

CHAPTER 4-1

INVERTEBRATES: INTRODUCTION

TABLE OF CONTENTS

The Invertebrate Fauna.....	4-1-2
Sampling	4-1-9
Preservation of Specimens	4-1-11
Community Patterns.....	4-1-12
Terrestrial/Limnoterrestrial	4-1-12
Lobules as Habitat.....	4-1-14
Aquatic	4-1-14
Altitudinal Gradients.....	4-1-16
Food Webs	4-1-16
Pollution	4-1-18
Harvesting Dangers	4-1-18
Summary	4-1-19
Acknowledgments.....	4-1-19
Literature Cited	4-1-19

CHAPTER 4-1

INVERTEBRATES: INTRODUCTION



Figure 1. *Marchantia polymorpha* that has been nibbled by an unknown organism. Note holes in the thallus. Photo by C. R. Stevenson, with permission.

The Invertebrate Fauna

Einstein is credited with saying that the most incomprehensible fact about nature is that it is comprehensible (Miller 1992). The invertebrate community associated with bryophytes, especially in terrestrial habitats, needs still to be comprehended.

Dendy (1895) coined the term **cryptozoic fauna** to describe "the assemblage of small terrestrial animals found dwelling in darkness beneath stones, rotten logs, the bark of trees, and in other similar situations." Although not specifically mentioned, bryophytes surely belong among the "other similar situations," as evidenced by the browsed patches on the liverwort in Figure 1. A comparable term for such bryophyte dwellers in the aquatic realm is **meiofauna**, defined as "**benthic** (living on the bottom of a body of water) animals that can fit a mesh size of 1 mm and be retained on a mesh size of 42 μm " (Brave New Biosphere 1999). Although living among bryophytes directly contradicts being on the bottom, the bryophytes do occupy the bottom, and one might think of the habitat they create as simply an extension of that bottom.

For many of the invertebrates, the bryophytes represent a moist island among the drier sites. Invertebrates living there because they are able to survive in interstitial collections of water droplets are considered **limnoterrestrial**, and this **limnoterrestrial habitat** houses many organisms better known in aquatic habitats, such as copepods, gastrotrichs, rotifers, and tardigrades (Thorp & Covich 2010).

The invertebrate fauna are likely to play an important role in nutrient cycling within the bryophyte community, thus facilitating return of detrital matter to ecosystem level nutrient cycling. Merrifield and Ingham (1998) suggested that the diversity of feeding strategies found in moss invertebrate communities provides evidence of within-bryophyte-community nutrient cycling. Studies by Davis (1981) seem to support this suggestion. He found that the moss turf community and the moss carpet community in the maritime Antarctic on Signy Island showed similar levels of productivity, trophic structure, and efficiencies of organic matter transfer, but they differed in **Collembola**

(springtails) and **Acari** (mites) standing crops, turnover of mosses, and accumulation of dead organic matter. Both communities [turf of *Polytrichum strictum* (= *P. alpestre*; Figure 2-Figure 3) and *Chorisodontium aciphyllum* (Figure 4-Figure 5) and carpet of *Calliergon sarmentosum* (Figure 6), *Calliergidium austro-stramineum* (Figure 7), *Sanionia uncinata* (Figure 8), and *Cephaloziella varians* – a liverwort (Figure 9)] had fauna of **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola**. Despite the diverse fauna, Davis found no evidence that the mosses would have been eaten. However, he based this on known feeding groups of the organisms and not on direct evidence. Nevertheless, it is likely that detrital matter and predation were primary food pathways, permitting nutrient cycling.



Figure 2. *Polytrichum strictum* cushions in Alaska, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo courtesy of Andres Baron Lopez.



Figure 3. *Polytrichum strictum*, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by Jan-Peter Frahm, with permission.



Figure 4. *Chorisodontium aciphyllum* in Antarctica, home of **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola**. Photo from Polar Institute, through Creative Commons.



Figure 5. *Chorisodontium aciphyllum*, home of **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola**. Photo by Jan-Peter Frahm, with permission.



Figure 6. *Calliergon sarmentosum*, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by David T. Holyoak, with permission.



Figure 7. *Calliergidium austro-stramineum*, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by Bill Malcolm, with permission.



Figure 8. *Sanionia uncinata*, home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by Michael Lüth, with permission.



Figure 9. *Cephaloziella varians* (among mosses), home for **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola** in the Antarctic. Photo by Kristian Peters, with permission.

Nelson and Hauser (2012) examined what would seem to be a very different habitat from that of the Antarctic samples of Davis (1981) – epiphytic mosses and liverworts of the Pacific Northwest, USA. Despite that seeming difference in climate, the same six groups were dominant: Acari, Tardigrada, Collembola, Nematoda, and Rotifera, in that order. Protozoa were also abundant, but they did not quantify those. They found no differences in major groups between mosses and liverworts, but suggested that there may have been differences between species.

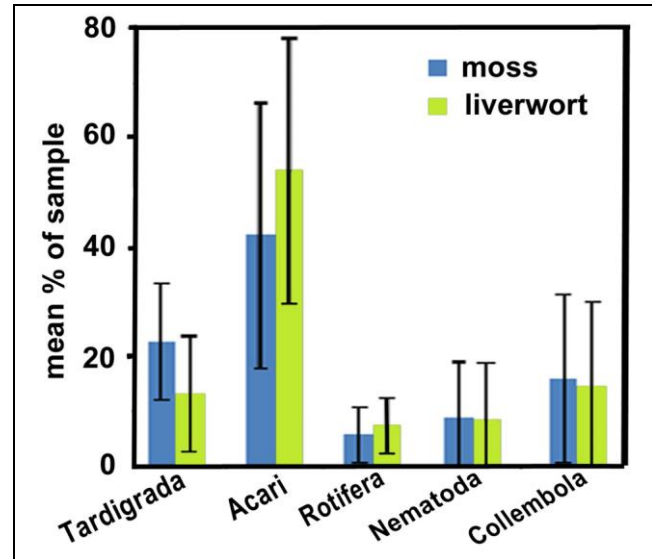


Figure 10. Mean percent and standard deviation of organisms for each of the five dominant taxa groups in epiphytic mosses and liverworts at Tryon Creek State Natural Area, 1, 7, and 17 October 2011, calculated for all samples together. Redrawn from Neslon & Hauser 2012.

In the Czech Republic, Božanić *et al.* (2013) attempted to elucidate the factors that determined which invertebrates inhabited bryophyte clumps. They examined the fauna on 15 bryophyte species (61 total samples) and identified 45 invertebrate species in 13 higher taxonomic groups. They found that the two most important factors determining the invertebrate fauna were the size of the moss clump (Figure 12) and the height above ground (Figure 13). The moss genus *Brachythecium* housed the most invertebrate taxa, with the species *Brachythecium curtum* (Figure 11) on rotten trees housing the most.



Figure 11. *Brachythecium curtum* on rotten wood, home for the most invertebrate taxa in a Czech Republic study. Photo by Janice Glime.

Millipedes preferred bryophyte habitats higher above ground, with *Nemasoma varicorne* (Figure 14) being the most abundant (Božanić *et al.* 2013). Mites (**Acarina**), pseudoscorpions (**Pseudoscorpiones**), and ants (**Formicidae**) were only in the lower levels. Interestingly, tree diameter also played a role in locations, with the isopods *Trichoniscus pusillus* (Figure 15) and *Porcellium collicola* (Figure 16) occupying mosses on smaller trees, whereas the isopod *Trachelipus rathkii* (Figure 17) and centipedes *Lithobius mutabilis* and juveniles of other *Lithobius* species preferred larger trees.

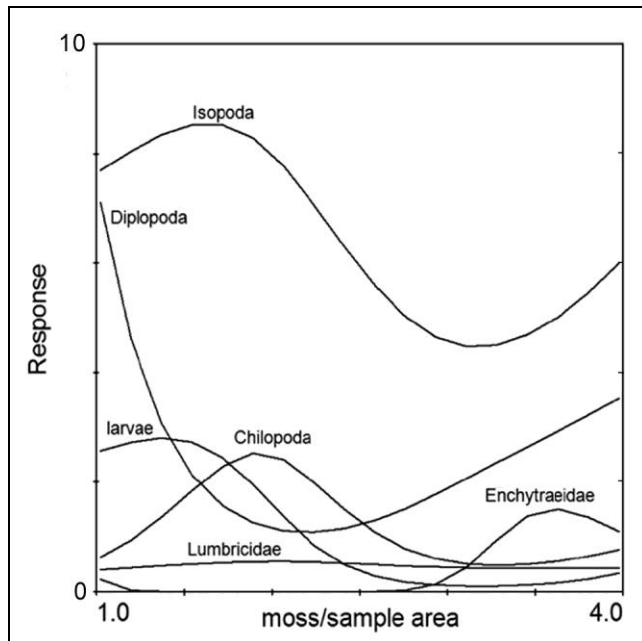


Figure 12. Relative numbers of invertebrate groups on bryophytes vs moss sample area. Redrawn from Božanić *et al.* 2013.

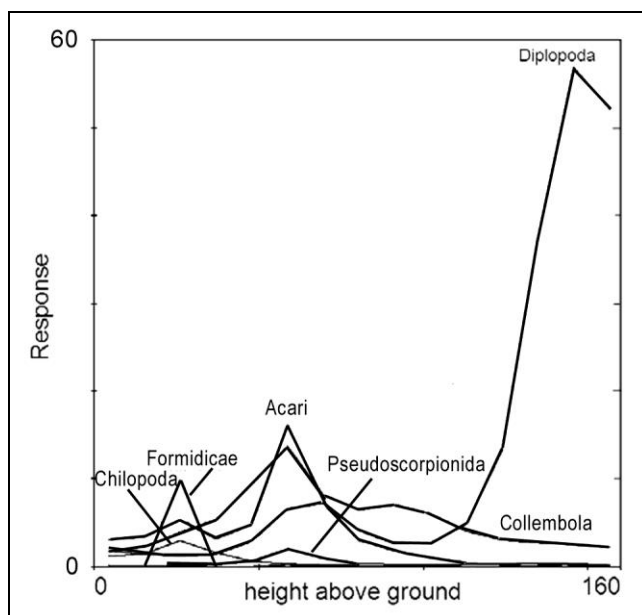


Figure 13. Relative numbers of invertebrate groups on bryophytes vs height above ground. Redrawn from Božanić *et al.* 2013.



Figure 14. *Nemasoma varicorne* female, an abundant above ground millipede that can be found among bryophytes. Photo by Walter Pfliegler, with permission.



Figure 15. *Trichoniscus pusillus*, a species among mosses on smaller trees. Photo by Andy Murray, through Creative Commons.



Figure 16. *Porcellium collicola*, a species among mosses on smaller trees. Photo by Dragisa Savic, with permission.



Figure 17. *Trachelipus rathkii*, a species among mosses on larger trees. Photo by Joerg Spelda, SNSB, Zoologische Staatssammlung Muenchen, through Creative commons.



Figure 18. *Lithobius mutabilis*, a species among mosses on larger trees. Photo by Joerg Spelda, SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Dražina *et al.* (2011) examined the meiofauna of bryophytes in Europe. These included **Turbellaria** (flatworms), **Rotifera** (rotifers), **Nematoda** (nematodes), **Gastrotricha**, **Oligochaeta** (segmented worms), **Tardigrada** (tardigrades), and **Crustacea**, as well as small, immature insects. They found more than 100 taxa, with rotifers dominating (52 taxa) and nematodes second (27 taxa). In fast water, rotifers averaged an abundance of 219 individuals cm^{-3} . Velocity accounted for much of the variation in locations, with rotifers being most abundant in high velocity and gastrotrichs, tardigrades, and microturbellarians having a negative relationship to flow velocity.

Perić *et al.* (2014) studied the invertebrate drift and found that the meiofauna formed a "considerable" portion of it among moss-rich areas in a karst stream. They found 60 invertebrate taxa in the drift. Only six taxa, all in the annelid and arthropod meiofauna, comprised 35% of the total drift density. Most of the Macroinvertebrates were immature insects. The **Cladocera** (*Alona* spp.; Figure 19) comprised 26.7%, *Riolus* spp. (Coleoptera: Elmidae; Figure 20) comprised 13.2%, *Simulium* spp. (Diptera: Simuliidae; Figure 21) 12.2%, **Enchytraeidae** (Annelida; Figure 22) 10.4%, **Hydrachnidia** (mites; Figure 23) 6.3%, **Orthocladinae** (Diptera: Chironomidae; Figure 24) 3.9%, and **Naididae** (Annelida; Figure 25) 3.6%.



Figure 19. *Alona*, a bryophyte dweller that is most common among them in the drift. Photo by Yuuji Tsukkii, with permission.



Figure 20. *Riolus subviolaceus* adult, a genus that is common in mosses and common in stream drift. Photo from Naturalis Biodiversity Center, through Creative Commons.



Figure 21. *Simulium* larvae, bryophyte dwellers that are common in the drift. Photo from USDA, through Public Domain.



Figure 22. **Enchytraeidae**, a family with bryophyte dwellers that are common in the drift. Photo by Aina Maerk Aspaas, NTNU University Museum, Department of Natural History, through Creative Commons.



Figure 25. **Naididae**, a family with bryophyte dwellers that are common in the drift. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

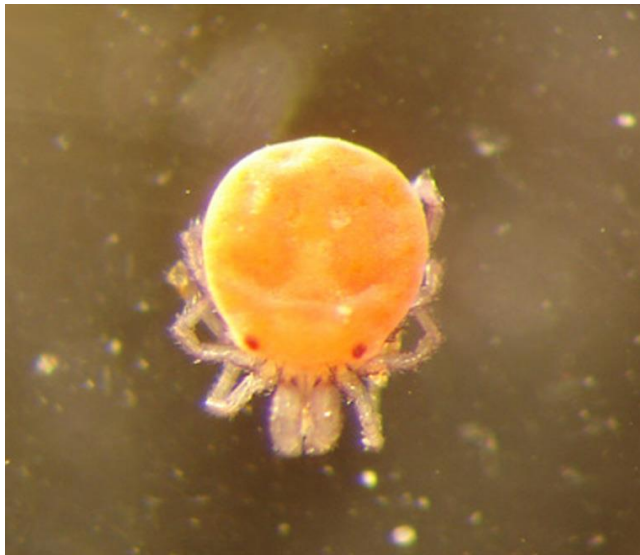


Figure 23. **Hydrachnidia**, a mite group with bryophyte dwellers that are common in the drift. Photo by Mnolf, through Creative Commons.



Figure 24. *Synorthocladius* larva, a member of **Orthocladiinae**; members of this subfamily are common among stream mosses and stream drift. Photo from Stroud Water Research Center, through Creative Commons.

Drozd *et al.* (2009) conducted studies in bryophyte fauna in the forests of the submountain and mountain areas of the Czech Republic. They concluded that moisture, bryophyte presence, and surprisingly, bryophyte species were the important characteristics determining total abundance. Their study area bryophytes included the mosses *Polytrichum commune* (Figure 26), *Polytrichastrum formosum* (Figure 27), *Sphagnum teres* (Figure 28), *Sphagnum girgensohnii* (Figure 29), *Sphagnum fallax* (Figure 30), *Pleurozium schreberi* (Figure 31-Figure 32), *Eurhynchium angustirete* (Figure 33), *Oligotrichum hercynicum* (Figure 34), and the leafy liverwort *Bazzania trilobata* (Figure 35-Figure 36).



Figure 26. *Polytrichum commune* habitat, a species of the submountain and mountain areas of the Czech Republic. Photo by Sten Porse, through Creative Commons.



Figure 27. *Polytrichastrum formosum*, a species of the submountain and mountain areas of the Czech Republic. Photo by David T. Holyoak, with permission.



Figure 30. *Sphagnum fallax*, a species of the submountain and mountain areas of the Czech Republic. Photo from <www.aphotofauna.com>, with permission.



Figure 28. *Sphagnum teres*, a species of the submountain and mountain areas of the Czech Republic. Photo by J. C. Schou, with permission.



Figure 31. *Pleurozium schreberi*, a species of the submountain and mountain areas of the Czech Republic. Photo by Bob Klips, with permission.



Figure 29. *Sphagnum girgensohnii*, a species of the submountain and mountain areas of the Czech Republic. Photo by Martin Hutten, with permission.



Figure 32. *Pleurozium schreberi*, a species of the submountain and mountain areas of the Czech Republic. Photo by Michael Lüth, with permission.



Figure 33. *Eurhynchium angustirete*, a species of the submountain and mountain areas of the Czech Republic. Photo by Hermann Schachner, through Creative Commons.



Figure 36. *Bazzania trilobata*, a species of the submountain and mountain areas of the Czech Republic. Photo by Barry Stewart, with permission.



Figure 34. *Oligotrichum hercynicum*, a species of the submountain and mountain areas of the Czech Republic. Photo by David T. Holyoak, with permission.



Figure 35. *Bazzania trilobata*, a species of the submountain and mountain areas of the Czech Republic. Photo by Michael Lüth, with permission.

Sampling

Drozd *et al.* (2009) lamented the paucity of comprehensive studies, citing many studies that included only one taxonomic group. They studied the bryophyte fauna using 66 traps in three mountain ranges in the Czech Republic. These traps collected more than 55,000 individuals in 5 sites with a mean of 850 individuals per trap. Litter samples had higher arthropod abundance than did moss cushions. They suggested this was probably influenced by the behavior of the detritivorous arthropods that do not have to move about in search of food. They also suggested that the arthropods might use the bryophytes only as a temporary shelter against predators and desiccation.

Quantitative field sampling of bryophytes is a challenge, and what works for one species may not work for another. Hynes (1961) collected mosses by hand and stuffed them into a 180 cc jar until it reached capacity, a sample of ca 300 cm². But this may not work well for some large growths of *Fontinalis* spp and produces a large sample to be sorted. Furthermore, adding material from other locations in the clump or different clumps diminishes the ability to detect variability and prevents examining subtle effects of stream location. Pulling the moss from the water generally loses few animals because they are adapted to clinging within the moss mat, but pulling the moss apart to make a smaller sample to fit into 180 cc will dislodge even some of the best adapted. Cutting the moss into smaller segments would be less disruptive, but if no bases are samples, some organisms with preferences for bases may be missed. And increasing the sample size of all collections to one suitable for large clumps of *Fontinalis* (Figure 37) would create a prohibitive sorting size. I found that collecting a handful, preferably to fit into a baby food jar, worked well (Glime1994). The samples were quantified on the basis of moss dry weight after sorting by hand. Frost (1942) used 200 g wet weight for her moss sample size. Since many of the invertebrates disintegrate quickly, 90-95% ethanol should be added immediately. Lower concentrations become too dilute. This method worked well for insects, but may not be suitable for all the non-chitonous invertebrates. These methods will be discussed with the various groups.



Figure 37. *Fontinalis antipyretica*, a large aquatic moss that is difficult to sort through. Photo by Bernd Haynold, through Creative Commons.

Hynes (1961) solved the sorting problem by floating the organisms with a saturated solution of calcium chloride. Even with repeated stirring, those organisms with spines and clinging legs may remain in the mosses, as will those nestled at the bases of leaves that curl around them, creating a bias in the sampling.

Determining the faunal composition and community structure of these microhabitats is not an easy task. The most obvious method of sampling invertebrates is sorting them from the bryophytes under the dissecting microscope. But this method is tedious, very time-consuming, and often misses the smaller organisms (personal experience!). The method of wringing and squeezing is much less tedious and faster, a method used by Morgan (1977), but certainly many get left behind, and attached organisms are likely to be preferentially left behind, not to mention damage to larger organisms. To help in this time-consuming task, Paul Davison (pers. comm. 21 June 2006) modified the **Baermann funnel** (Figure 38) for extracting turbellarians (as well as nematodes, copepods, and tardigrades) from bryophytes. A piece of cheese cloth, muslin, or tissue paper is placed in a funnel to hold a sample (Tylka Nematology Lab 2005). This is usually supported by a piece of screening (Figure 38). Then water is run through the sample with rubber tubing clamped at the end of the funnel. After the sample sits overnight or longer, the water is released from the funnel and collected. The first few drops will have a concentration of nematodes, which are heavier than water.

Another method is use of the **Berlese funnel**, which does not have water, using a light and/or temperature gradient that separates mobile organisms such as **arthropods** and **annelids**, but that method leaves the non-mobile ones behind, and doesn't work for nematodes (ED-STEPP). If it is too hot, organisms die before they can drop.

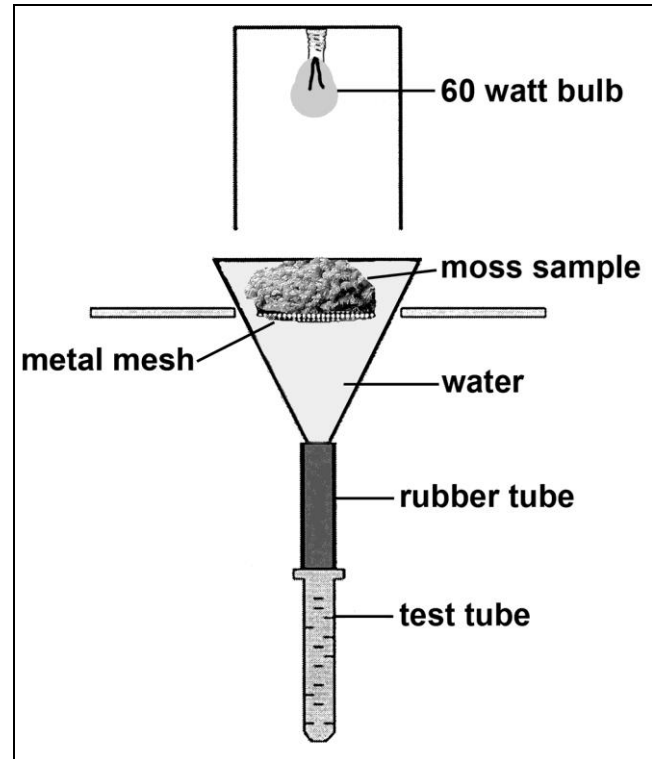


Figure 38. Baermann funnel using moss sample. Water can be replaced with air for non-aquatic organisms, thus making it similar to the Berlese funnel. Modified from Briones 2006.

Nelson and Hauser (2012) discovered that the Berlese funnel and soaking in water gave very different results. For the water extraction, they placed the bryophytes in 200 mL water and allowed to settle for at least two hours, following the protocol for tardigrades described by Thorpe and Covich (2010). The sample was taken by sucking up sediment with a dropper and placing two drops on a depression slide. The Berlese funnel method has a strong bias toward arthropods, in this case mites (Acari), whereas the water method found at least 6 types of tardigrades and many algae and protozoa. They found "almost no taxa overlap" between the two extraction methods!

Kreutz and Foissner (2006) likewise used liquid extraction. They placed mud on a slide, but for bryophytes it is necessary to wash the bryophytes into water in something like a Petri plate. Detritus and unattached organisms will be dislodged if the bryophytes are stirred into the water. The precipitated detritus can be placed on a slide and separated using the slide-on-slide method described in Chapter 2-6, Protozoa Ecology.

Jennings (1979) used the Baerman funnel to extract invertebrates from mosses on Signy Island in the Antarctic. Fairchild *et al.* (1987) have taken advantage of the behavior of these invertebrates to develop an extraction method. By creating a vertical temperature and oxygen gradient in samples of *Sphagnum* (Figure 28-Figure 30), they were able to obtain an 85% efficiency. Merrifield and Ingham (1998) compared several methods of extracting invertebrates. In a study of *Eurhynchium oregonum* (Figure 39) in the Oregon Coast Range, USA, Merrifield and Ingham first verified extraction efficiency for **nematodes** and other invertebrates using the Baermann funnel. First, invertebrates were collected from the funnel

apparatus, then more were collected from the mosses on subsequent days, and finally more were collected by squeezing and agitation of the moss. More than 90% of cumulative final counts of the nematodes *Monhystera* spp. (Figure 40) and *Prionchulus muscorum* (Figure 41) were extracted by the Baermann funnel technique by day 4 of extraction. Tardigrade extraction was even more efficient, reaching 95% by day 4. Rotifers, however, were less efficiently extracted, with only 42% by day 4 and 55% by day 7.



Figure 39. *Eurhynchium oreganum*, home for nematodes. Photo by Matt Goff, with permission.

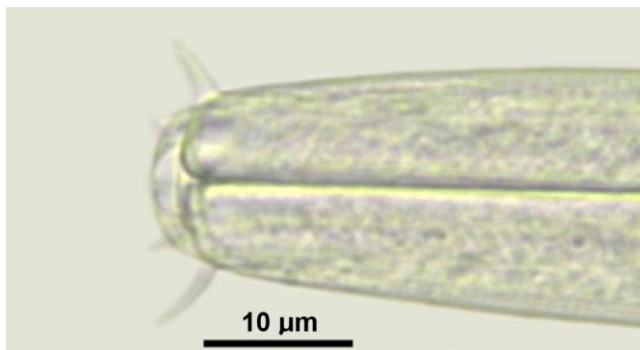


Figure 40. *Monhystera* sp., a nematode that is extracted effectively from bryophytes by a Baerman funnel. Photo by Peter Mullin, with permission.

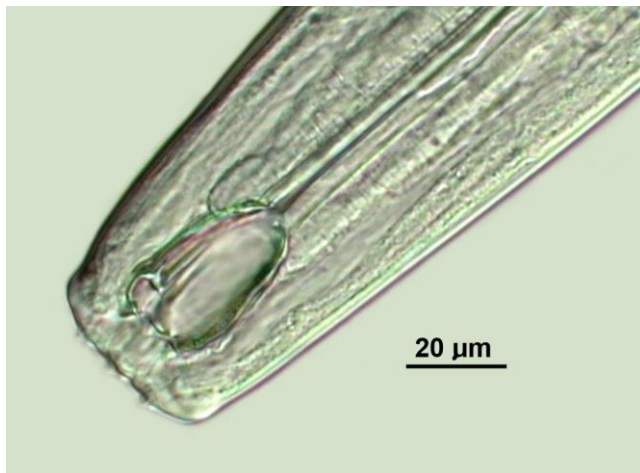


Figure 41. *Prionchulus muscorum*, a nematode that is extracted effectively from bryophytes by a Baerman funnel. Photo by Peter Mullin, with permission.

Andrew and Rodgerson (1999) investigated diversity gradients of invertebrates on bryophytes on two mountains in Tasmania. they compared two extraction techniques for their effectiveness in representing diversity – Tullgren funnels and sugar flotation – with a new technique using kerosene phase separation. When using two samples bulked together, they found that the kerosene phase separation extracted more total individuals and more Acari (mites) and Collembola (springtails). When they compared single samples (1.5 cm x 2.5 cm), the abundance results were the same, but only three of the nine taxa found in the bulked samples were extracted from the single samples. They therefore recommended that two samples be taken and used as replicates (not bulked).

Preservation of Specimens

Ecologists take note. Simply identifying and counting the faunal organisms and getting someone to identify the bryophytes isn't enough! Whereas you may be confident that your expert has identified everything correctly, it is likely that the expert is less confident and has provided you with the "best" determination possible with the material provided. But ecological specimens typically lack reproductive organs, are not well preserved, and may not even be the whole organism. Systematists always pay careful attention to keeping specimens and publishing their location. Ecologists and physiologists should also. Both the bryophytes and the fauna should be preserved and their locations in permanent, reputable herbaria and museums should be part of any publication based on the data. Furthermore, the specimens should be clearly labelled as voucher specimens, referencing the study.

Species concepts change; often physiological and ecological properties are not uniform among members of the earlier species concept. In the absence of a specimen, the data become useless. Yet, in 1950, Fosberg examined 270 ecological publications with discussions of species. Locations of preserved specimens were provided in only five of these publications! I decided to see if the situation had improved by using a much smaller sample size of three recent ecological journals and three recent bryological journals. In the 15 papers I examined from ecological journals, there was no mention of preserving or keeping specimens. In the three bryological journals, all 15 papers dealing with systematics or checklists provided the herbaria locations. However, even among this group of biologists who share the same journals, none of the six ecological papers in the same issues mentioned any preservation of specimens from the species included in the study. This practice of providing no preserved reference material defies the concept that scientific data must be verifiable.

I disagree with Fosberg (1950) when he pokes fun at stating the source of the nomenclature. Unlike his concept that this is presented to "verify" the identity of the organism, the source of nomenclature demonstrates the species concept used and provides a link to a source where a description may be found. Thus, if one uses *Drepanocladus* from Crum 1973, we know that a broad concept of the genus is used and that *Sanionia*, *Warnstorfia*, or other genus might now apply instead.

Community Patterns

When only aquatic vs terrestrial are considered, we find a difference in groups dominating the bryophytes. In terrestrial habitats, arthropods dominate (Kinchin 1992). Nevertheless, few arthropods spend their entire life cycle among mosses (Kinchin 1990a). The aquatic fauna, Kinchin (1992) contends, is dominated by nematodes, tardigrades, and rotifers. It is not clear if he includes the peatlands in this aquatic grouping, but I have examined the preserved fauna of stream bryophytes, where I have found **insects** to be the dominant organisms (Glime 1994). I must admit, however, that my bias was to describe the insect communities.

A particularly good reference for the identification of species in *Sphagnum* pools (Figure 42), particularly in Germany, is that of Kreutz and Foissner (2006). However, those on mosses are not distinguished from those in open water.



Figure 42. *Sphagnum cuspidatum* and *S. denticulatum* with bog pools. Photo by Jonathan Sleath, with permission

Terrestrial/Limnoterrestrial

Kinchin (1992) reviewed the invertebrate fauna among bryophytes in the British Isles and provided us with a summary of the "moss" habitat. He found that acrocarpous cushions support a richer fauna than the more loosely packed pleurocarpous mosses, attributing this to the greater ability of acrocarpous cushions to hold water. He demonstrated this ability experimentally, showing that at 100% saturation a cushion of the acrocarpous *Bryum argenteum* (Figure 43) held 277% of its "dry" weight in water. The pleurocarpous moss *Hypnum cupressiforme* (Figure 44), on the other hand, held 1496%. *Bryum argenteum* held 85% of its dry weight as soil trapped among the rhizoids, whereas *H. cupressiforme* has less than 1%. But perhaps most importantly, *B. argenteum* required 180 hours to reach steady dryness, whereas *H. cupressiforme* required only 132, and this was in a moss starting with more than 5X as much water!



Figure 43. *Bryum argenteum* showing its compact habit. Photo by Dick Haaksma, with permission.



Figure 44. Mat of *Hypnum cupressiforme*. Photo by Dick Haaksma, with permission.

Slow drying, as you will soon see, is a prerequisite for survival in many of these faunal organisms. Supporting his argument, Kinchin found that the *Bryum argenteum* (Figure 43) fauna was much richer than that of *Hypnum cupressiforme* (Figure 44). Interestingly, he found that mosses such as *Tortula muralis* (Figure 45) and *Grimmia pulvinata* (Figure 46) with long hair points have particularly rich fauna, which might again result from a mechanism for slow drying.



Figure 45. *Tortula muralis* in a rock crevice. Photo by Michael Lüth, with permission.



Figure 46. *Grimmia pulvinata* on boulder. Photo by Michael Lüth, with permission.

The wonderful fauna of bryophytes led Gadsby (1926) to publish his paper, "Meanderings 'mong mosses." Even after a fire bryophytes such as *Funaria hygrometrica* (Figure 47) and *Ceratodon purpureus* (Figure 48) accumulate organic matter and dust, permitting invertebrates to colonize (Clément & Touffet 1981). Others are quick to colonize areas of harvested peat (Curry *et al.* 1989). Even glacial land in the Antarctic (Schwarz *et al.* 1993) and geothermal areas of Iceland (Elmarsdottir 2003) and Ireland (Fahy 1974) sport their own bryophyte invertebrate fauna, most likely facilitated by the ameliorating effect of the microclimate within the bryophyte clone. In the Antarctic, Sohlenius *et al.* (2004) found highest invertebrate densities where there were moss communities.

In addition to the protozoa already discussed, these leaves are home to large numbers of rotifers, nematodes, and oribatid mites, and the associated bacteria, fungi, and algae provide their sustenance. Some of the species, particularly *Sphagnum* (Figure 41) inhabitants, are not found elsewhere. Many live as epiphytes on the leaf, but some live as endophytes, gaining entrance to the cells through pores in *Sphagnum* leaf and stem cells. These specialists are often elusive by standard sampling techniques. Nevertheless, Hingley showed that 50% of the taxa were present in a single drop of water!



Figure 47. *Funaria hygrometrica*, a common colonizer after fires that collects organic matter, permitting invertebrates to colonize. Photo by Michael Lüth, with permission.



Figure 48. *Ceratodon purpureus*, a common colonizer after fire, accumulates organic matter, permitting invertebrate fauna to develop. Photo by Michael Lüth, with permission.

Jones *et al.* (1994) described mosses as ecosystem engineers that provide living spaces by providing a suitable physical structure. Although *Sphagnum* (Figure 42) is the most cosmopolitan engineer, bryophytes create habitats for invertebrates in many ecosystems. Sayre and Brunson (1971) compared the moss inhabitants in a variety of habitats to determine what faunal taxa were most common (Figure 49).

One of the primary determinants of faunal inhabitants is the film of water surrounding moss leaves, especially *Sphagnum* (Hingley 1999). Bryophyte habitats generally influence the faunal community structure based on their moisture availability. Five classes can be recognized (Hofmann 1987; Hofmann & Eichelberg 1987):

- I Submerged mosses
- II Mosses that are permanently moist
- III Mosses that are only rarely dry
- IV Mosses that are frequently dry
- V Exposed mosses that are often dry for long periods

In desert cryptogamic crusts, bryophytes seem to be important to the soil fauna (Brantley & Shepherd 2004). Among these invertebrates are **arachnids**, **mites**, **nematodes**, **springtails**, **tardigrades**, and other small **arthropods**. Mixed lichen and moss patches supported 27 taxa at sites in New Mexico, whereas mosses had 29 taxa. Abundance and diversity were higher in winter than in summer, most likely due to a lower water stress. Even the moss *Syntrichia ruralis* var. *pseudodesertorum* (Figure 50) may have its own invertebrate community (Kaplin & Ovezova 1986; Ovezova 1989).

In **Vaccinium heaths**, the moss litter is difficult to break down (Frak & Ponge 2002). The invertebrate fauna process the litter, convert it to animal feces, and transform the soil to mor.

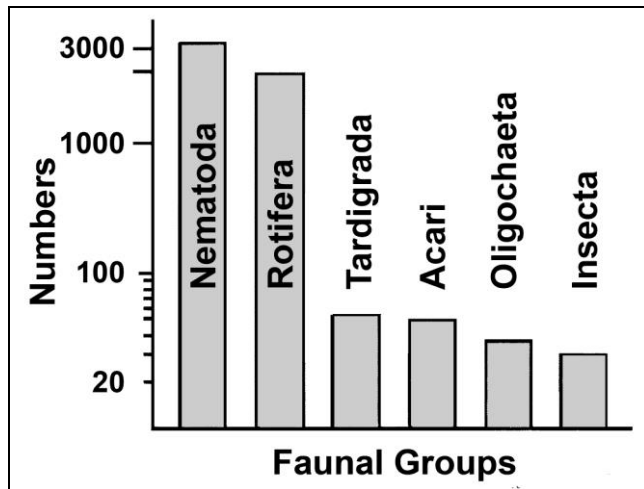


Figure 49. Mean population numbers of faunal groups from 3 2.5-cm diameter cores per moss sample, plotted on a logarithmic scale. Samples represent a variety of habitats from 26 locations in Maryland and Virginia, USA. Redrawn from Sayre & Brunson 1971.



Figure 50. *Syntrichia ruralis* var. *pseudodesertorum* may have its own invertebrate community. Photo by Paul Slichter, with permission.

In the Antarctic, the structure of the mosses [*Calliergon sarmentosum* (Figure 51), *Drepanocladus* sp. (possibly *Sanionia uncinata*)] provides a complex community where epiphytic algae and invertebrates form a higher diversity than the surrounding algal community (Priddle & Dartnall 1978). For example, *Calliergon sarmentosum* provides the site of most abundant algae in leaf axils. Six stem zones result from deterioration of basal portions. Benthic invertebrates move actively among these mosses. Six species of **rotifers** are common in the middle stem zones where there is the greatest abundance of epiphytes. Of these, two colonize the bare underside of leaves whereas four live mostly in leaf axils. Wind-induced mixing in the summer provides transportation for at least some of the epiphytes from the shallow portions of the lake. **Rotifers** settle there as larvae.



Figure 51. *Calliergon sarmentosum*, a common component of the moss-invertebrate community in the Antarctic. Photo by Michael Lüth, with permission.

The invertebrate representation can be more limited in the Antarctic than in many other parts of the world. Schwarz *et al.* (1993) found that the moss-dominated flushes near the Canada Glacier supported a community where **Protozoa**, **rotifers**, **worms**, and **tardigrades** dominated, with all but the **Protozoa** occurring at 5-10.83 mm depth in the moss. Following melt, more of the organisms were found in the upper 5 mm of the moss habitat. **Mites** occurred in lesser quantities and **Collembola** were nearly absent. On the other hand, a catenulid **flatworm** in that habitat was a rare find; **microturbellarians** are quite rare in Antarctica.

Bryophytic epiphytes are important habitats for invertebrates. Kellar (1999) and Milne and Short (1999) demonstrated this for *Dicranoloma* in the cool temperate rainforest of Victoria, Australia. Nadkarni and Longino (1990) have demonstrated this for the neotropics.

Lobules as Habitat

As discussed in the chapters on micro-organisms and rotifers, the water-holding lobules of some leafy liverworts may house a variety of invertebrates. In fact, these invertebrates seem in some cases to be attracted to the plants and readily enter the lobules (Hess *et al.* 2005). In the leafy liverwort *Pleurozia purpurea* (Figure 52-Figure 53), the fauna include **Ciliata**, **Rhizopoda** (protozoans), **flatworms**, **nematodes**, **annelids**, **rotifers**, **tardigrades**, and **copepods**. A detailed discussion of the "trapping" mechanism of the lobules is in sub-Chapter 2-6 on protozoa. Whether these invertebrates are truly trapped and consumed by the liverworts remains unknown. Decaying inhabitants provide food for other members of the community and provide a proximal source of nutrients for the liverwort leaves. These organisms form a unique faunal community where organisms live, consume, die, and decay.

Aquatic

Bryophytes can offer communities that mimic those of riffles, or house very different communities. In her study of the River Liffey, Ireland, Frost (1942) found that the

numbers of organisms found in 23 bryophyte samples differed little between an acid (ca 282,000 organisms) and an alkaline (ca 306,900 organisms) stream, but the composition of the organism differed. On the other hand, Elgmork and Sæther (1970) found that at least some species exhibited larger numbers of individuals at locations with moss cover on the stones than those without mosses, suggesting that the mosses could accommodate a much larger number of invertebrates.



Figure 52. The leafy liverwort *Pleurozia purpurea*, showing the protective nature of the curved leaves. The lobules are underneath. Photo by Sebastian Hess, with permission.



Figure 53. **Left:** Worm, probably an *oligochaete*, from the lobule of the leafy liverwort *Pleurozia purpurea*. **Right:** Lobule of the liverwort, *Pleurozia purpurea*. Photos by Sebastian Hess, with permission.

In a study of Doe Run, Meade County, Kentucky, USA, Minckley (1963) found that the invertebrate abundance in beds of the moss *Fissidens fontanus* (Figure 54) "strongly reflected the fauna of unvegetated riffles." This seems to be almost a contradiction since the same study demonstrated that the closely matted *F. fontanus* created a "pool environment in the midst of riffles."

Minckley suggested that those animals that were relatively scarce in the moss beds but much more abundant in the rubble of smaller riffles may have been driven there by the preference of crustaceans for the mosses. Inhabiting the riffles permitted the smaller invertebrates to avoid being dinner for the crustaceans.



Figure 54. *Fissidens fontanus*, an aquatic moss that creates a quiet refuge in the middle of riffles. Photo by Tan Sze Wei Aquamoss website <www.aquamoss.net>, with permission.

Kinchin (1992) considered the faunal inhabitants to grade from unspecialized among the submerged mosses to more specialized, drought-resistant or drought-tolerant toward the dry end. Carpenter and Lodge (1986) found that submerged plants, including bryophytes, affect the physical environment through light extinction, temperature modulation, hydrodynamics, and substrate. They alter the chemistry by providing oxygen, altering inorganic and organic carbon, and sequestering nutrients. Nevertheless, some habitats, while appearing suitable, are not colonized by any species.

Aquatic bryophytes in streams generally house the largest and probably the most diverse fauna among the various stream communities (see *e.g.* Percival & Whitehead 1929; Frost 1942; Badcock 1953; Hynes 1961; Minckley 1963; Thorum 1966; Stern & Stern 1969; Michaelis 1977; Cowie & Winterbourn 1979; Carpenter & Lodge 1986; Suren 1988, 1991a, b; Vlčková *et al.* 2001/2002; Paavola 2003). Amos (1999) described the torrent among the *Fontinalis* branches (Figure 55) in a poetic fashion: "All was quiet at the bottom of the torrent moss world, despite the storm of rushing water overhead." Here one could find zones of algae – diatoms, desmids, and filamentous species. Inhabitants included **round** and **segmented worms**, **rotifers**, **gastrotrichs**, **water fleas**, **copepods**, **scuds**, and a variety of larval **insects** as well as adults of tiny species. The **mountain midge** larva anchors there with suction cups that are even better than those of the squid and octopus. Yet Kinchin (1990b, 1992) paints a different picture of the waterfalls in Ein Gedi Nature Reserve, Israel, where the fauna is relatively poor.



Figure 55. *Fontinalis antipyretica* houses a wide range of invertebrates in streams and lakes, giving them a refuge from rapid flow and predators. Photo by Michael Lüth, with permission.

Specificity for particular bryophytes may be more a result of the habitat where each bryophyte lives. Paavola (2003) attempted to show the relationship between bryophytes, macroinvertebrates, and fish, with a goal to show concordance and usefulness in predictive power. Bryophytes and macroinvertebrates showed a weak congruence with weak predictive power, but neither had a good congruence with fish. Cowie and Winterbourn (1979) found distinct preferences for certain bryophyte species among the invertebrates in a New Zealand stream, but these differences also reflected habitat differences such as position in stream. *Fissidens rigidulus* occurred in the torrential water in mid channel. *Pterygophyllum quadrifarium* occurred where it was water saturated by the inner spray zone of a waterfall. *Cratoneuropsis relaxa* grew in the outer spray zone. Cowie and Winterbourn suggested that the invertebrates responded to differences in water saturation, flow rates, and detritus-trapping ability by the mosses, the latter also relating to flow rate but including aspects of the moss morphology.

In aquatic habitats, bryophytes are particularly important in contributing to faunal diversity (Priddle & Dartnall 1978; Suren & Winterbourn 1992a). In the Antarctic, these faunal groups are dominated by **Protozoa**, **Rotifera**, **Nematoda**, **Turbellaria**, **Tardigrada**, **Oligochaeta**, and **Acari** (Ingole & Parulekar 1990). In alpine streams of New Zealand, bryophytes provide shelter with reduced flow (Suren 1991b) and catchment for algae and detritus, thus creating a habitat with both shelter and food (Suren 1992), and in some cases materials for constructing larval cases (Suren 1987). Among 23 invertebrate taxa, 14 were found with bryophyte fragments in their gut, but their presence in the gut was only common in several of the aquatic insects (Suren & Winterbourn 1991). Bryophytes contained more indigestible compounds than did other plants, making them less nutritious. Rather, it appears that detritus and periphyton were the primary food sources (Suren & Winterbourn 1992b).

In these New Zealand streams, the bryophyte faunal communities were greater in streams above the treeline (Suren 1993). Greater invertebrate density occurred within bryophyte communities with periphyton than those with detritus (Suren 1993). Bryophyte communities were dominated by aquatic **insects** and **Nematoda**, **oribatid mites**, **Hydracarina**, **Copepoda**, and **Ostracoda** (Suren

1988). When artificial mosses were used in place of real ones, similar invertebrate communities developed, but some, e.g. **Nematoda**, **Acarina**, **Tardigrada**, **Ostracoda**, seemed to suffer from loss of the food supply (Suren 1991a).

Linhart *et al.* (2002) examined the fauna of *Fontinalis antipyretica* (Figure 55) growing on rocks used to stabilize a side channel of the Morava River in the Czech Republic. The means of moss-dwelling meiofauna were $253,917 \pm 178,335$ (\pm SD) per 10 g dry weight of moss and $7,160,461 \pm 5,029,047$ per 1 m² of the bottom area during October 1999–November 2000. **Bdelloidea** (rotifers) formed the dominant group (76%), followed by **Monogononta** (rotifers) (11.23%), **Nematoda** (6.38%), **Chironomidae** (midges) (4.08%), and **Oligochaeta** (worms) (1.06%). Linhart and coworkers (2002) considered that fine particulate matter trapped by the mosses would serve as both a habitat and a food source. They found that about 4% of the trapped matter was coarse matter (500–1000 μ m), 14% medium (10–500 μ m), and 82% fine (30–300 μ m). Only 10% of the trapped matter is organic. The size and content of the trapped matter were significantly correlated ($P < 0.05$) with densities of **Oligochaeta** (segmented worms), **Hydrachnidia** (mites), **Cladocera**, **Copepoda**, and **Chironomidae**. They reported that the bryophyte habitat houses considerably greater numbers of meiofauna compared to the stream gravel bed. Table 1 compares the numbers of moss-dwelling organisms in streams.

Even in the Antarctic, bryophytes are important habitats for invertebrates. In the flushes of meltwater, moss-dwelling invertebrates are dominated by protozoa, rotifers, nematodes, and tardigrades that live at moss depths of 5–10.8 mm. The upper 5 mm of the moss housed more members of all groups in post-melt samples than in pre-melt samples. Mites were less important than in more temperate climates. On the other hand, a flatworm, which is rare in the Antarctic, occurred there.

Altitudinal Gradients

Altitudinal gradients are often followed by community and diversity gradients. But surprisingly, the greatest diversity often occurs at mid altitudes rather than decreasing toward the summit. Andrew *et al.* (2003) investigated diversity gradients of invertebrates on bryophytes on mountains in Tasmania and New Zealand. Although they found altitudinal relationships, these were not consistent among the four mountains they studied. Rather, there were strong geographic differences. Mt. Field in Tasmania had the highest invertebrate and bryophyte diversity at 750 m, whereas Mt. Rufus had low diversity of both throughout its entire altitudinal gradient. In New Zealand, Otira had the highest bryophyte and invertebrate diversity at low altitudes, but Kaikoura had the highest invertebrate diversity at the highest altitude where the bryophyte diversity was lowest.

Food Webs

The aquatic food web is quite complex. It appears that detritus and periphyton may play a major role in the presence and abundance of invertebrates on the bryophytes (Percival & Whitehead 1929). Suren (1988) experimented with artificial bryophytes made of nylon cord woven into a

4 mm mesh mat. In the stream where the mat was highly colonized by periphyton and detritus, the invertebrates were far more abundant than in the stream with little periphyton and detritus on the mat. There was little difference between the number of invertebrates on the artificial and real mosses. But some groups were significantly reduced on the artificial mosses: **Acarina** (mites), **Collembola** (springtails), **Tardigrada** (water bears), **Dorylaimoidea** (nematode worms), and **Ostracoda**, possibly due to the loss of the bryophytes as a food source. It appears that the **aquatic insects** do not depend on the bryophytes for food, but some of the other invertebrates do. Aquatic insect relationships will be discussed in the chapter on aquatic insects, since they are major players in the aquatic bryophyte realm.

Much less is known about the terrestrial food webs in bryophyte microcosms. Sayre and Brunson (1971) pointed out that these ecosystems have the same four basic food units as larger ecosystems described by Odum (1963):

abiotic, producer, consumer, and decomposer. In fact, there are often secondary consumers and even some tertiary consumers.

The **abiotic** portion of the habitat includes dust and other particles gained from the atmosphere, organic leachates from the bryophytes (and host trees for epiphytes), decaying bryophyte parts, and the remains of dead inhabitants. The water film enveloping the bryophytes is essential to their survival in active states, but like the bryophytes, most of the organisms living here are capable of dormancy when the water dries up. They gain the advantage that the bryophytes dry slowly compared to most other available substrata.

The bryophytes themselves are **producers**, but they often also have algae on them (yes, even those on trees) and may have lichens associated with them, both of which add to the carbon fixation.

Table 1. Comparison of numbers of invertebrate organisms in moss collections from streams. **NR** means not reported.

	Sample Size	Hydrozoa	Platyhelminthes	Nematoda	Annelida	Rotifera	Gastroticha	Tardigrada	Non-Insect Arthropoda	Insecta	Mollusca	Reference
Straffan, River Liffey, Ireland	200 g	NR	0.1	56.0	48.0	NR	NR	NR	489	12755	0.7	Frost 1942
Ballysmuttan, River Liffey, Ireland	200 g	NR	0.1	38.0	36.0	NR	NR	NR	160	12051	+	Frost 1942
Cold Springbrook, Tennessee, USA	0.1 m ²	NR	1.1	NR	NR	NR	NR	NR	18.9	255	NR	Stern & Stern 1969
Bystřice, Czech Republic	10 g dry	34	319	18305	1355	54561	1347	736	1817	46426	NR	Vičková <i>et al.</i> 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	0.0	37	16198	3602	222084	189	277	427	11229	NR	Vičková <i>et al.</i> 2001-2002
Welsh Dee Tributary, Wales	~300 cm ²	NR	0.5	1.8	11.5	NR	NR	NR			NR	Hynes 1961
Mouse Stream, alpine, New Zealand	1 m ²	NR	NR	87430	NR	NR	NR	5640			NR	Suren 1991a
Tim's Creek, alpine, New Zealand	1 m ²	NR	NR	6810	NR	NR	NR	0			NR	Suren 1991a
West Riding, Yorkshire, GB - loose moss	%	NR	NR	NR	4.6	0.0	NR	NR	4.6	90	0.4	Percival & Whitehead 1929
West Riding, Yorkshire, GB - thick moss	%	NR	NR	NR	0.0	0.0	NR	NR	4.7	63	4.1	Percival & Whitehead 1929
alpine unshaded stream, New Zealand	% top 10	NR	NR	22.1	NR	NR	NR	2.4	12.9	61		Suren 1991b
alpine shaded stream, New Zealand	% top 10	NR	NR	12.5	NR	NR	NR	0.0	8.1	74		Suren 1991b

The **consumer** component of the bryophyte community has seldom been investigated. We know that **tardigrades** are often specifically adapted to sucking contents from bryophyte cells and may be the primary consumers (Pennak 1953; LeGros 1958). However, many **tardigrades** are also carnivores; Sayre and Brunson (1971) suggest that most of those in their study were secondary consumers, *i.e.* predators/carnivores. Higgins (1959) suggested **rotifers** were a food source for **tardigrades**. As one of the two most abundant invertebrates in samples of Sayre and Brunson (1971), **rotifers** are a good source of food. **Tardigrades** also feed on **nematodes** (Sayre 1969).

As in other habitats, fungi and bacteria break down the debris that accumulates among the bryophytes. The bacteria and the by-products of their decomposition provide food for **nematodes**, **rotifers**, and **oligochaetes** (Sayre & Brunson 1971). Hence, one could hypothesize a simple food web (Figure 56).

Frost (1942) considered the mosses in some habitats to be a fallback substrate. She thought that those organisms that reach large numbers on other kinds of plants could colonize the moss when the other plants became overcrowded. This would increase the importance of the mosses in the food web. In other cases, they provide a winter substrate when tracheophytes are dormant.

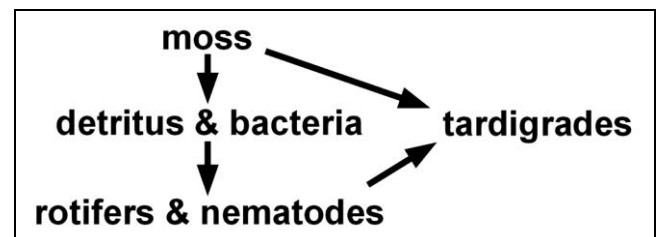


Figure 56. Theoretical food web involving mosses and lower invertebrates. **Mollusks**, **insects**, and other **arthropods** could form secondary and tertiary consumers in this web.

Pollution

One predicted consequence of acidification is a shift from tracheophytes to bryophytes, especially in lakes (Carpenter & Lodge 1986). This may also be so in slow streams, whereas fast streams are typically dominated by bryophytes from the start. A consequence of this shift is likely to be a decrease in rates of decomposition in the sediment and an increase in the diffusion of phosphorus, iron, and possibly other metal ions into the water column. These chemical changes relate to the inability of bryophyte rhizoids and shoots to oxidize the sediments. These changes are likely to result in changes to the faunal community, but the interactions are too complex to make good predictions.

Mosses are well known for their ability to monitor and indicate pollution. But it appears that their fauna may also be important indicators of the assault by heavy metals and other air pollutants (Steiner 1994a, b, c). Zullini and Peretti (1986) found that lead pollution affects **nematodes** living among mosses. Species richness declines and communities become more uniform as pollution levels rise, especially for the **oribatid mites** (Figure 58) (Steiner 1995a). Moss communities of **nematodes**, **rotifers**, and **tardigrades** change composition in response to SO₂ fumigation (Steiner 1995b). Both **nematodes** and **tardigrades** were greatly reduced in numbers by the highest SO₂ levels (0.225 ppm), particularly the nematodes *Chiloplectus cf. andrassyi* and *Paratripyla intermedia*. Nevertheless, the tardigrade *Macrobiotus persimilis* (Figure 57) actually increased with increasing SO₂ levels. More attention should be paid to these organisms whose population numbers can serve as suitable indicators of pollution.



Figure 57. *Macrobiotus cf. furciger*, a tardigrade that seems to thrive in higher SO₂ levels. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Although the **arthropods** in aquatic systems have often been used as indicators, in terrestrial moss communities they seem to be less sensitive to pollution than **nematodes** and **tardigrades** (Steiner 1995b).

Harvesting Dangers

It would be irresponsible to include this and the succeeding chapters without reminding the readers of the dangers lurking in harvested mosses. Such mosses, like their living counterparts, harbor numerous invertebrates

(Peck *et al.* 1996), many that can become dormant for extended periods of time. The danger is not one to your safety, but to safety of ecosystems that may be disturbed, first in one from which you remove the bryophytes, and second to one to which they are transported.

Muir (2004) reported 81 million pounds of moss per year, the equivalent of about 10,500 semi-trucks, harvested in the Pacific Northwest. This massive harvest on logs can take 10-23 years to recover (Peck 2006). Most likely a greater recovery time is needed for epiphytes.

Using a Berlese funnel for extraction, Peck and Moldenke (1999) identified 125 invertebrate taxa from 200 moss mats in Oregon, USA. Greater overall numbers were present at shrub bases than at tips. However, this pattern did not exist for all organism groups (Peck & Moldenke 1999). **Coleoptera** (beetles) and **Thysanoptera** (thrips) exhibited greater numbers per gram at the base, as did detritivores in general, but spiders and predators in general were actually lower in numbers at the bases. Turtle-mites characterized basal samples [*Ceratoppia* sp. (Figure 58), *Hermannia*, and *Phthiracarus* sp. (Figure 60)], whereas microspiders (**Micryphantidae**) and springtails (*Sminthurus*; Figure 61) were typical of tips.



Figure 58. *Ceratoppia* sp., a genus that lives among bryophytes at the bases of shrubs in Oregon, USA. Photo by Dragiša Savić, with permission.



Figure 59. *Hermannia* sp., a turtle-mite that lives among bryophytes at the bases of shrubs in Oregon, USA. Photo by Tom Murray, through Creative Commons.



Figure 60. *Phthiracarus* sp., a mite species that lives among bryophytes at the bases of shrubs in Oregon, USA. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 61. *Sminthurus viridis*; *Sminthurus* is typical of bryophytes at the tips of shrub branches in Oregon, USA. Photo by AfroBrazilian, through Creative Commons.

Moss harvesting therefore creates two problems. At first it creates the possibility of endangering specific inhabitants that thrive only among bryophytes. Secondly, transport of harvested mosses will undoubtedly also transport the invertebrate fauna, providing the possibility for these creatures to invade areas where they did not exist before, most likely altering their new ecosystem, often to the detriment of the native fauna and flora. Details of harvesting will be discussed in a different volume.

Summary

The invertebrate fauna living among bryophytes can be variously categorized as **cryptozoic fauna** (hidden animals), **meiofauna** (retained on a mesh size of 42 μm , and **benthic** (living on the bottom of a body of water). The non-arthropod fauna include primarily **nematodes**, **rotifers**, **tardigrades**, and **annelids**, generally in that order of abundance. Their diverse feeding strategies engage them in nutrient cycling.

Sampling can be difficult and often requires extraction by hand or use of a **Baermann or Berlese funnel**. Whenever possible, specimens should be preserved in a recognized museum and that location published along with any studies involving them.

In aquatic habitats, the bryophytes provide a safe site away from torrents and large predators, where invertebrates are known to number as much as 25,400 per g dry weight of *Fontinalis*. Detrital matter trapped by the moss is a ready food source. In prairies and desert regions, bryophytes may provide the most important suitable habitat. In the Antarctic, epiphytic algae provide food for the meiofauna.

Most of the organisms do not eat bryophytes and depend on adhering detritus and bacteria for food (**rotifers & nematodes**). **Tardigrades**, however, may also eat bryophytes.

Because of their ability to respond to heavy metals and other pollutants, the invertebrates provide a suitable group to monitor air pollution, along with their bryophyte habitat.

On one hand, harvesting of bryophytes can remove endangered invertebrate species, and on the other may distribute species to new areas where they may become invasive or disruptive to new ecosystems.

Acknowledgments

Thank you to Aldo Zullini for pointing me to the interesting paper by Sayre and Brunson. María Jesús Iglesias Briones was helpful in many ways in the preparation of this chapter. Bryonettors have been wonderful in making their photographs available to me and seeking photographs from others.

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