocyclops vernalis* female with egg sacs. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

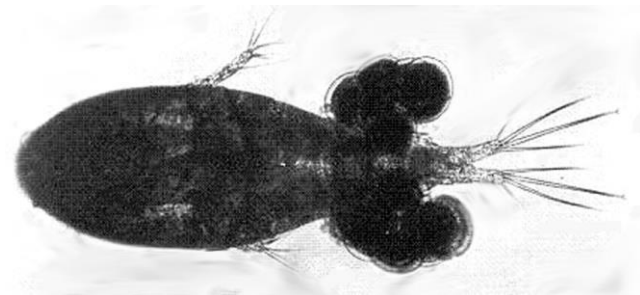


Figure 40. *Thermocyclops* sp. with egg sacs. Photo through Creative Commons.

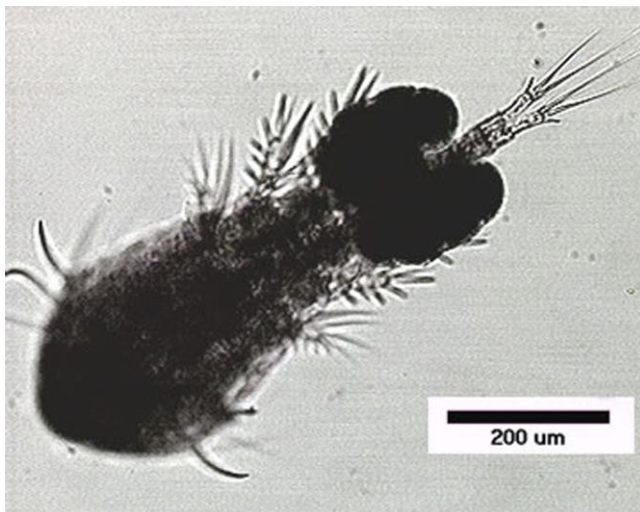


Figure 41. *Tropocyclops prasinus* with egg sacs. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.



Figure 43. *Sphagnum* blanket bog. Photo through Creative Commons.

Peat bogs, with a ground cover of *Sphagnum* species (Figure 43), provide the film of water needed by limnoterrestrial copepods. *Diacyclops languidus* and *D. hypnicola* (see Figure 44) are small species adapted to living in the water film on the mosses and characteristic of peat bogs in the Alps, Apennines, and central and northern Europe (Minelli 2004). Among European alpine *Sphagnum* and other moss cushions one can find *Bryocamptus pygmaeus*, *Epactophanes richardi* (Figure 54), and *Phyllognathopus viguieri*. Barclay (1969) found the latter species in New Zealand among mosses at the base of gravel piles in the winter when the mosses become quite soggy. A species of *Bryocyclops* is common in this same habitat.



Figure 44. *Diacyclops* sp., a genus of small copepods with some species adapted for living in the water film of bog mosses. Photo from USGS, through public domain.

Stoch (1998b) originally described the new species *Moraria alpina* and re-described *M. radovnae* (see Figure 45) from the Alps of Italy and Slovenia, where they occurred among mosses, in bogs, and in interstitial spaces in brooks. Additional European alpine species, for example *Bryocamptus veidovskji*, *Elaphoidella gracilis*, *Moraria mrazeki*, *M. alpina*, *Maraenobiotus veidovskji*, and *Hypocamptus brehmi*, live only in peat bogs and interstitial mountain habitats (Minelli 2004). In Britain, one can find *Moraria arboricola* among *Sphagnum* (Figure 43), as well as in leaf litter and tree hole pools (Fryer 1993). It seems none of these are strict **tyrphobionts** (living only in peat bogs and mires).



Figure 45. *Moraria laurentica* female, member of a genus including moss dwellers in the Antarctic South Georgia Island and known from mossy swamps and wet mosses on stream banks in the Great Lakes area, USA. Photo from US Geological Survey, through public domain.

Herbst (1959) reported *Metacyclops paludicola* and *Ectocyclops herbsti* (see Figure 46) from a *Sphagnum* bog in São Paulo, Brazil. Hingley (1993) reported *Moraria sphagnicola* (see Figure 45) and *Canthocamptus weberi* (see Figure 47) as associated with *Sphagnum* (Figure 43) in Europe. In addition to living in mossy tarns, *Attheyella (Delachauxiella) brehmi* and *Attheyella (Chappuisiella) maorica* (see Figure 35) occur among *Sphagnum* in New Zealand (Lewis 1972a).

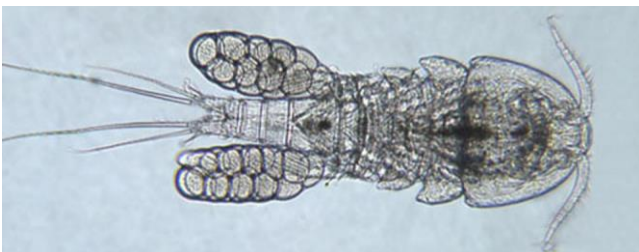


Figure 46. *Ectocyclops phaleratus* with egg sacs, member of a genus in which some species occur in peat bogs. Photo from Haney *et al.* 2013, with permission

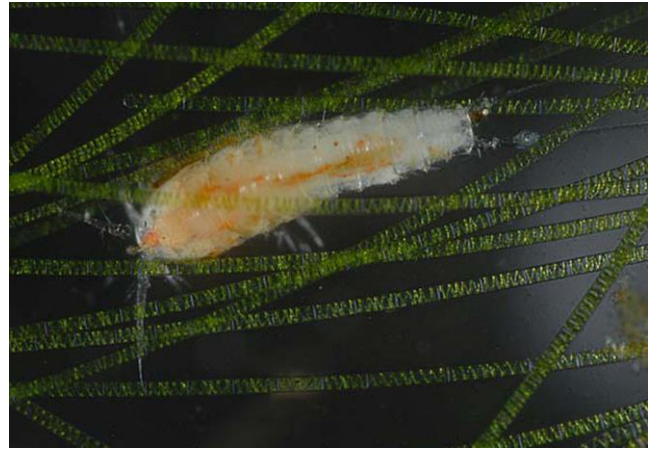


Figure 47. *Canthocamptus* sp. on the alga *Spirogyra*. Photo by Gerard Visser through Creative Commons.

In peatlands, the mosses can have an indirect influence on the fauna due to the tracheophytes they support. The rare North American copepod *Paracyclops canadensis* (Figure 48) is common in the pool of water in the leaves of the pitcher plant (*Sarracenia purpurea*, Figure 49) (Hamilton *et al.* 2000). In *Sphagnum* (Figure 43) peatlands, the mosses are a necessary habitat element to support the growth of pitcher plants.

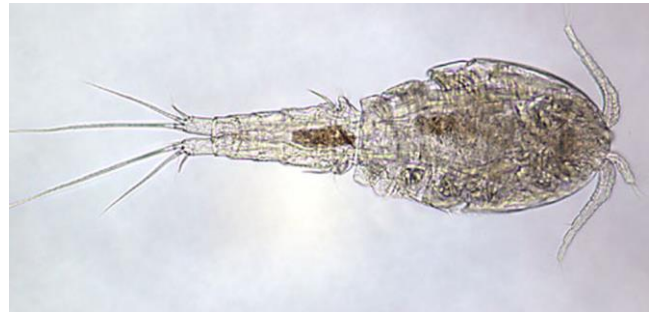


Figure 48. *Paracyclops canadensis*, an inhabitant of pitcher plants. Photo from US Geological Survey, through public domain.



Figure 49. *Sarracenia purpurea* leaf amid *Sphagnum* where copepods can live in the pool formed within the leaf. Photo by Janice Glime.

Aquatic

Reid (2001) reported that squeezing aquatic mosses would reveal small copepods such as members of *Acanthocyclops* (Figure 50-Figure 51), *Diacyclops* (Figure 52), and other small cyclopoid genera (Gurney 1932; Scourfield 1932, 1939). Aquatic bryophytes can provide cyclopoid genera with safe sites from strong flow, hide them from predators, and trap particulate matter that serves as food.



Figure 50. *Acanthocyclops venustoides*, genus of the small copepods that live among aquatic mosses. Photo by US Geological Survey, through public domain.



Figure 51. *Acanthocyclops robustus*, member of a genus of small copepods that live among bryophytes. Photo from Haney, J. F. *et al.* 2013. An Image-Based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.



Figure 52. *Diacyclops navus*, genus of the small copepods that live among aquatic mosses. Photo from US Geological Survey, through public domain.

Mossy Tarns

Tarns (Figure 53) are small mountain lakes. For the crustaceans, the mossy tarn habitat is similar in many ways to peatland pools, but it may differ in its pH and does not necessarily have *Sphagnum* (Figure 43) or may have different *Sphagnum* species. Several copepod species seem to prefer mossy tarns in New Zealand (Lewis 1972a). Among these are *Attheyella* (*Delachauxiella*) *brehmi* and *Attheyella* (*Chappuisiella*) *maorica* (species known to occur among *Sphagnum*; see Figure 35) and *Attheyella* (*Delachauxiella*) *bennetti*, genera known also from peatlands.



Figure 53. Tarn in Siskiyou Wilderness, CA, USA. Photo by Miguel Vieira, through Creative Commons.

Springs

Stoch (2007) found that mosses in springs in Italy were particularly good habitats for copepods, supporting large numbers. This may be due to their complex structure and highly available food sources. At the same time, the spring-dwelling species are often not true **crenobionts** (occurring only in springs and spring brooks) (Stoch 1998a), also occurring in other damp or aquatic habitats such as the littoral zone of lakes, moist mosses elsewhere, in groundwater, and in the epirithral region (upstream stream region suitable for trout) (Gerecke *et al.* 1998; Jersabek *et al.* 2001; Galassi *et al.* 2002; Stoch 1998a, 2003, 2006, 2007). Within the springs, species often segregate into microhabitats that supply their needs, including hygropetric rivulets, mosses, and patches of sediments with different characteristics (Stoch 2003; Fiasca *et al.* 2005). Bottazzi *et al.* (2011) reported **crenophilous** ("loving" springs and spring brooks) crustaceans from mosses in the Northern Apennine **rheocrene** springs (springs that flow to surface from underground), with pH and temperature best explaining their distribution and diversity pattern. In fact, the harpacticoid copepods and ostracods dominated the moss fauna, along with stoneflies and Chironomidae. The mosses were important contributors to the biodiversity.

We know that the copepod genera *Morarina* (Figure 45) and *Bryocamptus* are associated with wet or submerged mosses in Europe, including springs (Harding 1953). In their Italian study, Bottazzi *et al.* (2008) used traps, tubes, and moss samples to determine the copepod fauna of **rheocrene springs** (those that exhibit flow immediately after emerging from the substrate). They found 63% of the copepod taxa in these springs were represented among the

mosses, including a species of *Moraria*, in this case, *M. poppei*. Some of the copepod taxa occurred only in the moss habitat (i.e., were not collected in traps). These were the harpacticoid copepods *Bryocamptus tatrensis*, *B. alpestris* (see Figure 31), *Moraria vej dovski*, *M. vej dovski truncatus*, *M. poppei*, *Epactophanes richardi* (Figure 54), *Attheyella crassa* (see Figure 35), and the cyclopoid *Eucyclops serrulatus* (Figure 55). *Bryocamptus* species were evenly recorded from both moss and trap samples.

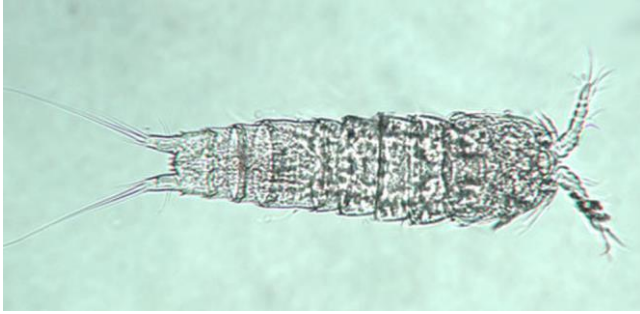


Figure 54. *Epactophanes richardi* female, a harpacticoid copepod of rheocene springs that seems to prefer mosses. Photo from US Geological Survey, through public domain.



Figure 55. *Eucyclops serrulatus*, a harpacticoid copepod that lives among mosses of rheocene springs. Photo by Fausto at <microscopio.it.gg>, with permission.

Bottazzi *et al.* (2011) also reported that the taxa most represented in the Northern Apennine rheocene springs were the harpacticoid copepods: *Bryocamptus zschokkei* (Figure 31) (mean number of individuals per sample = 2 for traps, 14 for mosses) and *B. pygmaeus* (1 individual/sample for traps, 5 for mosses). Out of their total of 3,284 invertebrates collected, **Ostracoda**, **harpacticoid Copepoda**, and **Diptera** were the most abundant among the 54 taxa. Bottazzi and coworkers considered the mosses to be a favorable habitat that contributed to the high species diversity.

Rivulets

Rivulets, often as outflow from springs, often have mosses that serve as copepod habitats. Stoch (2003, 2007) reported copepods from mosses in **hygropetric** rivulets (having water forming a surface film on rocks). Genera such as *Moraria* (Figure 45), *Epactophanes* (Figure 54), *Arcticocamptus*, *Nitocrella*, *Parastenocaris* (see Figure 33), *Speocyclops*, and *Diacyclops* (Figure 52) occur among hygropetric rivulet mosses (Fiasca *et al.* 2005).

Streams

It appears that copepods are important bryophyte inhabitants in mountain streams of New Zealand. In unshaded areas of the streams, Suren (1992) found *Canthocamptus howardorum*, *C. maoricus* (see Figure 56), *Attheyella stillicidarum*, *A. cf. brehmi* (see Figure 35), *Antarctobiotus elongatus*, and *A. cf. diversus*, all in the **Harpacticoida** (Figure 57). In 1992, Suren suggested that the large numbers of Copepoda found in association with bryophytes there may relate to the high food value of abundant periphyton that grow on the surfaces and the ability of the bryophytes to serve as safe sites against fast water currents. But in 1993, he refined his assessment to suggest that the copepods are especially important on bryophytes that are covered with detritus rather than periphyton (Suren 1993).

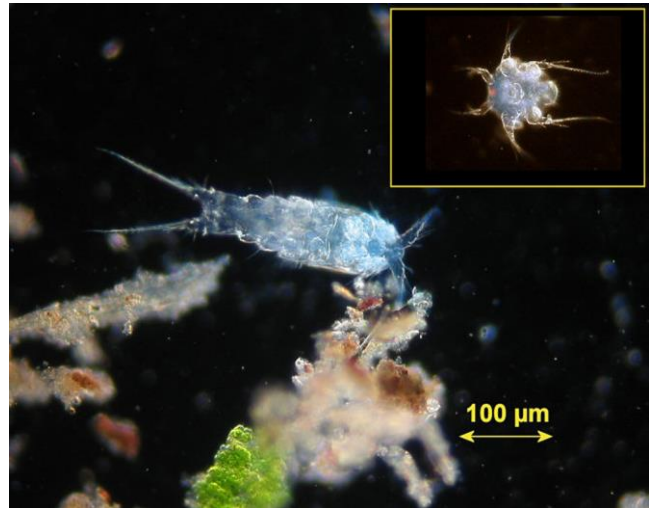


Figure 56. *Canthocamptus* from moss; note nauplius in insert. Photo by Graham Matthews <http://www.micromagus.net/microscopes/pondlife_copepoda.html>, with permission.



Figure 57. Harpacticoid copepod on leaf of *Fontinalis antipyretica*, demonstrating how tiny it is. Photo by Dan Spitale, with permission.

Leaf axils of bryophytes can be particularly protective against the current, but they also serve as collection sites for detritus. The differences in periphyton vs organic detritus may relate to location in sun vs shade. Cox (1988) found that bryophytes from an unshaded location had predominantly periphyton associated with them, whereas

those from the shaded site had predominately fine amorphous detritus associated with them. This is reasonable, as more light would promote greater algal growth. But flow rates will play into this as well, and oxygen content will differ with both flow rate and periphyton vs detrital matter.

Chironomidae (midges) are typically the dominant group on stream bryophytes [see, for example Williams (1989) in southern Ontario, Canada, and Nolte (1991) in Germany, who found that chironomids dominated on the submerged moss *Hygroamblystegium tenax* (Figure 58)]. In New Zealand alpine streams, Suren (1992) found that harpacticoid copepods and ostracods were among the most abundant groups of non-chironomids. Suren found that there was a "strong positive relationship" between copepod density and high water velocity, with densities among the bryophytes there reaching twice that of macroinvertebrates. At first, this seems like a contradiction because meiofauna are intolerant of high water velocity (Winner 1975) and avoid it by burrowing into the hyporheic zone (sediment). Suren (1992) pointed out that the copepods *Bryocamptus vej dovskiyi* and *B. zschokkei* (Figure 31) in Minnesota, USA, can only be found in the hyporheos in fast-flowing streams. He suggests that the bryophytes provide a "biotic hyporheic zone." The studies by Suren (1992) in New Zealand are in sharp contrast to those of Cox (1988) who found that in streams in Tennessee, USA, it was rotifers that dominated the bryophytic "hyporheic zone" in the mosses *Fontinalis novae-angliae* (Figure 59) and *Platyhypnidium riparioides* (Figure 60).



Figure 58. *Hygroamblystegium tenax*, a submerged moss dominated by Chironomidae (midges - Diptera) rather than copepods in Germany. Photo by Barry Stewart, with permission.



Figure 59. *Fontinalis novae-angliae* at edge of stream, a moss that supports dominant rotifer fauna, not copepod fauna, in the hyporheic zone in Tennessee, USA. Photo by Janice Glime.



Figure 60. *Platyhypnidium riparioides*, a moss that supports a dominant rotifer fauna rather than a copepod fauna in the hyporheic zone in Tennessee, USA. Photo by Michael Lüth, with permission.

Splash Zones

Stream edges and waterfall splash zones provide a suitable habitat for some limnoterrestrial copepods (Lewis 1972a). In New Zealand one can find such taxa as *Attheyella stillicidarum* (see Figure 35) among the mosses and liverworts, preferring either permanently dripping mossy banks or areas in the splash zones of streams, apparently requiring moving (fresh, not stagnant) water. *Attheyella humidarum* and *Attheyella fluviatilis* likewise prefer dripping mossy banks and damp "bush" moss. In addition to these *Attheyella* species, Lewis (1972b) also described six new species in the genus *Antarctobiotus* (*A. ignobilis*, *A. diversus*, *A. elongatus*, *A. australis*, *A. exiguus*, *A. triplex*) from damp mosses in New Zealand.

Cave Pool

Galas *et al.* (1996) examined the decomposition of litter in a cave pool in Poland. These pools included copepods, among other fauna. Respiration released more energy by activity of microorganisms on mosses (*Polytrichum*, Figure 61) than on the litter of *Sorbus* and *Alnus* in the pool. This higher rate among the bryophytes suggests that they may have provided a better food source of fine particulates and microorganisms for small organisms such as copepods than that associated with the submersed leaf litter.



Figure 61. *Polytrichum commune* in a geothermal spring, Yellowstone, WY, USA. Photo by Janice Glime.

Summary

Microcrustacea are primarily aquatic and marine, but some, including Copepoda and Cladocera, have developed characteristics that permit them to live on land in such habitats as wet bryophytes. Moisture, water chemistry, pH, and roughness of the moss habitat can be important determinants of microcrustacean diversity.

Adaptations to land may include separate sexes, ability to change sex, and parthenogenesis. Cyclopoid copepods have short life cycles that permits them to increase recruitment. They can sometimes disperse with their bryophyte substrate.

Truly terrestrial Cladocera are few, with *Bryospilus* being best represented among this group. Springs seem to be a transitional habitat between aquatic and terrestrial systems, with bryophytes serving as a refuge vertically and horizontally as moisture levels change. In streams, bryophytes can serve as a safety net to catch drifting organisms. The bottom of the moss clump provides a safe haven from the torrential waters above while being a collection site for food. Food is often fine detritus trapped by the bryophytes. In these aquatic and wet habitats, the bryophytes can contribute significantly to increasing the faunal diversity. Peatlands/*Sphagnum* bogs increase diversity by offering multiple niches both in the mosses and among the tracheophyte vegetation. *Alona* and *Alonella* are among the most common there; *Alona* is also the most common drift cladoceran in streams.

Cladoceran adaptations can include appendage reduction, shorter life cycle, eggs placed in dense masses of vegetation, and ability to swim in a thin film of water.

Copepods on land use their antennae to swim in the larval stage. Dormancy permits them to survive dry periods, including resting eggs, arrested development, and encystment of both juveniles and adults.

The ability of land-dwelling copepods to live among bryophytes is reflected in such names as *Muscocyclops*, *Bryocyclops*, and *Epactophanes muscicola*. Bryophytes can provide moist islands when copepods move from one location to another. Other species live among canopy epiphytes. Some even live among bryophytes in the Antarctic. *Attheyella* and *Moraria* are among the genera known from peat bogs, with genera such as *Paracyclops* found in pitcher plants there. Small copepods hide among the aquatic bryophytes. Harpacticoid copepods can dominate the moss fauna in springs, where temperature and pH are important factors in diversity. *Canthocamptus* and *Attheyella* are well represented in streams in New Zealand. Like the Cladocera, copepods often feed on periphyton or detritus among the bryophytes.

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CHAPTER 10-2

ARTHROPODS: CRUSTACEA – OSTRACODA AND AMPHIPODA

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CHAPTER 10-2

ARTHROPODS: CRUSTACEA – OSTRACODA AND AMPHIPODA



Figure 1. Terrestrial amphipod on leafy liverworts from New Zealand. Photo by Paddy Ryan, with permission.

The amphipods (Figure 1) and ostracods (Figure 2) might be considered as mimics that live in the bryophyte world. The amphipods look like miniature shrimp and the ostracods look like miniature mussel shells with a shrimp inside instead of a mussel.

CLASS OSTRACODA

Mark Papp (pers. comm. 19 November 2011) reported to me that he had a very sore neck and shoulders, but no ostracods to report. He had been looking at roof mosses where he had originally taken many ostracods at Chalfont St. Peter, UK. Their identity as ostracods was confirmed by a marine ecologist. He did find the remains of a copepod. The ostracods are evasive, making it that much more delightful when you find them. Those on the roof had apparently moved on.

The name **Ostracoda** comes from the Greek *óstrakon*, meaning shell. Ostracods (sometimes known as seed shrimp) look like miniature clams (or seeds) with a tiny shrimp-like animal living inside the shell. They typically are marine and freshwater organisms, but some have

become terrestrialized. They are not common among bryophytes, but they do sometimes occur there.



Figure 2. Ostracod, showing internal digestive system through the shell. Photo by Anna Syme through Wikipedia Commons.

Adaptations

Harding (1953) claimed the first find of a terrestrial ostracod (*Mesocypris terrestris*) as a new species occurring among mosses at the source of a small stream on Mt. Elgon in Kenya. Another occurred among mosses in a waterfall. But this ostracod is too large and globular for close alliance to the aquatic environment, so Harding (1953) reasoned that it must be more truly terrestrial. This ostracod is blind, presumably surviving loss of eyes because eyes are of little use among the mosses, and their swimming setae are very reduced as well. Instead, the second pair of antennae is especially powerful and Harding suggested that it might aid in movement in the water film among the mosses, a movement typically accomplished on mosses and liverworts by crawling (Powers & Bliss 1983). Excretion seems to be poorly understood, but some form of nitrogenous waste is excreted through glands on the maxillae, antennae, or both (Barnes 1982). Their food includes diatoms, bacteria, and detritus (Miracle 2014), items found not only in aquatic habitats, but also among terrestrial bryophytes.

Swimming to Crawling

A loss of ability to swim seems to be the result of an evolutionary loss of setae on antennae and reduction of setae on antennules (Harding 1953; De Deckker 1983; Martens *et al.* 2004). Instead, the terrestrial ostracods use their antennae to move along solid surfaces, much as benthic ostracods move along the bottom surface (Harding 1953; De Deckker 1983). On a moss, the ostracod is surrounded by a film of water at the bottom of the carapace (shell). This water is trapped by numerous hairs, especially ventrally and laterally, to about mid-height. This mechanism seems to work only on moist substrates. When *Austromesocypris australiensis* (= *Mesocypris australiensis*) was placed on a dry Petri plate, it was unable to retain all of the water when it moved (De Deckker 1983). Whereas most ostracods lie on their sides when at rest, this moss-dweller remains upright. As members of this species dry, they migrate to wetter conditions, but when it is too dry they close their shells (compare Figure 3 to Figure 9) to curtail water loss.



Figure 3. Dead ostracod with its shell open, revealing the exoskeleton. When taken out of water, this shell immediately closes. Photo by Paul Davison, with permission.

Reproduction

About half the non-marine ostracod species belong to the family **Cyprididae** (Wikipedia 2014). Many of these occur in temporary water bodies, requiring a degree of terrestrialization, and have drought-resistant eggs, mixed sexual and parthenogenetic reproduction, preadapting them to terrestrialization, and to living among bryophytes (Powers & Bliss 1983). There seems to be a prevalence of asexual reproduction among terrestrial ostracods compared to their aquatic counterparts (Pinto *et al.* 2005a). Nevertheless, terrestrialization of some may include retention of the fertilized eggs, protecting them from desiccation. Observations by Chapman (1961) suggest that the developing embryos of the moss-dweller *Scottia audax* (= *Mesocypris audax*) may be retained within the shell of the mother until they become free-living juveniles.

Habitats

Terrestrial

Although most ostracods are marine or aquatic, some, such as *Mesocypris* spp., live in wet terrestrial habitats, including mosses (Introduction to the Ostracoda 2002). This genus seems to be widespread among bryophytes in the Eastern Hemisphere from the Russian Far East (I'm unable to confirm this record) to Australia (Martens *et al.* 2004). Terrestrial species also occur in South America (Pinto *et al.* 2005a, b).

Although Harding (1953) claimed the first record of terrestrial ostracods in Africa with his finding of *Mesocypris terrestris*, this one was still in the wet habitats of a waterfall and source waters of a stream among mosses. De Deckker (1983) collected *Austromesocypris australiensis* from Cammoo Caves in Queensland, Australia, from wet moss. De Deckker points out that although most ostracods are aquatic or marine, several species are able to live among leaf litter and mosses that are able to provide a moist environment. Among these, the type specimen of *Austromesocypris australiensis* was found among mosses, and others were living among *Sphagnum* (Figure 4) on the side of a road near a small creek in New South Wales, Australia. In fact, these individuals were unable to swim freely even in free water.



Figure 4. *Sphagnum cristatum* from a soil bank in New Zealand. Photo by Janice Glime.

In Queensland, the terrestrial ostracod *Scottia audax* (also known from mosses in New Zealand; Chapman 1961) occurred along with *Austromesocypris australiensis* in mosses (De Deckker 1983). *Scottia birigida* (Figure 5)

occurs among mosses in Japan (Robin James Smith, pers. comm. 31 March 2014). In Tasmania, *Mesocypris tasmaniensis* likewise occurs among mosses as well as litter (De Deckker 1983). Røen (1956) named *Bryocypris grandipes* from Africa (GBIF 2013), but I have only its name to suggest it dwells among bryophytes. De Deckker stated that terrestrial ostracods are known only from Gondwanaland: Africa, Madagascar, Australia, and New Zealand, but they have since been found in Europe (Pieri *et al.* 2009; Mark Papp, pers. comm. 19 November 2011) and South America, where *Caaporacandona iguassuensis* occurs among moist Brazilian forest mosses (Pinto *et al.* 2005a). Although members of the **Cyprididae** occur in North America, thus far terrestrial representatives seem to be undocumented. Nevertheless, Paul Davison (pers. comm. 31 May 2014) reports them from dripping cliffs (Figure 6) among algae and suspects they could inhabit bryophytes under similar conditions. Bryologists should watch for them!



Figure 5. *Scottia birigida*, a moss dweller in Japan. Photo by Robin James Smith, with permission.

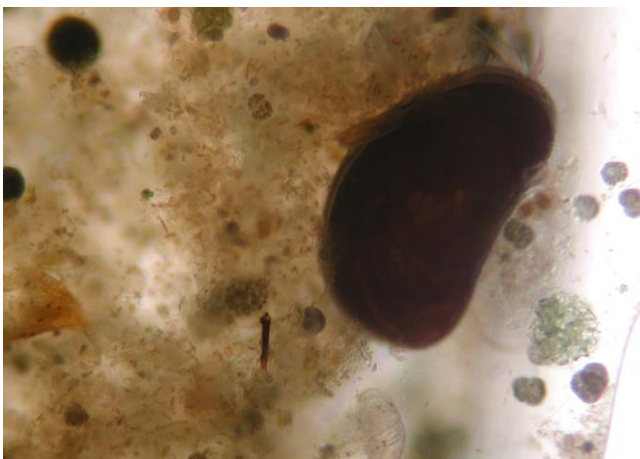


Figure 6. Ostracod from wet wall, a potential bryophyte dweller. Photo by Paul Davison, with permission.

Pieri *et al.* (2009), reporting on ostracods from Friuli Venezia Giulia, Italy, found three species distributed on mosses: *Cypria ophthalmica* (Figure 7), *Cyclocypris laevis* (Figure 8), *Cyclocypris ovum* (Figure 9). It is not clear what the habitat was for these mosses. *Cypria*

ophthalmica is known as a widespread species from the karst region of Italy (Wagenleitner 1990). All three species occur at the margins of lakes in the reed belt among the vegetation and on the sediment surface (Kiss 2007). The mosses were only examined from one site. One should note that these three species are also among the three most common taxa in the study (Figure 10), which included all the likely habitats for ostracods in the study area.

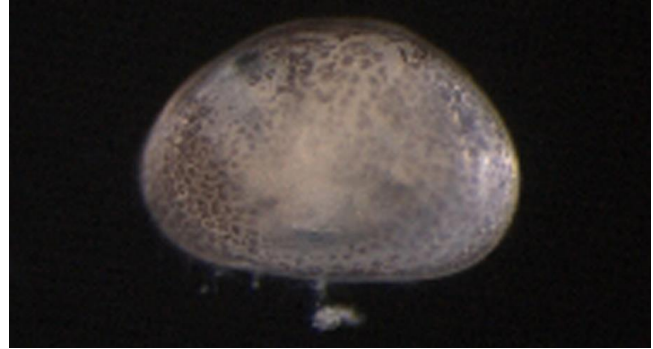


Figure 7. *Cypria ophthalmica*, a moss-dweller in Italy. Photo from Bold Systems through Creative Commons.

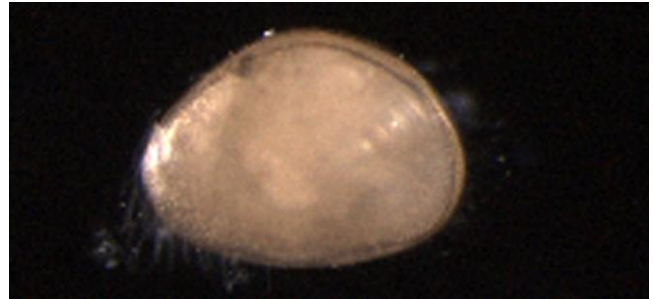


Figure 8. *Cyclocypris laevis*, a moss-dweller in Italy. Photo from Bold Systems through Creative Commons.

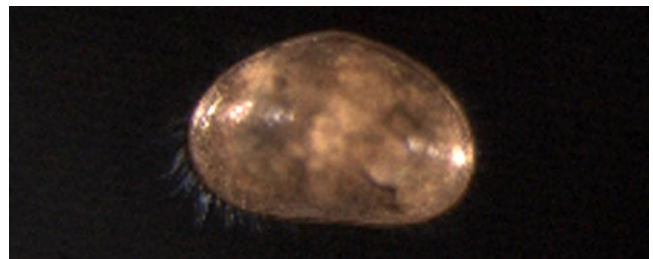


Figure 9. *Cyclocypris ovum*, a moss-dweller in Italy, with its shell closed. Photo by Bold Systems Creative Commons.

Peat Bogs

Peat bogs seem to be a rich site for ostracod species. Harding (1953, 1955) states that ostracods tend to occur in *Sphagnum* (Figure 11) as well as in forest litter. Bryophytes influence the species composition by creating a diversity of niches, from pools to dry hummock tops, and many microniches among the stems and leaves. Likewise, a gradation of *pH* can sometimes be found vertically and horizontally, providing more niche choices. Temperature differs between the surface and deeper portions of peat. Figure 10 shows the relationships of four environmental parameters with the five most common ostracod species in 200 sites in the sampling of surface, interstitial, and ground waters of Friuli Venezia Giulia, Italy (Pieri *et al.* 2009).

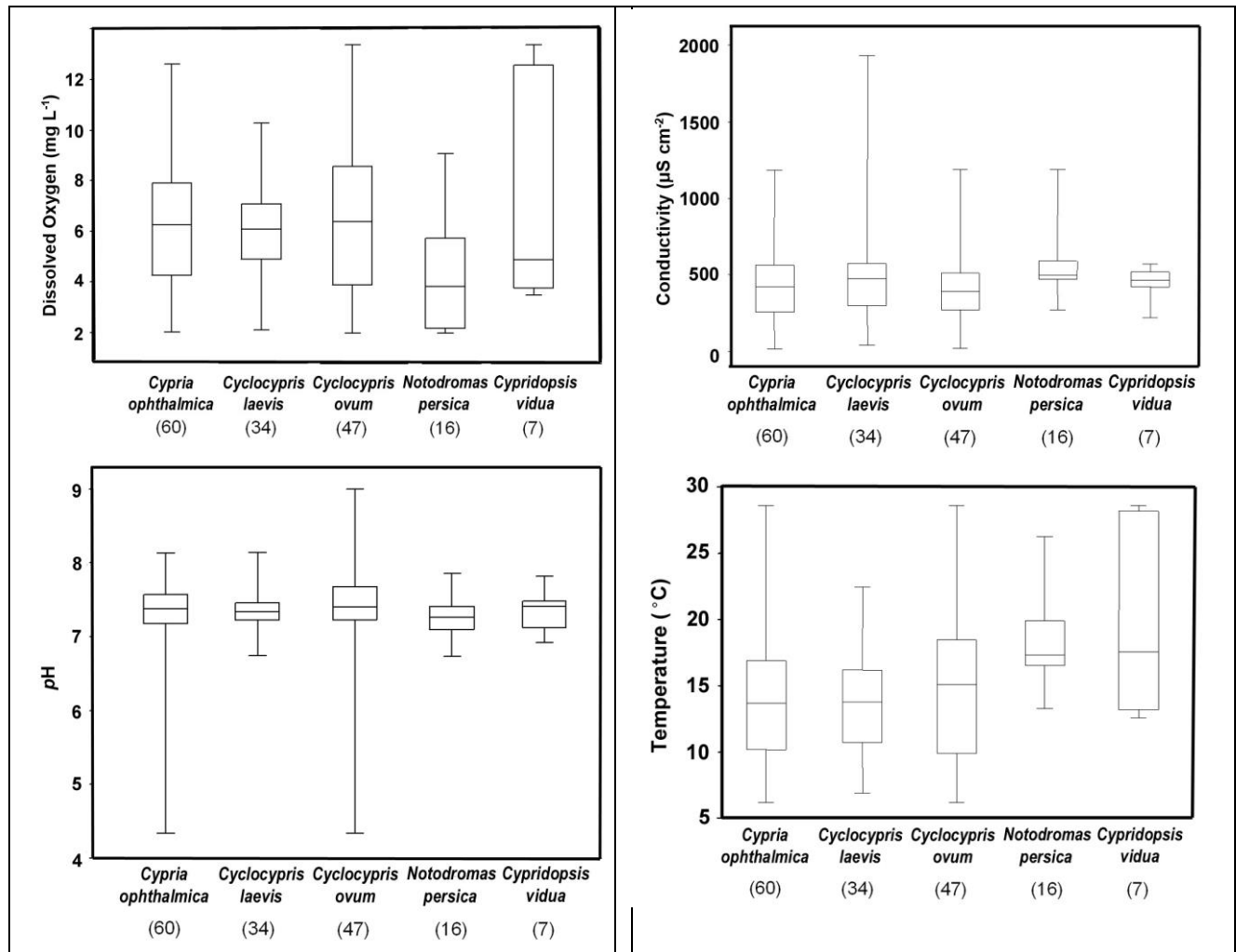


Figure 10. Comparison of environmental parameters for the five most common species in Friuli Venezia Giulia, Italy that also occur in peat bogs. The boxes show 25-75% quartiles. The horizontal line is the median, and vertical bars (whiskers) show the maximum and minimum values. The numbers of analyzed samples appear in parentheses below the species names. Redrawn from Pieri *et al.* 2009.



Figure 11. *Sphagnum capillifolium* representing a genus that houses several species of terrestrial ostracods. Photo by Blanka Shaw, with permission.

At Friuli Venezia Giulia, Italy, the five most widespread and common species of ostracods also occurred in peatlands (Pieri *et al.* 2009). Pieri and coworkers reported 24 species in 16 genera from peat bogs (Table 1).

Table 1. Ostracod species among those at Friuli Venezia Giulia, Italy, that occurred in peat bogs. From Pieri *et al.* 2009.

<i>Darwinula stevensoni</i> Figure 12	<i>Cycloocypris ovum</i> Figure 9
<i>Penthesilenula brasiliensis</i>	<i>Ilyocypris bradyi</i> Figure 29
<i>Microdarwinula zimмери</i> Figure 13	<i>Ilyocypris inermis</i> Figure 19
<i>Pseudocandona lobipes</i>	<i>Notodromas persica</i> Figure 20
<i>Pseudocandona compressa</i> Figure 14	<i>Eucypris pigra</i> Figure 21
<i>Pseudocandona pratensis</i> Figure 15	<i>Herpetocypris</i> sp. Figure 22
<i>Pseudocandona</i> cf. <i>sucki</i>	<i>Herpetocypris reptans</i> Figure 22
<i>Cryptocandona vavrai</i>	<i>Scottia pseudobrowniana</i>
<i>Candonopsis scourfieldi</i> see Figure 16	<i>Cypridopsis elongata</i> Figure 23
<i>Cypria ophthalmica</i> Figure 7	<i>Cypridopsis vidua</i> Figure 24
<i>Cycloocypris globosa</i> Figure 17	<i>Cavernocypris subterranea</i>
<i>Cycloocypris laevis</i> Figure 18	<i>Metacypris cordata</i> Figure 25

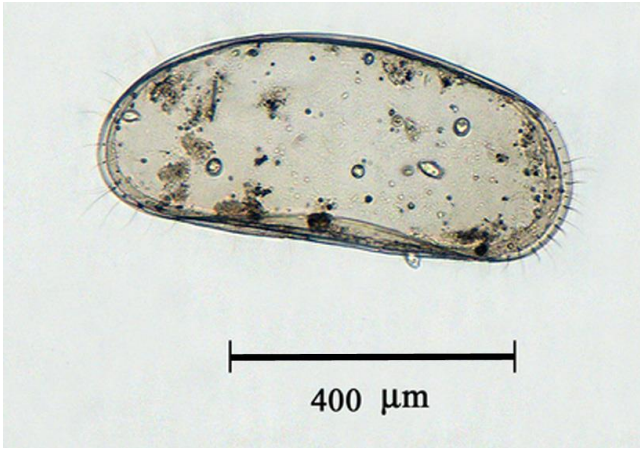


Figure 12. *Darwinula stevensoni*, an ostracod from mosses in peatlands in Italy. William Dembrowski through Creative Commons.

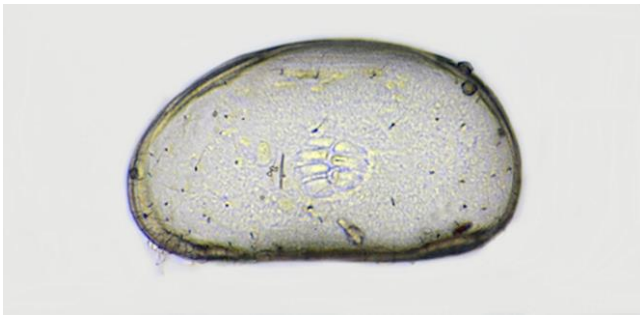


Figure 13. *Microdarwinula zimneri*, a peat moss ostracod. Photo by Robin J. Smith, with permission.

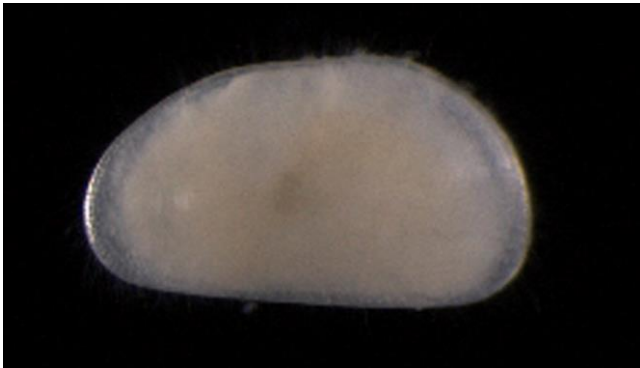


Figure 14. *Pseudocandona compressa*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.



Figure 15. *Pseudocandona pratensis*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.



Figure 16. *Candonopsis kingsleii*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

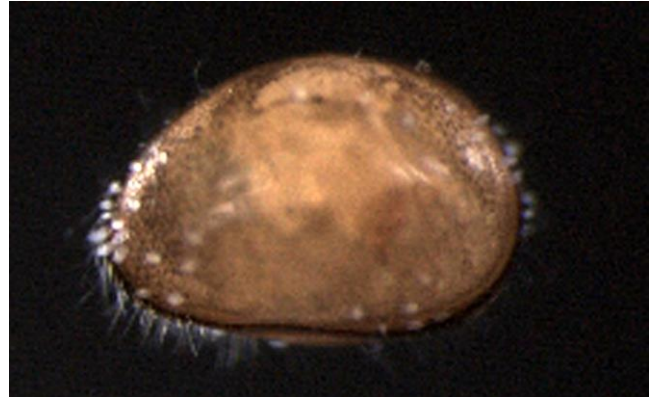


Figure 17. *Cyclocypris globosa*, a peat bog species in Italy. Those white ovals near its surface are attached protozoa. Photo from Bold Systems through Creative Commons.

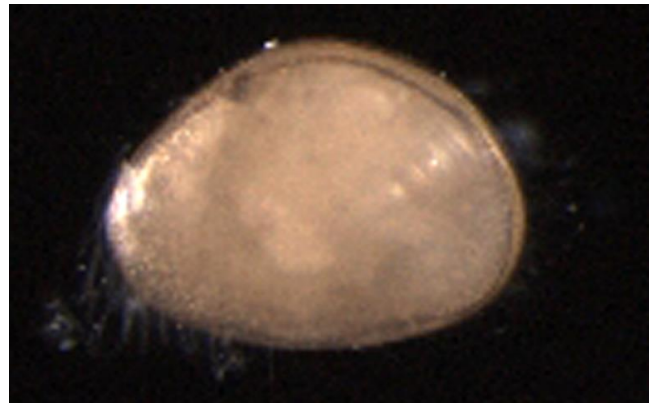


Figure 18. *Cyclocypris laevis*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

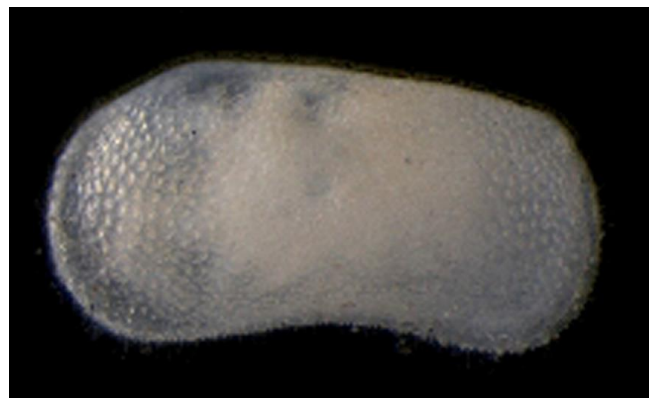


Figure 19. *Ilyocypris inermis*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.



Figure 20. *Notodromus* sp., a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

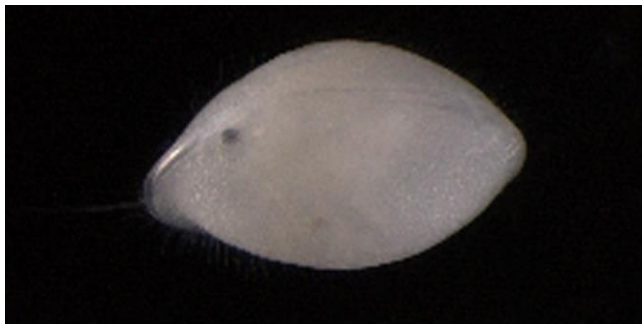


Figure 21. *Eucypris pigra*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

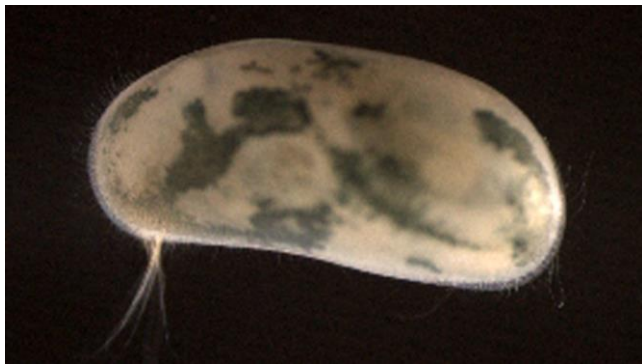


Figure 22. *Herpetocypris reptans*, a genus with members living in peat bogs in Italy. Photo from Bold Systems through Creative Commons.



Figure 23. *Cypridopsis elongata*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

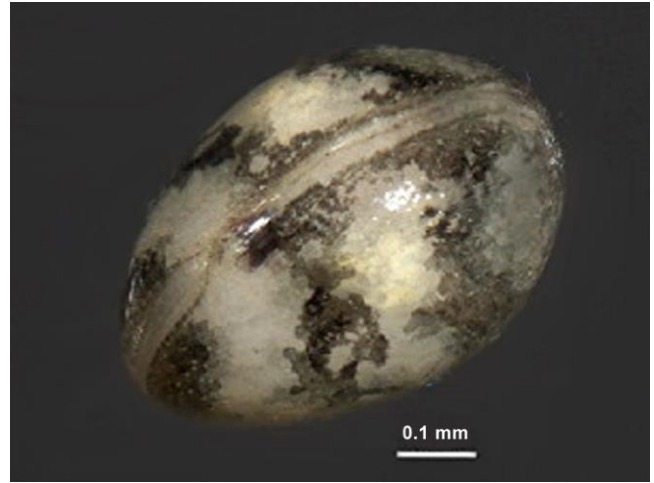


Figure 24. *Cypridopsis vidua*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.



Figure 25. *Metacypris cordata*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

It is interesting that some of these Italian bog-dwelling species are so widespread. For example, *Penthesilenula brasiliensis* is known on all the continents except Antarctica and North America (Pieri *et al.* 2009). Its wide range of habitats (rivers, streams, interstitial water, bromeliad basins, rain forest leaf litter, and bog mosses) may permit this widespread geographic distribution. Furthermore, three of the most common species in this part of Italy have a wide altitudinal distribution (Figure 26). Surely they occur among bryophytes in other European countries as well.

Some species seem to be restricted to bogs, making them **tyrphobionts**. In their study of Friuli Venezia Giulia, Italy, *Cavernocypris subterranea* and *Cryptocandona vavrai* were apparently restricted to peat bogs at high altitudes (Pieri *et al.* 2009). Barclay (1968) reported the new species *Penthesilenula sphagna* (= *Darwinula sphagna*) from New Zealand, living above the water among *Sphagnum* (Figure 4). Similar relationships of ostracods to *Sphagnum* are known from eastern Africa (Menzel 1916).

The importance of mosses in bogs can be indirect. In *Sphagnum* (Figure 11) peatlands, mosses are a necessary habitat element to support the growth of pitcher plants (*Sarracenia purpurea*; Figure 27). The leaves of these plants form pitchers of water that provide a suitable habitat

for some ostracods in North America (Hamilton *et al.* 2000), including those in Florida, USA (Harvey & Miller 1996).

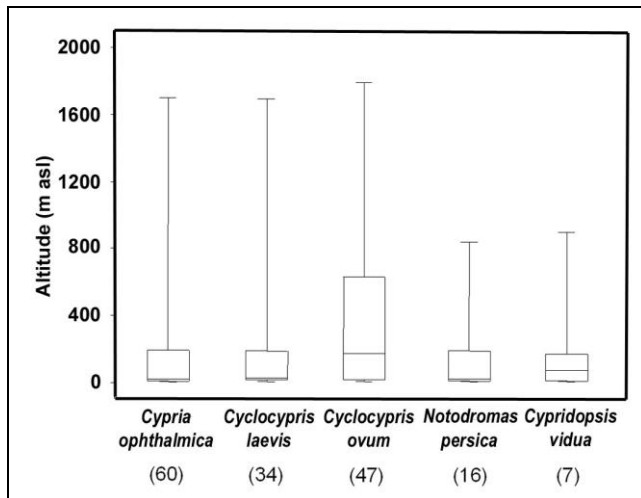


Figure 26. Comparison of altitudinal ranges of the five most common ostracods in Friuli Venezia Giulia, Italy, all five of which also occur in peat bogs. The boxes show the 25-75% quartiles. The horizontal line is the median, and the vertical bars (whiskers) show the maximum and minimum values. The numbers of analyzed samples appear in parentheses below the species names. Redrawn from Pieri *et al.* (2009).



Figure 27. *Sarracenia purpurea* in a *Sphagnum* bog. Photo from Wikimedia Creative Commons.

Aquatic

Streams

Potamocypris pallida (Figure 28) in Macedonia occurs in moss cushions on the sandy and rocky bottoms of mountain springs and brooks (Petrovski & Meisch 1995). In my own stream bryophyte collections in Appalachian Mountain, USA, streams, I rarely encountered ostracods and considered them to be accidental or temporary residents since they more commonly occur in quiet water.

Springs

Spring habitats have a number of features in common with peat bogs. They typically have a dominant bryophyte flora, and they can be dry during part of the year. But their

pH range can reach into basic values, creating conditions that favor different communities.

Bottazzi *et al.* (2011) compared ostracods collected in traps with those collected from mosses in **rheocrene** springs (where aquifer water reaches the surface) of the Northern Apennines. Ostracods were among the most abundant taxa, particularly among the permanent meiofauna. Such common inhabitants of springs can be called **crenophiles** (literally, spring-lovers). Only *Psychrodromus bertharrami* was collected in both traps and mosses, with similar numbers (20 individuals per sample in traps, 17 for mosses). *Ilyocypris bradyi* (Figure 29) was only recovered from mosses. All other taxa (except one of questionable identity) were collected in traps. Fryer (1955) described *Potamocypris thienemanni* (see Figure 28) as new to Britain, inhabiting bryophytes, including *Sphagnum* (Figure 11), in a spring. This species was also known from three springs in Germany.

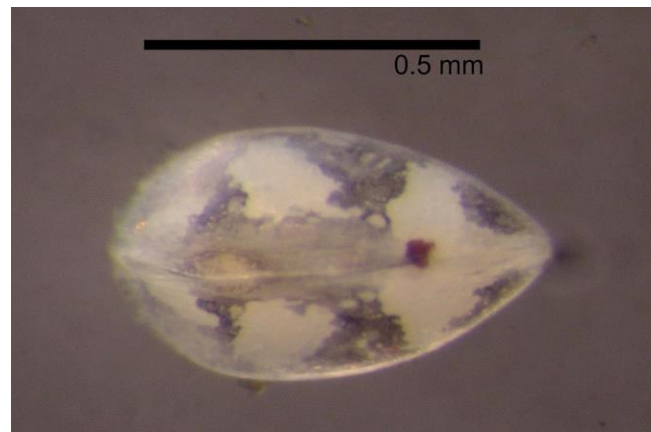


Figure 28. *Potamocypris pallida*, moss-dweller on sandy and rocky bottoms of Macedonian mountain springs and streams.. Photo by Elissa Dey, Zooplankton Project. Accessed 13 May 2014 at <http://www.biology.missouristate.edu/ostracods/Default.htm>.



Figure 29. *Ilyocypris bradyi*, an ostracod that in the northern Apennine springs seems to be limited to living among mosses. Note the hairy carapace that is typical of terrestrial ostracods. Photo from Bold Systems through Creative Commons.

CLASS MALACOSTRACA, ORDER AMPHIPODA

I have occasionally found amphipods in my collections of stream mosses, but they are more typically in quiet water

of larger streams. Nevertheless, it appears that in some cases they can be an important part of the aquatic moss faunal community (Minckley 1963; Minckley & Cole 1963; Matonickin & Pavletic 1964; Willoughby & Sutcliffe 1976). Badcock (1949) found *Gammarus* (Figure 30) to be most numerous in mosses and other protected niches, reporting an estimated fifty in a single tuft of moss (Cheney 1895). They are even known from terrestrial mosses (Merrifield & Ingham 1998).



Figure 30. *Gammarus pulex* showing the massive numbers in shallow pools. Photo through Creative Commons.

In some systems, amphipods can be quite abundant among the bryophytes. Wulfhorst (1994) found this to be true in two acid streams in the Harz Mountains, Germany, where they far exceeded those in the interstitial spaces (Figure 31).

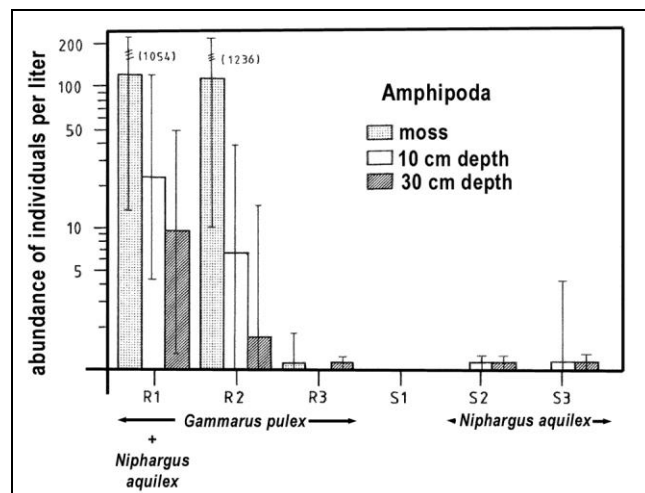


Figure 31. Abundance (number of individuals per liter) of the amphipods *Gammarus pulex* and *Niphargus aquilex* (Figure 32) among mosses and the interstitial spaces at 10 and 30 cm depth at six stations in two Harz Mountain streams. Bars indicate 95% confidence interval; n = 14 for mosses and 28-36 for interstitial spaces. Redrawn from Wulfhorst 1994.



Figure 32. *Niphargus aquilex*, a moss dweller. Photo by Grabow-Universität Koblenz-Landau, permission pending.

Adaptations to Land – and Bryophytes

Stout (1963) summarized three evolutionary pathways for terrestrial plankton. Among these, Hurley (1959) proposed that amphipods moved from the **supralittoral** (splash zone) fauna directly to the forest floor. Another suggestion is that fauna such as amphipods may have originated in freshwater streams, extended to the wet mossy banks and *Sphagnum* (Figure 11) bogs to the forest floor and ultimately to mineral soil. Stout considers the latter route to be the most convincing.

Hurley (1959, 1968) reported that all the terrestrial species of amphipods are in the family **Talitridae**, occurring in damp habitats. To survive in these terrestrial habitats required several morphological and behavioral changes, not to mention the physiological changes needed. They needed to become air breathers, jump instead of swim (accomplished by reduced **pleopods**, *i.e.* swimmerets, – to stumps in some species), adapt their life cycle to the changes in the seasons (Hurley 1959), and excrete uric acid instead of ammonia (Dresel & Moyle 1950). But they can have more than 50% ammonia excretion (Hurley 1959), perhaps releasing their ammonia as a gas like the isopods (O'Donnell & Wright 1995). It appears that they may have evolved different solutions to some of these problems from those of some of the other crustacean groups.

We can understand the small number of terrestrial amphipod species by comparing them to the isopods, where both aquatic and terrestrial species likewise exist. Terrestrial amphipods are less adapted to their terrestrial life than the isopods, being restricted to more narrow niches (Hurley 1968). The amphipods lack the isopod advantages of evaporative cooling at high temperatures and have exoskeletons with greater permeability, leading to greater risk of desiccation (Hurley 1959). Terrestrial isopods have lost their antennae, whereas in amphipods they are merely simplified. Both groups have modified their behavior to stay where it is cool and moist.

In wet leaf litter, the amphipods may move upward, a behavior we should look for among mosses (Hurley 1968). It is interesting that in the Fiordland of New Zealand the high level of rainfall and saturated ground has driven the amphipods to living among mosses or under bark of trees rather than their usual habitat of leaf litter. Avoidance of leaf litter there seems to be especially true for *Arcitalitrus sylvaticus* (= *Talitrus sylvaticus*; Figure 33). Its relative

Arcitalitrus dorrieni (Figure 34) also occurs with mosses on bark in Australia.



Figure 33. *Arcitalitrus sylvaticus*, an amphipod that avoids leaf litter and lives among mosses in the New Zealand Fiordland. Photo by Arthur Scott Macmillan through Creative Commons.



Figure 34. *Arcitalitrus dorrieni* on bark among mosses. Photo by Dluogs through Creative Commons.

Obtaining water, no problem for aquatic species, requires special behavioral techniques for the land dwellers. It is interesting that the water-obtaining behavior is similar to that of the terrestrial oniscid isopods. The terrestrial amphipods both gain and eliminate water by dabbing the uropod tips (tails) onto wet or dry substrata, respectively (Moore & Richardson 1992). The water is exchanged rapidly in or out of the central channel through the capillary spaces between the body parts. Beating **pleopods** (abdominal appendages also known as swimmerets) transfer water from the abdomen to the thorax in most terrestrial taxa. Water that pools beneath the tail is taken in by anal drinking.

Reproduction and Early Development

Among amphipods, the male is typically larger than the female and mounts her dorsally when she is ready to molt (Sutcliffe 1992). This behavior of having the male carry the female beneath him, known as **mate guarding**, helps to protect her during the crucial mating molt while

she is more vulnerable to predation, and on land to desiccation. The eggs are deposited in the external brood pouch when she molts, followed by deposition of the sperm by the male. Following fertilization, embryos are carried by the female, but hatchlings, resembling miniature adults, are on their own. The terrestrial *Talitrus saltator* (a sandhopper; Figure 35) lays its eggs four days after molting, compared to laying them immediately after copulation (Figure 36) in the aquatic *Gammarus* (Hurley 1959). The latter species can hold the spermatozoa in a brood pouch for up to four days. The aquatic male *Gammarus* carries the female under him for several days (Figure 36), whereas the terrestrial male of *Talitrus saltator* does not carry the female, a behavior difference that seems backwards until you realize he is jumping around on the sand and the female would get in the way. The 1-10 terrestrial eggs are much larger than the small and numerous aquatic eggs. The eggs of the terrestrial species furthermore remain in the brood pouch longer, affording them greater protection from desiccation.



Figure 35. *Talitrus saltator*, a sand hopper that holds its eggs four days after molting. Photo by Arnold Paul through Wikimedia Commons.



Figure 36. *Gammarus pulex* copulating, with the larger male on top. Photo by J. C. Schou, with permission.

A further means to conserve both energy and water is **neoteny**. *Orchestia* (Figure 37) reaches sexual maturity at an earlier growth stage and smaller size (Powers & Bliss 1983). This results in fewer offspring. They have a female bias, somewhat compensating for the smaller number of offspring, and females are larger than males, which is atypical for amphipods. Stephensen (1935) reported *Orchestia floresiana* from moss in Java, where it grows in waterfalls, rivulets, and fountains.



Figure 37. *Orchestia cavimana* at Colwick Park, Notts, UK. This terrestrial genus has females larger than males. Photo by Roger S. Key, with permission.

Food among the Bryophytes

Felten *et al.* (2008) found that some aquatic amphipods, or at least *Gammarus fossarum* (Figure 38), eat mosses, and that the relative proportion in the diet increases as they grow from 2 mm to 4 mm, increasing only slightly after that (Figure 39). Conversely, the proportion of fine amorphous detritus steadily decreases as the amphipods grow. Felten *et al.* suggest that the younger (smaller) amphipods do not have mouth parts that are developed well enough to eat the larger food items like bryophytes. The proportion of bryophytes in the diet also depends on where they are living, with those living among bryophytes eating a greater proportion of bryophytes (Figure 40). It is interesting that those in the detrital pools have a greater proportion of minerals, suggesting that they are unable to sort out the nutritious items from the non-nutritious items that surround them. It was unclear if the detrital pool populations were actually nibbling on the bryophytes or just eating fragments that had collected where they were.



Figure 38. *Gammarus fossarum*, an aquatic amphipod that eats mosses when its mouth parts are developed well enough to do so. Photo from BioLib.cz through public domain.

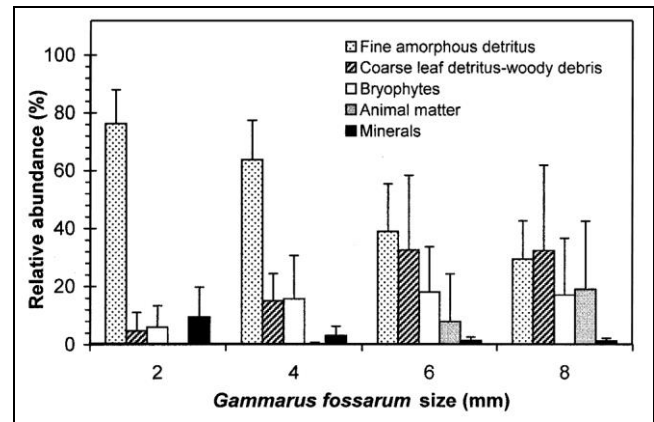


Figure 39. Comparison of mean percentage food types \pm SD. of *Gammarus fossarum* as it relates to size. Modified from Felten *et al.* 2008.

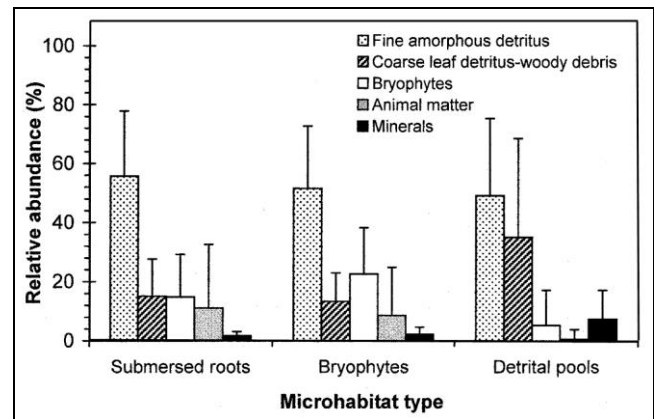


Figure 40. Comparison of mean proportion (\pm SD) of bryophytes vs other food items eaten by *Gammarus fossarum* in three habitat types. Modified from Felten *et al.* 2008.

Gladyshev *et al.* (2000) examined the gut contents of *Gammarus lacustris* (Figure 41) and found that they ingested mostly seston, obtaining omega 3 fatty acids from bottom sediment particles. They also consumed cells of the green alga *Botryococcus*. This alga not only survived the digestive tract, but its photosynthetic activity increased. They considered this activity to contribute to the dispersal of the alga, causing blooms in the littoral zone. Could this also be true of bryophytes they consume?



Figure 41. *Gammarus lacustris*, an amphipod that consumes mostly seston. Photo by Bold Systems Creative Commons.

Food particle size can determine which species are able to survive in a habitat. Graca *et al.* (1994) found that *Gammarus pulex* (Figure 30-Figure 36) occupies different zones in rivers from those of the isopod *Asellus aquaticus* (Figure 42). The researchers found that the selection of substrate by *G. pulex* was based on size, with larger individuals choosing larger-sized substratum particles; juveniles were mostly associated with plants, including mosses. The substrate choices were most likely food choices. For the aquatic amphipods, it is likely that the detritus collected by the mosses serves as a food source. It would be interesting to determine the role of food sources in the choices of terrestrial amphipods for particular bryophytes.



Figure 42. *Asellus aquaticus*, an aquatic isopod shown here on leaf litter. Photo by Malcolm Storey through Discover Life.

Acosta and Prat (2011) partially supported the idea of mosses as food collectors for the amphipod *Hyaella* sp. (Figure 43) in the headwaters of a High Andes river. Those living among layers of travertine had 69.5% fine particulate organic matter (FPOM), but even the bryophyte-dwellers had 56.8% FPOM. Those from leaf litter, on the other hand, had 68% of their gut contents from coarse particulate organic matter, suggesting a high level of flexibility in the diet.



Figure 43. *Hyaella azteca*, a common bryophyte dweller in streams and rivers. Photo by Barbara Albrecht at <<http://www.ipm.ucdavis.edu/WATER/U/hyaella.html>>, with permission.

One hypothesis is that increased density of bryophytes would increase available organic detritus and thereby increase invertebrate abundance. However, Suren and Winterbourn (1992) found that reducing stem density of mosses had little effect on periphyton biomass, but that the detrital biomass was reduced on low-density artificial mosses. In any case, stem density had little effect on invertebrate abundance. Nevertheless, detrital and periphyton availability seemed to be the determining factor for invertebrate density.

Gladyshev *et al.* (2012) examined the gut contents of gammarids as part of a food chain study including *Fontinalis antipyretica* (Figure 44). Following Kalachova *et al.* (2011), they used acetylenic acids, considered as biomarkers for *Fontinalis antipyretica*, to trace the food through the mosses, periphyton, Trichoptera, gammarids, and Siberian grayling (Gladyshev *et al.* 2012). Gladyshev *et al.* (2012) found small amounts of consumption of the mosses among both the Trichoptera (caddisflies) and the gammarid *Eulimnogammarus* (*Philolimnogammarus*) *viridis*. The latter species had the highest concentrations of acetylenic acids in the winter and the lowest in summer (Kalachova *et al.* 2011), suggesting a shift to mosses in winter. It is likely that both the caddisflies and gammarids ate the moss to gain the periphyton and detritus accumulated there. The moss and associated periphyton and detritus are especially important in winter when other food sources are scarce (Gladyshev *et al.* 2012).



Figure 44. *Fontinalis antipyretica* var *gracilis*, home for the amphipod *Eulimnogammarus* (*Philolimnogammarus*) *viridis*. Photo by Des Callaghan, with permission.

But Parker *et al.* (2007) found that even when the moss *Fontinalis novae-angliae* (Figure 52) was cleaned of particulate matter, the amphipods still ate significant quantities of it. Earlier studies by Minckley and Cole (1963) likewise indicated that amphipods ate mosses. On the other hand, Mulholland *et al.* (2000) found that the amphipod *Gammarus minus* (Figure 45) depended on fine benthic (bottom) organic matter, despite the presence of bryophytes.

One feeding possibility in nature that might not be evident in laboratory studies is the role of fungi. Barlocher and Porter (1986) demonstrated that *Gammarus tigrinus* (Figure 46) was able to digest plant polysaccharides and release sugars from maple leaves. They also had the right enzymes to break down glycosidic linkages in small molecules, much as that done in microbial decomposition.

Furthermore, fungal carbohydrases ingested with the food of the *Gammarus* remained active in the gut. The implication seems to be that *Gammarus* could benefit from fungi associated with bryophytes in the field. Similarly, Sarah Lloyd (pers. comm.) has documented that terrestrial amphipods eat slime molds that live on mosses (Figure 47).



Figure 45. *Gammarus minus*, an amphipod that seems to prefer fine benthic organic matter over bryophytes. Photo through Creative Commons.



Figure 46. *Gammarus tigrinus*, an amphipod that can digest fungi from leaves. Photo by Hugh MacIsaac, with permission.



Figure 47. Amphipod, probably *Keratoides*, possibly *K. vulgaris*, eating a slime mold (probably *Diderma* sp.) on moss. Photo by Sarah Lloyd, with permission.

It appears that at least some bryophytes are not suitable food for *Gammarus* (Figure 30-Figure 36). Willoughby and Sutcliffe (1976) conducted feeding experiments on *Gammarus pulex* (Figure 30) from the River Dutton. They found that those provided with only the liverwort *Nardia* sp. (Figure 48) were unable to grow or survive.



Figure 48. *Nardia scalaris*, a leafy liverwort genus in which a European species failed to sustain *Gammarus pulex* as a food source. Photo from Europe by Michael Lüth, with permission.

Habitats

Terrestrial

Terrestrial amphipods are rare, but bryophytes can provide the kind of moist habitat needed for them to survive. Merrifield and Ingham (1998) found amphipods in their Oregon Coast Range, USA, study of the fauna of *Eurhynchium oregonum* (Figure 49). In most months they were not evident, but in the December collection their numbers rose to 1 per gram of moss in 10 5-cm samples. The second "peak" was in April, with 0.6 per gram. Sarah Lloyd (pers. comm.) found what appears to be *Keratoides*, possibly *K. vulgaris*, among mosses in a wet eucalypt forest in northern Tasmania.



Figure 49. *Eurhynchium oregonum*, a moss that is known to house amphipods in North America. Photo by Adolf Ceska, with permission.



Figure 50. Terrestrial amphipod, probably *Keratoides*, possibly *K. vulgaris*, on mosses in wet sclerophyll (eucalypt) forest at Birrallee in Northern Tasmania, Australia. Photo courtesy of Sarah Lloyd.

Friend (1987) described the new species *Orchestiella neambulans* from litter that accumulated between mosses in Tasmania.

The Antarctic seems to be the most likely place to find limnoterrestrial Crustacea among mosses, but the amphipods are poorly represented. Pugh *et al.* (2002) found only one (*Makawe insularis*) in their study, a species with a broad niche of wood, leaf litter, lichens, tussock grass, under stones, penguin nests, and...among mosses.

Aquatic

Rocky streams are often dominated by mosses and liverworts in extensive mats over the rocks. These provide a foothold that protects their inhabitants from being swept away. Macan and Worthington (1951) found that amphipods such as *Gammarus* (Figure 30-Figure 36) were more likely on mosses that were not so thick, whereas thicker mosses were dominated by Chironomidae. They found that fish food organisms increased in number when the streams had rooted plants or mosses. One problem faced by the inhabitants of tracheophytes is that the plants begin die-off in late summer and the amphipods must find a new substrate with sufficient periphyton and detritus to provide food. *Gammarus* is among the slow colonizers (Fontaine & Nigh 1983), so it might benefit from the stable year-round habitat of bryophytes as a source of shelter and detrital and periphytic food.

Elliott (2005) found that *Gammarus pulex* had significant day-night differences in its habitat distribution. These were explained by dry weights of bryophytes, leaf material, organic detritus, distance from bank, water depth, water velocity, and particle size class. The bryophyte weight correlated positively with larger particle sizes and negatively with smaller particle sizes, perhaps explaining some of the choices by *G. pulex* for bryophytes. But this correlation may have been due to the preference of

bryophytes for larger stones. Juvenile densities in the daytime correlated positively with smaller particles and negatively to larger particles, also correlating with the weight of bryophytes. However, at night the densities were unrelated to particle sizes or bryophyte weight.

Parker *et al.* (2007) found that the amphipod *Crangonyx gracilis* (see Figure 51) was a common inhabitant of the brook moss *Fontinalis novae-angliae* (Figure 52), where it used the moss shelter as a food source. Badcock (1949) found that *Gammarus* (Figure 30-Figure 36) species were more numerous in sheltered sites such as mosses. Minckley (1963) found *Gammarus* among the moss *Fissidens* sp. (Figure 53) in a Kentucky, USA, stream. It not only lived there, but ate the moss that served as its home (Minckley & Cole 1963).



Figure 51. *Crangonyx pseudogracilis*, relative of *C. gracilis* that lives among *Fontinalis novae-angliae* and also eats it. Photo from Discover Life - Creative Commons.



Figure 52. *Fontinalis novae-angliae*, shelter for *Crangonyx gracilis*. Photo by Janice Glime.

In an unlikely place, the depths of Yellowstone Lake, associated with active geothermal vents, *Fontinalis* abounds (Lovalvo *et al.* 2010). Associated with this unusual inhabitant are, among other invertebrates, the amphipods *Hyaella* (Figure 43) and *Gammarus* (Figure 30-Figure 36, Figure 41, Figure 45).



Figure 53. *Fissidens fontanus*, both a home and food for some species of *Gammarus*. Photo by Michael Lüth, with permission.

Summary

Both Ostracoda and Amphipoda are primarily marine, with fewer species in freshwater and much fewer in terrestrial habitats. Nevertheless, ostracods are known from roof mosses, and the genus *Mesocypris* is a common terrestrial moss dweller, especially in the Southern Hemisphere.

Their adaptations to living among bryophytes (and other terrestrial locations) include swimming instead of crawling, small size, loss of eyes in some, reduced setae (used for swimming), excretion of nitrogenous waste from maxillae, antennae, or possibly through the carapace (perhaps as gaseous ammonia), drought-resistant eggs, and parthenogenesis. Food often consists of detritus, algae, and bacteria, but some amphipods eat bryophytes as well.

Bogs offer habitats where ostracods can migrate vertically or horizontally to find suitable conditions as the temperature and moisture change. Some are even true **tyrphobionts**. But there appear to be few, if any, records for amphipods. Some ostracods live among the pitcher plants in the bogs.

Few ostracods are known from among mosses in streams, but several amphipods can be found there. However springs seem to be suitable habitats for several species in both groups.

The microcrustacea may have advanced onto land through wet mosses of springs and stream banks. They are represented by few families, the **Cypridae** among the ostracods and the **Talitridae** among the amphipods.

Terrestrial amphipods are not well known, and thus far their presence among *Sphagnum* does not seem to be documented.

Acknowledgments

Sarah Lloyd and her colleagues have been of invaluable help in this chapter by providing me with

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CHAPTER 10-3

ARTHROPODS: CRUSTACEA – ISOPODA, MYSIDA, AND DECAPODA

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CHAPTER 10-3

ARTHROPODS: CRUSTACEA – ISOPODA, MYSIDA, AND DECAPODA

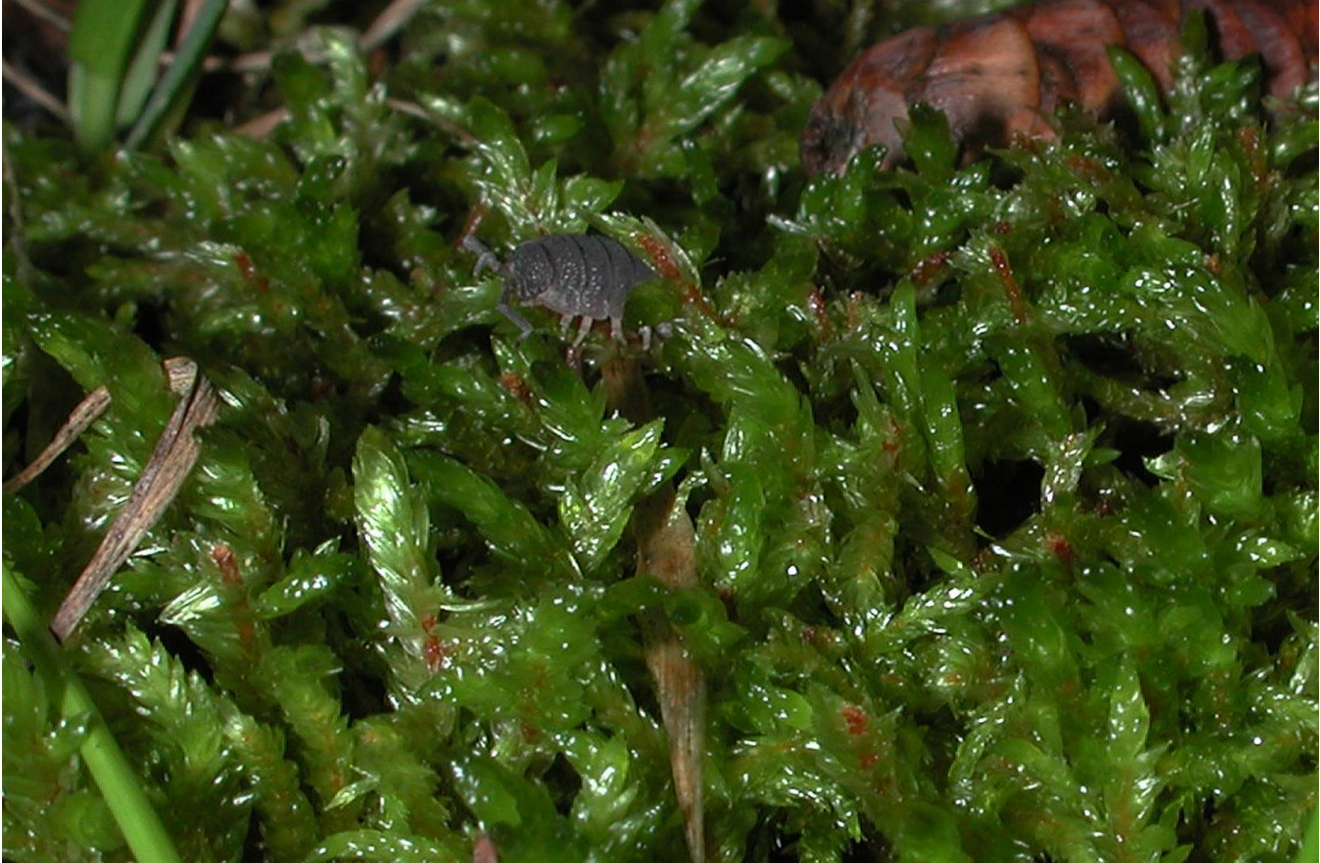


Figure 1. *Porcellio scaber* eating *Pleurozium schreberi* at midnight in Houghton, Michigan, USA. Photo by John Hribljan, with permission.

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 **multi**pedes, 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), **Opiliona** (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).

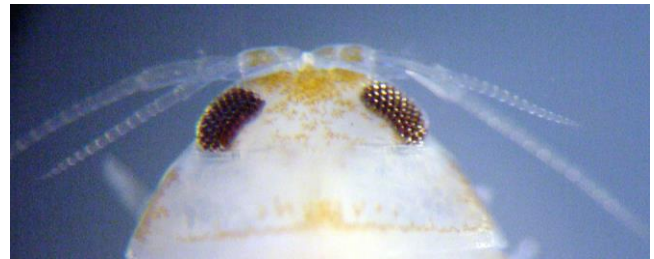


Figure 5. Isopod head showing compound eyes. Note the multiple small sections in each eye. Photo from NOAA, through public domain.

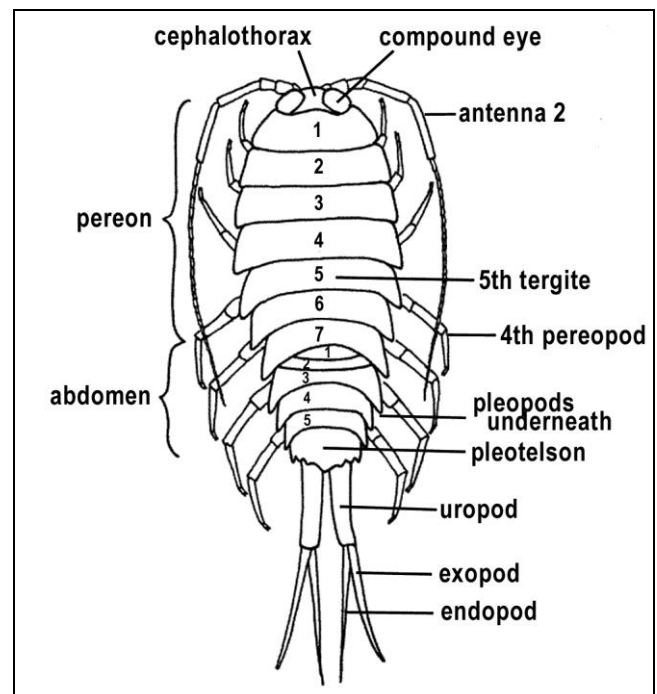


Figure 6. *Ligia*, a genus that sometimes inhabits bryophytes, showing typical isopod external anatomy. Redrawn from Richard Fox.

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 **peropods** (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 Giuseppe 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 hoffmannseggii* (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 hoffmannseggii*, 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 *Rhytidadelphus 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 pH 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 pH in the hindgut lumen was nearly constant. Zimmer and Brune (2005) suggested that the pH 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.

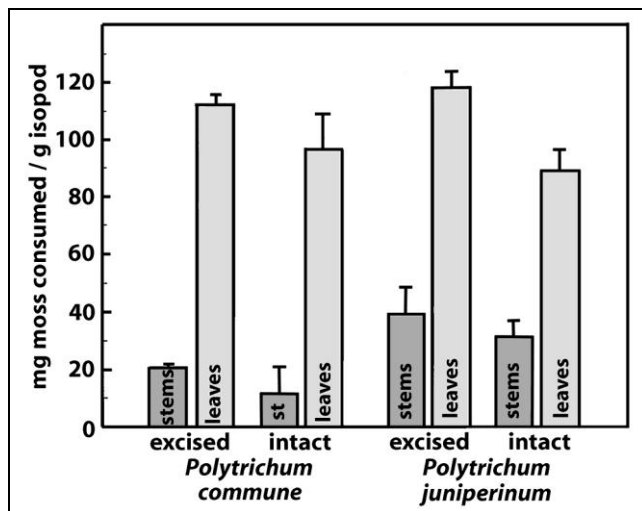


Figure 35. Comparison of mean isopod (*Porcellio*) consumption \pm 95% CI of excised leaves and stems vs intact leaves and stems in two species of moss. Data based on unpublished laboratory data of Weston 1995; Liao & Glime unpublished data; n = 3.

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).

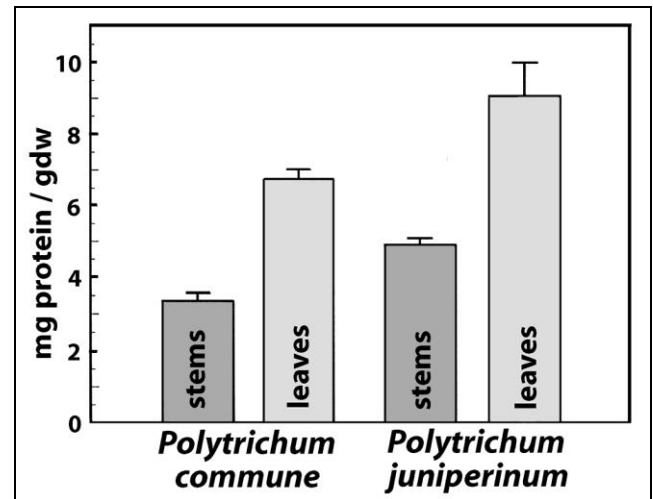


Figure 36. Comparison of mean protein \pm 95% CI in stems and leaves of two *Polytrichum* species. Based on Weston 1995; Liao & Glime unpublished data; Bradford's (1976) test, n = 3.

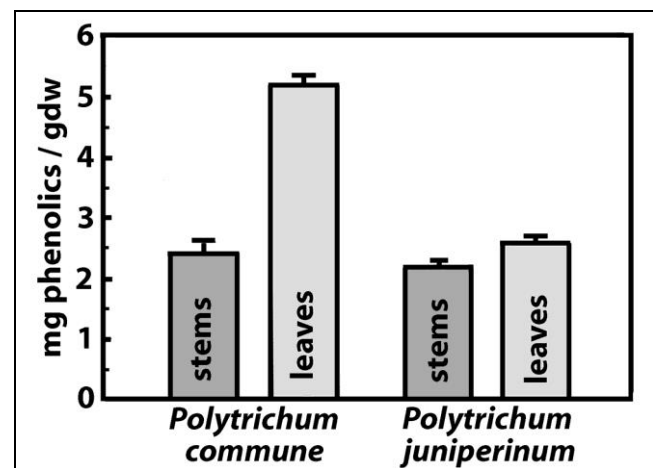


Figure 37. Comparison of mean phenolic content \pm 95% CI in stems and leaves of two *Polytrichum* species. Based on Weston 1995; Liao & Glime unpublished data; Folin-Denis test (Swain & Hillis 1959) and Prussian Blue test for tannin; n = 3.



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

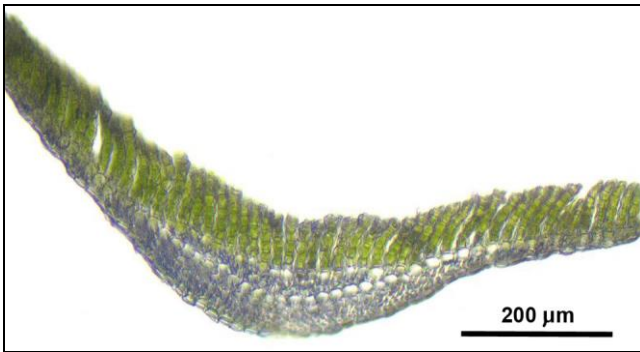


Figure 39. *Polytrichum commune* leaf cross section showing absence of rolled over leaf margin, thus giving exposure to all the lamellae. Photo by Kristian Peters, through Creative Commons.

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), Adebisi *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.

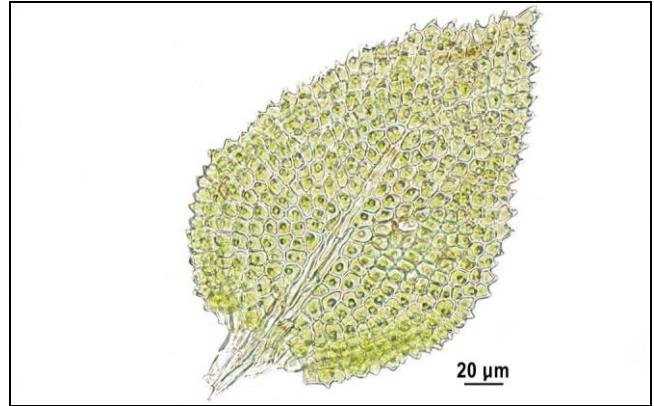


Figure 41. *Thuidium delicatulum* branch leaf showing small cells and papillae (note bumps on cells). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



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.

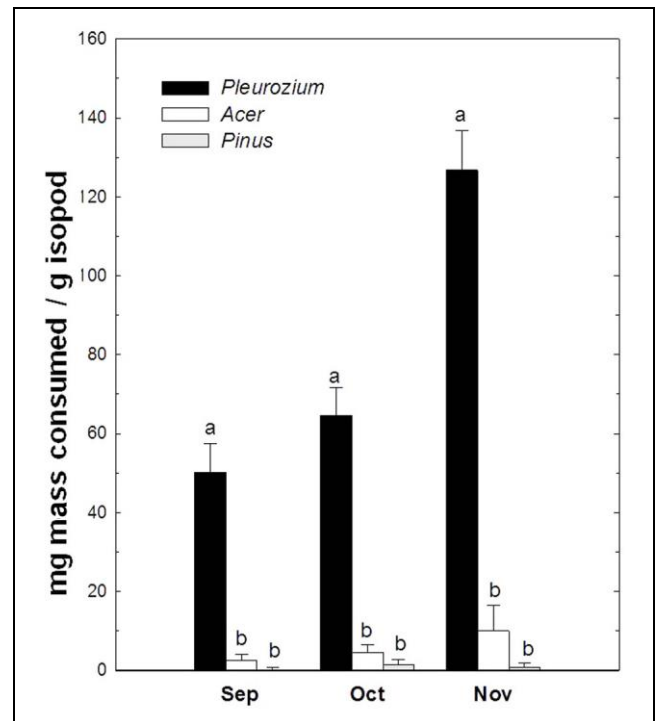


Figure 47. Comparison of mean air-dried mass ($\pm 95\%$ CI) consumed by isopods in 24 hours when given the choice of the moss *Pleurozium schreberi* and the tree leaves of *Acer saccharum* and *Pinus strobus*. The same letters signify means that are not significantly different from each other ($\alpha = 0.05$ 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.

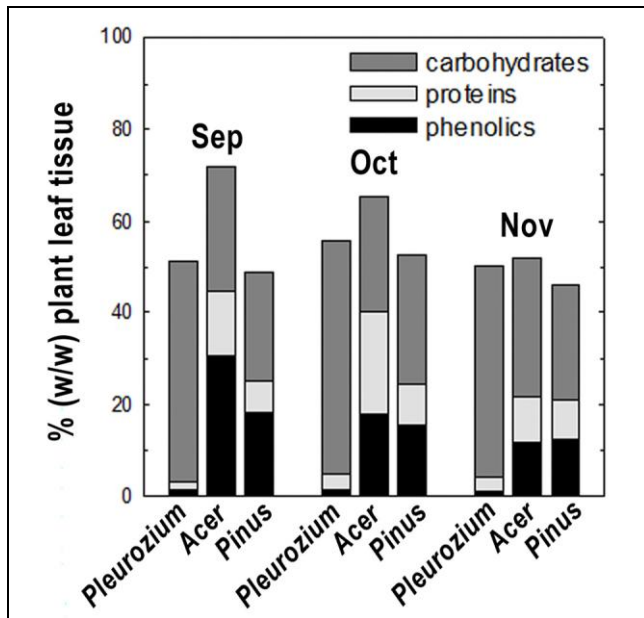


Figure 48. Comparison of percent of carbohydrates, proteins, and phenolics in freeze-dried leaves of the moss *Pleurozium schreberi*, sugar maple tree *Acer saccharum*, and white pine *Pinus strobus*. Samples were taken once each month during to compare stages of decay in the tree leaves. Values are 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.

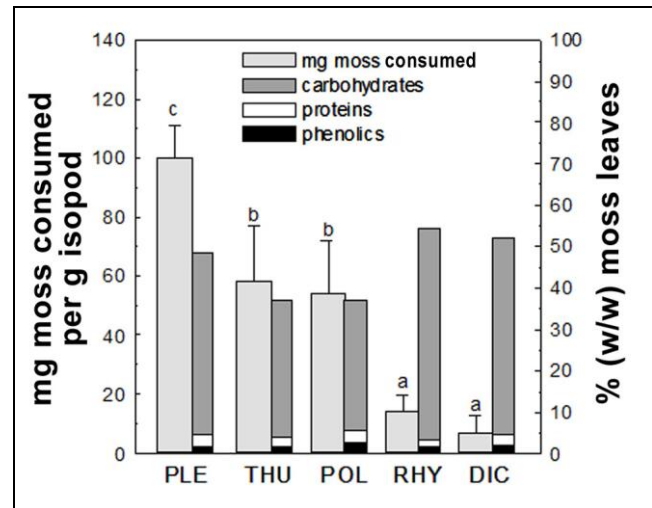


Figure 50. Comparison of moss consumed (mean \pm 95% CI) with mean percent by weight of phenolics, proteins, and carbohydrates in leaves of the mosses *Pleurozium schreberi* (PLE), *Thuidium delicatulum* (THU), *Polytrichum juniperinum* (POL), *Rhytidiadelphus triquetrus* (RHY), and *Dicranum polysetum*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

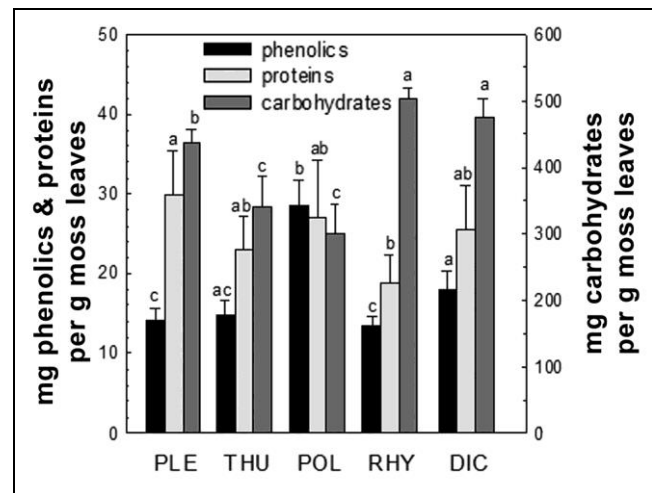


Figure 51. Comparison of means \pm 95% CI of phenolics, proteins, and carbohydrates in leaves of the mosses (arranged from most to least eaten) *Pleurozium schreberi* (PLE), *Thuidium delicatulum* (THU), *Polytrichum juniperinum* (POL), *Rhytidiadelphus triquetrus* (RHY), and *Dicranum polysetum* (DIC).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



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.

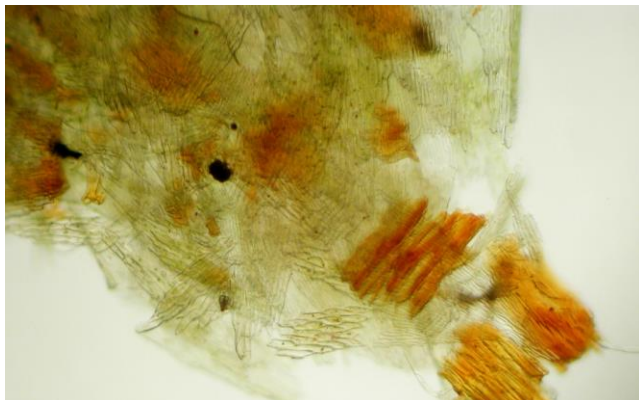


Figure 54. Moss leaf fragments extracted from feces of *Porcellio scaber* fed only *Rhytidiadelphus triquetrus*. Photo by John Hribljan, with permission.

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 crane fly *Tipula montana*, a moss-food-avoider, cannot (Smith *et al.* 2001).

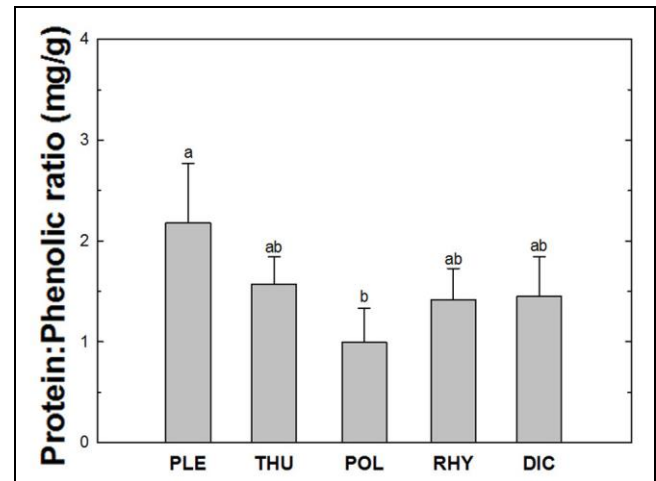


Figure 55. The mean protein:phenolic ratio of leaves (\pm 95% CI), arranged in order from most to least consumption, of freeze-dried mosses *Pleurozium schreberi* (PLE), *Thuidium delicatulum* (THU), *Polytrichum juniperinum* (POL), *Rhytidiadelphus triquetrus* (RHY), and *Dicranum polysetum* (DIC).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

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).

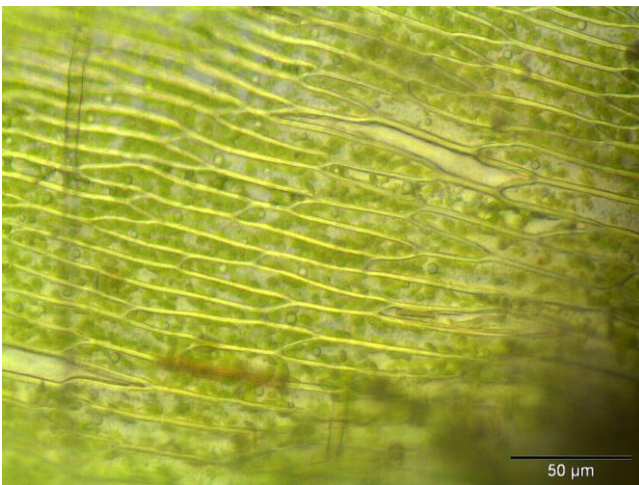


Figure 58. Leaf cell structure of *Pleurozium schreberi* showing thin cell wall and high ratio of cell contents to cell wall. This species was most consumed among the five moss species in the study by Hribljan and Glime (in prep.). Photo from Wikimedia Commons.

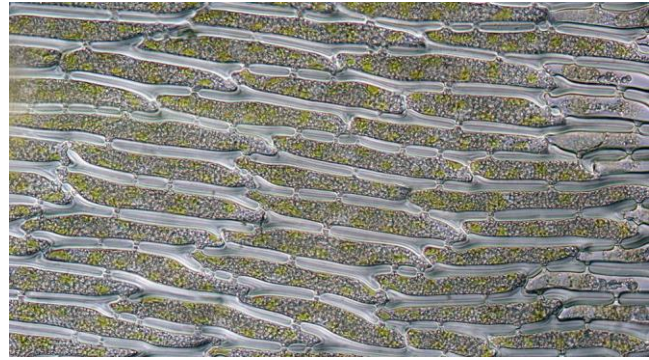


Figure 59. Leaf cell structure of *Dicranum polysetum* showing thick cell wall and low ratio of cell contents to cell wall. This species was least consumed among the five moss species in the study by Hribljan and Glime (in prep.). Photo by Walter Obermayer, with permission.

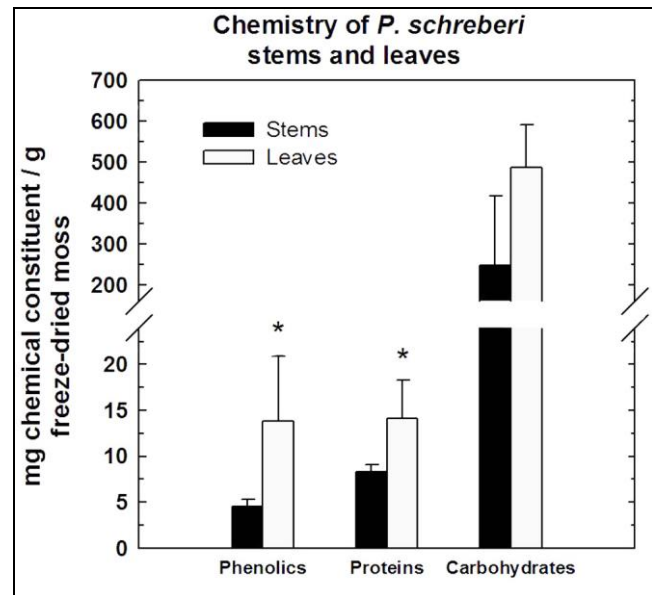


Figure 60. Comparison of mean phenolic, protein, and carbohydrate content (\pm 95% CI) of *Pleurozium schreberi* between freeze-dried leaves and stems (paired t-test, an asterisk indicates a significant difference between the two bars, $\alpha = 0.05$, $n = 3$).

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; Adebisi *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.

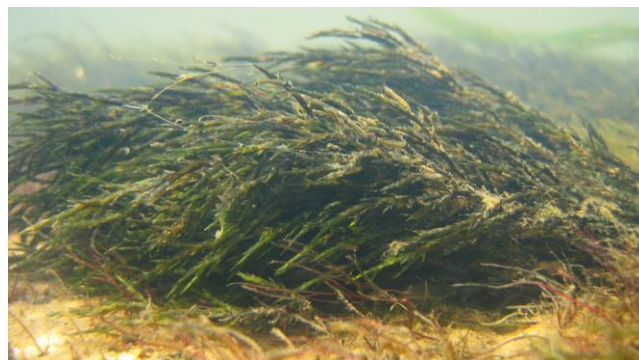


Figure 62. *Fontinalis novae-angliae*, a habitat and a food source for species of *Asellus*. Photo by John Parker, with permission.

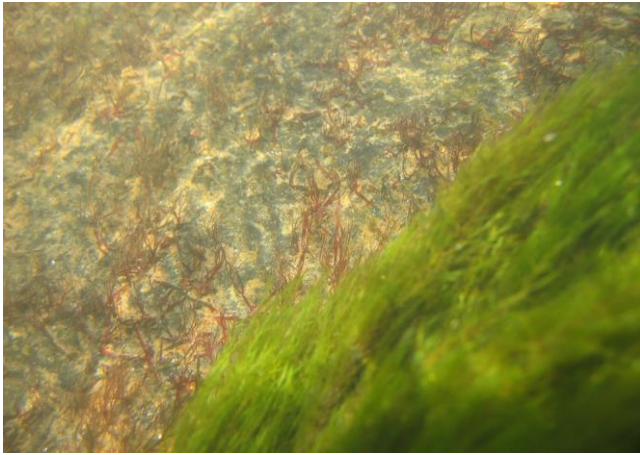


Figure 63. *Podostemum ceratophyllum* (riverweed) in upper left, appearing as fine red threads here. This plant has been heavily grazed, whereas the *Fontinalis novae-angliae* on the right has not. Photo by John Parker, with permission.



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.

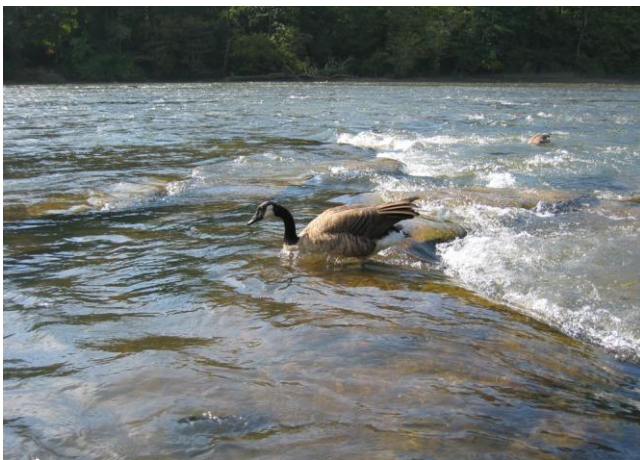


Figure 65. *Branta canadensis* (Canada Goose), a large bird that avoids mosses, thus permitting the mosses to protect would-be food items that hide there. This one is feeding on riverweed (*Podostemum ceratophyllum*). Photo by John Parker, with permission.

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.

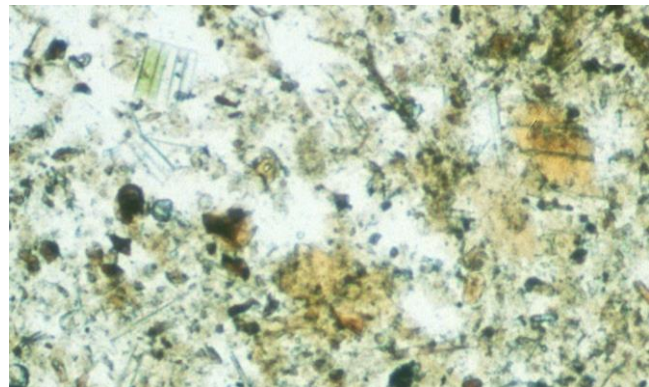


Figure 68. *Fontinalis antipyretica* and diatoms in gut of *Asellus cf. militaris*. Photo by Jacob LaCroix, with permission.

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.

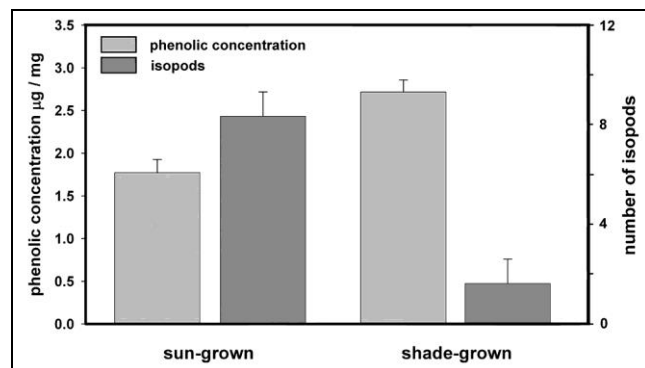


Figure 69. Comparison of moss *Fontinalis antipyretica* mean phenolic content (\pm 95% CI) and number of moss-dwelling isopods *Asellus cf. militaris* (\pm 95% CI) choosing to inhabit it. Most of the isopods in the lab chose to go to the sun-grown *Fontinalis antipyretica* that had a lower phenolic content 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 Calmejdane, 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. *Plagiommium 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. *Styloniscus nicholli* 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 pH 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, Vandell (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. *Cratoneuroopsis relaxa*, genus of mosses that occur in springbrooks in the Southern Alps of New Zealand and home to *Styloniscus otakensis*. Photo by Tom Thekathyl, 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 pH 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 opossum 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 (Weihrach *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 *Paranephrops* 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 C₁₈ 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.

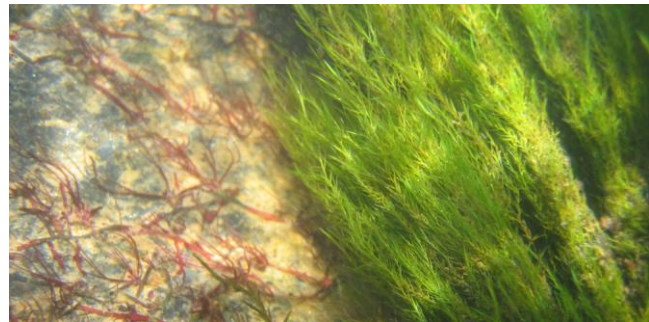


Figure 96. *Podostemum ceratophyllum* (left) and *Fontinalis novae-angliae* (right) showing effects of grazing by the crayfish *Procambarus spiculifer* on the *P. ceratophyllum*. The moss remains untouched. Photo by John Parker, with permission.

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 descendants 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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