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CHAPTER 4-1
INVERTEBRATES: INTRODUCTION

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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 interstial 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.

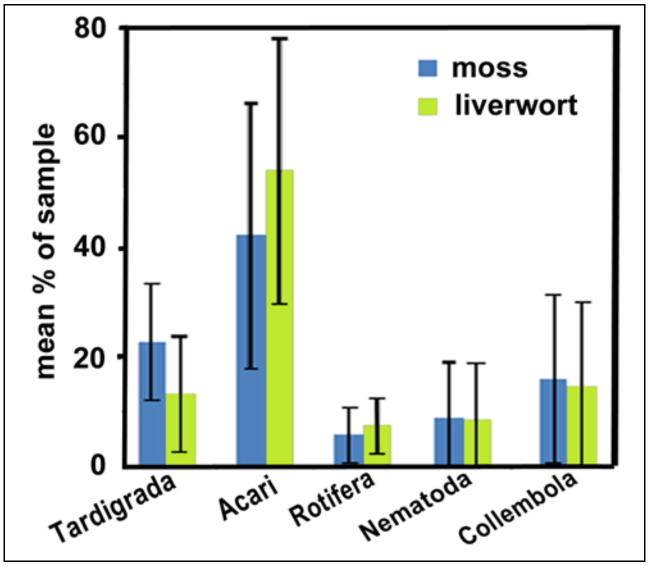

Figure 10. Mean percent and standard deviation of organisms for each of the five dominant taxa groups in epiphytic mosses and liverworts at Tryon Creek State Natural Area, 1, 7, and 17 October 2011, calculated for all samples together. Redrawn from Neslon & Hauser 2012.

In the Czech Republic, Božanić *et al*. (2013) attempted to illucidate 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.

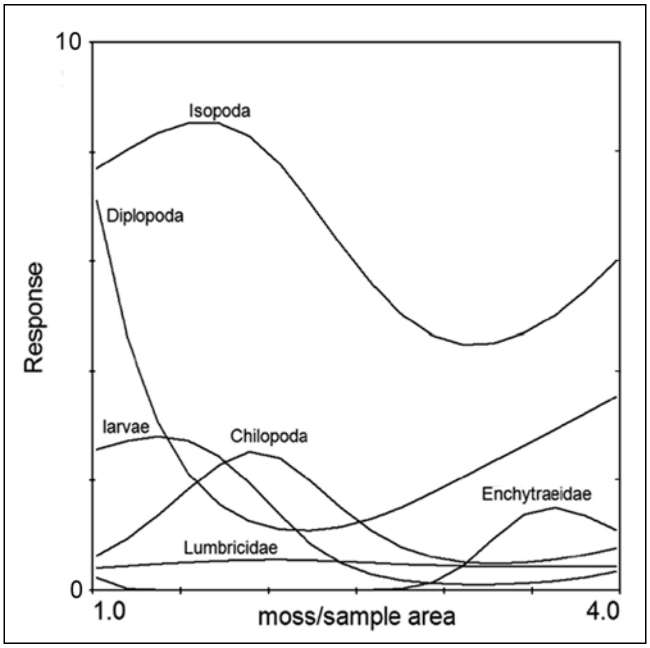

Figure 12. Relative numbers of invertebrate groups on bryophytes vs moss sample area. Redrawn from Božanić *et al*. 2013.

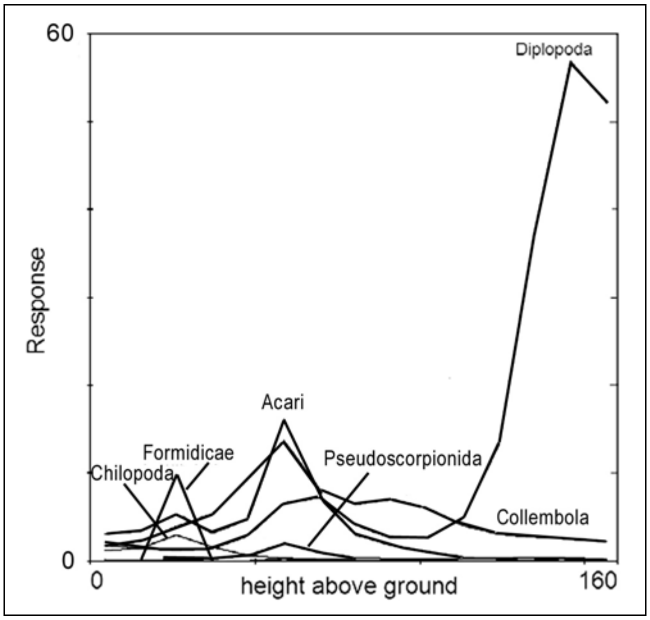

Figure 13. Relative numbers of invertebrate groups on bryophytes vs height above ground. Redrawn from Božanić *et al*. 2013.

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 mieofauna 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%, **Orthocladiinae** (**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.

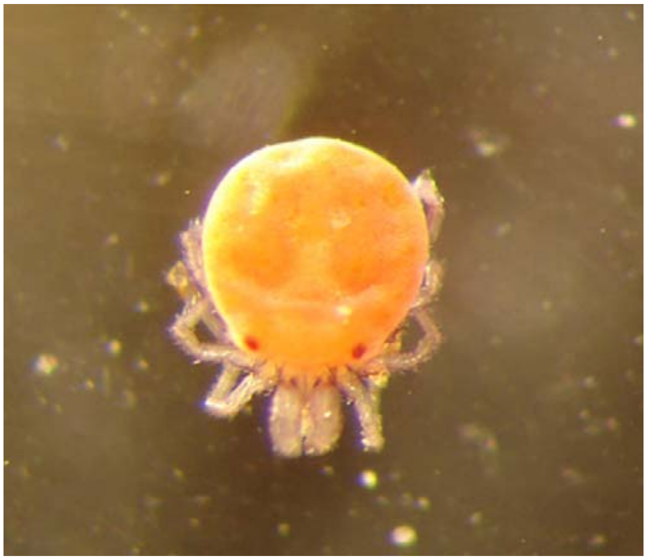

Figure 23. **Hydrachnidia**, a mite group with bryophyte dwellers that are common in the drift. Photo by Mnolf, through Creative Commons.

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.

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.

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 28. ***Sphagnum teres***, a species of the submountain and mountain areas of the Czech Republic. Photo by J. C. Schou, 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 30. ***Sphagnum fallax***, a species of the submountain and mountain areas of the Czech Republic. Photo from <www.aphotofauna.com>, 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 32. ***Pleurozium schreberi***, a species of the submountain and mountain areas of the Czech Republic. Photo by Michael Lüth, with permission.

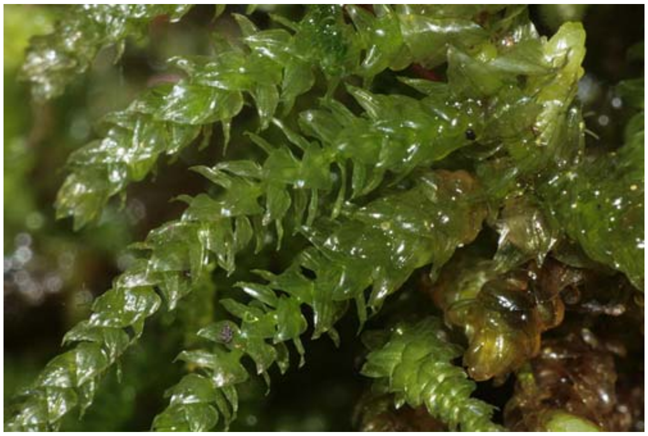

Figure 33. ***Eurhynchium angustirete***, a species of the submountain and mountain areas of the Czech Republic. Photo by Hermann Schachner, through Creative Commons.

Figure 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.

Figure 36. ***Bazzania trilobata***, a species of the submountain and mountain areas of the Czech Republic. Photo by Barry Stewart, 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 saples 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 cm^2. 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-STEEP). If it is too hot, organisms die before they can drop.

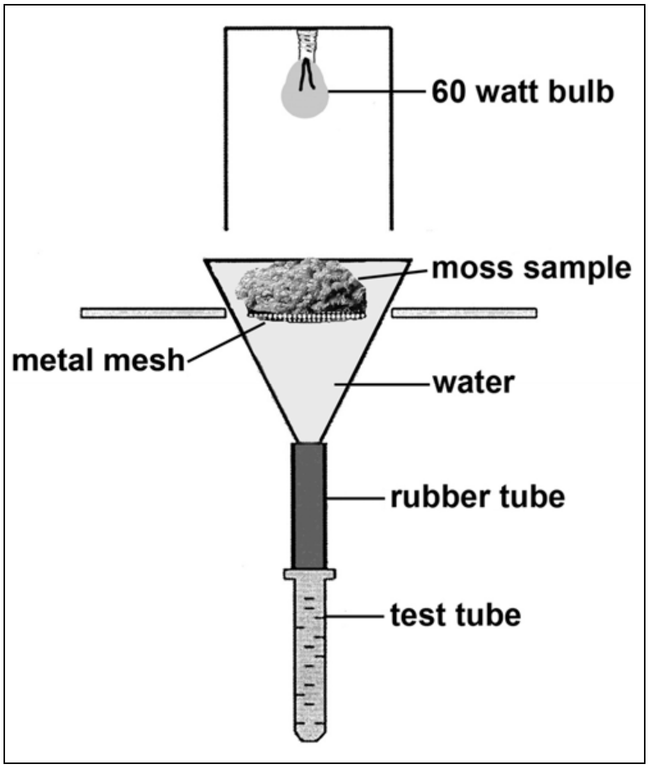

Figure 38. Baermann funnel using moss sample. Water can be replaced with air for non-aquatic organisms, thus making it similar to the Berlese funnel. Modified from Briones 2006.

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 precipidated 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 oreganum*** (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.

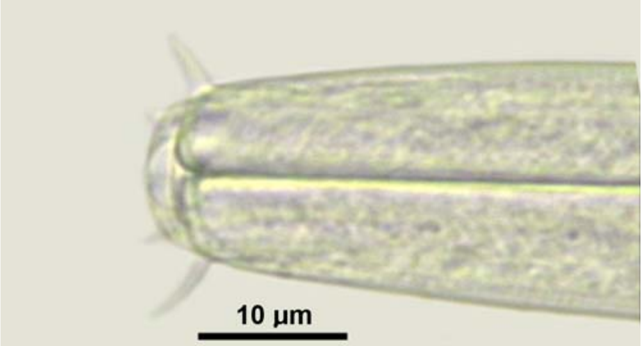

Figure 40. ***Monhystera*** sp., a nematode that is extracted effectively from bryophytes by a Baerman funnel. Photo by Peter Mullin, with permission.

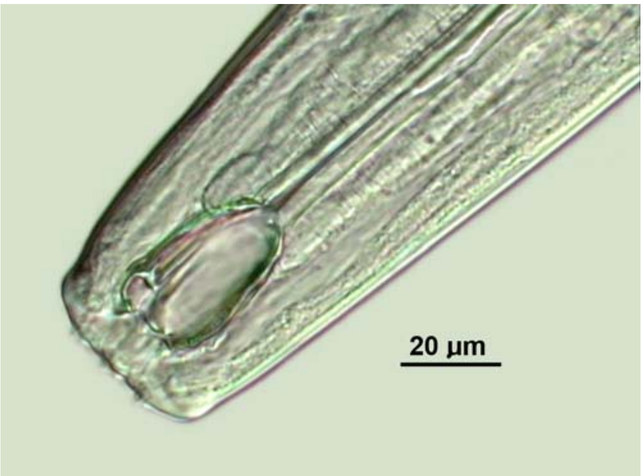

Figure 41. ***Prionchulus muscorum***, a nematode that is extracted effectively from bryophytes by a Baerman funnel. Photo by Peter Mullin, with permission.

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.

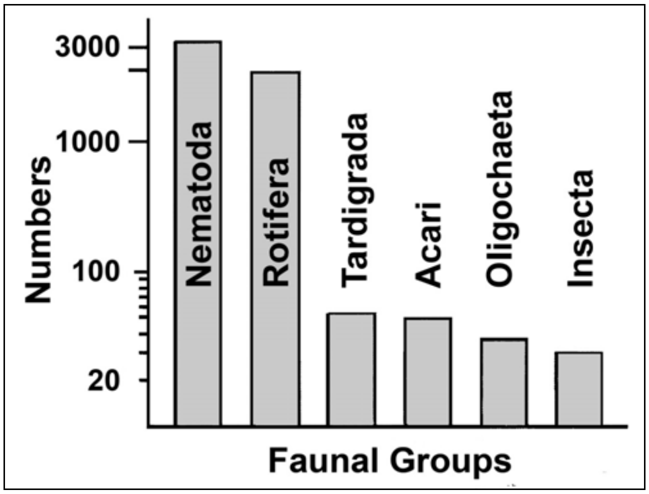

Figure 49. Mean population numbers of faunal groups from 3 2.5-cm diameter cores per moss sample, plotted on a logarithmic scale. Samples represent a variety of habitats from 26 locations in Maryland and Virginia, USA. Redrawn from Sayre & Brunson 1971.

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 sream. ***Fissidens rigidulus*** occurred in the torrential water in mid channel. ***Pterygophyllu 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 ± 178,335 (± SD) per 10 g dry weight of moss and 7,160,461 ± 5,029,047 per 1 m^2 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 µm), 14% medium (10-500 µm), and 82% fine (30-300 µm). 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 compates 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 inertebrates 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	Gastrotricha	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	Vlčková *et al.* 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	0.0	37	16198	3602	222084	189	277	427	11229	NR	Vlčková *et al.* 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.

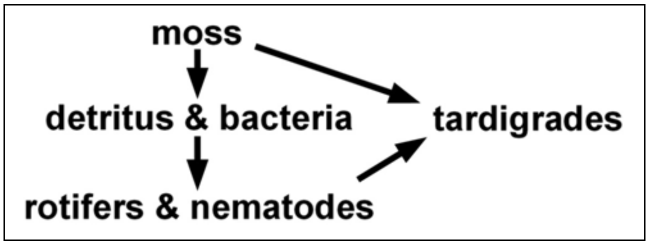

Figure 56. Theoretical food web involving mosses and lower invertebrates. **Mollusks**, **insects**, and other **arthropods** could form secondary and tertiary consumers in this web.

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 increasse 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 SO_2 fumigation (Steiner 1995b). Both **nematodes** and **tardigrades** were greatly reduced in numbers by the highest SO_2 levels (0.225 ppm), particularly the nematodes ***Chiloplectus*** *cf.* ***andrassyi*** and ***Paratripyla intermedia***. Nevertheless, the tardigrade ***Macrobiotus persimilis*** (Figure 57) actually increased with increasing SO_2 levels. More attention should be paid to these organisms whose population numbers can serve as suitable indicators of pollution.

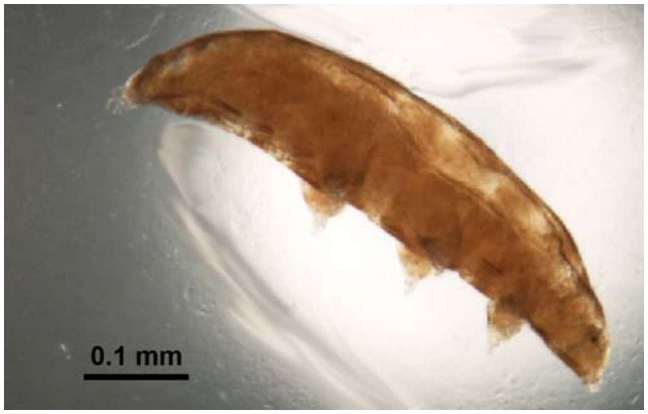

Figure 57. ***Macrobiotus*** cf. ***furciger***, a tardigrade that seems to thrive in higher SO_2 levels. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

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.

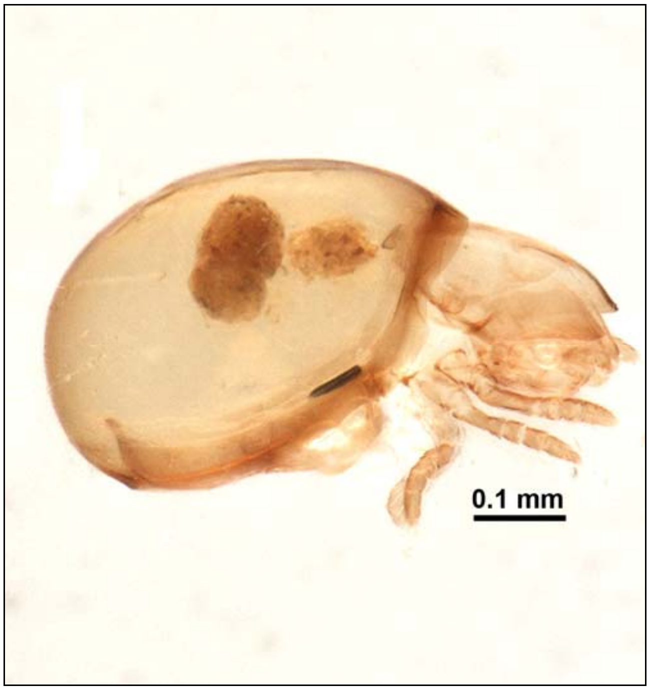

Figure 60. ***Phthiracarus*** sp., a mite species that lives among bryophytes at the bases of shrubs in Oregon, USA. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

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.

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CHAPTER 4-2
INVERTEBRATES: SPONGES, GASTROTRICHS, NEMERTEANS, AND FLATWORMS

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Figure 1. This **planarian, *Polycladus gayi***, is navigating a mat of the liverwort ***Lepidozia cordulifera***. The planarian is a native of Valdivian rainforests of southern Chile, where it hunts for food on bryophytes and other substrata. Photo courtesy of Filipe Osorio.

Cnidaria

Members of the **Hydrozoa** (hydroids) are not common among bryophytes, but they can occur there. Jones (1951) reported ***Hydra viridissima*** (Figure 2) from ***Fontinalis antipyretica*** (Figure 3) on bedrock in the River Towy, Wales.

Figure 2. ***Hydra viridissima***, occasional bryophyte dweller. Photo from Proyecto Agua, with permission.

Figure 3. ***Fontianlis antipyretica*** growing in a stream where it can offer a protected substrate for a number of invertebrates. Photo by Andrew Spink, with permission.

Porifera – Sponges

Sponges don't seem to have any particular appreciation of bryophytes, being unknown from that habitat. However, it appears that the moss genus ***Fissidens*** has a special fondness for sponges. I know of no other bryophyte genus that finds this a suitable habitat, but ***Fissidens fontanus*** (Figure 4) in Europe is epizootic on **sponges** (Sowter 1972) and ***F. brachypus*** lives only on freshwater sponges in the Amazon (Buck & Pursell 1980). ***Fissidens*** seems to like animal habitats, living on the openings of wombat holes, termite mounds, and in this case, on a sponge.

Although a moss-sponge combination in nature is rare, humans seem to have found this combination useful. A patent application by Albert G. Morey, dated 13 October 1968, for an "improved mattress" extols the virtues of placing a large **sponge** (mattress) over a layer of only slightly spongy material such as moss. A three-layer mattress is considered to be superior, with the lower layer of moss sustaining the middle layer of woody fiber or excelsior, again with a layer of elastic **sponge** on top. It appears that this was a real sponge (or lots of them) and predates the use of cellulose sponges. The improvement seems to have been the addition of the moss and fibrous layers.

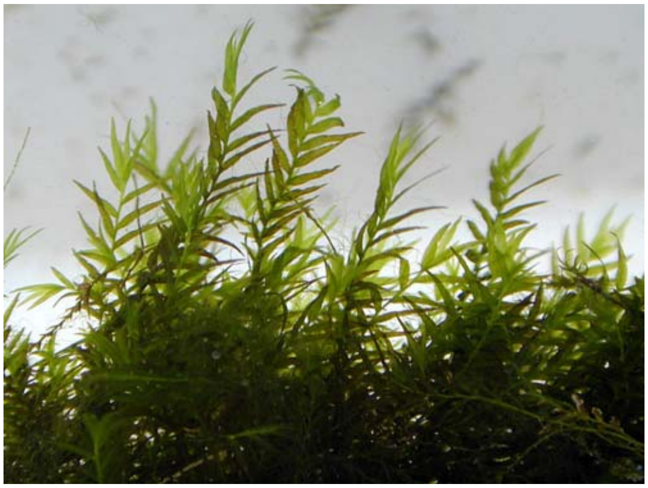

Figure 4. ***Fissidens fontanus***, a species that can be epizootic on **sponges**. Photo by Michael Lüth, with permission.

Gastrotrichs

These small animals with "hairs on their stomachs" use them to beat against such surfaces as moss leaves to glide forward (Figure 5-Figure 11; Hingley 1993). They lack a coelom, like flatworms, and move in a similar motion. Like nematodes, rotifers, and tardigrades, freshwater **gastrotrichs** are all **parthenogenetic**, producing viable unfertilized eggs. Adults are unable to go dormant, but when unfavorable conditions arise, they produce larger eggs with heavier shells that survive not only desiccation, but also low and high temperatures. They adhere using cement glands in two terminal projections (Gastrotrich 2009). One of the glands conveniently secretes a de-adhesion to release them.

They may be found occasionally on aquatic bryophytes. The **Dichaeturidae** is a rare family that has been found in cisterns, in underground water, and among mosses (Remane 1935-1936; Ruttner-Kolisko 1955). In the Czech Republic, Vlčková *et al.* (2001/2002) reported 2823 of these invertebrates on 100 ml of the aquatic moss ***Fontinalis antipyretica*** (Figure 3) in Bystřice, whereas in Mlýnský náhon there were only 371 per 100 ml. In Bystřice the mosses held a food source of organic matter in the size range of 30-100 µm. Linhart *et al.* (2002) found that abundance was negatively influenced by flow velocity in both of these streams, and the gastrotrichs were significantly fewer in riffles, suggesting that bryophytes could act as refugia in areas of high flow. On the other hand, sediment also was reduced in areas of high velocity, resulting in more available food in sediments in low velocity areas.

In a peatland complex in northern Italy, Balsamo and Todaro (1993) identified 21 species of **gastrotrichs**. Hingley (1993) found the following gastrotrichs among the peatlands mosses in her study of the British Isles:

Chaetonotus heterocanthus
Chaetonotus maximus
Chaetonotus ophiogaster
Chaetonotus polyspinosus
Chaetonotus voigti
Chaetonotus zelinkai
Heterolepidoderma ocellatum
Ichthydium forcipatum
Lepidodermella squamatum
Stylochaeta fusiformis

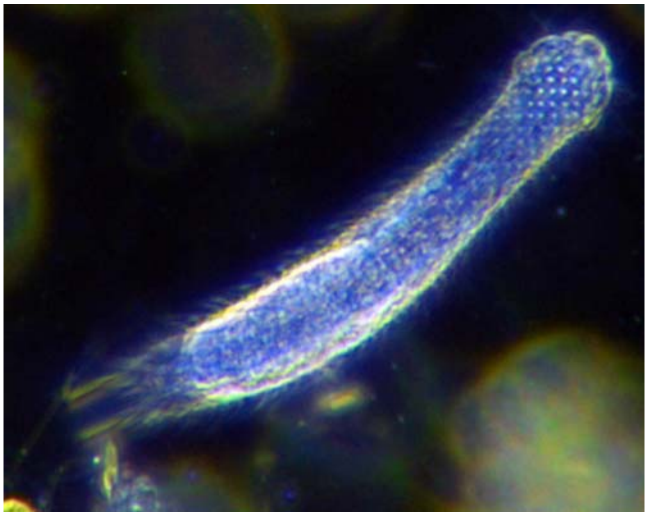

Figure 5. **Gastrotrich** showing two tails and cilia. Photo by Jasper Nance through Wikimedia Commons.

Figure 6. **Gastrotrichs** awakened from dry soil. Photo by Paul G. Davison, with permission.

Figure 7. ***Heterolepiderma***, a genus that has moss-dwelling gastrotrichs. Photo by Yuuji Tsukii, with permission.

Figure 8. ***Chaetonotus cordiformis*** next to a desmid. Photo by Yuuji Tsukii, with permission.

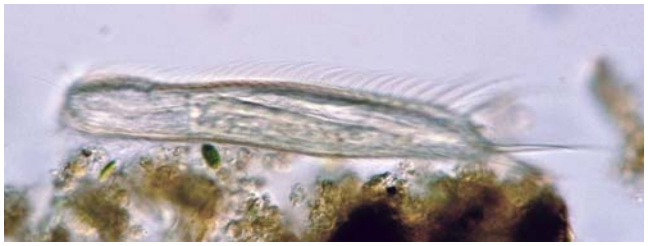

Figure 9. ***Chaetonotus zelinkai***, a moss-dwelling gastrotrich. Photo by Yuuji Tsukii, with permission.

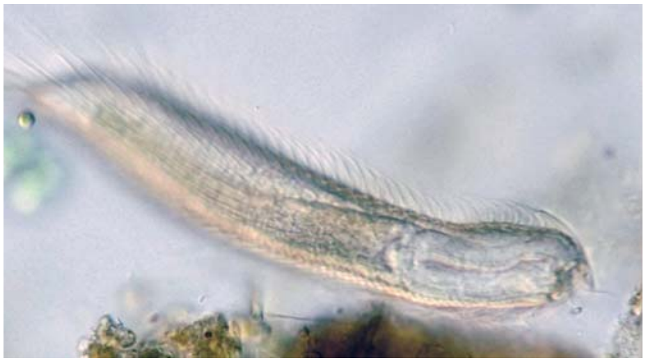

Figure 10. ***Chaetonotus zelinkai***, a peatland gastrotrich. Photo by Yuuji Tsukii, with permission.

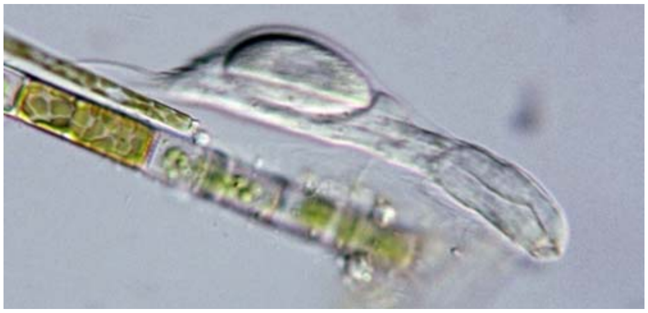

Figure 11. ***Ichthydium forficula***, a member of a genus that can occupy peatlands. Photo by Yuuji Tsukii, with permission.

Nemertea – Ribbon Worms

The ribbon worms are an unknown phylum to most of us. But those nemertines that live on land have learned about bryophytes. In 1915, Dakin described one of these as a new species *Geonemertes dendyi*, later moved to ***Argonemertes dendyi*** (Figure 12), from Western Australia. Anderson (1980) reported this species from Ireland, where it can be found among a thin layer of mosses on branches. Later, Anderson (1986) reported it from mosses and under bark in Ireland. Ribbon worms are clandestine species that one can rarely find in the open (Winsor 2001, pers. comm. 29 February 2012).

Argonemertes dendyi (Figure 12) is among the small fauna, measuring only 15 mm (Dakin 1915). It has multiple eyes, numbering as many as 30 or 40. As descendents from marine organisms, one of the major adaptations required by terrestrial nemerteans was a way to maintain sufficient hydration (Moore & Gibson 1985). The physiological mechanisms are not well understood but seem to involve mucous glands, blood and excretory system, and modulation of osmotic properties. These worms often travel with potted plants, and consequently they can be found in far-flung parts of the planet (Gibson 1995; Moore *et al*. 2001). Their hermaphroditic reproduction makes establishment of these travellers more likely to succeed.

Figure 12. ***Argonemertes dendyi***. Photo by Malcolm Storey through Creative Commons.

Leigh Winsor (pers. comm., 16 February 2012) is an avid seeker of terrestrial flatworms, but occasionally he also finds nemertines (Winsor 1985). He reports finding ***Argonemertes australiensis*** (Figure 13) under a thick mat of moss where it resided on a rotting log in a closed forest in southwest Tasmania. That is impressive for a worm that is 40 mm long (Hickman 1963; Moore 1975; Mesibov 1994). The egg capsules typically occur in rotting logs in August and March (Winsor 1996/97). These eggs are clear, jelly-like, and oblong, ca 10 mm long X 3 mm diameter.

Figure 13. ***Argonemertes australiensis*** extracted from moss on a log. Photo by Leigh Winsor, with permission.

This strange nemertine uses its proboscis to escape. When in a hurry, the worm quickly everts the proboscis and uses it as a muscled anchor to pull its body forward rapidly as the proboscis once again returns to its internal lodging (Figure 14). This rapid proboscis also out-paces its Collembola and other prey, permitting the worm to capture its dinner. This species comes in three very distinct color varieties (Mesibov 1994), most likely permitting it to survive in its diverse habitat where different predators may lurk in different locations, a phenomenon we will discuss later for tropical frogs.

Figure 14. ***Argonemertes australiensis*** with an extended proboscis. Photo by Leigh Winsor, with permission.

Platyhelminthes – Flatworms

Most of us in the pre-DNA-biology generations learned about flatworms in high school because it was easy to do experiments with ***Dugesia*** (see *e.g.* Saló & Baguñà 2002), known to most of us as *Planaria*. This animal has a distinguishable head with two eyes, and it was relatively easy to cut the head in half and watch two heads develop. This novel exercise opened discussions about development and other topics and provided a memorable experience that endeared the flatworms to us for life.

Most of the **turbellaria** (Figure 1), formerly a class within the phylum **Platyhelminthes**, are nocturnal and free-living, and it is among this group that one finds a small number of bryophyte-dwellers. The group is not monophyletic and is no longer recognized taxonomically, but the concept of **turbellaria** is useful for our purposes as all the bryophyte dwellers are in this group of non-parasites. The **turbellaria** lack a true body cavity and are shaped like a large ciliate protozoan and actually have a covering of cilia that permits them to glide (Hingley 1993). But they are multicellular, somewhat flattened, as their phylum name implies, where *platy* means flat and *helminth* means worm. This flattening permits them to obtain oxygen throughout their bodies, which lack circulatory and respiratory organs. They sport a simple digestive system, nervous system, and excretory system, and they seem to lack any sort of physiological or anatomical adaptations for conserving water, but they may be able to conserve water through alternative biochemical excretory pathways (Winsor *et al*. 2004). They even have eyespots and a simple brain (Hingley 1993).

Reproduction in the phylum may be by simple division (fission), whereas almost all turbellarians are **simultaneous hermaphrodites** (have both sexes at the same time). Among the family Typhloplanidae, the eggs may be thin-shelled in summer and hatch within days of being laid, but winter eggs are often thick-shelled and may be dormant (Pennak 1953; Domenici & Gremigni 1977; Hingley 1993). In the Typhloplanidae, these thick-shelled eggs can survive desiccation, whereas mature individuals might migrate to more moist, deeper levels. In other terrestrial flatworms, egg shells are typically thick (Figure 15), but the process of laying down the shell is different from those of the Typhloplanidae, and their ability to survive harsh conditions is unknown. These process differences may relate to differences between freshwater and terrestrial triclads (Winsor 1998a).

Figure 15. Eggs of a terrestrial flatworm. Photo by Alastair Robertson and Maria Minor, Massey University, Copyright SoilBugs, published by permission.

Bryophyte Habitat Constraints

Leigh Winsor, who has spent more than 40 years studying terrestrial flatworms, says that in wet forests the bryophytes are generally too adherent to the substrate to permit the (large) flatworms to move beneath the moss (Leigh Winsor, pers. comm. 16 February 2012).

Furthermore, unlike many of the invertebrates that seek mosses to maintain moisture, the flatworms seek a fairly smooth surface to which they can adhere their ventral surface, thus minimizing water loss. I would suggest further that the hygroscopic mosses might actually absorb surface water from the flatworms in drying conditions, further drying them. Nevertheless, the bryophyte mats do offer a substrate where the flatworms can pursue their prey (Leigh Winsor, pers. comm. 16 February 2012). And some seem to solve the problem of water loss by twisting into a knot that glues the ventral surface to itself (Figure 16). On the other hand, in excessively wet conditions, the terrestrial flatworms may use mosses to prevent getting too wet by crawling up into the moss and away from **frank water** (obvious pools of water).

Figure 16. ***Australopacifica*** sp. in knot on moss in New Zealand. Photo by Alastair Robertson and Maria Minor, Massey University, Copyright SoilBugs, published by permission.

Following Schultze (1857), who suggested that terrestrial planarians are likely to exhibit a rich fauna concealed in damp mosses, under stones, and other habitats where moisture is sufficient to maintain them, Davison *et al.* (2008, 2009) report on bryophilous microturbellarians from northwest Alabama, USA. These smaller versions are able to live among mosses on tree trunks and rocks.

The terrestrial flatworm ***Tasmanoplana tasmaniana*** (Figure 17), a species widespread in a variety of habitats throughout Tasmania, has also been found beneath moss in a temperate rainforest near Fourteen Mile Creek, SW Tasmania (Leigh Winsor, pers. comm. 16 February 2012). The area was very wet and the bryophytes and logs were saturated with water.

Figure 17. ***Tasmanoplana tasmaniana***, a flatworm that lives in mosses in Tasmania. Photo by Leigh Winsor, with permission.

Bryophytes provide a moist habitat where zoospores of such parasites as the **chytridiomycosis** fungus can survive (Dewel *et al.* 1985). One must wonder how bryophytes may play a role in harboring other parasites, or conversely, in providing antibiotics that deter them.

One mossy habitat that may be suitable for larger planarians is on leaves covered with epiphylls, as seen in ***Pseudogeoplana panamensis*** (Figure 18). The surface is relatively flat, and the mosses, liverworts, and other epiphylls can maintain greater moisture levels than a "clean" leaf surface. This relationship remains unstudied.

Figure 18. This flatworm, possibly ***Pseudogeoplana panamensis***, is on a palm leaf covered with lichens. Photo by Brian Gratwicke through Creative Commons.

Food Sources

When active, **microflatworms** feed on **protozoa**, **nematodes**, **rotifers**, **tardigrades**, **insect** larvae (Figure 19), and **algae** (Kolasa 1991; Davison *et al.* 2008) with which they share their mossy home. As suggested by Davison, it appears that one attraction for these **flatworms** in moss communities is the available **tardigrades** (Figure 20). **Flatworms** are known to eat **mosquito** larvae (Figure 19), so it is likely that they are able to eat **Chironomidae** (**midge**) larvae that live among the leaves of aquatic mosses and liverworts. Some **microturbellarians** are known to house green **algae** as symbionts (Kolasa 1991), presumably contributing to oxygen, but possibly also contributing carbohydrates. Such a relationship is unknown among moss-dwellers, but certainly it would be worthwhile to search for such symbionts. We do know that some of the tardigrades eat diatoms, a group of algae common on bryophytes, even in some terrestrial habitats, making algae part of the food chain (Bartels 2005).

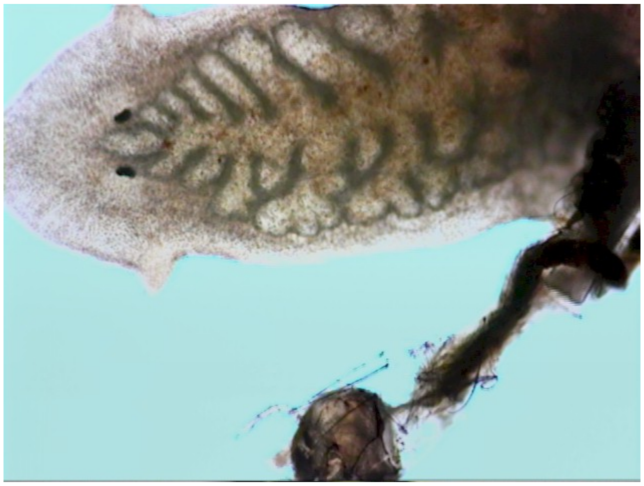

Figure 19. **Flatworm** feeding on a **mosquito** larva. Photo by Paul G. Davison, with permission.

Figure 20. **Flatworm** eating **tardigrade**. Photo by Paul G. Davison, with permission.

Davison *et al.* (2009) experimented with prey choice among flatworms from epiphytic mosses in Alabama, USA. The flatworms had a strong preference for the rotifer ***Philodina roseola*** (Figure 21) over the nematode ***Panagrolaimus***, both of which occur on bryophytes (Hirschfelder *et al.* 1993; Shannon *et al.* 2005). They either ingested these prey or sucked the contents out.

Figure 21. ***Philodina roseola***, a preferred prey organism for some flatworms. Photo from Proyecto Agua, with permission.

Protection or Predation?

The terrestrial flatworms seem to be relatively well protected from predation. Vertebrates seem to avoid them, most likely due to their mucous secretions when disturbed (Arndt & Manteufel 1925; McGee *et al.* 1996; Cannon *et al.* 1999). ***Arthurdendyus triangulatus*** (Figure 22) invokes violent reactions in earthworms when they make contact (Blackshaw & Stewart 1992 in Winsor *et al.* 2004). The flatworm wraps itself around the earthworm and secretes strong enzymes that turn the poor earthworm into soup! But then, earthworms are their primary source of food (Winsor *et al.* 2004). When this species is unable to find any food, it can survive more than 15 months at 12°C by digesting its own tissues – and shrinking (Blackshaw 1992, 1997; Christensen & Mather 1998a, 2001). However, at 20°C it dies within three weeks without food (Blackshaw 1992), so its presence at warmer temperatures needs to be timed with availability of a food source.

Figure 22. ***Arthurdendyus triangulatus*** on a bed of damp mosses. Photo © Roy Anderson, with permission.

Mosses can deprive the stoneflies of their flatworm prey. Wright (1975) found that flatworms in streams of North Wales were scarce on the undersides of stones and spent their lives confined to patches of mosses. Those that emerged from the mosses to venture to the undersides of rocks became easy prey for the stonefly *Dinocras cephalotes*.

Watch Out for Invasive Species

Arthurdendyus triangulatus (New Zealand flatworm, formerly *Artioposthia triangulata*; Figure 22) lives in damp terrestrial habitats such as those under logs, decaying wood, mosses, and leaves (Willis & Edwards 1977). ***Arthurdendyus triangulatus*** is a flatworm about 50 mm long, but can extend to 200 mm when in motion. Unlike the lab planaria with two large eyespots, ***Arthurdendyus triangulatus*** has a row of tiny black eyes extending down the pale-colored margin. These, as in planaria, are light sensitive and aid the animal in its navigation.

Arthurdendyus triangulatus (Figure 22) originated in New Zealand, but most likely hitch-hiked its way to Ireland among nursery plants, where it was able to spread to Scotland and Britain (Willis & Edwards 1977; Christensen & Mather 1998b; Baird *et al.* 2005). A member of this genus has also found its way to Macquarie Island in the subAntarctic (Winsor 2001). With its ability to travel at the rate of 28 cm per minute (Mather & Christensen 1995) and migrate as much as 20 m (Mather & Christensen 1998), there is concern about its spread in the British Isles where its habit of eating earthworms may be detrimental to their role in aerating the soil (Willis & Edwards 1977; Blackshaw 1990, 1997; Christensen & Mather 1995; Boag & Yeates 2001; Mather & Christensen 2001; Baird *et al.* 2005). One individual can eat about 1.4 *Eisenia foetida* earthworms each week (Blackshaw 1991) and has no species preference among earthworms. Furthermore, ***Arthurdendyus triangulatus*** thrives better in habitats with more earthworms (Mather & Christensen 2003).

Baird *et al.* (2005), concerned with its potential to drastically reduce the earthworm populations, studied the survival strategies of ***Arthurdendyus triangulatus*** (Figure 22) and its reproductive behavior under multiple conditions. As noted, planarians can survive for long periods of time without food, utilizing reabsorbed body tissue instead (Calow 1977; Ball & Reynoldson 1981). This permits them to survive winter and even allows them to lay eggs during that season (Baird *et al.* 2005). Whereas Christensen and Mather (1995) demonstrated that these flatworms could survive at least 15 months at 12°C without food, at lower temperatures (8°C), there was even less weight loss. In the lab, they had 100% survival under starvation for 4 weeks at 10°C, but at 15°C, 30% died during that time (Blackshaw & Stewart 1992). This greater loss of weight at temperatures above 14°C and the reduced survival at the warmer temperatures explains the greater spread seen in the northern compared to southern parts of the UK (Blackshaw 1992; Boag *et al.* 1993, 1995, 1998; Baird *et al.* 2005).

Because of these low temperature requirements, it is often necessary for these flatworms to burrow into the soil or travel down tunnels made by other invertebrates. The presence of bryophytes is likely to enhance the habitat by moderating the temperature and maintaining a greater level of moisture, but such bryophyte linkages have not been explored.

This species is a **K strategist** and is a hermaphrodite. Baird *et al.* (2005) demonstrated that ***Arthurdendyus triangulatus*** (Figure 22) could lay nine egg capsules in four months, with a mean of 4 eggs per capsule, producing 45 eggs per individual per year. It is able to store sperm after copulation (Baird 2002). Individuals cultured alone were able to produce eggs for up to eight months, indicating that sperm could be stored at least that long (Baird *et al*. 2005).

At temperatures above 10°C, there was a considerable decrease in hatching success, but eggs took longer to hatch at 10°C (Baird *et al*. 2000, 2005). These eggs, like the adults, can easily travel with potted plants from one country to another, and although the nursery trade is highly regulated, internet sales usually escape this close scrutiny.

Desiccation Tolerance

If there is a niche, there is most likely an organism to fill it. And eventually, there is most likely a biologist to study it, but for moss-dwelling **flatworms**, this has been a long time in coming. Although **flatworms**, known to most of us as human parasites and freshwater organisms, can be quite abundant among bryophytes, their presence there is barely known (Paul Davison, pers. comm., 8 August 2007).

Unlike rhizopods and other kinds of protozoa, moss-dwelling **microflatworms** are not known to enter a state of **cryptobiosis**. Davison has collected several ***Bryoplana xerophila*** (Figure 23) from mosses on a concrete wall and taken them to room-dry conditions, then revived them (Figure 24). These relatively unknown members of the bryophyte community do form cysts and resistant eggs (Figure 25-Figure 26) that permit them to survive the alternating wet and dry conditions found among bryophytes, especially those on tree trunks, despite the thinness of their mucous covering (Davison *et al*. 2008, 2009; Van Steenkiste *et al*. 2010). But for the Australian and New Zealand fauna, these cysts do not seem to occur on the bryophytes (Leigh Winsor, pers. comm. 16 February 2012). Winsor considers the bryophyte habitat there to be too exposed for the cysts or eggs and young to survive.

Figure 23. ***Bryoplana xerophila***, a moss-dwelling **microturbellarian** from Alabama. Photo by Paul G. Davison.

But for ***Bryoplana xerophila*** (Figure 23-Figure 26) survival on rocks is facilitated by the ability to encyst (Van Steenkiste *et al*. 2010). The cysts typically occur in concavities between moss leaves and the stem connection where interstitial water slows water loss. Once rewet, they begin moving within the cyst and within minutes (up to 15 minutes) break through the cyst wall and are on their way to an active life once again. They further ensure survival of the species by laying one or two eggs as they go into encystment.

Figure 24. Recently excysted terrestrial flatworm, ***Bryoplana xerophila***, and empty cysts. The dark brown eggs formed during encystment provide a second means of surviving. These **flatworms** were living in the moss ***Entodon seductrix*** (Figure 44) from a concrete block wall in Florence, Alabama, induced to encyst on a glass slide, then brought back to an active state. Photo by Paul G. Davison, with permission.

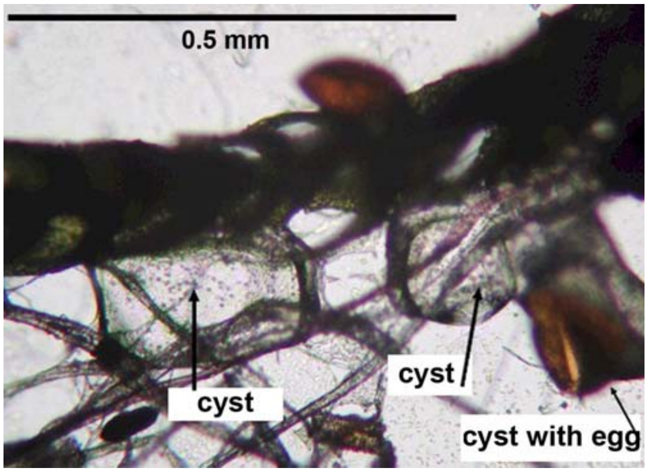

Figure 25. Cysts of flatworms, ***Bryoplana xerophila***, in desiccated state on moss. Photo by Paul G. Davison, with permission.

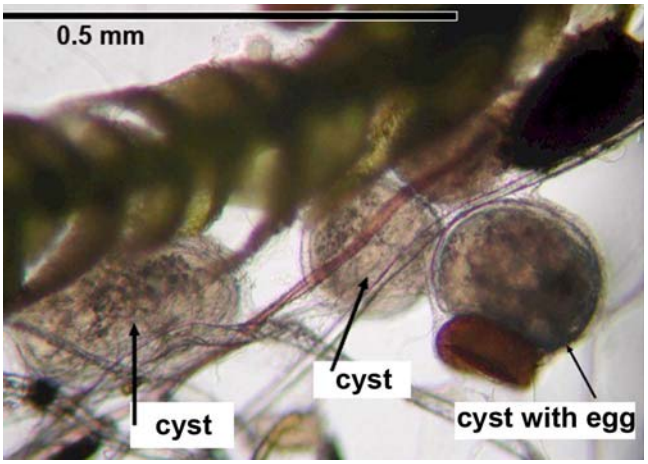

Figure 26. Cysts of flatworms, ***Bryoplana xerophila***, on a moss after rehydration. Photo by Paul G. Davison, with permission.

Terrestrial (Limnoterrestrial)

Fletchamia sugdeni (**Sugden's flatworm**, also known as **canary worm**; Figure 27-Figure 28) is a native of wet and dry forests in Victoria and Tasmania, Australia

(Winsor, 1977; Ogren & Kawakatsu 1991), where it can sometimes be found among bryophytes. Dendy (1890) noted that ***Fletchamia sugdeni*** was "remarkable for its habit of wandering about in broad daylight." That is truly remarkable for this bright yellow planarian. But the bright color might actually be a warning color that would be more useful in daylight.

Figure 27. ***Fletchamia sugdeni*** (**Sugden's flatworm, canary worm**), Victoria, Australia. Photo by Leigh Winsor, with permission.

Figure 28. ***Fletchamia sugdeni*** (**Sugden's flatworm, canary worm**) traversing a moss-covered substrate in Tasmania. This planarian certainly does not have camouflage on this bryophyte with its bright yellow color, but may gain protection with this warning coloration. Photo courtesy of Sarah Lloyd.

The bright yellow ***Caenoplana citrina*** (*C. barringtonensis* syn.; Figure 29) is known from mosses at Barrington Tops, New South Wales (Wood 1926). It resembles ***Fletchamia sugdeni*** (Figure 27-Figure 28), but has two stripes down its dorsal surface.

Wood (1926) noted that ***Caenoplana coerulea*** (Figure 30-Figure 31) was the commonest species collected near the Barrington River, New South Wales, being found on rocks, damp moss, the trunks of trees, and under rotten logs. Its thick-walled egg is in Figure 32.

Figure 29. A bright-colored flatworm, probably ***Caenoplana citrina*** (formerly *C. barringtonensis*), on a bed of mosses. Photo by Ian Sutton through Flickr Creative Commons.

Figure 30. ***Caenoplana coerulea***, a moss-dweller, among other habitats, displaying its blue color. Photo by Peter Woodard through Wikimedia Commons.

Figure 31. ***Caenoplana coerulea***, a moss dweller in a darker form. Photo from <www.aphotofauna.com>, with permission.

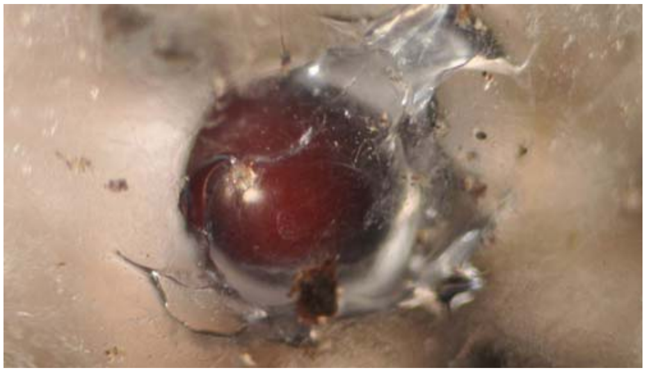

Figure 32. ***Caenoplana coerulea*** egg laid in captivity. Photo by Jacobo Martin through Flickr Creative Commons.

Elsewhere in Great Britain, McDonald and Jones (2007) compared habitat and food preferences for two species of ***Microplana***, a terrestrial flatworm. The habitat choices in the experiment were not germane to bryophytes, but in addition to the artificial cover, they did find cocoons at a 7 cm depth in ***Sphagnum*** in the garden. This genus is likely to occur among bryophytes elsewhere and thus should be sought there. The food preferences of ***Microplana terrestris*** (Figure 33) were gastropods [***Arion hortensis*** (slugs, Figure 34) and ***Discus rotundatus*** (snail, Figure 36)]. ***Microplana scharffi*** (Figure 37) preferred earthworms but also ate slugs. Both of these species avoided eating live animals and instead fed on damaged animals (see Figure 35). McDonald and Jones suggested that centipedes may contribute to that damage in nature.

Figure 33. ***Microplana terrestris*** in its grey form. Photo by Brian Eversham, with permission.

Figure 34. ***Arion hortensis***, a food source (when dead) for ***Microplana terrestris***. Photo © Roy Anderson, with permission.

Figure 35. Land planarians eating dead earthworm and dead springtails in a rainforest gully, Canberra, Australia. Photo by Andras Keszei, with permission.

Leigh Winsor (pers. comm. 16 February 2012) reports that some terrestrial flatworms have a "most unpleasant taste" (he tasted some species!) that may have a repugnatorial function. Whether brightly colored Australian flatworm species have a repugnant or toxic taste to birds or other predators is not presently known, but the yellow coloration could serve as either Batesian or Muellerian mimicry.

Figure 36. ***Discus retundatus***, a food source (when dead) for ***Microplana terrestris***. Photo by Francisco Welter Schultes through Creative Commons.

Figure 37. ***Microplana scharffi***, a flatworm that eats dead earthworms and slugs among bryophytes and elsewhere. Photo from <www.aphotofauna.com>, with permission.

Hyman (1957) reported the planarian ***Gigantea cameliae*** (identified at that time as *Geoplana cameliae* and moved to *Gigantea* by Ogren & Kawakatsu 1990) on wet mosses at night in Trinidad. This 25 mm, up to 50 mm (Hyman 1941), planarian is larger than most moss dwellers, especially among the terrestrial taxa. This species is also present in Panama (Hyman 1941), but there seem to be no reports of it from bryophytes there.

One mossy habitat where these **microturbellarians** seem to be quite rare, however, is in the Antarctic. Nevertheless, Schwarz *et al*. (1993) did find one **catenulid flatworm** inhabiting the mosses of flushes near the Canada Glacier on continental Antarctica.

Epiphyte Dwellers

The **microturbellarians** are those free-living flatworms (Platyhelminthes) generally <1 mm in length (*e.g.* Figure 23; Davison *et al*. 2008). They typically live in water films, making them essentially aquatic (**limnoterrestrial**). Bryophytes can provide such water films, so it is no real surprise that they (**Rhabdocoela**,

Typhloplanidae) are common 1-2 m above ground among epiphytic mosses. Davison *et al.* (2008) sampled longleaf pine-mixed hardwoods, *Juniperus* in limestone cedar glades, northern hardwoods above 1600 m elevation, dwarf oak forest, upland hardwoods-pine, and planted roadside pecan trees in the southeastern USA. They found that the tree trunk dwellers are rare in cool, mossy stream ravines, where one might have expected them, but are common in areas prone to rapid drying following rainfall – mosses on tree trunks fit this need well. In such locations, Davison *et al*. have found that flatworms are quite common in association with mosses on hackberries and other trees in Florence, Alabama, USA. These mosses include ***Leucodon julaceus*** (Figure 38) on *Cornus florida* and ***Clasmatodon*** (Figure 39) on *Paulownia tomentosa*, all at least 0.3 m above ground, as well as on trees of open, urban habitats, including *Catalpa* sp., *Celtis* sp., *Cornus florida*, *Fraxinus* sp., *Liquidambar*, *Magnolia grandiflora*, *Quercus* spp., and *Ulmus* spp. They survive these habitats by forming thin-coated transparent mucous cysts, a mechanism not familiar in other habitats.

Figure 38. Epiphytic ***Leucodon julaceus***, a known habitat for flatworms. Photo by Janice Glime.

Figure 39. ***Clasmatodon parvulus*** with capsule, a home for flatworms. Photo by Paul G. Davison, with permission.

Davison later collected **flatworms** from mosses on two white oaks in northern Tennessee, suggesting that they may be widespread, at least in these south temperate areas (Paul Davison, pers. comm. 12 January 2008). The collections were from the mosses ***Forsstroemia trichomitria*** (Figure 40) and ***Haplohymenium triste*** (Figure 41) growing 1.7-2 m above the ground. Although these had 10 and 6 turbellarians, a sample of ***Hypnum curvifolium*** (Figure 42) from the tree base produced only one flatworm. Davison suggests that the **water bears** (tardigrades) are important determinants of the location of the **flatworms** as a food source, and **water bears** were much less abundant at the tree base.

Figure 40. ***Forsstroemia trichomitria*** on a tree trunk, providing a suitable habitat for flatworms. Photo by Janice Glime.

Figure 41. ***Haplohymenium triste*** on bark, a suitable habitat for flatworms. Photo by Robert Klips, with permission.

Figure 42. ***Hypnum curvifolium*** on bark at base of tree, a habitat unsuitable for tardigrades and flatworms. Photo by Robert Klips, with permission.

Although **flatworms** are known from dry mosses on rocks, these observations by Davison and coworkers (2008, 2009) appear to be the first discovery of their living among epiphytic bryophytes. There is at least one report of moss-dwelling turbellarians (on ***Eurhynchium oreganum***, Figure 43) on a wet log (Merrifield & Ingham 1998), but that is hardly similar to the dry habitat of a tree trunk. The **flatworms** are seldom abundant, with four or fewer from a clump being common. However, they can be as abundant as 20 in a palm-sized patch of moss. Although they are not abundant, they are frequent, despite the apparent dispersal problems they are likely to have.

Figure 43. ***Eurhynchium oreganum***, sometimes home to flatworms. Photo by Matt Goff, with permission.

Epilithic Dwellers

The **epilithic** (rock) dwellers, like the epiphytic dwellers, must tolerate frequent drying on a very xeric habitat. For these limnoterrestrial microturbellarians, a bare rock is a challenge beyond their means. But bryophytes hold moisture and accumulate soil, making this austere habitat more turbellarian friendly. It was from this habitat that Van Steenkiste and co-workers (2010) described the new genus – ***Bryoplana***. They appropriately named the new species, the first in the genus, ***Bryoplana xerophila*** (Figure 23-Figure 26). This one was found among mosses, including ***Entodon seductrix*** (Figure 44), and soil on a concrete wall in northern Alabama, USA. Not only is it a new genus, but it is the first limnoterrestrial member of the **Protoplanellinae** to be found in North America and is among only a few rhabdocoels from a dry habitat. This species is easy to miss, measuring only 0.4-0.5 mm long.

Figure 44. ***Entodon seductrix***, a moss where the flatworm ***Bryoplana xerophila*** is known to encyst. Photo by Robert Klips, with permission.

These particular **microturbellarians** had guts filled with **bdelloid rotifers**, common inhabitants of mosses (Van Steenkiste *et al.* 2010). They ingested small ones within a minute, but for larger rotifers, they drained them instead, using a sucking action by the pharynx.

Other genera and species of limnoterrestrial turbellarian moss-dwellers include ***Acrochordonoposthia***, ***Adenocerca***, ***Chorizogynopora***, ***Haplorhynchella paludicola***, ***Olisthanellinella***, ***Olisthanellinella rotundula***, ***Perandropera***(?), and ***Rhomboplanilla bryophila*** (Van Steenkiste *et al.* 2010). Association of ***Acrochordonoposthia conica*** with mosses seems to be particularly well documented (Reisinger 1924; Steinböck 1932; Luther 1963). ***Rhomboplanilla bryophila*** is even named for its preference for a bryophyte habitat. The absence of images of these taxa on the internet is a testimony to how little we know of them.

Aquatic Bryophyte Habitats

Most of the non-parasitic **flatworms** (formerly **Turbellaria**) are known from aquatic habitats. Stern and Stern (1969) found numbers among cold springbrook mosses (***Fontinalis antipyretica***, Figure 3) in Tennessee to be similar to those on stones, ranging 1-5 per 0.1 m^2 on stones and 1-4 per 0.1 m^2 among the moss-algae associations. Frost (1942) found the fauna of **turbellarians** among mosses [mostly ***Fontinalis squamosa*** (Figure 45), ***F. antipyretica***, and ***Platyhypnidium riparioides*** (Figure 46)] in her River Liffey Survey, Ireland, to be less than 0.1% of the non-microscopic fauna. Berg and Petersen (1956) reported ***Schmidtea lugubris*** (formerly *Planaria lugubris*; Figure 47) and ***Dendrocoelum lacteum*** (Figure 48-Figure 49) from beds of ***Fontinalis dalecarlica*** (Figure 51) in Store Gribsø Lake, Denmark. **Turbellarians** are not generally a dominant component of the aquatic bryophyte fauna.

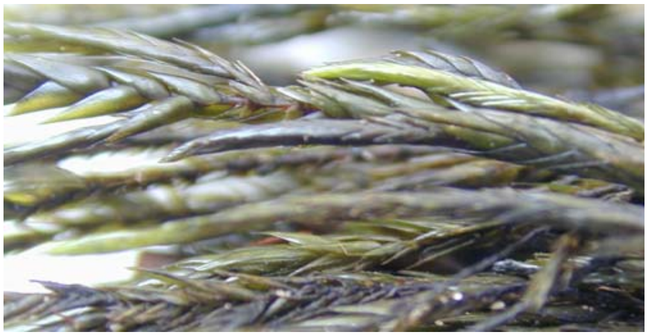

Figure 45. ***Fontinalis squamosa***, a common habitat for stream fauna, including flatworms. Photo by Michael Lüth, with permission.

In a springbrook in Meade County, Kentucky, USA, flatworms were very abundant at one sampling station on the flattened moss ***Fissidens fontanus*** (Figure 52), ranging from ~92 per 0.1 m^2 in June to ~1200 in January, but at another station, the same moss had numbers ranging from ~7 to ~300 in November and March respectively. In the marl riffles, the highest number was 1, and in rubble riffles it was not found. The flatworm ***Phagocata velata*** (see Figure 53) was the most abundant flatworm on ***Fissidens fontanus*** as well as under flat stones, logs, twigs, and debris, always in fast currents.

Figure 46. ***Platyhypnidium riparioides*** in Europe. This species can be submerged or emergent. Photo by Michael Lüth, with permission.

Figure 47. ***Schmidtea lugubris*** (formerly ***Dugesia lugubris***) from Crowland, Lincs, UK. Photo by Roger S Key, with permission.

Figure 48. ***Dendrocoelum lacteum*** female in extended position. Crowland, Lincs, UK. Photo by Roger S. Key, with permission.

Figure 49. ***Dendrocoelum lacteum*** female in contracted position. Note the two eyes. Crowland, Lincs, UK. Photo by Roger S. Key, with permission.

Figure 50. ***Dendrocoelum lacteum*** female with recently deposited egg. Crowland, Lincs, UK. Photo by Roger S. Key, with permission.

Figure 51. ***Fontinalis dalecarlica***, suitable home for the flatworm ***Dendrocoelum lacteum***. Photo by Janice Glime.

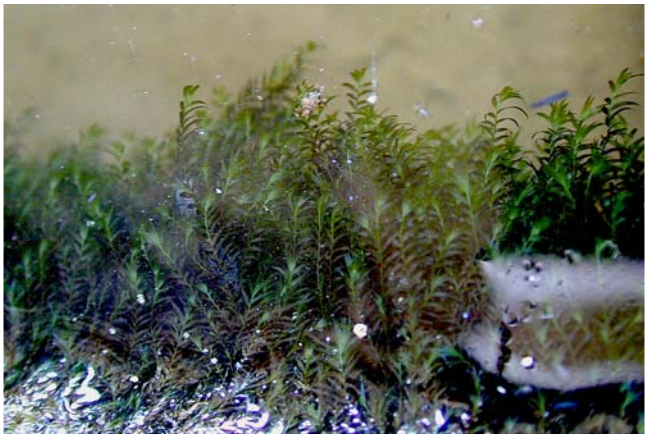

Figure 52. ***Fissidens fontanus***, showing the flat fronds. Photo by Michael Lüth, with permission.

The well-known planarian ***Dugesia dorotocephala*** finds "moss and sand quite acceptable," preferring them over silt, but less than rocks or leaves (Figure 54; Speight & Chandler 1980). ***Phagocata gracilis***, a moss-preferring species, selected temperatures of 4-22°C, preferring 14.8°C on rocks and 12.6°C on moss. I have to wonder if that was oxygen-related, with mosses taking up oxygen at night. ***Phagocata velata***, on the other hand, preferred living on rocks and migrated mostly to a temperature range of 16.0-20.5ºC, with a temperature preference of 17.8ºC.

Figure 53. ***Phagocata vitta***. Photo by Malcolm Storey through Creative Commons.

Figure 54. ***Dugesia*** sp. in its rock habitat, which is usually preferred to mosses. Photo by Janice Glime.

In a New Zealand springbrook, ***Neppia montana*** (Figure 55) seemed to have a preference for the ***Achrophyllum quadrifarium*** (=***Pterygophyllum quadrifarium***; Figure 56) over the other two mosses in the stream (***Fissidens rigidulus***, ***Cratoneuropsis relaxa***) (Cowie & Winterbourn 1979). The ***A. quadrifarium*** occurred in a zone extending from the stream margins on up the banks where it received spray from the rapidly moving water. This is a large, pleurocarpous moss with flattened branches.

Figure 55. ***Neppia montana***, a flatworm that prefers ***Achrophyllum quadrifarium*** over other moss species in its stream. Photo by Paddy Ryan, with permission.

Figure 56. ***Achrophyllum quadrifarium***, home of the flatworm ***Neppia montana*** in a New Zealand springbrook. Photo by Jan-Peter Frahm, with permission.

Extraction and Observation Techniques

The **flatworms** represent a little known fauna of terrestrial bryophytes. Brigham (2008) suggests that one reason for this may be the lack of a satisfactory extraction technique. She compared the traditional beaker extraction method with a Baermann funnel method modified by Paul Davison (see Vol 2, Chapter 4-1). Using the beaker method, she was unable to find any **microturbellarians** among the mosses. However, she found them in multiple samples using the modified Baermann funnel.

Since these organisms are too small and too numerous for quantification in the field, they must be transported to the laboratory for extraction. Examination of live organisms makes them both easier to locate and easier to identify (Kolasa 2000). Warm temperatures and lack of oxygen quickly become lethal, not to mention confined but hungry predators, so samples must be kept in a cooler (Stead *et al*. 2003) and processed within a few hours of collection. Preserved animals usually cannot be identified.

Winsor (1998b) suggests narcotizing the flatworms with 10% ethanol, then preserving them with a formaldehyde calcium cobalt fixative. They can be cleared for examination in terpineol, imbedded in paraffin wax, and serially sectioned. The sections can be stained to make internal systems more visible. Long-term storage may require 80% ethanol, and those for DNA extraction should be fixed in 100% ethanol.

Slowing down live animals for identification can be challenging, but Thorp and Covich (1991) recommend placing them in a small volume of water on ice. Alternatively, they can be anaesthetized with a mix of 7% ethanol, 0.1% chloretone, and 1% hydroxylamine hydrochloride.

One trick to help in identification of soft-bodied taxa when time is at a premium is to use a video camera on a sample under appropriate microscope magnification (Stead *et al*. 2003). Davison and Kittle (2004) suggest making a miniature aquarium using microscope slides as a housing for both culturing these organisms and examining them (Figure 57-Figure 59).

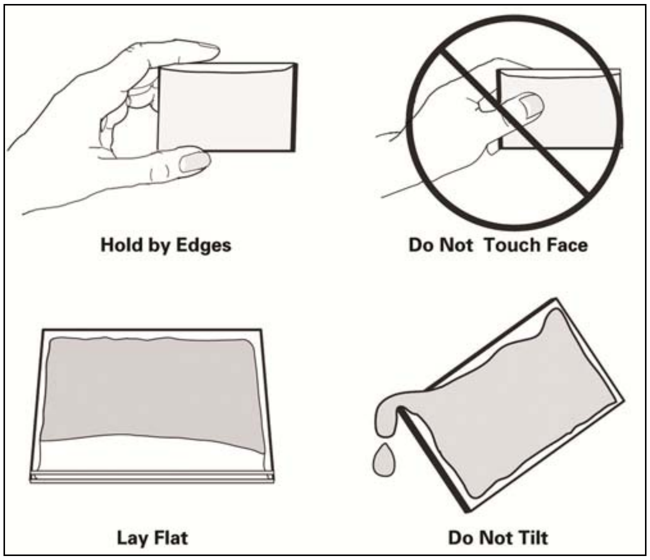

Figure 57. Method for constructing a microchamber for observing flatworms and other small invertebrates. Modified from Davison 2006.

Food choices in the lab may differ from those in the field where a wider array of choices is available. Gut analyses are used for larger organisms to determine diet in the field. But obtaining samples for gut analysis in flatworms and other tiny invertebrates is a bit more tricky than that used for insects and larger invertebrates. One can't pull or dissect the gut from the animal. Instead, Young (1973) sacrificed the animals another way. He squashed them with a coverslip on a glass slide. But first the flatworms had to take a bath by crawling around in tap water to remove adhering items that might look like food in the squash. Then they were placed on the "squash" slide, all within an hour of collection to avoid extensive digestion of the food items.

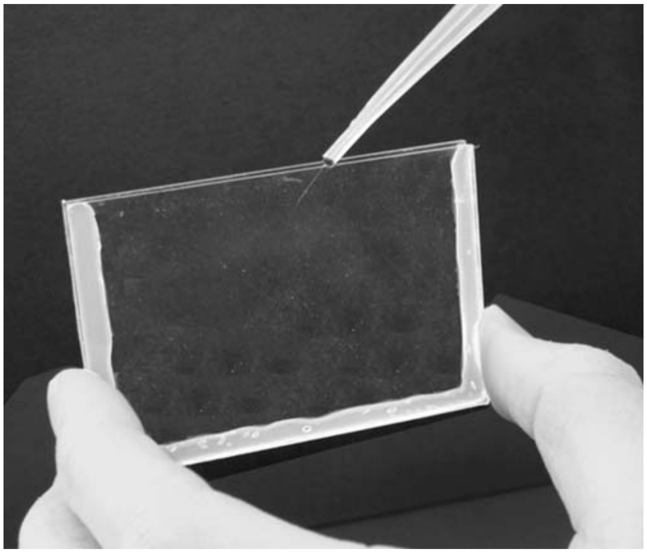

Figure 58. Filling completed microchamber built by above construction. Photo by Paul G. Davison from Davison 2006.

In 1979, Feller *et al*. demonstrated the usefulness of immunological techniques for identifying major taxonomic groups in the guts of these small organisms. Young and Gee (1993) used the precipitin test, a serological technique, to identify major taxonomic groups in the gut. Schmid-Araya *et al*. (2002) first anaesthetized the organisms with CO_2 to prevent regurgitation, although it was not clear if this method was used to identify flatworm gut contents. More recently, DNA extraction and amplification provide a means of identifying gut material from such small meiofauna (Martin *et al*. 2006), providing a potential tool for flatworms.

Figure 59. Occupied microchamber (with flatworms and moss). Image modified from Davison 2006.

Summary

Fissidens fontanus and ***F. brachypus*** can grow epizootically on **sponges**. Humans may enjoy a mattress made with mosses and sponges.

Gastrotrichs survive the dry stages of mosses by producing larger eggs that survive due to heavier shells. They seem to prefer lower velocity areas where sediments can accumulate and can be relatively common in peatlands.

Microflatworms are mostly from aquatic habitats where they are known from ***Fontinalis antipyretica***, ***F. squamosa***, and ***Platyhypnidium riparioides***. They survive winter and dry periods like the **gastrotrichs**, as thick-shelled eggs, but they can also form cysts, particularly among epiphytic mosses. They are actually more abundant on tree trunks that are prone to drying out than they are in cool, mossy stream ravines. These terrestrial species seem to be most abundant among the mosses where they can find **tardigrades** to eat. The triclad flatworm ***Phagocata gracilis*** actually prefers moss habitats.

A Baermann funnel seems to work best for extracting microturbellarians from terrestrial mosses.

Acknowledgments

Paul Davison kept me informed of new finds, which were especially important for these groups where so little is known of their bryophyte relationships. Filipe Osorio added information on tropical Platyhelminthes. Sarah Lloyd has kept me in mind as she finds new invertebrates and takes pictures for me, including the canary worm. Yuuji Tsukii gave me permission to use his wonderful collection of images. Leigh Winsor has been invaluable in helping me to identify the flatworm and nemertine worm pictures, to understand these species better, and to review the revised chapter (February 2012). Thank you to Larry Williams for catching some of my errors and notifying me.

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CHAPTER 4-3
INVERTEBRATES: NEMATODES

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CHAPTER 4-3
INVERTEBRATES: NEMATODES

Figure 1. Nematode taken from epiphytic bryophytes. Photo by Paul G. Davison, with permission.

Nematoda – Roundworms

The failure of many soil biologists to distinguish between bryophytes and what the rest of us think of as soil (*i.e.* not including bryophytes) has made researching the bryophyte-dwelling nematodes and annelids particularly difficult. Although we usually think of the nematodes (roundworms as soil organisms, they join the many other invertebrates in living among bryophytes as well (Allgén 1929; Overgaard-Nielsen 1948, 1949; Zullini 1970, 1977; Wood 1973; Yeates 1979; Caldwell 1981a, b; Zullini & Peretti 1986; Kinchin 1989; Merrifield 1992; Steiner 1994a, b, c, 1995a, b; Gadea 1964a, b, 1995; Linhart *et al.* 2000a, b, 2002a). Even the pendant moss ***Barbella asperifolia*** (see Figure 2) can be inhabited by nematodes (Noguchi 1956). The most common moss-dwelling nematodes worldwide are ***Plectus*** (Figure 3) (named for its twisted excretory tract) and ***Eudorylaimus*** (Figure 4; Overgaard-Nielsen 1948; Brzeski 1962a, b; Gadea 1964b; Eliava 1966, Spaull 1973).

Figure 2. ***Barbella*** sp., demonstrating the aerial habitat of some **nematodes**, with another pendant moss, ***Meteorium*** sp. Photo by Janice Glime.

Figure 3. The tail end of the nematode genus ***Plectus***. Photo by Peter Mullin, with permission.

Figure 4. Head of ***Eudorylaimus*** juvenile from Costa Rica. Photo by Melianie Raymond, with permission.

Most of the nematodes that inhabit mosses are less than 1 cm in length (Poinar 1991). Their digestive tract has a. mouth and anus, and it is the structure of this tract that determines many species differences in these animals. They get their gases by simple diffusion, and thus living deep in mosses can present a problem. The head possesses sensory papillae. Reproduction may be sexual or by parthenogenesis. No known species is hermaphroditic.

Densities and Richness

Kinchin (1992) claims that nematodes are common in most moss samples and are easy to see while they are alive due their thrashing movements. Fantham and Porter (1945) reported up to 480 per gram of moss. In their survey of Canadian moss fauna, they considered them to be the most abundant of the (terrestrial) metazoan fauna. Frost (1942) reported a mean of 56 and 38 individuals per stream sample (200 g). These represented only 0.41 and 0.3% of the fauna, respectively. In a high mountain brook, in the Colorado Rocky Mountains, Elgmork and Sæther (1970) reported that nematodes, primarily from the family Tylenchidae, were most abundant in the locations where there were mosses, but were not necessarily on the mosses – they were in all locations in the stream.

Despite the large numbers, not many species are known from bryophytes. Hingley (1993) reported that only 30 species were known from ***Sphagnum*** (Figure 5), despite 30,000 species known from soil or fresh water. One reason for the small number of species known is that they are quite difficult to identify. Table 1 indicates species richness of nematodes in a number of locations, demonstrating several habitats.

Figure 5. Mix of ***Sphagnum*** typical of that found in north temperate bogs and providing suitable nematode habitat. Photo by Janice Glime.

Table 1. Comparison of species richness of nematodes among mosses in various habitats. Table based on Hoschitz 2003.

Locality	# spp	Reference
Grassland & other non-woody		
Seeland, Denmark	48	Micoletzky 1929
Signy Island, Antarctic	30	Spaull 1973
Mols, Denmark	27	Nielsen 1949
Pamir, Asia	10	Micoletzky 1929
Polar		
Ross Island, Antarctica	6	Wharton & Brown 1989
Dry Valleys, Antarctica	4	Freckman & Virginia 1993
Ross Island, Antarctica	2	Yeates 1970
Alpine Summit		
Dachstein, Austria	2	Hoschitz 2003

Habitat Needs

Some of the mossy habitats, especially in streams, might make it easy for a nematode to become dislodged. Kinchin (1989) points out that many of the moss taxa have a caudal adhesive organ that permits them to anchor themselves.

Moisture Requirements

The moss cushion is not homogeneous. Generally, one can identify a leafy canopy layer, a stem layer with reduced leaf cover, and the rhizoid layer (Kinchin 1989). Many nematodes are able to migrate vertically through these layers diurnally to escape the dry upper canopy in the daytime (Overgaard-Nielsen 1948, 1949). Overgaard-Nielsen recognized three ecological groups, based on their behavior in dealing with moisture needs:

1. Members of the largest group, including ***Plectus*** (Figure 3), migrate from the rhizoid layer to the canopy layer when the moss is damp.

2. Worms such as ***Aphelenchoides*** (Figure 6) with modest migrations move only from the rhizoid layer to the stem layer and only when the moss is saturated.
3. Non-migrating worms such as ***Dorylaimus*** (Figure 7) never venture from the rhizoid layer, regardless of the moisture level.

Figure 6. ***Aphelenchoides*** sp., a moss dweller in the rhizoid layer. Photo by Peter Mullin, with permission.

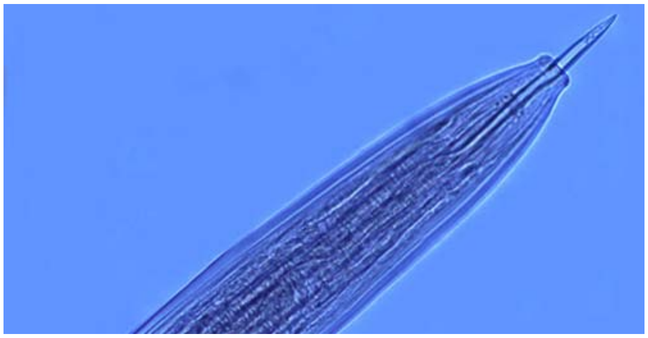

Figure 7. ***Dorylaimus*** sp. Photo by Aldo Zullini, with permission.

Moist mosses have more nematode species than dry ones (Kinchin 1989). Mosses that experience frequent desiccation episodes tend to have a more specialized moss fauna. In the ones that are dry most of the time, the fauna is primarily comprised of ***Plectus rhizophilus*** (Figure 8), a species that does not occur in the soil beneath the moss (Overgaard-Nielsen 1948, 1949). **Acrocarpous** moss cushions typically have more nematodes than **pleurocarpous** feather mosses (Kinchin 1989). Kinchin suggests that the water content in cushions is more favorable for movement.

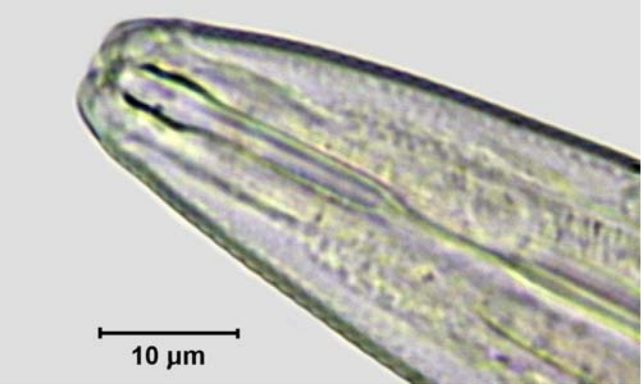

Figure 8. ***Plectus rhizophilus***, a nematode that specializes in dry moss habitats. Photo by Peter Mullin, with permission.

As in most non-arthropod invertebrates, water can be a limiting factor for nematodes. Womersley (1987) (in Wharton 2004) considered most of the moss-dwelling nematodes to be slow-dehydration strategists, whereas other nematodes may tolerate rapid dehydration of the habitat by having mechanisms that make their own dehydration slow. Hence, despite their need for water, they can be common in cryptogamic crusts. In just one of its faunal genera, the Konza Prairie crusts support 16 species in the genus ***Plectus*** (Figure 3; Figure 8). Beasley (1981) and Kinchin (1990) suggested that some nematodes actually require a dry phase in their life cycle.

Food Supply

Food supply may at times be an overriding factor in determining locations of moss-dwelling nematodes. Several researchers have suggested that food supply was a major controlling factor for nematode density in soil (Bunt 1954; Winslow 1964; Yeates 1967). Spaull (1973) suggested that food was likely to also be a determining factor in the moss community, at least in the Antarctic. Predominant food strategies of bryophyte-dwelling nematodes include predators (Barbuto & Zullini 2006) and bacteriovores (Lazarova *et al*. 2000) and food includes bacteria, algae, and protozoa (Poinar 1991). Mosses usually collect detrital matter that provides suitable habitat for Protozoa and bacteria.

Quality of Food

However, it is possible that it is the quality of food that matters. Spaull (1973) found that nematode abundance was not related to water content on Signy Island, but correlated with a low ratio of C:N (favoring bacteria) in the soil (including mosses), seemingly explaining the greater numbers associated with the grass *Deschampsia antarctica*, where C:N ratios were the lowest. Hingley (1993) indicated that the peatland nematodes did not eat the moss ***Sphagnum*** (Figure 5). Rather, they are likely to eat bacteria, protozoa, and small invertebrates.

Warming Effect among Bryophytes

Spaull (1973) and Holdgate (1964) consider the warming effect of solar radiation within the upper portion of the moss mat to determine activity of nematode moss dwellers. But this influence is only important near the surface, with its influence diminishing with depth (Longton & Holdgate 1967; Cameron *et al*. 1970). Nevertheless, bryophytes buffer the temperature of the soil beneath them, keeping it cooler in summer and insulating it against an early frost or cold when there is no snow cover.

Unusual Bryophyte Dwellings

It appears that some nematodes have found a cozy niche in **antheridia** of mosses (Figure 9). Lars Hedenäs (pers. comm. Aug. 2007) has found such nematodes in old perigonia of ***Homalothecium lutescens*** (Figure 10) collected in France by Gillis Een with one actually inside the spent antheridium. Could this be a common niche for some nematode taxa, or was this just an opportunist and rare occurrence?

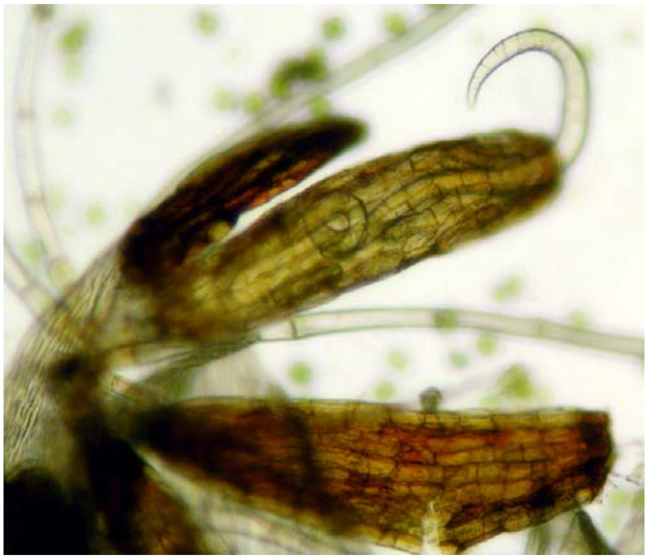

Figure 9. This nematode chose an antheridium of the moss ***Homalothecium lutescens*** for its home. Photo by Lars Hedenäs, with permission.

Figure 10. ***Homalothecium lutescens***, a moss where nematodes may dwell in the antheridia. Photo by Michael Lüth, with permission.

Substrate Preferences

Barbuto and Zullini (2006) found that despite highly variable densities of nematodes between samples and substrate of the mosses, the diversity and trophic group structure varied little. Predators dominated in these Italian samples. Soil as a substrate for the mosses seemed to favor a greater species richness and biomass, particularly for large species such as ***Aporcelaimellus obtusicaudatus*** (Figure 11-Figure 12; most likely a species complex; Mike Hodda, personal communication). In their study, ***Tripylella intermedia*** seemed to occur exclusively on mosses on rocks, but any other relationship to substrate was not clear. On the other hand, Eyualem-Abebe *et al.* (2006) reported it as a species of both mosses and soil. As in many other geographic areas, Barbuto and Zullini (2006) found that the two most common species were ***Prionchulus muscorum*** (Figure 13) and ***Plectus acuminatus***, occurring in nearly all samples. The greatest differences among European communities seemed to be between continental and Mediterranean communities.

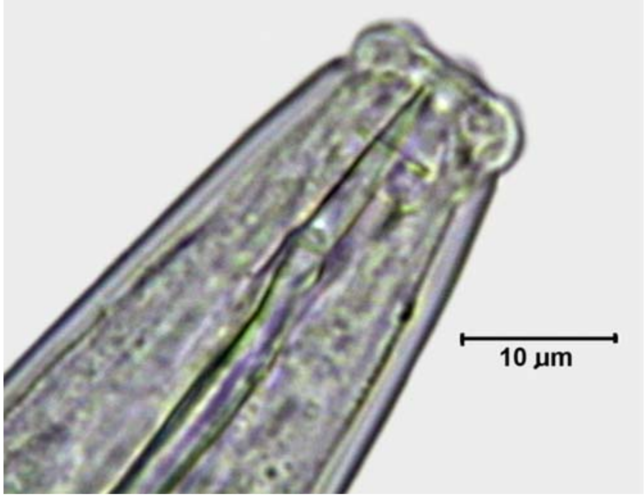

Figure 11. Head view of ***Aporcelaimellus***, a genus with the large ***A. obtusicaudatus*** preferring mosses on soil in an Italian study. Photo by Peter Mullin, with permission.

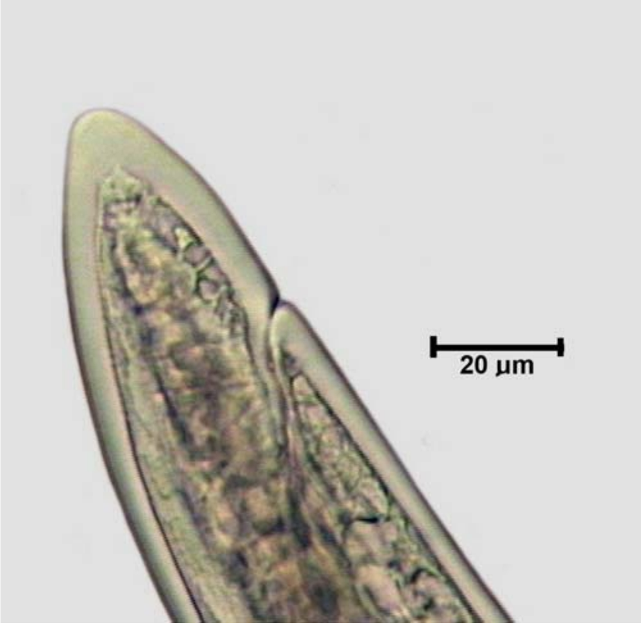

Figure 12. Tail view of ***Aporcelaimellus***. Photo by Peter Mullin, with permission.

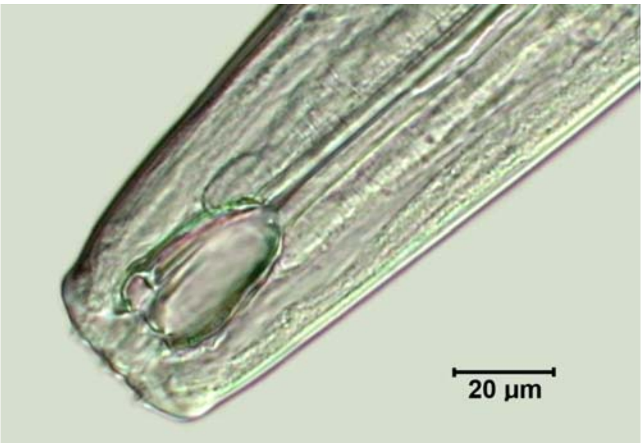

Figure 13. ***Prionchulus muscorum***, one of the two most common species among mosses in an Italian study. Photo by Peter Mullin, with permission.

Lazarova *et al*. (2000), in comparing nematode communities on the moss ***Hypnum cupressiforme*** (Figure 14) in Bulgaria, likewise found that abundance was quite variable among substrata (soil, stone, & tree trunks) and samples, and these likewise were similar in diversity, trophic group structure, and generic composition. They did, however, vary in species composition. Contrasting to the predatory dominance of nematodes in the broader range of European mosses studied by Barbuto and Zullini (2006), they found that the most abundant ***H. cupressiforme*** nematodes were bacteriovores. The proportion of predatory and omnivorous nematodes was quite low. They also found no clear substrate dependence of any species except for ***Chiloplectus andrassyi*** (Figure 15), which was most abundant among ***H. cupressiforme*** on stone.

Figure 14. ***Hypnum cupressiforme***, a preferred habitat for ***Chiloplectus andrassyi***. Photo by Michael Lüth, with permission.

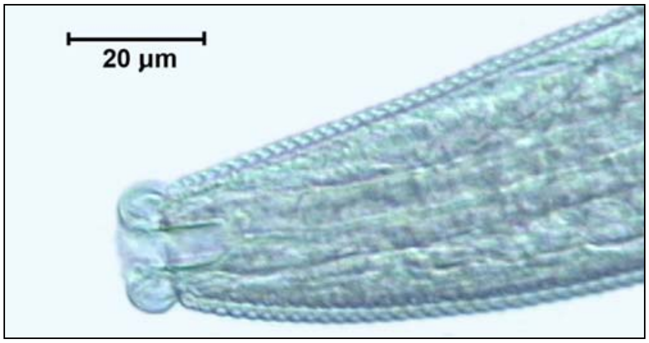

Figure 15. ***Chiloplectus*** sp., a member of a genus in which ***C. andrassyi*** seems to prefer ***Hypnum cupressiforme*** on stone. Photo by Peter Mullin, with permission.

Motility Constraints

Merrifield and Ingham (1998) considered that low densities of nematodes in some mosses may result from interference by the moss with the motility efficiency of the nematodes. Kinchin (1992) commented that live nematodes in mosses were easy to locate because of their thrashing movements. Overgaard-Nielsen (1948) described the genera ***Aphelenchoides*** (Figure 6), ***Monhystera*** (Figure 16), ***Plectus*** (Figure 8), ***Prionchulus*** (Figure 13), ***Teratocephalus*** (Figure 17), and ***Tylenchus*** (Figure 18) as moving by swimming (a rare event for most nematodes), thus requiring an accumulation of large quantities of water, but more likely they crawl in a thin film of water (Mike Hodda, personal communication). Nematodes are heavier than water and thus sink. The members of ***Eudorylaimus*** (Figure 19) are "powerful benders" that can move in a thin film of water. Although ***Eudorylaimus*** species are unable to inch or swim where they live on the moss, their bending ability permits them to attain a patchy distribution (Merrifield & Ingham 1998). The genera ***Monhystera*** and ***Plectus*** move like inchworms, using their caudal and labial gland adhesives (Overgaard-Nielsen 1948). But ***Tylenchus***, lacking the caudal glands, cannot creep, and basically becomes confined to its original location.

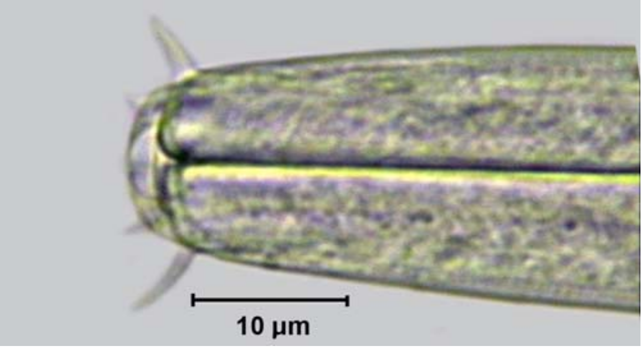

Figure 16. ***Monhystera*** sp., a nematode that moves like an inchworm among the mosses. Photo by Peter Mullin, with permission.

Figure 17. ***Teratocephalus terrestris***, representing a genus that is abundant in the Antarctic moss turf. Photo by Peter Mullin, with permission.

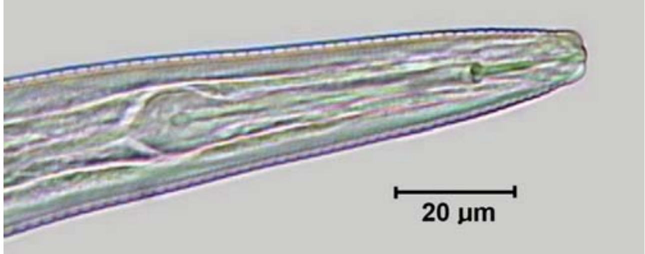

Figure 18. ***Tylenchus davainei***, in a genus where ***Tylenchus polyhypnus*** sets the record for a long dormancy of 39 years on a moss herbarium specimen. Photo by Peter Mullin, with permission.

Figure 19. ***Eudorylaimus*** juvenile. Photo by Peter Mullin, with permission.

Drought Strategies

As one would expect in a diverse group of organisms, the strategies for survival in a widely varying environment are also diverse. Like their mossy substrate, nematodes are able to go dormant for long periods of time (McSorley 2003). The record seems to be that of ***Tylenchus polyhypnus*** (literally meaning many sleeps). This moss-dweller became active again after 39 years of sleeping on a moss herbarium specimen! (Figure 18; Steiner & Albin 1946).

Eggs have a long longevity that permits them to remain quiescent until favorable conditions for growth and development return (Hingley 1993). They can survive drought, lack of oxygen, and a series of freeze-thaw cycles. Sex ratios can change to provide a more favorable ratio for the conditions at hand. And worms can cluster together in great aggregations in the soil, although I know of no reports of this phenomenon within moss habitats. Even adults can survive long periods of **anhydrobiosis**, a dormant state in which some invertebrates can survive desiccation. The lack of water prevents all enzymatic metabolic reactions (Clegg 1973; Barrett 1982).

Panagrolaimus (Figure 20) is known from a wide range of niches, including bryophytes, and they are bacterial feeders, a strategy that suits them well for dwelling among bryophytes (Shannon *et al*. 2005). They furthermore have the ability to survive extreme desiccation by entering the dormant state of **anhydrobiosis**, thus being able to dry as the bryophytes dry. Many of the ***Panagrolaimus*** species require preconditioning through slow desiccation. ***Panagrolaimus superbus***, on the other hand, has a fast desiccation strategy in which it can survive rapid desiccation, but whose chance of survival increases with preconditioning. Just as found for freezing tolerance (Crowe *et al*. 1984), there is a high correlation between **trehalose** induction and desiccation/anhydrobiosis survival (Shannon *et al*. 2005). It is therefore not surprising that ***P. superbus*** maintains a high level of trehalose even in its fully hydrated state, *i.e.*, 10% of its dry mass! It is possible, then, that it is this ready supply of trehalose that preadapts this species to survival of desiccation.

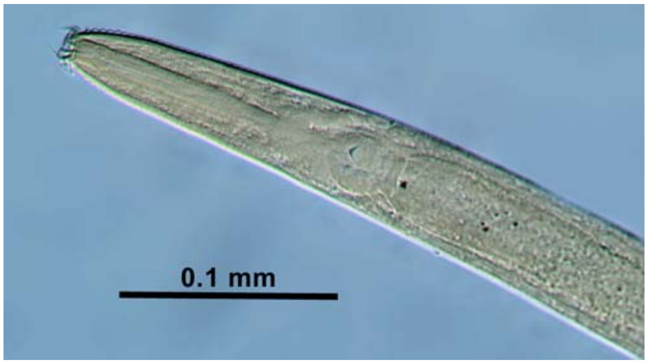

Figure 20. ***Panagrolaimus davidi***. Photo by Smithsonian Institution, National Museum of Natural History, Invertebrate Zoology through Creative Commons.

Panagrolaimus (Figure 20) species also exhibit behavioral adaptations to drying. They coil their bodies (Figure 21) and clump with other nematodes, both of which reduce the surface area from which water can be lost (Shannon *et al*. 2005).

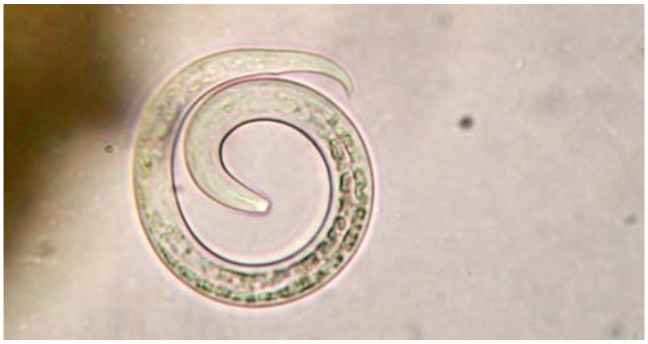

Figure 21. This moss-dwelling nematode is attempting to move with its longitudinal muscles. Coiled positions like this also reduce the rate of water loss as the habitat dries. Photo courtesy of Andi Cairns.

Both moss-dwelling nematodes and bryophytes have been described as **poikilohydrous**, meaning their water content will vary with that of the environment (Proctor 1979). Like most mosses, some nematodes can enter an anhydrobiotic state or become dormant. Unlike ***Panagrolaimus superbus***, most nematodes must dry slowly to survive (Crowe & Madin 1974) and eventually lose most of their water. ***Plectus*** (Figure 3), a common moss dweller, is a notable exception, being known as a "quick drier" (Mike Hodda, personal communication). Coiling their bodies (Figure 21) helps many nematodes to slow the water loss (Demeure *et al*. 1979), but Kinchin (1989) indicated that there are no observations to indicate whether or not this behavior is present in moss inhabitants Fortunately, Andi Cairns has photographed a moss-dwelling nematode doing just that (Figure 21).

Habitation of mosses themselves is a survival strategy. Mosses, especially cushions, dry slowly. A boundary layer of still air forms over the cushion. Evaporation must occur through this boundary layer. Thicker layers mean slower evaporation rates. The nematodes are nestled in the axils of leaves, so those in a cushion experience slower evaporation than those in more open habitats (Richardson 1981).

Some mosses may contribute to slowing evaporation not only of themselves, but also their inhabitants by curling their leaves, as in ***Atrichum*** spp. (Figure 22). Others, such as ***Syntrichia princeps*** (Figure 23) or ***S. intermedia*** (Figure 24), may wind their leaves helically around the stem.

Figure 22. ***Atrichum undulatum*** with moist leaves (upper right) and dry, curled leaves (lower middle). Curled leaves help to slow evaporation, permitting the nematodes to acclimate as they go dormant. Photo by Michael Lüth, with permission.

Figure 23. ***Syntrichia princeps***. Photo by Martin Hutten, with permission.

Figure 24. ***Syntrichia intermedia***, illustrating the twisting of leaves that can protect nematodes from rapid drying. Photo by Michael Lüth, with permission.

Kinchin (1992) observed that luxuriant growths of epiphytic bryophytes often had fewer species and reduced numbers compared to those bryophytes in lesser abundance. He suggested that the more open growth habit of these mosses in higher humidity were perhaps not suitable for the nematodes. He further suggested that some nematodes require alternate dry and wet phases in their life cycles, thus not faring well in the more moist dense moss growths (see also Kinchin 1990).

Succession

Moss age not only affects probability of arrival, but also influences the moisture of the habitat. The most specialized nematode species arrive first because they are adapted to the changing moisture regime. These include ***Plectus rhizophilus*** (Figure 25), a moss canopy species (Kinchin 1989). Members of the rhizoidal group (*e.g.* ***Dorylaimus***, Figure 7) are the last to arrive because they require the more stable moisture climate of a larger cushion. Although ***Dorylaimus*** is an aquatic genus, it can survive on very wet mosses (Aldo Zullini, pers. comm. 18 March 2009). On the other hand, Mike Hodda (personal communication) considers that they may arrive last because they have long life cycles and are slow to breed, whereas ***Plectus*** (Figure 27) is short-lived, fecund, and moves much more quickly.

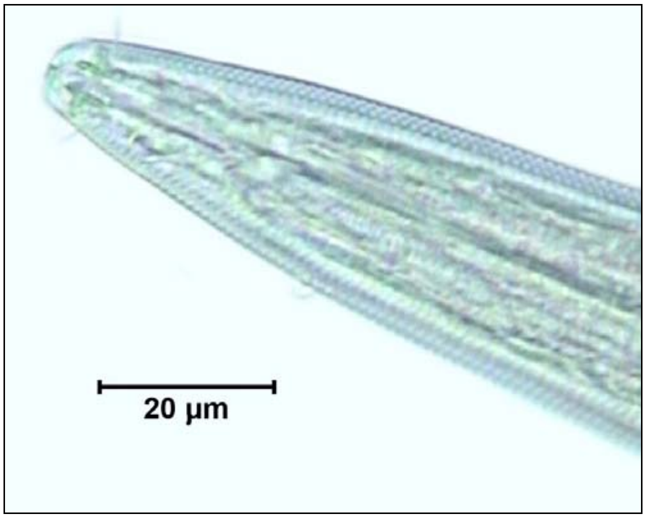

Figure 25. ***Plectus rhizophilus***, a nematode found among roof mosses. Photo by Peter Mullin, with permission.

Nematode communities in moss cushions are so sensitive to moisture regimes that they can be used to ascertain the moisture history of the cushion (Kinchin 1989). Fewer species would be present in cushions that are frequently desiccated. Thus even among populations of the same species, communities will differ based on the moisture history of the cushion. Overgaard-Nielsen (1967) demonstrated this by comparing communities associated with ***Ceratodon*** sp. (Figure 26) on north- and south-facing sides of a thatched roof (Table 2).

Figure 26. ***Ceratodon purpureus***, a common roof moss that has its own nematode fauna. Photo by Michael Lüth, with permission.

Table 2. Comparison of nematode densities (numbers per cm^2) in cushions of ***Ceratodon*** sp. (Figure 26) on a single thatched roof (Overgaard-Nielsen 1967).

	S-facing	**N-facing**	**Figure**
Plectus rhizophilus	330	51	Figure 25
Plectus cirratus	0	47	Figure 27
Aphelenchoides parietinus	0	8	Figure 28
Paraphelenchus pseudoparietinus	0	1	Figure 29
Prionchulus muscorum	0	1	Figure 13

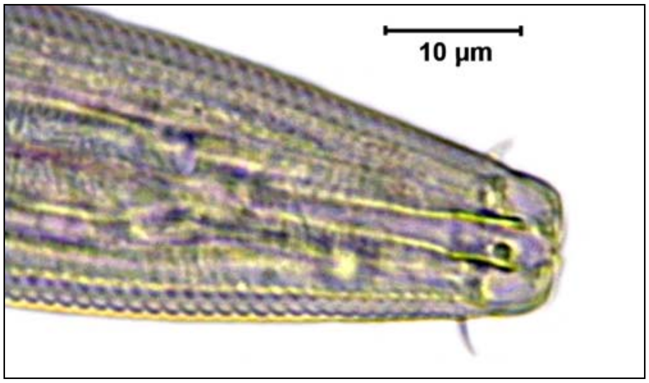

Figure 27. ***Plectus cirratus***, known from roof mosses. Photo by Peter Mullin, with permission.

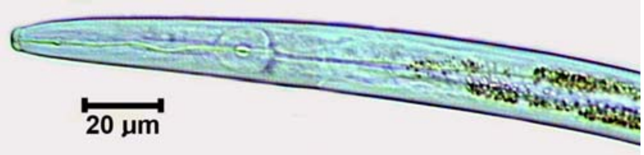

Figure 28. ***Aphelenchoides parietinus***, a roof moss dweller. Photo by Peter Mullin, with permission.

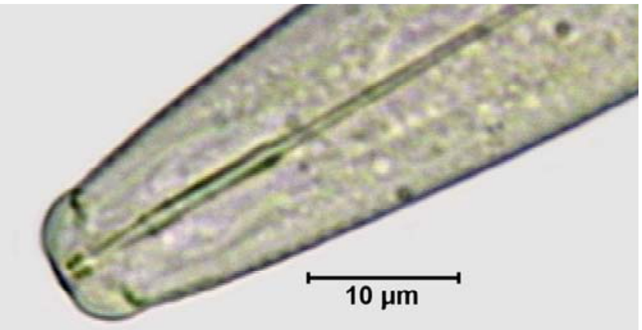

Figure 29. ***Paraphelenchus*** (=*Paraphelenchoides*) ***pseudoparietinus***, a roof moss inhabitant. Photo by Peter Mullin, with permission.

Seasonal Changes

Seasonal differences among the moss-dwelling nematodes can be pronounced, as reported by Steiner (1994d in Boag & Yeates 2004) for the Swiss Alps. In a study of nematodes dwelling on ***Eurhynchium oreganum*** (Figure 30) in the Oregon Coast Range, USA, comparison indicated that the densities of ***Eudorylaimus*** spp. (Figure 19) and ***Plectus*** spp. (Figure 25, Figure 27) differed between sampling dates, but that densities of ***Monhystera*** spp. (Figure 16), ***Prionchulus muscorum*** (Figure 13), and ***Tylenchus*** spp. (Figure 18) did not differ, resulting in total densities of nematodes that varied little between dates (Figure 31; Merrifield & Ingham 1998). Nevertheless, ***Monhystera*** (Figure 16) species reached a mean of 35 individuals per gram in August, but only 1 or fewer in winter and spring. Members of other genera occurred sporadically in low numbers: ***Aphelenchus*** (Figure 32), ***Acrobeles*** (Figure 33), ***Cuticonema***, ***Ecphyadophora***, ***Leptolaimus*** (Figure 34), ***Teratocephalus*** (Figure 17), and members of the order **Cromadorida**. The number of nematodes per gram of dry moss ranged from 21 in February to 64 in July, a density somewhat lower than that found in other studies on moss-dwelling nematodes.

Figure 30. ***Eurhynchium oreganum***, home to nematodes and other invertebrates in Oregon, USA. Photo by Matt Goff, <www.sitkanature.org>, with permission.

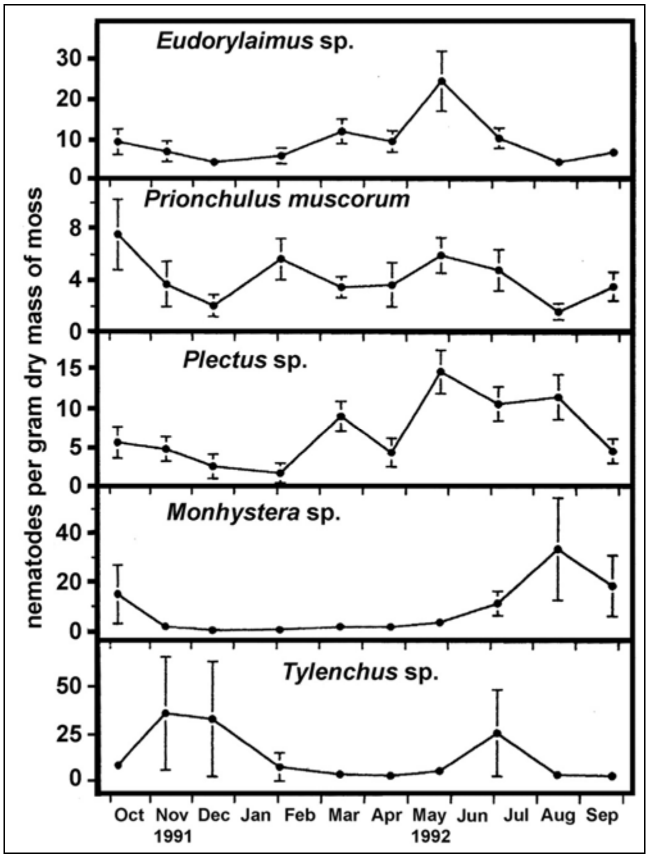

Figure 31. Seasonal changes in densities of nematodes on the moss ***Eurhynchium oreganum*** (Figure 30) from Mary's Peak, Oregon Coast Range, Oregon, USA. Vertical bars represent standard errors. Redrawn from Merrifield & Ingham 1998.

Figure 32. ***Aphelenchus avenae***, a member of a genus where some members live among mosses. Photo by Peter Mullin, with permission.

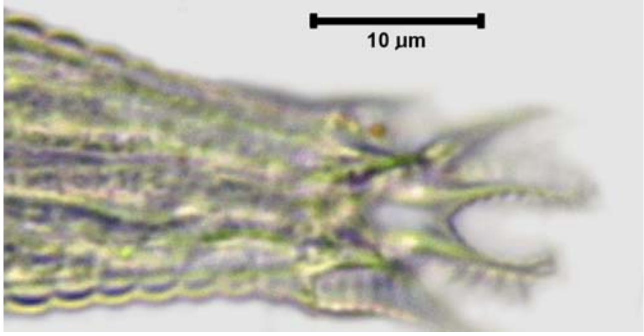

Figure 33. Head end of ***Acrobeles***, a sporadic genus on the moss ***Eurhynchium oreganum*** on the Oregon coast. Photo by Peter Mullin, with permission.

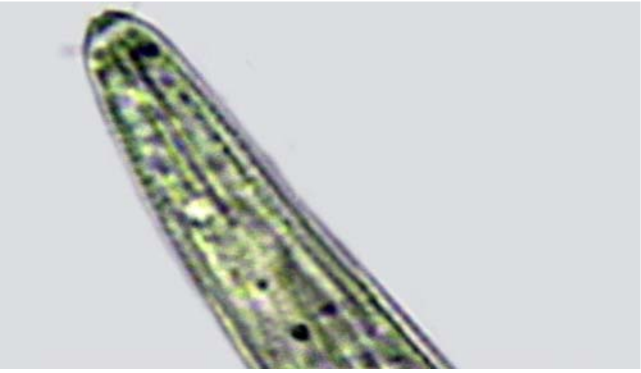

Figure 34. Head end of ***Leptolaimus***, an occasional dweller on the moss ***Eurhynchium oreganum*** (Figure 30). Photo by Peter Mullin, with permission.

Merrifield and Ingham (1998) suggested peaks of ***Eudorylaimus*** (Figure 19) and ***Plectus*** (Figure 3) species in association with the moss ***Eurhynchium oreganum*** (Figure 30) in the Oregon Coast Range in late May, continuing until August, could indicate optimal conditions during that time of year (Figure 31). It is not clear if food is a limiting factor because feeding habits of some species are not clear. In fact, these nematodes are often polyphagous, with some switching food items from bacteria to prey items as they grow (Yeates *et al*. 1993; Mike Hodda, personal communication). Merrifield (1994) examined the relationship between spore production of the moss ***Schistidium maritimum*** (Figure 35) and the omnivorous nematode ***Eudorylaimus*** at Yachats, Lincoln County, Oregon, USA, in a year-long study. She found a lag of one month between the peak of mature sporophytes and the maximum density of nematodes. Since there were no other invertebrates to serve as food, she suggested that the spores might serve as a food source.

Plectus sp. (Figure 3), a bacteriovore, ranged from 4 to 12 per gram dry weight (gdw) of moss on the northwest slope of Mary's Peak, Oregon, USA, throughout most of an October 1990-October 1991 sampling period, but reached 25 per gdw in June (Merrifield 1992). ***Monhystera*** sp. (Figure 16), on the other hand, peaked in September with 35 per gdw, whereas it remained mostly below 1 per gdw throughout the Oregon winter. The possibly fungus and plant feeder ***Tylenchus*** sp. (Figure 18) had a bimodal seasonal distribution, with highs in November (35) and July (25). ***Prionchulus*** sp. (Figure 13), a predator, peaked at 6-8 in summer and winter, with fluctuations throughout the year.

Figure 35. ***Schistidium maritimum*** in a typical shoreline habitat. Photo by Michael Lüth, with permission.

Spaull (1973) likewise found a vertical migration of moss-dwelling nematodes on Signy Island. In the summer and first half of winter the nematodes remained in the 3 cm nearest the surface, but when the cold of winter set in, they could be found primarily in the 3-6 cm layer. Spaull speculated that the freeze-thaw cycle near the surface resulted in a decline in numbers there, but that the lower positions also experienced slightly higher daytime temperatures in the autumn. Despite earlier studies suggesting the importance of moisture (Tilbrook 1967a, b), there seemed to be no relationship between vertical position and moisture in the mosses (Figure 36).

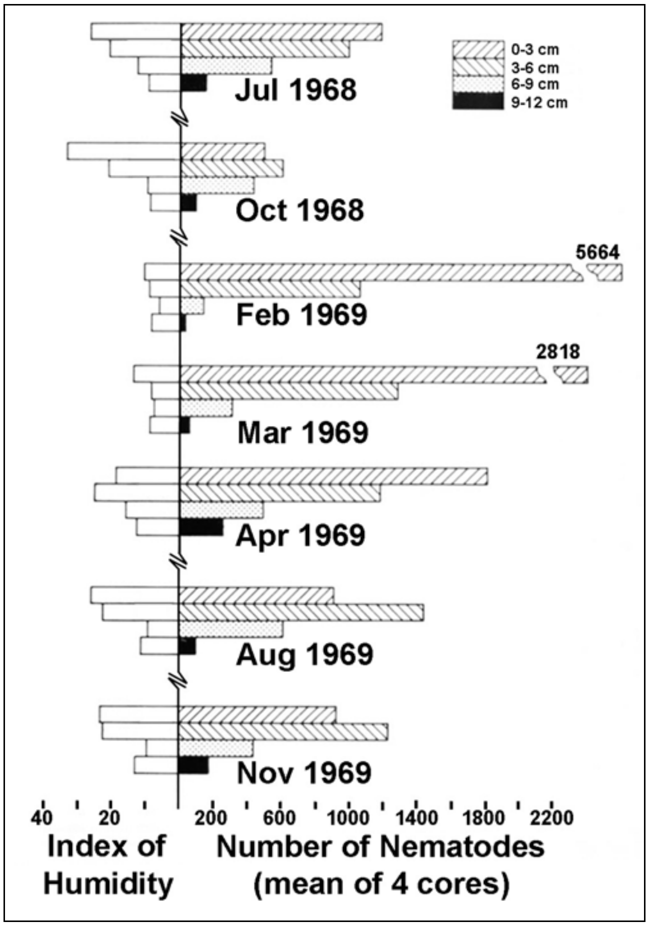

Figure 36. Seasonal depth distribution of nematodes compared to humidity levels in ***Calliergon*** (Figure 37)-***Calliergidium*** (Figure 38) cores on Signy Island, Antarctic region. Redrawn from Spaull (1973).

Figure 37. ***Calliergon sarmentosum***, a known host of nematode-trapping fungi on Signy Island in the Antarctic. Photo by Michael Lüth, with permission.

Some moss-dwelling nematodes can respond to seasonal changes by migrating. Of course they can't travel long distances like birds can. Whereas some nematodes migrate vertically on a daily basis, others move vertically within the moss community to survive changing seasons (Wharton 2004). In the Antarctic, Caldwell (1981b) and Maslen (1981) found that a seasonal migration existed in moss carpets, wherein the nematodes moved deep into the carpet in autumn and returned to the surface in spring. But it is interesting that they found no similar migration pattern in moss cushion forms.

Figure 38. ***Chorisodontium aciphyllum***, home to nematodes in the Antarctic. Photo by Jan-Peter Frahm, with permission.

Freeze Tolerance

Nematodes range at temperatures from snow pools to hot springs, with a species of ***Aphelenchoides*** (Figure 28) occurring at 61.3ºC (Hebert 2008). In fact, some Antarctic nematodes can withstand freezing at -80°C for more than six years (Newsham *et al*. 2006). On the liverwort ***Cephaloziella varians***, there were more live ***Coomansus gerlachei*** nematode individuals than of ***Rhyssocolpus paradoxus***. Nematodes had much greater survival (49%) than did tardigrades (13%) or rotifers (2%).

One factor that permits nematodes to succeed in climates of the Antarctic, alpine areas, and other areas with harsh winters is their ability to survive freezing conditions. But how does this tiny, watery worm do it? Several species in the genus ***Panagrolaimus*** (Figure 39-Figure 41) have been studied to reveal their freeze-tolerance secrets. Some day we may be able to freeze and thaw humans from what we learn about these moss inhabitants.

The transparency of the nematode body enabled Wharton and Ferns (1995) to discover that ***Panagrolaimus davidi*** (Figure 20) froze not only in its extracellular spaces, but also formed ice in living cells (Figure 39). They found that all body parts could experience freezing and thawing, including within cells (Figure 39). Freezing extends inward through body openings, mostly through the excretory pore. These nematodes, with intracellular freezing, can revive, grow, and reproduce, at least in culture (Figure 41-Figure 41).

Figure 39. Frozen female ***Panagrolaimus davidi*** that survives intracellular ice formation (Wharton & Ferns 1995). This female was frozen on a light microscope cold-stage. Freezing causes darkening in appearance, and ice can be seen throughout this nematode, except the egg, which remains unfrozen due to its protective shell. Photo by Melianie Raymond, with permission.

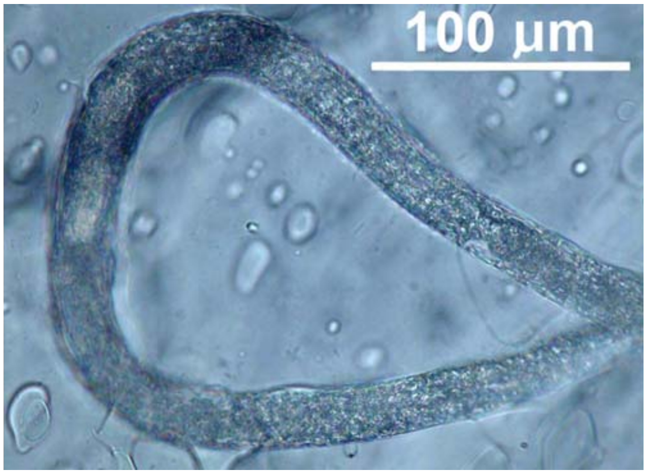

Figure 40. The same female ***Panagrolaimus davidi*** as in Figure 39, thawing from being completely frozen. Photo by Melianie Raymond, with permission.

But ***Panagrolaimus davidi*** (Figure 20) has more possibilities to survive freezing, and these may play a role in its desiccation story as well. These nematodes can avoid freezing by dehydration (Wharton *et al*. 2007). If nucleation of their surrounding medium occurs at a high subzero temperature, *e.g.* -1°C, the nematodes dehydrate instead of freezing. This occurs as a result of difference in vapor pressure between ice and super-cooled water at the same temperature. When they are cooled slowly, there is sufficient time for them to lose enough water to prevent freezing. It is only when they are cooled rapidly or at a lower nucleation temperature that they actually freeze internally, but still survive. These multiple strategies permit them to survive the harsh Antarctic environment.

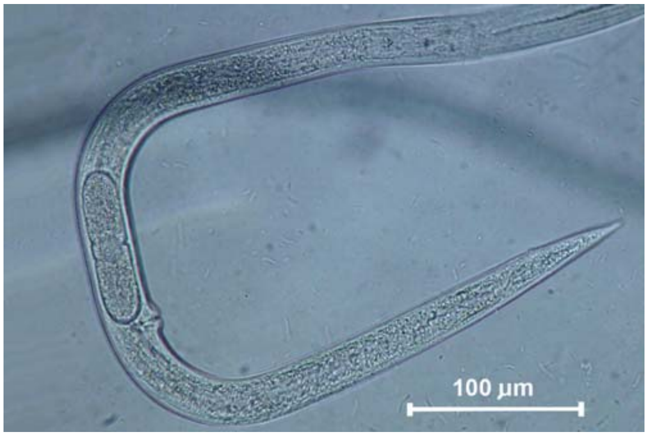

Figure 41. The same female ***Panagrolaimus davidi*** as in Figure 39, after thawing from being completely frozen, but undamaged. Photo by Melianie Raymond, with permission.

However, when these nematodes are in water, they are seeded by exogenous ice nucleation, a process in which a dust particle, protein, or other small particle (the "nucleus") forms the center for ice crystallization – the same process used for making artificial snow. Even under these conditions, some of the nematodes of this species do survive. One reason for their survival is that the formation of the ice seems to be restricted to the **pseudocoel** – the "false" body cavity. A major danger from ice crystallization is that the crystals are sharp and poke holes in cell membranes, or distort them, changing permeability. However, the pseudocoel is fluid and **acellular**, thus avoiding that danger.

Thermal history and age are important in determining which individuals survive (Wharton & Brown 1991). In arthropods, supercooling and freeze tolerance are thought to be mutually exclusive, but in nematodes, that is not the case. In the Antarctic, sub-zero temperatures can occur on any day of the year, making tolerance a necessity for survival. Even in the summer, moss temperatures can go down to -8.4ºC (Block 1985). The moss environment is usually saturated with water (Pickup 1990a, b), requiring that the nematodes either prevent ice nucleation or survive exogenous nucleation and subsequent freezing.

Panagrolaimus davidi (Figure 20; Figure 39-Figure 42) freezes when it is seeded by exogenous ice nucleation and is freezing tolerant (Wharton & Brown 1991). In the moss habitat, nematodes will usually experience low water loss rates; hence, an interaction between water loss and cold tolerance may occur under some conditions. This slow water loss rate may be a vital factor in its choice of the moss as a habitat (Wharton *et al*. 2003). When nucleation begins at subzero temperatures near -1ºC, this nematode dehydrates (Wharton *et al*. 2003). The difference in vapor pressure of ice and supercooled water, at the same temperature, drives the water loss from the nematode. If the process is slow enough, the nematode loses enough water to prevent freezing (Figure 42). It is likely that **trehalose**, an important molecule during dehydration, also acts to prevent or reduce freezing within the worm (Wharton 2003).

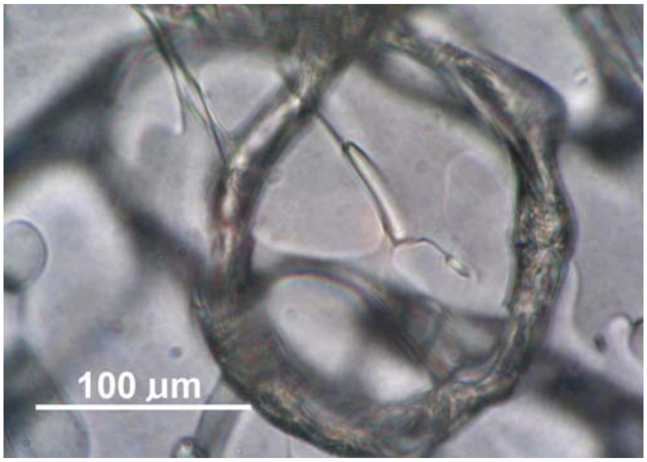

Figure 42. ***Panagrolaimus davidi*** showing cryoprotective dehydration. ***Panagrolaimus davidi*** can also survive exposure to freezing conditions by undergoing cryoprotective dehydration (Wharton *et al*. 2003). This photo shows a nematode encased in ice, unfrozen but dehydrated. Photo by Melianie Raymond, with permission.

To further combat its frigid environs, ***Panagrolaimus davidi*** (Figure 20; Figure 39-Figure 42) produces **ice-active proteins** (Wharton *et al*. 2005a). These proteins seem to have the ability to stabilize the ice after freezing by preventing **recrystallization** during minor freeze-thaw temperature fluctuations within the organism. Wharton *et al*. (2005b) examined the survival of these nematodes under several freezing scenarios. At sub-zero temperatures near 0ºC, three patterns of ice formation were evident: no ice, extracellular ice, and intracellular ice (Wharton *et al*. 2005b). In a slow-freezing regime (at -1ºC) mainly extracellular ice (70.4%) formed, with most of the ice in the pseudocoel. Cryoprotective dehydration accounted for ~25% of the individuals with no ice within their bodies. However, under a fast-freezing regime (at -4ºC) both intracellular (54%) and extracellular (42%) ice formed. Fortunately, the intracellular ice only formed in the cytoplasm of cells, while organelles remained in unfrozen spaces between the crystals. Nevertheless, those nematodes that experienced the fast freezing had only 53% survival compared to 92% for those that underwent slow freezing.

We have also learned that the Antarctic ***Panagrolaimus davidi*** (Figure 20; Figure 39-Figure 42) is able to survive freezing temperatures by supercooling when it is in air that permits it to be free of surface water (Figure 42) (Wharton & Brown 1991; Wharton *et al*. 2003). But, in these conditions, it is intolerant of freezing. In fact, it can survive better at sub-zero temperatures than other individuals of the species that have been kept at 15ºC in 99% relative humidity – not unlike the moisture relationships of bryophytes and their tolerance to temperature extremes.

The importance of mosses to the life cycle of ***Panagrolaimus davidi*** (Figure 20; Figure 39-Figure 42) is evidenced by the nematode's optimum temperature range of 25-30ºC (Brown *et al*. 2004). Population growth ceases at about 6.8ºC. Fortunately, egg incubation requires only 4.1-7.6ºC. This bacteriovore is **r-selected** (typically short-lived with lots of offspring like bacteria), more like temperate nematodes than its Antarctic compatriots. However, the cold polar environment forces it to become dormant for long periods of time and to grow in spurts; such longevity is more like that of **K-selected** organisms (long life span and few offspring, like humans), but is it right to count that dormancy period as part of its longevity?

Scientists have known about freezing of juveniles and eggs of other nematodes for some time, but the mechanisms were not understood. In some species (***Trichostrongylus colubriformis***), a sheath protects at least some juveniles from formation of exogenous ice nucleation, although this species also survives freezing (Wharton & Allan 1989). Worms of ***Ditylenchus dipsaci*** and the eggs of ***Globodera rostochiensis*** are able to survive freezing in wet conditions, but the researchers were unable to distinguish between survival of freezing and prevention of ice nucleation (Wharton *et al*. 1984; Perry & Wharton 1985).

But not all cold temperatures are in the high elevations and latitudes. In peatlands, freezing is common, yet nematodes survive. Some protection is afforded by their behavior of coiling (Hingley 1993). But the greater protection is most likely their chemical alteration. As unfavorable conditions approach, they decrease their concentrations of **fats**, **glycogen**, and **glucose** and increase **glycerine** and **trehalose** (Crowe *et al*. 1984). In addition to its probable role in preventing or reducing freezing (Wharton 2003), trehalose is able to stabilize dry membranes, a consequence of freezing as well as drought conditions (Crowe *et al*. 1984).

Gall-formers

Some of these bryophyte-dwelling nematodes are free-living and some are parasitic on the mosses (Gadea 1977, 1978a, b; Duggal & Koul 1985; Georgievska 1990). In fact, many kinds of nematodes induce the formation of galls (Sheldon 1936; Horikawa 1947) on both mosses [*e.g.* ***Racomitrium lanuiginosum*** (Figure 43) and ***R. heterostichum*** (Figure 44) (Deguchi 1977), ***Thuidium delicatulum*** (Figure 45) (Sheldon 1936; by ***Anguina askenasyi***, Steiner 1936, 1937), ***Phascopsis rubicunda*** (Stone 1980 in southern and western Australia), ***Dicranum*** sp., ***Thamnobryum alopecurum*** (Figure 46), ***Eurhynchium*** sp., ***Warnstorfia fluitans*** (Figure 47), and ***Hypnum cupressiforme*** (Figure 14; Gerson 1982), and others (Dixon 1905, 1908)] and liverworts [*e.g.* ***Cheilolejeunea*** *cf*. ***giraldiana*** (Asthana & Srivastava 1993) and ***Anastrophyllum minutum*** (Figure 48; Kitagawa 1974)].

Figure 43. ***Racomitrium lanuginosum***, a moss known for its nematode galls. Photo by Michael Lüth, with permission.

Figure 44. ***Racomitrium heterostichum***, a moss where nematodes are known to from galls. Photo by Michael Lüth, with permission.

Figure 45. ***Thuidium delicatulum***, a pleurocarpous moss that forms nematode galls. Photo by Michael Lüth, with permission.

Figure 46. ***Thamnobryum alopecurum***, a host to the gall-forming nematode ***Tylenchus davainii***. Photo by Michael Lüth, with permission.

Figure 47. ***Warnstorfia fluitans***, a widespread aquatic moss that gets nematode galls. Photo by Michael Lüth, with permission.

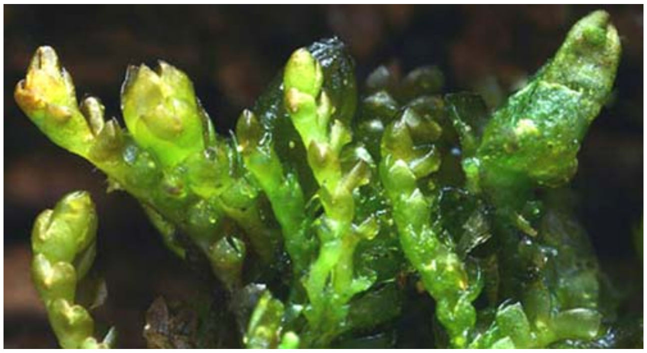

Figure 48. The leafy liverwort ***Anastrophyllum minutum*** a host to nematode galls. Photo by Des Callaghan, with permission.

Dixon (1905) reported the nematode ***Tylenchus davainii*** (Figure 49) to form galls on ***Thamnobryum alopecurum*** (Figure 46), ***Eurhynchium hians*** (=***E. swartzii***; Figure 50), and ***Hypnum cupressiforme*** (Figure 14) in Great Britain. Hedenäs (2000) found 59 individuals of the moss ***Abietinella abietina*** (Figure 51-Figure 52) (6.6% of those examined) to have nematode galls in the apices of their vegetative branches. Typically, where one gall existed, numerous ones could be found.

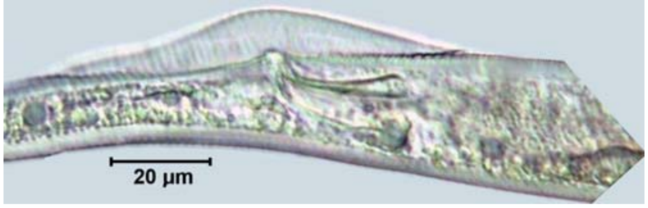

Figure 49. ***Tylenchus davainii***, a gall-forming nematode. Photo by Peter Mullin, with permission.

Figure 50. ***Eurhynchium hians***, home to gall-forming nematodes. Photo by Michael Lüth, with permission.

Figure 51. ***Abietinella abietina***, a moss that can have nematode galls. Photo by Michael Lüth, with permission.

Figure 52. ***Abietinella abietina*** with nematode galls on the branch tips. Photo by Lars Hedenäs, with permission.

Claudio Delgadillo has described to me (Bryonet 18 March 1996) a growth form of ***Bryum argenteum*** (Figure 53) from Mexico that is unusual and may represent the typical result of nematode gall formation (Figure 54). The presence of nematode galls caused the upper part of the stem to be modified. The upper leaves had a modified shape, color, and general structure that had the appearance of a fruiting cleistocarpous moss.

Figure 53. ***Bryum argenteum***, one of the mosses that houses nematode galls. Photo by Michael Lüth, with permission.

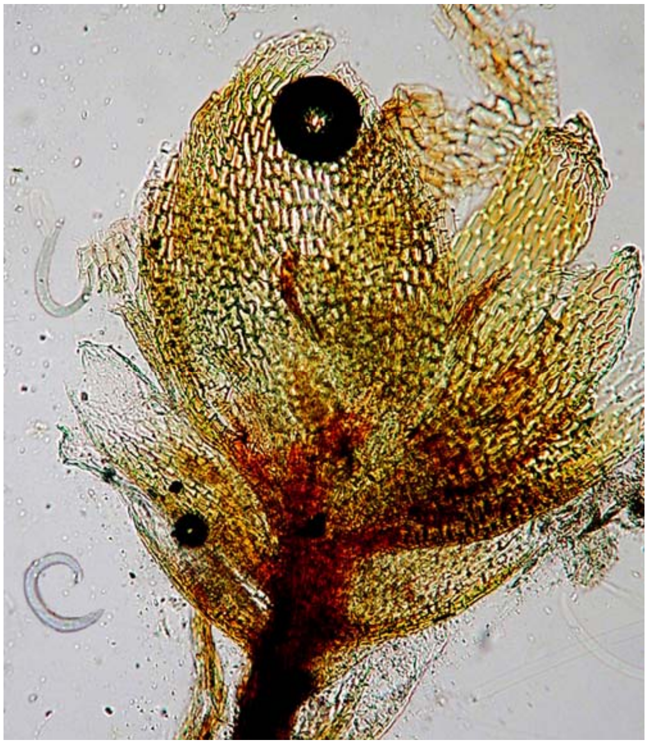

Figure 54. ***Bryum argenteum*** with a nematode gall at its tip. The cell walls are thickened and the leaves and stem apex have a different morphology from uninfected plants. Two C-shaped nematodes can be seen at left, collected near Temascalapa, Mexico. Photo by Claudio Delgadillo, with permission.

Stone (1978) commented that nematodes produced similar galls on male plants of ***Bryum pachytheca*** in Australia, again resembling cleistocarpous capsules. Both Stone (1980) for ***Phascopsis rubicunda*** and Delgadillo (Bryonet 1996) for ***Bryum argenteum*** (Figure 53-Figure 54) reported that the cell walls were thickened. Stone reported that the stems of ***Phascopsis rubicunda*** were hollow and necrosed, cell walls were reddened and glossy, and inner leaves were ecostate, and like Delgadillo, she considered the galls to resemble cleistocarpous capsules.

As I thought I was drawing this chapter to a close, a new report appeared in the Australasian Bryological Newsletter. Jolley and Hodda (2009) found nematode galls on a tiny Australian moss called ***Stonea oleaginosa*** (Figure 55-Figure 57), a fitting name commemorating Ilma Stone, who had reported nematodes in this moss under the moss name of ***Tortula oleaginosa*** (Stone 1978). This moss from the salt bush and mallee in Southern Australia is inconspicuous (<1 mm) as it hides among the sand grains, often nearly buried.

As in ***Phascopsis rubicunda***, Stone (1978) had reported hollow, elongated stems, but she had not observed galls. Like Delgadillo and Stone for other species of moss, Jolley and Hodda (2009) described the galls as resembling cleistocarpous moss capsules (Figure 57). And as in ***Phascopsis rubicunda***, the galls of ***Stonea oleaginosa*** (Figure 56-Figure 57) are modified leaves that are very broad, with thick cell walls. I have to wonder if some of those unidentifiable mosses I have seen in the field with what I thought were developing sessile capsules may have been bearing galls – did I really explore them thoroughly enough?

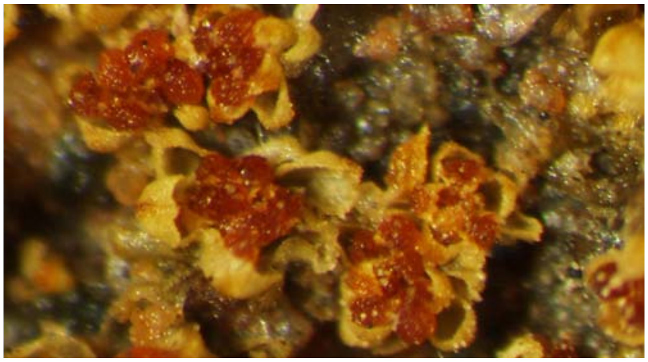

Figure 55. ***Stonea oleaginosa***, a microscopic moss. Photo by Helen Jolley, with permission.

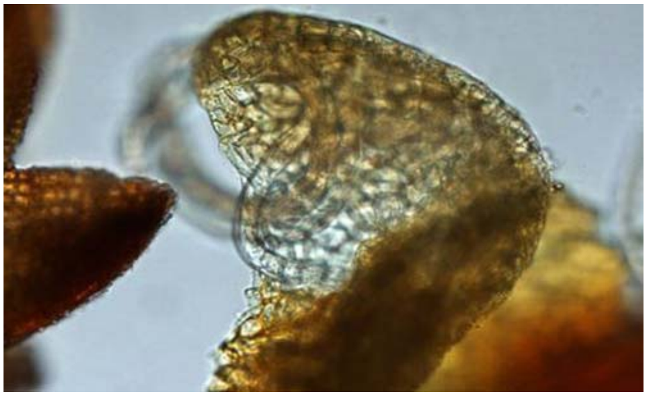

Figure 56. Gall leaf of ***Stonea oleaginosa***, caused by the nematode ***Nothanguina*** sp. nov. Photo by Helen Jolley, with permission.

Figure 57. Leaf gall of the nematode ***Nothanguina*** from the moss ***Stonea oleaginosa***. Note the encysted nematodes within. Photo by Helen Jolley, with permission.

Jolley and Hodda (2009) determined the nematode to be a species of ***Nothanguina*** (Figure 58), a species that occurs on several Australian moss taxa, including ***Phascopsis rubicunda***, and was a species as yet undescribed. (That is coming soon.) The genus is known to house up to five female adults, usually about the same number of males, and numerous eggs and juveniles in one gall. But in galls on ***Stonea oleaginosa*** (Figure 55-Figure 57), only female nematodes are known.

In ***Stonea oleaginosa*** (Figure 55-Figure 57), the galls are placed amid the archegonia of the moss, possibly modifying archegonia to inhibit fertilization. By interesting coincidence, only female plants are known in this moss, and inhibition of fertilization seems unnecessary, unless galls were so frequent that useless males were lost through evolution. Rather, females produce upper leaves that are modified into propagules that are rich in oils and break off the plant easily (Stone 1978). Could it be that some hormone inhibits male development in the moss and subsequently in the nematode? It would be interesting to follow the development of the gall to understand how tissues are modified to make the gall tissues and propagules.

Figure 58. ***Nothanguina*** sp. nov. from ***Stonea oleaginosa***. Photo by Helen Jolley, with permission.

Niklas Lönnell (pers. comm. 26 March 2012) described a nematode gall on ***Microbryum floerckeanum*** (Figure 59). This moss had a structure that looked like a strange capsule, but it proved to be a structure with a nematode resident.

Figure 59. ***Microbryum floerkeanum*** with capsules, home of a nematode gall. Photo by David Holyoak, with permission.

It appears that even ***Buxbaumia aphylla*** (Figure 60) may host nematodes. Misha Ignatov (Bryonet 7 April 2017) observed gametophytes that resembled sea urchins and had no trace of sporophytes. Instead, a nematode was often present inside. These occurred in September when the temperature was *ca*. 10ºC in their Middle European Russia location.

Figure 60. ***Buxbaumia aphylla*** showing nearly mature capsules. The gametophyte is merely a protonema (threadlike structure) and the leafy plants seen here belong to other mosses. Photo through public domain.

Unfortunately, few of the bryophyte gall-formers have been identified, so we don't know if they are unique to bryophytes. It is likely that at least some are. Ernie Bernard at the University of Tennessee is currently working with nematode galls from the moss ***Hypnum***. sp. (Paul G. Davison, pers. comm. 22 January 2012).

Terrestrial Moss Inhabitants

Hodda (2003) lists only three bryophytes as hosts for nematodes: ***Barbula*** sp. (Figure 61) – ***Aphelenchoides*** sp. (Figure 28); ***Tortula*** sp. (Figure 62) – ***Aphelenchus*** sp. (Figure 32), ***Aphelenchoides*** sp.; ***Grimmia pulvinata*** (Figure 63) – ***Laimaphelenchus pini***. But Kinchin (1992) reported that nearly all moss samples from the British Isles contained nematodes, often in large numbers.

Figure 61. ***Barbula convoluta***, a nematode host. Photo by Michael Lüth, with permission.

Figure 62. ***Syntrichia*** (=*Tortula*) ***intermedia***, a moss that houses nematodes. Photo by Michael Lüth, with permission.

Figure 63. ***Grimmia pulvinata***, a moss that hosts nematodes. Photo by Michael Lüth, with permission.

Eyualem-Abele *et al.* (2006) reported that ***Tripylella arenicola*** occurs on moss as well as in soil. Many aquatic taxa also are able to survive in the wet habitat provided by moisture held in capillary spaces among bryophyte leaves. I was able to document eighteen genera (Table 3) that have species known in and around moss clumps. There are most likely more that have never been identified, or even found.

Peatlands

Some of the ubiquitous nematodes reside in peat, but others are inhibited by the low *p*H. Glatzer and Ahlf (2001) found that the nematode ***Caenorhabditis elegans*** (Figure 64) was inhibited in growth in the sediments. When they tested eighteen different sediment combinations that mimicked those available, the optimum for growth and successful reproduction was a mixture with 5% ***Sphagnum*** peat (Figure 5), suggesting that this nematode may actually benefit from some characteristic of the peat. Nematodes such as the **mycophagous *Aphelenchoides compositicola*** and many **saprophytic** nematodes can be a problem in peat used for culture of mushrooms and must be eliminated with chemicals such as ethylene oxide (Nikandrow *et al.* 1982).

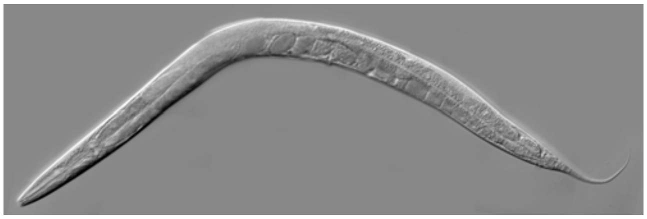

Figure 64. ***Caenorhabditis elegans***, a nematode that seems to benefit from some properties of ***Sphagnum***. Photo by Kbradnam through Creative Commons.

Some individuals coil up inside the hyaline cells of ***Sphagnum*** leaves (Figure 65), and nematodes even deposit eggs within these cells (Hingley 1993). Eggs of these species survive long periods of drought, anaerobic conditions, and repeated freeze-thaw cycles. Even adult worms can survive unfavorable conditions by encysting and decreasing fats, glycogen, and glucose, increasing glycerine and trehalose, and assuming a coiled position (Crowe *et al.* 1984).

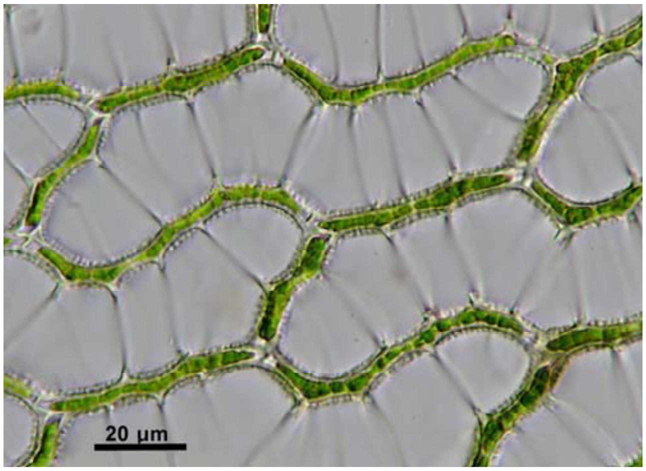

Figure 65. ***Sphagnum papillosum*** leaf cells. Nematodes may live in the hyaline cells. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

As noted earlier, although there are about 30,000 species of nematodes worldwide, only about 30 species are known from ***Sphagnum*** (Figure 5) (Hingley 1993). Knowledge about specific taxa on other mosses is likewise limited (Table 3), but Coleman pointed out in 1971 that our knowledge about nonparasitic nematodes in soils in many parts of the USA is nonexistent. With the important role they are perceived to play in soil compared to mosses, it is hardly surprising that knowledge about those among mosses is somewhat scant.

Woodland peat mosses are a somewhat preferred community (Hingley 1993). Some of these worms feed on detritus while others are predatory, feeding on protozoa and small invertebrates. The herbivorous species apparently never feed on the mosses. Nevertheless, nematodes living in the microbiotic soil crusts of prairies are known to eat moss rhizoids, among other things (Bamforth 2003).

Table 3. Nematode genera that are known to inhabit terrestrial bryophytes. Occasional taxa from the Antarctic are not included. *Indicates taxa also on the Table 4 aquatic list.

*Achromadora**	Kinchin 1989
Aphelenchoides	Kinchin 1989
Aphelenchus	Hodda 2003
Caenorhabditis	Glatzer & Ahlf 2001
Chromadorina	Kinchin 1989
Diplogaster	Kinchin 1989
*Dorylaimus**	Kinchin 1989
Monacrosporium	Duddington *et al.* 1973
Monhystera	Kinchin 1989
*Mononchus**	Kinchin 1989
Nothanguina	Jolley & Hodda 2009
Odontolaimus	Kinchin 1989
*Paraphelenchoide*s	Overgaard-Nielsen 1967
*Plectus**	Kinchin 1989
*Prionchulus**	Overgaard-Nielsen 1967
Rhabditis	Kinchin 1989
Thyronectria	Duddington *et al.* 1973
*Tylenchus**	Kinchin 1989
Tripylella	Eyualem-Abebe *et al.* 2006

Global Warming

Global warming has been a concern for the peatland habitat at all levels. Sohlenius and Boström (1999a) investigated the effect a rise in temperature might have on nematode communities of peatlands by transplanting peat blocks from northern Sweden to nine warmer sites within that country. After one year, they found that in all but the northernmost transplant site, these transplants resulted in increased numbers, but had no influence on species composition. The most abundant of the 35 taxa were ***Plectus*** (Figure 3) and ***Teratocephalus*** (Figure 17) (Sohlenius & Biström 1999b).

Hence, it appears that temperature alone may not have a serious effect on nematodes, but they cautioned that other changes in the ecosystem could alter the nematode communities. Furthermore, tardigrades, known to prey on nematodes, also increased in numbers, possibly damping the effect of temperature on the nematodes (Sohlenius & Boström 1999b). I would consider that one year is insufficient basis for a long-term assessment as the greater temperatures could lie within normal variation from year to year. Even Sohlenius and Boström (1999b) suggested that seasonal differences and the short duration of the experiment could be misleading. Numbers of nematodes increased in autumn, especially in warm sites, with a positive relationship between nematode numbers and temperature in November. Likewise, in spring there were more nematodes in warm sites than in cooler ones.

Population Size

In an ombrotrophic mire in northern Sweden, Sohlenius *et al.* (1997) found high densities of nematodes, especially in the moss surface layer. In fact, the nematodes dominated with a mean abundance of 9.4 million individuals per square meter. These were represented by 34 taxa. The surface layer was characterized by similar numbers of fungal vs bacterial feeders. By contrast, bacterial feeders dominated the underlying peat.

Aquatic Nematodes

In New Zealand alpine streams, nematodes were the most abundant moss-dwelling invertebrate (40.6%), exceeding **all** the insects (Suren 1993). This number was higher above the treeline (43.6%), but was exceeded by the Chironomidae (midges) below the treeline. In an unshaded alpine stream at Arthur's Pass National Park on South Island, NZ, Chironomidae were the most abundant (57.6%), with nematodes in second place (22.1%) (Suren 1991b). The same relationship existed in a shaded stream, but the Chironomidae became more dominant (63.4%) compared to only 12.5% nematodes. Numbers of nematodes were lower and their ranks dropped in the gravel in both streams. This was supported by the significant correlations of nematodes with bryophytes compared to gravels.

In the Czech Republic, Vlčková *et al.* (2001/2002) found similar percentages of nematodes among ***Fontinalis antipyretica*** (Figure 66) plants, with 38,350 per mL (14.6% of total meiofauna) in one stream and 31,813 per mL (6.4%) in another.

Figure 66. Streambed covered with dangling ***Fontinalis antipyretica***, where nematodes may be numerous. Photo by Andrew Spink, with permission.

Some aquatic mosses have a somewhat unique fauna. In a comparison of communities associated with ***Fontinalis antipyretica*** (Figure 66) and those of associated gravel, Linhart *et al.* (2000b) found six genera only in mosses and five only in gravel. Nine genera occurred in both habitats. The most abundant genera were the same as many terrestrial genera and Linhart *et al.* (2000b) considered that their feeding strategy explained locations of dominant genera: ***Plectus*** (Figure 67) – bacteriophagous, in moss; ***Mononchus*** (Figure 68), ***Tobrilus***, and ***Tripyla*** (Figure 69) – predators, in gravel; ***Eudorylaimus*** (Figure 70) – plant feeders, in moss; ***Dorylaimus*** (Figure 7) – omnivorous, both substrates. Table 4 lists taxa of nematodes known from aquatic bryophytes.

Table 4. Taxa of freshwater nematodes known from bryophytes, based on Eyualem-Abebe *et al*. (2006).

Achromadora terricola
Alaimus sp.
Anatonchus dolichurus
Clarkus papillatus
Cobbonchus palustris
Cobbonchus radiatus
Comiconchus trionchus
Coomansus intestinus
Coomansus parvus
Dorylaimus sp.
Enchodelus sp.
Eudorylaimus
Limonchulus bryophilus
Mesodorylaimus spp.
Metateratocephalus crassidens
Miconchus studeri
Mononchus
Mylonchulus brachyuris
Neotobrilus telekiensis
Oncholaimellus campbelli
Plectus sp.
Prionchulus muscorum
Prionchulus punctatus
Prismatolaimus intermedius
Rhabdolaimus terrestris
Tobrilus zakopanensis
Tripyla affinis
Tripyla filicaudata
Tripyla glomerans
Tripyla setifera
Tylenchus davainei

Figure 67. ***Plectus***, widespread genus with bacteriophagous moss dwellers. Photo by Yuuji Tsukii, with permission.

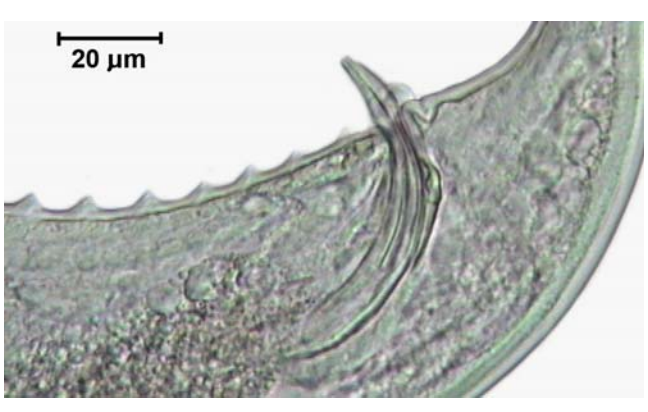

Figure 68. ***Monochus***, a predator. Photo by Peter Mullin, with permission.

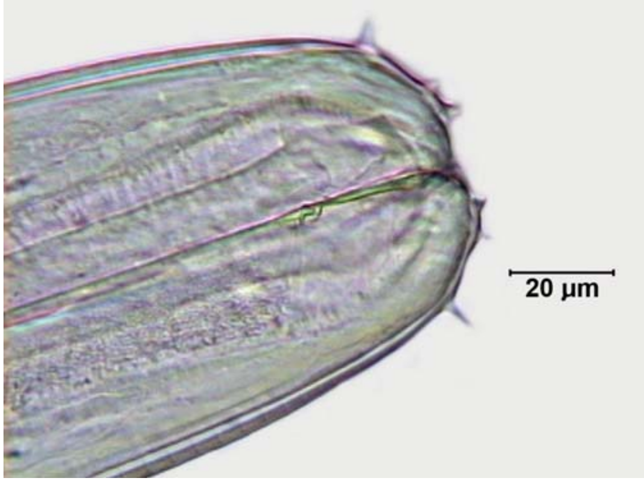

Figure 69. ***Tripyla*** sp. from an alpine habitat in the Rocky Mountains, USA. Photo by Peter Mullin, with permission.

Figure 70. ***Eudorylaimus*** sp., a plant feeder that lives among mosses. Photo by Melianie Raymond, with permission.

A study comparing artificial and real mosses [***Fissidens rigidulus*** (Figure 71), ***Cratoneuropsis relaxa***, ***Bryum blandum*** (Figure 72)] in New Zealand suggests that mosses may indeed have something unique to offer the nematodes (Suren 1991b). In three out of four trials, involving two streams, the artificial mosses made of nylon cord were poor mimics of the bryophyte habitat for the nematodes. Mosses had a mean of 84,000 & 90,000 (2 trials) per m^2 in mosses compared to 1560 & 2400 per m^2 in artificial mosses in one stream and 9840 & 3780 per m^2 in mosses compared to 1760 & 1320 in artificial mosses in a second stream. While it is unlikely that the bryophytes themselves provided food, they are a good source of periphyton and detritus.

On the other hand, when Hynes (1961) used silk in place of mosses, the percentage of organisms that were nematodes associated with the silk differed little from that associated with the mosses.

Figure 71. ***Fissidens rigidulus***. Photo by Bill and Nancy Malcolm, with permission.

Figure 72. ***Bryum blandum***, a moss superior to artificial mosses as a nematode habitat. Photo by Jan-Peter Frahm, with permission.

In streams, mosses can serve as nutrient traps, collecting detrital matter that is readily available to tiny organisms such as these (Suren 1991a; Linhart *et al.* 2002b). Food availability may account for moss-dwelling (***Fontinalis antipyretica***; Figure 66) nematodes whose numbers more closely resembled those in the gravel in that Austrian study: 2,850 per m^2 in the moss and 2,135 per m^2 in the gravel. When Linhart *et al.* (2000a) considered all meiofauna, mean abundances were as follows: moss at locality 1 – 182,672 individuals per 100 mL of moss, gravel at locality 1 – 1,206 individuals per 100 mL substrate, moss at locality 2 – 390,057 individuals per 100 mL moss. Mosses had more than 150 times as great a meiofauna density compared to the nearby mineral substrate. Nematodes were only about 22% of this moss meiofauna, but that is still greater than the entire meiofauna of the mineral substrate. Differences in fine particulate organic matter (FPOM, >30 µm) may account for differences in nematode densities. At locality 1, mosses trapped 19 times as much FPOM as the gravel and 3 times as much as the moss at locality 2. Likewise, nematodes at locality 2 comprised only 11% of the meiofauna. Everybody has to eat!

Even aquatic habitats dry out from time to time. Aquatic moss-dwelling nematodes are among the dominant invertebrates and tolerate these drying events in a state of **anhydrobiosis** (Overgaard-Nielsen 1949; Gilbert 1974; Crowe 1975; Nicholas 1975; Wright 1991), a capability that is not typical of other aquatic nematodes (Merrifield & Ingham 1998).

The Antarctic

Mosses are an important habitat for nematodes in the Antarctic (Figure 73). But not all mosses are created equal, and biologists in the Antarctic have been very aware of these differences. Caldwell (1981a) compared nematodes in moss turf with those in moss carpet on Signy Island. These two ecosystems differ markedly, with the carpets averaging 220-236 mg m^{-2} of nematode biomass and the turf 105-355 mg m^{-2}, showing a much greater variation. Despite these differences, the annual nematode population respiration was very similar: 1726.1 µL O_2 m^{-2} d^{-1} in the turf and 1761.0 µL O_2 m^{-2} d^{-1} in the carpets, accounting for 16% and 35% of metazoan respiration in the turf and carpet, respectively.

In Wilkes Land, East Antarctica, Petz (1997) found the highest abundance of soil microfauna occurred in mosses, with 513 nematodes per gram dry "soil" (moss). Distribution was non-random because the microfauna were often strongly correlated with each other and were related to water and organic matter. Air temperature and *p*H more likely had indirect effects through the food web, especially the detrital component.

Figure 73. Nematode from the terrestrial moss ***Sanionia uncinata*** on the Barton Peninsula of King George Island, Antarctica. Photo by Takeshi Ueno, with permission.

Spaull (1973) found 30 species in 19 genera among mosses on Signy Island, with summer population densities of 0.48 x $10^6/m^2$ in the upper 6 cm of ***Chorisodontium*** (Figure 38)-***Polytrichum*** (Figure 74) turf compared to 7.47 x $10^4/m^2$ in soil beneath the grass *Deschampsia antarctica*. Nevertheless, in alpine areas in ***Schistidium apocarpum*** (as ***S. grande***; Figure 75), Hoschitz (2003) and in the Antarctic (Figure 76; Caldwell 1981a, b), bryophytes and lichens provide a protected shelter in which nematodes may survive. In the Austrian Alps, ***Plectus*** sp. (Figure 3) and ***Eudorylaimus*** sp. (Figure 70) survive the extreme conditions of the Alps. ***Plectus murrayi*** (Figure 77) is likewise a moss inhabitant at Victoria Land in the Antarctic (Melianie Raymond, pers. comm. 2008). ***Teratocephalus tilbrooki*** and ***Plectus antarcticus*** coexist in the shelter of moss cushions and mats (Pickup 1990b) and were the most abundant taxa on Signy Island in the Antarctic (Spaull 1973). However, on Signy Island ***Plectus*** (Figure 3) reaches its greatest abundance in moss carpets and ***Teratocephalus*** (Figure 17) in moss turf, suggesting that moss form plays a role, most likely in moisture relations, but possibly also in temperature relations.

Figure 74. ***Polytrichum strictum*** in Alaska, a moss where nematodes are known to live in the upper 6 cm in the Antarctic. Photo by Andres Baron Lopez, with permission.

Figure 75. ***Schistidium apocarpum***, a moss that provides a survival refuge in the Antarctic and alpine areas. Photo by David T. Holyoak, with permission.

Figure 76. Moss (reddish) and lichens. This photo shows a typical habitat for ***Plectus murrayi*** and occasionally ***Panagrolaimus davidi*** and ***Eudorylaimus antarcticus***. The photo was taken near Gondwana Station, Terra Nova Bay, Victoria Land. Photo by Melianie Raymond, with permission.

Figure 77. Two individuals of ***Plectus murrayi***, an Antarctic endemic that is often found in moss beds. Photo by Melianie Raymond, with permission.

The common presence of ***Teratocephalus*** (Figure 17) seems to be unique to the Antarctic, where it is abundant in the moss turf (Spaull 1973). It survives the frigid cold by a fast dehydration strategy that reduces damage by ice crystals (Wharton 2003). It would be interesting to determine how this fast dehydration relates to its choices of moss species/form. ***Ditylenchus*** sp. B occurs in more exposed aerial thalli of lichens (Spaull 1973). The latter species exhibits supercooling ability, whereas the moss-dwelling species both have bimodal supercooling point distributions. The high group supercools to ~-7°C and the other at ~-22°C. Pickup (1990b) suggests that field temperatures are likely to reach even lower levels than that.

Spaull (1973) found ***Teratocephalus***, ***Plectus*** (Figure 3), and ***Eudorylaimus*** (Figure 70) in all the bryophyte sampling locations on Signy Island, with the former two accounting for more than 50% of the nematodes among mosses. Cushion-formers such as ***Andreaea*** (Figure 78) and ***Grimmia***, on the other hand, had a nematode community where ***Plectus*** comprised less than 3%. A similar small percentage of ***Teratocephalus*** occurred in ***Bryum***. ***Eudorylaimus*** is more abundant in moss carpets and cushions than elsewhere. ***Eudorylaimus*** sp. C, in particular, seems to prefer cushions of ***Andreaea*** (Figure 78), ***Grimmia***, and ***Tortula***, where it comprises 45% of the individuals in that genus, but it is rare elsewhere (Spaull 1973). ***Antarctenchus hooperi*** is less restricted, being common in cushions of ***Andreaea*** and ***Tortula*** and in carpet-forming ***Calliergon*** (Figure 37)-***Calliergidium*** (probably ***Warnstorfia austrostraminea***), but it is likewise rare or absent elsewhere. The tylenchids [***Antarctenchus***, ***Aphelenchoides***, ***Ditylenchus***, ***Tylenchus*** (Figure 18)] are more abundant in moss turf than elsewhere, whereas the monhysterids [***Monhystera*** (Figure 16), ***Prismatolaimus***] are less numerous in moss turf than in other bryophyte formations.

Figure 78. ***Andreaea gainii*** (blackish) in Antarctica, showing cushion growth where nematodes may lurk. Photo from Polar Institute through Creative Commons.

The genus ***Eudorylaimus*** is particularly common in the Antarctic. Melianie Raymond (pers. comm. 2008) found ***Eudorylaimus antarcticus*** (Figure 79) among mosses in the Antarctic. In the McMurdo Dry Valleys, ***Eudorylaimus*** species are unaffected by vegetation type, including bryophytes (Simmons *et al.* 2009). ***Plectus*** (Figure 3) species, although bryophyte dwellers, are more abundant in algae. Its abundance above ground and below ground were significantly correlated in both the microbial mats and mosses. That is, the above ground abundance was a good indicator of below-ground abundance. The ability of ***Plectus*** species to migrate vertically is likely to benefit it in this changeable and extreme climate (Overgaard-Nielsen 1948; Kinchin 1989).

Kito *et al.* (1996) found a new species of ***Eudorylaimus*** (***E. shirasei***), bringing the Antarctic total in that genus to seven. Some of the specimens for this new species were collected from moss clumps at Cape Ryugu on the Prince Olav Coast, East Antarctica. It is odd among the members of ***Eudorylaimus*** (Figure 70) in having multinucleate intestinal cells, a factor that could simply have been overlooked elsewhere, but that raises questions about the possible effects of the severe Antarctic climate in causing or selecting for this multinucleate state. New species of moss nematodes will most likely continue to be described, particularly in the Antarctic.

Sohlenius and Boström (2006) found that 64% of 91 moss cushion samples from nunataks in East Antarctica had nematodes in them. In this harsh environment, 8% of the samples had no microfauna (nematodes, rotifers, or tardigrades) at all. The researchers considered the patchy distribution of nematodes and other organisms among the mosses to be a product of patch dynamics where stochastic processes determined colonization. They further supported this notion with the fact that nematodes in different cushions had different developmental stages, but it is possible that these may reflect differences in temperature that would affect rate of development. Competition with tardigrades that share their food sources seems also to be a limiting factor within a cushion.

Figure 79. ***Eudorylaimus antarcticus***, a common nematode among Antarctic mosses. Photo by Melianie Raymond, with permission.

In nunataks of Vestfjella, Heimefrontfjella, and Schimacher Oasis in East Antarctica, the faunal communities associated with mosses lacked organization and represented early stages of succession (Sohlenius *et al.* 2004). In these exposed nunatak moss habitats, species of ***Plectus*** (Figure 3) and ***Panagrolaimus*** (Figure 20) were the most frequent of the nematodes, occurring in 26% and 5% of the samples, respectively.

Dangers Lurking among Bryophytes

Fungal Interactions

Who would think that fungal treachery looms amid the mosses! Although nematode-trapping fungi are known worldwide, they were unknown in the Antarctic until 1973. In their examination of Signy Island mosses, Duddington *et al.* (1973) found nematode-trapping fungi on a number of moss species: ***Brachythecium austrosalebrosum***, ***Calliergon sarmentosum*** (Figure 37), ***Sanionia uncinata*** (Figure 80) (all hydrophytic), and ***Andreaea depressinervis*** (mesophytic-xerophytic). These fungi sport rings (Figure 81) that are able to constrict around nematodes that wander through them, thus ensnaring them. Several specimens of the predatory ***Thyronectria antarctica*** var. ***hyperantarctica*** had indeed trapped nematodes within their mossy home. Spaull (in Duddington *et al.* 1973) also noted fungi with such loops in a sample of the leafy liverwort ***Cephaloziella*** sp. (Figure 82) mixed with the lichen ***Cladonia metacorallifera*** from Terra Firma Islands in Marguerite Bay (latitude 68º42'S).

Figure 80. ***Sanionia uncinata***, common home of nematodes and nematode-trapping fungi. Photo by Michael Lüth, with permission.

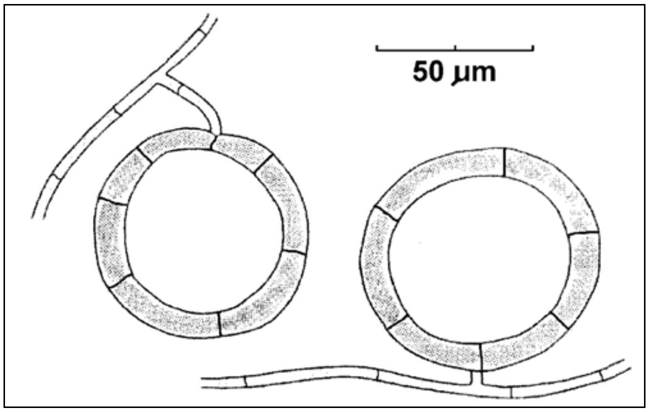

Figure 81. Nematode-trapping fungus, possibly ***Monacrosporium cionopagum***, isolated from the moss ***Calliergidium cf. austro-stramineum*** on Signy Island in the Antarctic. Redrawn from Duddington *et al*. 1973.

Figure 82. Leafy liverwort ***Cephaloziella turneri***, member of a genus that is home to nematode-trapping fungi. Photo by Michael Lüth, with permission.

The Antarctic sports at least 18 taxa that either trap nematodes or become endozoic parasites of members of this phylum (Gray *et al*. 1982). Many of these have been found among the mosses. Among the Hyphomycetes that snare nematodes, ***Monacrosporium ellipsosporum*** and ***M. cionopagum*** were the most widely distributed. The most frequent of the endozoic taxa was ***Harposporium anguillulae*** (Figure 83). These fungi seemed to have some bryological preferences, with ***M. ellipsosporum*** preferring calcicolous mosses. In fact, it appears that acidic habitats might provide a safe haven - the nematophagous fungi were absent from permanently saturated moss carpets and the strongly acidic turf-forming mosses of Polytrichaceae.

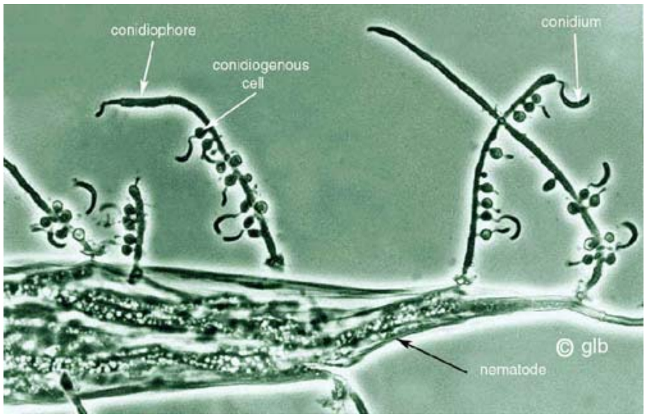

Figure 83. ***Harposporium anguillulae***, fungal parasite with conidiophores and conidia, on a dead nematode. Photo by George Barron, with permission.

These ensnaring fungi are not restricted to the Antarctic. Duddington (1951) considered the abundance of such fungi among mosses to result from the large amount of water among the shoots and leaves, making the environment favorable for both nematodes and fungi. In the Antarctic, the mosses provide the added benefit of being warmer than the air in summer.

Both nematodes and fungi live among ***Sphagnum*** (Figure 5). And here we also find nematode ensnaring fungi. In particular, the genus ***Sporotrichum*** (Figure 84), known for causing **sporotrichosis** in those who handle ***Sphagnum***, is able to trap the nematodes that reside there (Dollfus 1946).

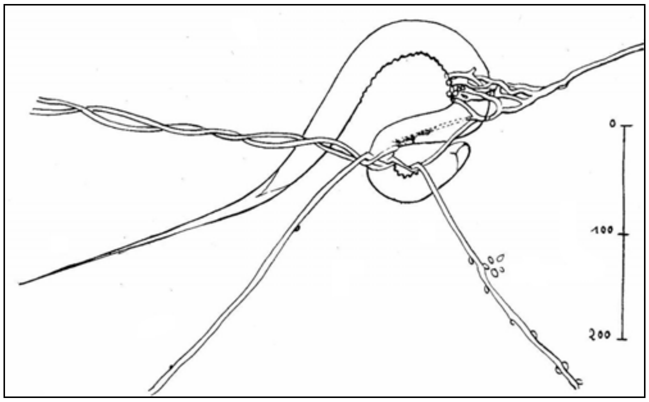

Figure 84. The nematode-ensnaring fungus ***Sporotrichum*** sp. in action. This is the same genus known so well for causing sporotrichosis in people who work with ***Sphagnum***. Image from Dollfus 1946.

Other fungal treachery looms, although not so dramatically. Several species of nematode-dwelling parasites await. Among these on Signy Island in the Antarctic are ***Harposporium*** sp. (Figure 83) and ***Acrostalagmus*** sp.

The widespread fungus ***Catenaria anguillulae*** (Figure 85-Figure 88) parasitizes nematodes (Sayre & Keeley 1969). Its **zoospores** (swimming spores) are attracted to the nematodes by exudates from the mouth, anus, or other opening of the nematode, including wounds. Once attached, the zoospores encyst, typically in clusters. These eventually germinate and penetrate through the nearby orifice to attack their host, the nematode. Success of the fungus is favored by high temperatures (optimum at 28°C) and moisture, the latter provided by bryophytes.

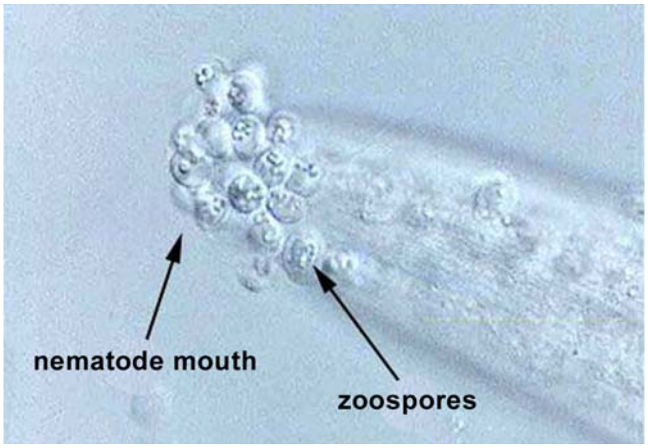

Figure 85. Nematode with zoospores of fungus ***Catenaria anguillulae*** surrounding its mouth. Photo by George Barron, with permission.

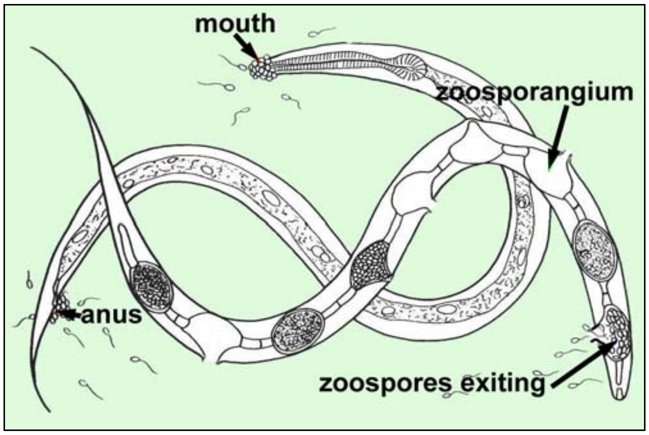

Figure 86. Nematodes showing infestation by ***Catenaria anguillulae***. Modified from George Barron's image, with permission.

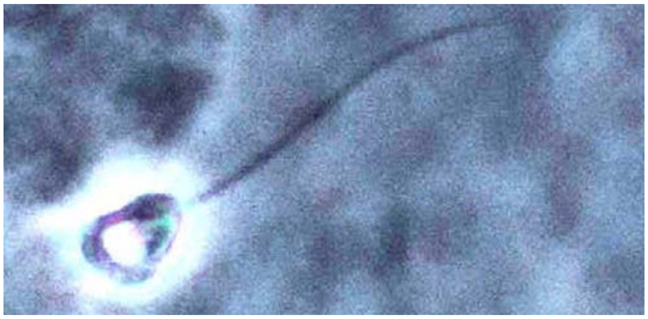

Figure 87. Zoospore of ***Catenaria anguillulae***. Photo by George Barron, with permission.

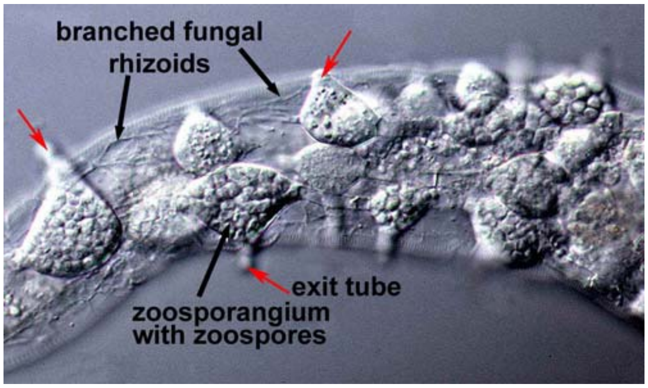

Figure 88. Zoosporangia of ***Catenaria anguillulae*** within a nematode. Red arrows indicate the exit tubes where zoospores escape. Photo by George Barron, with permission.

Safe Site from Predation

One advantage to living in a habitat with only small chambers is that large organisms don't fit. This affords some protection from predation, but nematodes are definitely not free from it. Some are preyed on by co-habiting tardigrades (Doncaster & Hooper 1961); under experimental conditions, one tardigrade, ***Macrobiotus richtersi*** (Figure 89), consumed 61 nematodes per day – no small threat (Sánchez-Moreno *et al*. 2008). Others must surely fall prey to insects. Even the protozoa may be a threat (Yeates & Foissner 1995). The Testacea (amoebae) can ingest nematodes, attacking mostly from the tail. In New Zealand, it was the protozoa ***Nebela*** (*Apodera*) ***vas*** (Figure 90) and ***Difflugia*** sp. (Figure 91) that waged the attacks, mostly on ***Dorylaimus*** (Figure 7) and ***Plectus*** (Figure 3) species among common bryophyte inhabitants.

Figure 89. ***Macrobiotus richtersi***, a moss-dwelling tardigrade that devours numerous nematodes. Photo through Creative Commons.

Pollution

Even aquatic organisms can suffer from air pollution. Steiner (1995b) tested responses of several groups of aquatic moss-dwelling invertebrates to SO_2 pollution. Nematodes, rotifers, and tardigrades changed their community composition. SO_2 at 0.225 ppm for 18 months significantly reduced the numbers of several nematode species. Responses were not so clear at 0.075 ppm, with some species increasing and others decreasing in numbers.

Lead can also considerably alter the moss-dwelling nematode community. Zullini and Peretti (1986) found that increased lead content in the moss resulted in a significant decrease in diversity, richness, and biomass, but not the density. The **Dorylaimina** suborder suffered the most by far.

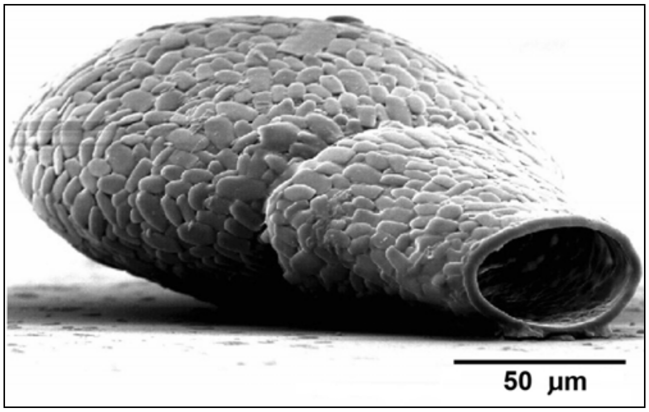

Figure 90. ***Nebela*** (=*Aphodera*) ***vas***, a protozoan that is a nematode predator. Photo by Edward Mitchell, with permission.

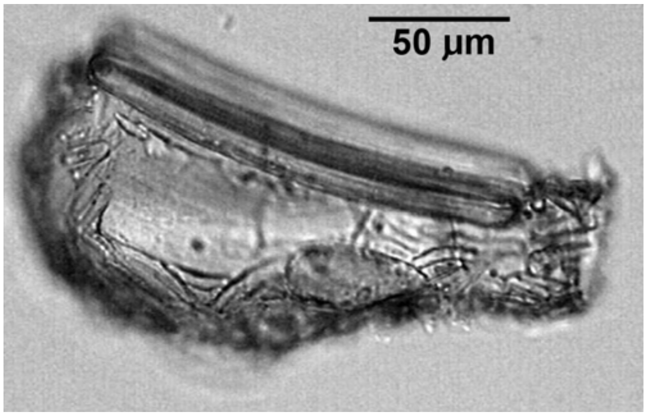

Figure 91. ***Difflugia bacillifera***, a moss-dwelling protozoan that preys on nematodes. Photo by Edward Mitchell, with permission.

Summary

Among the most common bryophyte-dwelling nematodes are members of the genera ***Plectus*** and ***Eudorylaimus***. These nematodes are usually less than 1 cm in length and many are much smaller. Although bryophyte-inhabiting nematodes are rarely studied, they are common there and can reach 480 individuals in just 1 g of moss.

Many nematodes adhere to the mosses with an **adhesive organ**. Water is their most limiting factor. They can migrate vertically among the bryophytes to adjust their moisture level. Some migrate from rhizoids to canopy when the moss is too wet, some move from the rhizoids to the stems when the moss is saturated, and some never leave the rhizoids. The most specialized nematodes, such as ***Plectus rhizophilus***, live in the bryophytes that experience the most events of desiccation, such as the epiphytes.

Members of ***Plectus*** are quick driers. Acrocarpous cushions are more favorable habitats than pleurocarpous feather mosses. Slow dehydration is important to their survival in a state of **anhydrobiosis**; some achieve this by **coiling**. Water is also necessary for their motility, where they can swim, crawl, inch, or bend to move. Some survive by living and reproducing inside the hyaline cells of ***Sphagnum***. **Eggs** likewise have a long survival and can even survive lack of oxygen.

Food strategies are mostly bacteriovores and predators. Some are **mycophagous** or **saprophytic**. Woodland mosses often feed on the detritus. They seem to do best in habitats with a low C:N ratio in the food source. Stream mosses serve as nutrient traps that favor nematodes.

Bryophytes can provide a safe site against would-be predators. However nematode-trapping fungi and fungal parasites may loom there. Bryophytes can also make a safe site by buffering the temperature both in the bryophyte and in the soil beneath. Even antheridia can serve as habitat, and in other cases the nematodes nestle among archegonia to make nematode galls. Galls seem to occur on many species of bryophytes and house nematodes that are often less than 1 mm long.

Numbers usually are highest in summer and lowest in winter, with some species migrating to greater depths in winter. Some species among ***Panagrolaimus*** can freeze and recover. Others, such as one ***Aphelenchoides***, can tolerate temperatures ranging from meltwater to 61.3ºC. **Trehalose** can protect some from freezing damage as well as from dehydration damage, most likely by stabilizing membranes.

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CHAPTER 4-4
INVERTEBRATES: ANNELIDS

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CHAPTER 4-4
INVERTEBRATES: ANNELIDS

Figure 1. ***Aeolsoma***, an aquatic annelid that sometimes inhabits mosses such as ***Fontinalis***. Photo by Yuuji Tsukii, with permission.

Annelida – Segmented Worms

Among the bryophyte-dwelling **Annelida** are worms that qualify as **mesofauna** (Figure 1). These are organisms, also including **mites** (**Acari**) and **springtails** (**Collembola**), that can occupy pore spaces that have a diameter of less than 2 mm (Briones 2006). In other words, these are small annelids, primarily in the subclass **Oligochaeta**.

Among the annelids, the family **Enchytraeidae** is a worldwide but little known family that can be found among the bryophytes. They reach their greatest abundance in the moist temperate soils (Block & Christensen 1985). Unlike the large, pink-red earthworms, these worms are usually grey-white (Briones 2006). Their identification is based primarily on internal characters, hence making them unknowns to the casual observer. And they must be live to be identified because preservatives make them opaque. **Enchytraeids** are important consumers in the Arctic tundra sedge-moss meadow habitat (Ryan 1977).

Although annelids are not as common as some other invertebrates in bryophytic habitats, there are at least some notable exceptions. ***Fontinalis*** (Figure 2) has been known to house 67 **oligochaetes** and 5 **leeches** (**Hirudinea**) in a square meter (Berg & Peterson in Macan 1966). Moss balls of ***Drepanocladus*** (Figure 3) and ***Fontinalis*** also house these annelids. In New Zealand Suren (1993) found **oligochaetes** to occupy 12.3% of the bryophyte fauna.

Three of the most common Enchytraeids in peatlands are ***Cognettia sphagnetorum***, ***Marionina clavata***, and ***Achaeta eiseni*** (Figure 4; Briones *et al.* 1997; Briones pers. comm. 17 March 2009). Nevertheless, Standen and Latter (1977) demonstrated that the common ***C. sphagnetorum*** is less common among ***Sphagnum*** than it is among *Eriophorum* or *Calluna* in a blanket bog at Moor House in Cumbria. ***Marionina clavata*** is aided in its survival by laying two types of eggs, one taking ~112 days and another taking ~271 days for the worms to reach maturity at 10ºC, thus potentially providing them with two different sets of conditions (Springett 1970). A tolerance for low *p*H levels in ***C. sphagnetorum*** and ***M. clavata*** (2.9-4) suggests their suitability for peatland habitation (Graefe & Beylich 2003).

Figure 2. **Brook moss**, ***Fontinalis duriaei***, where **annelids** can be common. Photo by Janice Glime.

In a Dutch Scots pine forest these three had a vertical zonation pattern in the same order, with ***Cognettia sphagnetorum*** (Figure 5) being the first to colonize new needle litter (Didden & de Fluiter 1998).

Figure 3. Moss ball of ***Drepanocladus*** from Lake Kucharo, Japan. Photo by Janice Glime.

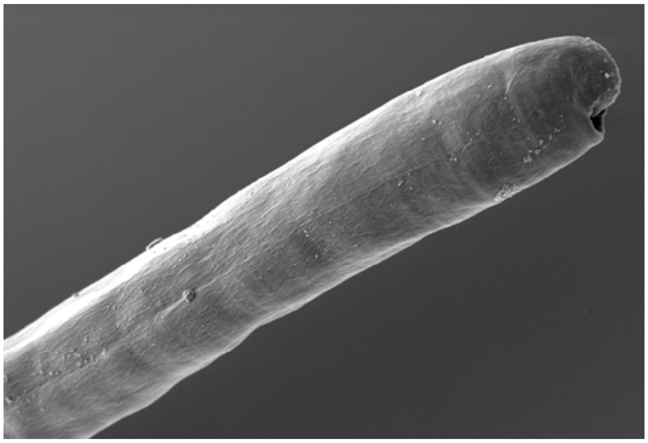

Figure 4. SEM image of *Achaeta* sp. Photo by María Jesús Iglesias Briones, with permission.

Water Relations

Very small annelids (**Enchytraeidae**) occur among ***Sphagnum*** plants. Springett (1970) found six species associated with peat. The moisture changes can result in diurnal vertical migrations (upwards at night), at least in ***Cognettia sphagnetorum*** (Springett *et al.* 1970; Hingley 1993; Briones *et al.* 1997), a widespread species known from aquatic habitats, ***Sphagnum*** peatlands, and on South Georgia in the Antarctic from ***Polytrichum*** (Figure 6) clumps (Block & Christensen 1985).

Cognettia sphagnetorum (Figure 5) has no cocoon stage, thus permitting it to take full advantage of the growing season in cold, wet climates of places like the Antarctic (Hingley 1993).

Several species of ***Achaeta*** (Figure 4) are morphologically adapted to drought by having a thicker cuticle. However, it appears that physiological adaptations to drought in the enchytraeids may be limited.

On the other hand, they seem also to be intolerant of too much water. In a study on the effects of drainage on the mesofauna of peatlands in Finland, Silvan *et al.* (2000) found that water-level drawdown resulting from peatland drainage caused an increase in the numbers of all the mesofauna studied, including the **Enchytraeidae**, with numbers ten times as great after 60 years. Because of a proportionally larger increase in Collembola, the proportion of **Enchytraeidae** in the fauna dropped slightly. More than 60% of the **enchytraeids** occurred in the top 4 cm of the peat. Within two years after water was returned to a drained peatland, the numbers dropped abruptly to levels near that of pre-drainage.

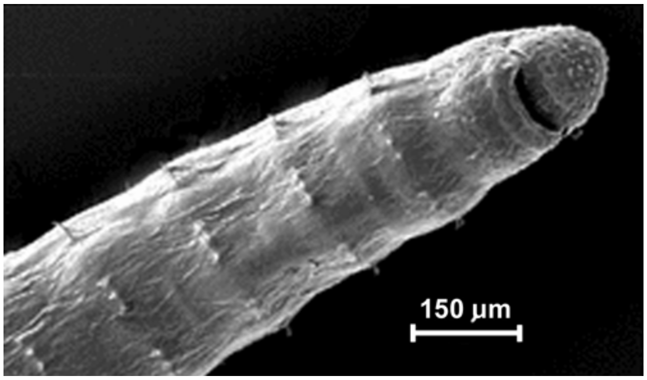

Figure 5. SEM image of ***Cognettia sphagnetorum***. Photo © María Jesús Iglesias Briones, with permission.

Figure 6. Clump of ***Polytrichum*** that could house **annelids**. Photo by Michael Lüth, with permission.

Temperature Tolerance

In peatlands and elsewhere, the **Enchytraeidae** are sensitive to temperature, which seems to be a major differentiating factor for population size. ***Cognettia sphagnetorum*** increases its reproductive rate, most likely through its capability of fragmentation as a reproductive strategy, in response to warmer temperatures (Briones *et al.* 1997). Warming seems to result in greater numbers without a concomitant vertical migration. Despite this advantage, Briones *et al.* (2007) considered that an increase in temperature to a maximum mean annual threshold of 16ºC could cause total loss of this species from some regions.

Achaeta eiseni, also a peatland species, is resistant to higher temperatures, increasing in numbers as temperatures increase, whereas numbers of ***Cernosvitoviella atrata*** (Figure 7) are greatly reduced by higher temperatures (Briones 2006, pers. comm. 17 March 2009). The latter species is inhibited by its inability to avoid dry conditions, resulting in death at high temperatures (Briones *et al.* 1997).

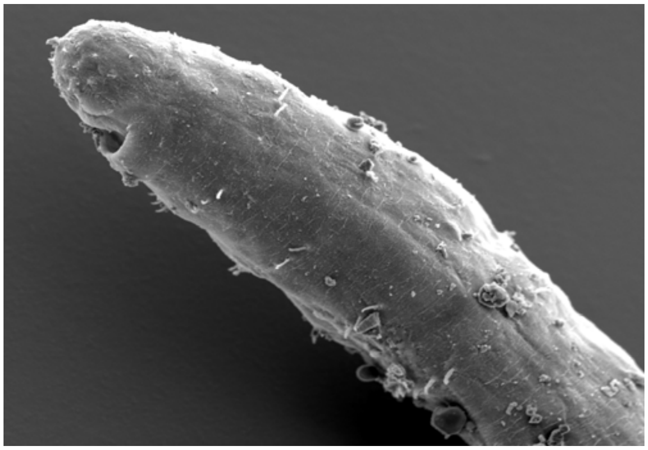

Figure 7. SEM image of ***Cernosvitoviella atrata***. Photo by María Jesús Iglesias Briones, with permission.

Cognettia sphagnetorum and ***C. glandulosa*** (known from moss banks and elsewhere; Block & Christensen 1985) are also prepared for the seasonal inundation of the peatlands. They are able to produce red blood under very wet conditions (Healy & Bolger 1984) to survive the low oxygen conditions that arise. Healy and Bolger showed that 35% of the Irish taxa of **enchytraeids** preferred habitats that were submerged or frequently flooded.

Reproduction

Any successful inhabitant of mosses must have a life cycle that is coordinated with the moss habitat. One advantage to some **Oligochaetes** is their ability to reproduce by fragmentation. Christensen (1959) pointed out that the **Enchytraeidae** contrast with other Oligochaeta in their inability to reproduce by fragmentation. At the same time, he reported on asexual reproduction in three species among the 78 Dutch **Enchytraeidae** studied by that time. In fact, one species apparently had only asexual reproduction, by fragmentation. Honda *et al*. (2003) described fragmentation in ***Enchytraeus japonensis***. This worm uses stem cells to accomplish its regeneration. Segments form as organs regenerate. They showed that cells with newly synthesized DNA appeared first as a ring in the tail area. The labelling then migrated, suggesting that the formation of segments occurs before organ regeneration. This regeneration cycle can take as few as ten days (Myohara *et al*. 1999; Nakamura 2004), and both ends of the worm can regenerate (Nakamura 2004). Nakamura (2004), in a six-and-a-half-year study, determined that the average fragmentation cycle length for the species was 20.4 days. The maximum number of fragmentation events in the life of the worm was 122, with an average of 35.3. The number of fragments in one event was 6.3. The cycle can repeat until the worm is starved or the population density is low, at which time it will differentiate gonads and reproduce once sexually (Honda *et al*. 2003). At this time I don't know how the number of annelid species using fragmentation relates to bryophytes as a habitat.

Food Relations

Springett and Latter (1977) experimented with various fungal diets on agar and found they could not keep many ***Cognettia sphagnetorum*** alive on the combinations they tried. Exudates from the mycelia of Basidiomycetes proved most harmful, resulting in 100% mortality in 20 days. They concluded that micro-organisms did not form any part of the natural diet of moorland Enchytraeidae. Hingley (1993) considered peat to be a poor source for food (Hingley 1993), with the moss itself seemingly of poor quality for annelids; only stem material of ***Sphagnum*** has been found in gut analyses (Figure 8; Standen & Latter 1977). Nevertheless, these worms feed on items that are generally unpalatable to other animals (Hingley 1993). After these are processed by the **annelids**, the feces are colonized by fungi and bacteria, which are in turn ingested by **Protozoa**, **rotifers**, and **nematodes**. Hence a food web emerges and peat is processed.

Briones (pers. comm.) challenged the suggestion that peatlands offered poor food quality, stating that enchytraeids are known to consume bacteria and dead organic matter, both of which are associated with the peatlands. Briones *et al*. (2004) used ^{14}C to match the gut contents with the substrate and found that most of the assimilated food came from sediment that is 5-10 years old. Their vertical movements in response to changing moisture did not affect their food source, but at higher temperatures it seemed that they had altered their carbon source since there was a lower ^{14}C enrichment with depth.

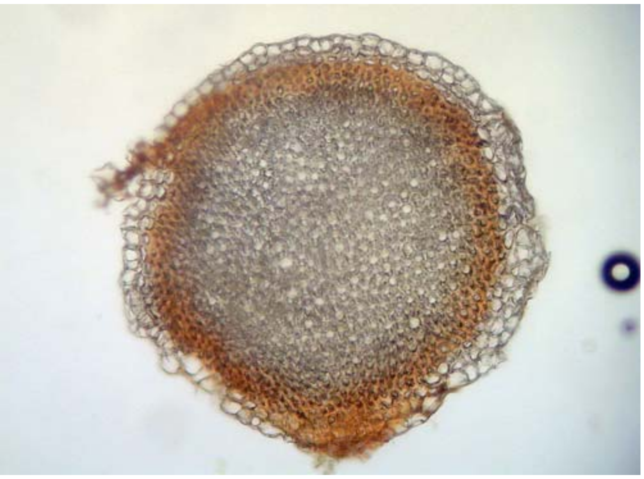

Figure 8. Stem section of ***Sphagnum contortum***, like those found in an annelid gut. Photo by Michael Lüth, with permission.

Guts from worms in substrata of ***Sphagnum***, *Calluna*, and *Eriophorum* at Moorhouse, Great Britain, all contained mixed decomposing litter, including cellulosic or humified plant material, amorphous humus, and associated fungal mycelia, again suggesting equal nutritional availability in the peatlands (Standen & Latter 1977). The ***Sphagnum*** stem material extracted from the gut of ***Cognettia sphagnetorum*** (Figure 5) causes one to question if these stems provide nutrition or merely serve to help in grinding other foods, much like the role of sand. In any case, the very high numbers of worms reached in peatlands provides witness that these are not bad systems for **enchytraeids** (Briones pers. comm.).

In the blanket bog at Moor House, Great Britain, the numbers of ***Cognettia sphagnetorum*** were significantly less in ***Sphagnum*** than they were in *Calluna* and *Eriophorum,* suggesting that ***Sphagnum*** was not an ideal habitat. However, when these were converted to numbers per gram dry weight of substrate, there were no significant differences among substrata. The species was in greatest numbers in association with older decomposing litter of *Eriophorum* and *Calluna* and with surface layers of ***Sphagnum***. The numbers of worms correlated weakly with unstained fungi, cocci, and moisture.

Sampling

Annelids are generally extracted from core samples. Researchers typically use some modification of a Berlese funnel (Didden *et al.* 1997; See Chapter 4-1). For annelids, a wet funnel is the most common, as suggested by O'Connor (1955) and Overgaard-Nielsen (1948, 1949). The moss samples are placed in a water-filled funnel and the temperature is gradually increased to about 40ºC (~3 hours). The high temperature causes the worms to vacate the mosses and drop down to the funnel. In organic soils, the efficiency is often 95% or more (Healy 1987), but can be less than 50% in some samples (Willard 1972 in Didden *et al.* 1997). Variations on this include soil cores in an earthenware cylinder suspended over a heated water bath (O'Connor 1955). The worms are driven upward to a layer of cool sand on top of the soil core. The worms are recovered by washing them from the sand.

An alternative method is to squeeze water from the mosses onto a microscope slide or into a Petri dish (Hingley 1993). Repeated extraction can be accomplished by soaking the moss in water and squeezing again, repeating this for a standard number of times. A paint brush or strip of filter paper can be used to transfer them to a drop of water on a slide. The sample could be transferred to a test tube, then centrifuged. A concentrated sample can then be removed from the bottom of the test tube with a long pipette.

Andrew and Rodgerson (1999) tested three methods of extracting invertebrates from Tasmanian bryophytes: Tullgren funnels, sugar flotation, and kerosene phase separation. When two samples were combined, the kerosene phase separation method extracted more total individuals, more **mites**, and more **Collembola**. Nevertheless, only three of the nine taxa were found in the single samples, suggesting that replicate samples are needed. Andrew and Rodgerson attributed this to differences caused by spatial scales. They further found that there is site scale variation at 2 km or less that may be more important that altitudinal variation.

Habitats

Aquatic

Aquatic bryophytes can serve as annelid (subclass Oligochaeta) habitat, especially for **Naididae**, reaching as much as 33% of the invertebrate fauna (1968 per dm^2) in thick moss vegetation of streams in the West Riding of Yorkshire, UK (Percival & Whitehead 1929). Their numbers were exceeded only by the Chironomidae (midges). This is a sharp contrast to their apparent absence on *Potamogeton* in those streams. Brusven *et al.* (1990) found that annelids were the most common non-insect invertebrate in the South Fork of the Salmon River, Idaho, USA. In Brazil, Gorni and da Gama Alves (2007) collected ***Fissidens*** and ***Philonotis*** (Figure 9) in winter and spring. Bryophytes adhering to rocks in the rapids of the Jacaré Pepira River, Brotas, São Paulo, Brazil, and to a vertical rock wall of a waterfall near the river provided a home for 191 Naididae individuals of ***Nais communis***, ***Pristinella jenkinae***, and ***P. menoni***. Among the identifiable species, ***P. jenkinae*** was dominant, representing 96.8% of all individuals. This species occupied both the submerged mosses of stream beds and the rock wall mosses with little water. But often the annelids are not very common. In ***Fontinalis antipyretica*** in the Czech Republic, Vlčková *et al.* (2001/2002) found that only about 1.1% of the fauna were annelids in one stream and about 1.4% in another.

Figure 9. ***Philonotis fontana***, representing a genus where ***Nais communis***, ***Pristinella jenkinae***, and ***P. menoni*** dwell in Brazil. Photo by Michael Lüth, with permission.

Naididae occupancy of mosses may provide several benefits to these worms. Mosses provide a safe site where the current is reduced in fast water (Vlčková *et al.* 2001/2002; Habdija *et al.* 2004). This is important for a group of organism that lack any adaptations for clinging or anchoring. Abundance and diversity are likely to increase with an increase in moss biomass, and more biomass makes available more periphyton and detritus (Egglishaw 1969; Suren 1993; Vlčková *et al.* 2001/2002; Linhart *et al.* 2002a, b).

Like Thienemann (1912), I rarely found oligochaetes among the bryophytes in Appalachian Mountain, USA, streams (Glime 1968). But Percival and Whitehead (1929) found that ***Eiseniella tetraëdra*** was a frequent inhabitant among the mosses in shallow water (3-4 cm). Nevertheless, even in thick moss beds, it reached a density of only 6 per dm^2. The Naididae (***Nais elinguis***), on the other hand, reached as many as 12,000 per dm^2 among the thick moss beds. Thickness of moss growth, as well as time of year and recent history of river conditions, influenced the density of oligochaetes. Percival and Whitehead suggest that the much smaller numbers of these naidids in the loose moss mats may be due to "feeble" setae and no ability to attach to the moss.

Hynes (1961) compared the oligochaetes, including ***Eiseniella tetraëdra***, on mosses and silk in a Welsh mountain stream and found little difference in the percentage of organisms, suggesting that the moss need not be a living organism and might only provide a substrate, perhaps with trapped detritus as a food source.

Peatlands

Unlike many other kinds of animals, the annelids are not very diverse in peatlands. Hingley (1993) reported that only three families of **Oligochaeta** occur in peatlands, with the most common being the Enchytraeidae. Duinen *et al.* (2006) found that in Estonia and The Netherlands, only ***Cognettia sphagnetorum*** occurred in ombrotrophic raised bogs, *i.e.*, in the most nutrient-poor situations. In Estonia, ***Nais variabilis*** (Figure 10), ***Lumbriculus*** (=*Lumbricus*) ***variegatus*** (Figure 11), and species with sexual reproduction occur only in more minerotrophic water bodies with a higher decomposition rate and consequent higher nutrient content. The lagg zone (marginal area around the bog where nutrients are often higher) fares somewhat better, having ten species of oligochaetes. This zone is absent in The Netherlands due to agriculture.

Figure 10. ***Nais variabilis***, a moss-dwelling annelid. Photo by Yuuji Tsukii, with permission.

Figure 11. ***Lumbriculus*** (=*Lumbricus*) ***variegatus***, an annelid that is used to feed pets and that lives in minerotrophic peatlands. Photo from Wikimedia Commons.

Prairie Worms

It is possible that mosses may provide refugia for one rare species. The giant **Palouse earthworm** (***Driloleirus americanus***; Figure 12), named because it can reach nearly a meter in length, is the subject of a petition to declare it an endangered species and afford it protection (Palouse Prairie Foundation 2007). Few recent reports of its presence exist. In one such report, however, near Moscow, Idaho, USA, two researchers found it in a somewhat mesic area under forest canopy. The area had abundant mosses and these researchers found several of the worms near the surface under moss mats when looking for moss-feeding beetles in the Byrrhidae. In drier times it can burrow down as much as 5 m.

Figure 12. The giant **Palouse earthworm** (***Driloleirus americanus***), an endangered worm that seems to seek moisture under mosses in the Palouse Prairie. Photo by Yaniria Sanchez-de Leon, with permission.

Antarctic

As in the peatlands, the **Enchytraeidae** are common in the Antarctic bryophytes. Block and Christensen (1985) found ***Cognettia sphagnetorum*** in ***Polytrichum*** clumps and ***C. glandulosa*** in moss banks. On South Georgia and Signy Island, they found seven taxa in soil and peat, but suspected that five of those had been introduced by human activity on the islands.

Dispersal Agents?

The presence of bryophyte diaspores in earthworm castings suggests a possible dispersal mechanism (During *et al.* 1987). Van Tooren and During (1988) found various spores and vegetative diaspores in the guts of terrestrial **earthworms** [***Allolobophora caliginosa***, ***A. chlorotica***, and ***Lumbricus terrestris*** (Figure 13-Figure 14)] in The Netherlands. Especially rhizoid tubers and spores occurred. However, it is not clear that these provided any nutritional value to the worms because some remained viable and grew new plants, suggesting digestion was not possible. Rather, they most likely were simply mixed in with the soil that was being consumed.

Figure 13. ***Lumbricus terrestris***, the common earthworm, is able to transport various diaspores, thus being a potential dispersal agent for bryophytes. Photo by Michael Linnenbach through GNU Free Documentation.

Figure 14. ***Lumbricus terrestris*** wending its way in a clump of the moss ***Rhynchostegium confertum***. Photo by Serhat Ursavas, with permission.

From a bryological point of view, it thus appears that the worms might serve as dispersal agents, although it was spores, not the more easily established tubers, that remained viable after traversing the **earthworm** gut (Van Tooren & During 1988). Tubers seemed unable to survive the journey through the gut. Twenty-five species of mosses germinated from diaspores from gut contents, with ***Pottia/Phascum*** (Figure 15) being the most common. This compares to the presence of only eight species of mosses in the samples of **earthworms**, indicating transport from other locations. For buried diaspores, **earthworms** may facilitate their movement from beneath the surface to the castings above ground where they are exposed to light and able to germinate. On the other hand, ***Bryum rubens*** (Figure 16) is not known to produce sporophytes in this area and relies on vegetative diaspores. It is one of the most common species in the area, but is not common above ground. It was also rare in the worm samples, causing Van Tooren and During to suggest that mechanical and chemical processes in the gut cause high mortality of the rhizoidal tubers in this species.

Figure 15. ***Pottia bryoides***, a member of one of the genera that had the highest germination in cultures from earthworm guts. Photo by Michael Lüth, with permission.

Earthworm Culture

Peatmoss is recommended as an additive to rich soil for rearing earthworms (Mascio 2006; How to Grow Your Own Earthworms 2009; Oliver 2009)

Most farmers seem to consider **earthworms** to be their friends because they reputedly aerate the soil. However, they can also be a nuisance. One person complained that the earthworms were the largest deterrent to the establishment of a moss garden. The worms would "plow" up the surface and detach the moss from the soil. It appeared that they also chewed up the moss, but there seems to be only circumstantial evidence of that.

Figure 16. Clump of ***Bryum rubens***, a moss that does not produce sporophytes and relies on dispersal of vegetative diaspores. Photo by Michael Lüth, with permission.

Polychaetes

I completely overlooked this mostly marine group when I wrote this chapter (Figure 17). It was only when two people posted pictures on Bryonet of strange organisms they found among bryophytes that I realized there are terrestrial polychaetes that may inhabit bryophytes. These Bryonet organisms were not polychaetes, but they did raise the question. However, I have been unable to find any published documentation that polychaetes ever occur on bryophytes.

Figure 17. Syllid polychaete undergoing epitoky – becoming sexually mature. Photo by Megan McCuller, through Creative Commons.

Storch and Welsch (1972) described adaptations to air breathing in polychaetes from the mangrove swamps of Sumatra. Their exterior is protected by a cuticle that varies in thickness. The gills have extracellular spaces that have blood lacunae in the epidermis in at least one species. But the terrestrial polychaetes seem to be poorly known.

Thank you to Bryonet and its wonderful subscribers! *Parergodrilus heideri* and *Hrabeiella periglandulata* are the only terrestrial European flatworms, where they live in forest soils (Dumnicka & Rozen 2002) and would seem to be likely candidates for bryophyte dwelling (Juan Larrain, pers. comm. 29 February 2012). But both Larrain and I searched the web for links to bryophytes to no avail. Rather, Schlaghamerský and Šídová (2009) examined the vertical distribution of a population in the Czech Republic of *Hrabeiella periglandulata* in soil and determined that they avoided the organic layer, which would include bryophytes. Perhaps the minute *Parergodrilus heideri* (Rota 1997) and *Hrabeiella periglandulata* (Rota 1998) are hiding among them somewhere with the right moisture conditions. But it is more likely that the temperature of their environment is modified by the presence of bryophytes at the surface.

Summary

Many bryophyte-inhabiting annelids (segmented worms) are **mesofauna**, *i.e.* able to occupy spaces with a diameter < 2 mm. The **Enchytraeidae** are among the most common. Bryophyte-dwelling annelids may form zones in the soil and bryophytes and some species may migrate up and down daily in response to changing moisture conditions. **Enchytraeids** have a wide tolerance to water, but have little adaptation to drought. Some species produce red blood to survive low oxygen conditions.

Although most **Enchytraeidae** cannot reproduce by fragmentation, some enchytraeids can reproduce by this method in a cycle of ~20.4 days. ***Cognettia sphagnetorum*** increases its reproductive rate when temperatures get warmer, but an annual mean above 16ºC could cause annihilation. Some species thrive in higher temperatures, whereas others are seriously affected.

Neither mosses nor fungi seem to serve as food for the annelids, although ***Sphagnum*** stems have been found in guts. In peatlands, 5-10-year old sediments seem to be an important food source. Bryophytes in streams can provide safe sites where reduced current provides more debris for food. Despite their apparent distaste for bryophytes, annelids may disperse vegetative diaspores by eating them and depositing them elsewhere unharmed, indicating at least some are not digested..

Worms can be extracted from bryophyte samples using funnel systems. Smaller taxa can be extracted by squeezing water onto a microscope slide.

The **Palouse earthworm** (***Driloleirus americanus***) is a rare species that occurs under moss mats in the prairie.

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CHAPTER 4-5

INVERTEBRATES: ROTIFERS

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CHAPTER 4-5

INVERTEBRATES: ROTIFERS

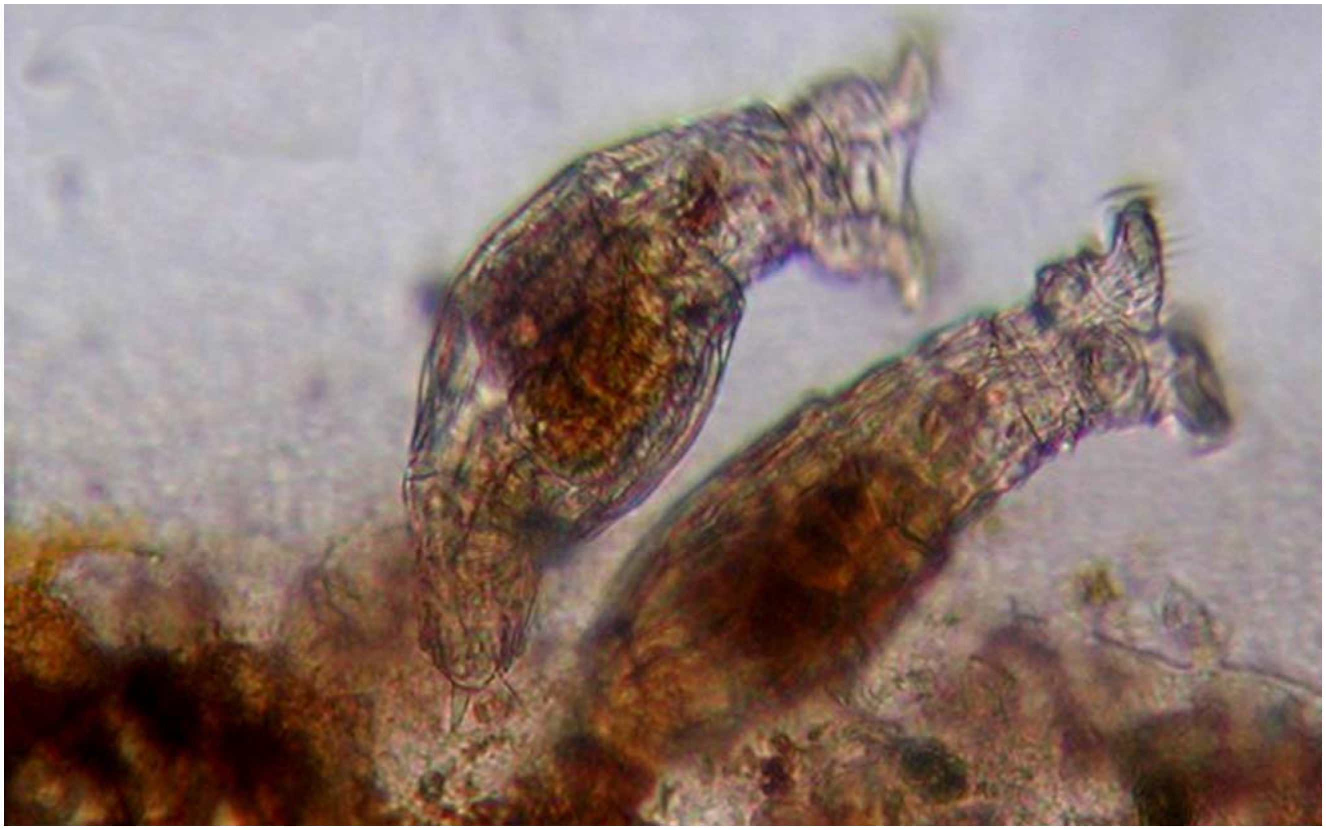

Figure 1. Two **bdelloid rotifers** that commonly inhabit bryophytes. Photo by Paul Davison, with permission.

Rotifera – Rotifers

Rotifers, also known as wheel animals, are so-named because of the ciliated **corona** on the head. The corona creates a circular movement that is used to direct food to the mouth. Rotifers have up to five simple eyes (Figure 2) that are light-sensitive and often are red. This sensitivity to light permits some species to be **phototactic** (moving toward or away from light).

Rotifers are natural partners for organisms like bryophytes that often experience extended periods of drought. Pourriot (1979) considered the number of species that inhabit mosses to be over 200. The number is surely larger now.

Anthony von Leeuwenhoek discovered in 1702 that rotifers could tolerate months in a state of desiccation, hence marking the earliest studies on **cryptobiosis**, or life in a dormant state without water (Alpert 2000). This desiccation tolerance is particularly common in the class **Bdelloidea**. In this dry state, they are easily dispersed along with fragments of the mosses they inhabit.

Not much bigger than some protozoa (mostly 0.1-0.5 mm long, but up to 2 mm), they form a phylum of their own, the **Rotifera**, with at least 2000 species (Howey 1999). They are multicellular and even possess a primitive brain, at least in females (Hingley 1993).

Figure 2. ***Brachionus quadridentatus*** (**Monogononta**) showing red eyespot. Photo by Frank Fox, through Creative Commons.

Rotifers have a variety of means of protection. Some are encased in a **lorica** (rigid case or shell; Figure 3, Figure 13-Figure 14). Others build tubes or cases (Figure 53, Figure 82). Some have sharp spines (Figure 13). And some simply hide, many of which use bryophytes for hiding.

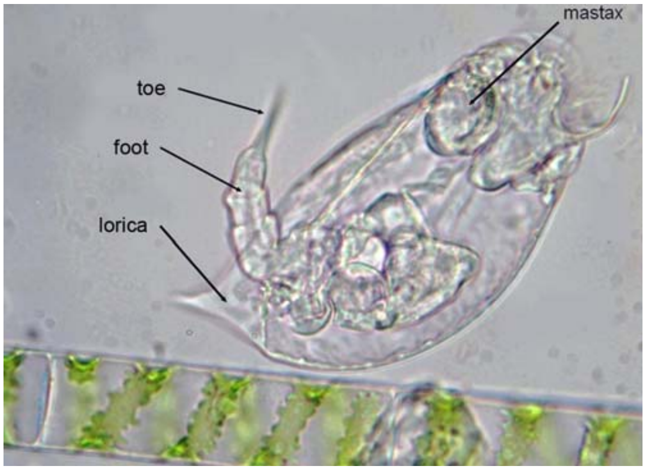

Figure 3. ***Colurella adriatica***, showing location of the mastax and other prominent features. This one is sitting on the green alga *Spirogyra* sp., but it sometimes occurs among mosses. Photo by Michel Verolet, with permission.

Moss-dwelling rotifers have been around for a long time. Waggoner and Poinar (1993) reported on fossil habrotrochid rotifers from Dominican amber. These revealed microfossils from the bracts of a moss from the Eocene-Oligocene (circa 34 million years ago) in the northern Dominican Republic. It is interesting that these match the **thecae** (sheath) of living moss dwellers in ***Habrotrocha***, being almost identical with ***H. angusticollis*** (Figure 4). These **parthenogenetic** (producing unfertilized eggs) bdelloid rotifers seem to have a well-adapted body plan that has persisted for 35 million years.

Figure 4. ***Habrotrocha angusticollis***, a moss inhabitant. Photo by Yuuji Tsukii, with permission.

It is likely that many species of rotifers remain to be described. The most likely habitat for these discoveries is that of bryophytes. The bryophyte dwellers are often very small, rarely swim, and go dormant (see below) as a **tun** (Figure 61) or a **resting egg**, all characteristics that make them less likely to be noticed and more difficult to identify. Shiel and Green (1996) remarked that considerably more rotifers in New Zealand and the Australasian region remain undescribed. At that time the region had 388 valid species in 66 genera. Yet less than 5% of these were endemic to the Australasian region.

With the potential differences in physiology and biochemistry, it is also likely that DNA analysis will reveal many microspecies and perhaps even different species that are not recognizable based on morphology alone. Kaya *et al*. (2009) compared "DNA species" with morphological species of bdelloid rotifers from mosses in Turkey and the United Kingdom. They found that traditional identification methods underestimate rotifer diversity by factors of 2 at the local level and 2.5 at a regional level. Each moss sample had 3-9 morphospecies, but the DNA species ranged 8-12 per moss sample. These DNA species numbers indicated greater differences in diversity among locations (**gamma diversity**) than within samples (**alpha diversity**). Rotifer biologists consider that the number of cryptic species that can be revealed by DNA taxonomy may be overwhelming (Suatoni *et al*. 2006; Fontaneto *et al*. 2008).

This knowledge that the **Rotifera** include many **cryptic species** (species that look alike but can't interbreed), as demonstrated by DNA, is supported by a diversity of narrow ecological niches (see, for example, Fontaneto *et al*. 2011). This allows for physiological/biochemical differences that permit the species to survive in a wide range of cosmopolitan habitats. This diversity and cosmopolitan distribution has led to superfluous names in many of the rotifer genera. This chapter follows the nomenclature of Segers (2007); for species described after that publication it follows EOL <http://eol.org/>.

Reproduction

The lifespan of many rotifers is as much as 30-40 days, not counting their time in dormant states (Ricci 2001). But Wikipedia (2016) considers it to be much shorter for **Monogononta**, ranging 2 days to 3 weeks for females. And species of these animals can often be found in active or dormant states on both aquatic/wetland (Priddle & Dartnall 1978; Bateman & Davis 1980; Ricci 1983; Ricci *et al*. 1989; Linhart *et al*. 2002a) and terrestrial mosses (Bartos 1949; Ramazotti 1958; Overgaard-Nielsen 1967; Kukhta *et al.* 1990). Several species are even known from the harsh environment of mosses growing on roofs (Hirschfelder *et al*. 1993).

Rotifers (depending on the taxon) have three types of individuals: **mictic** (mixing) females, **amictic** females (not reproducing sexually), and males. Rotifer eggs may be attached to a substrate (Figure 5-Figure 6) or remain attached to the parent (Figure 7) (EOL 2016). The female rotifers themselves live only a few days to a few weeks. The males have no digestive tract, are often sexually mature at birth, and are short-lived, as you might expect when they don't eat. Hence, it is also understandable that males are much smaller than females (Figure 8).

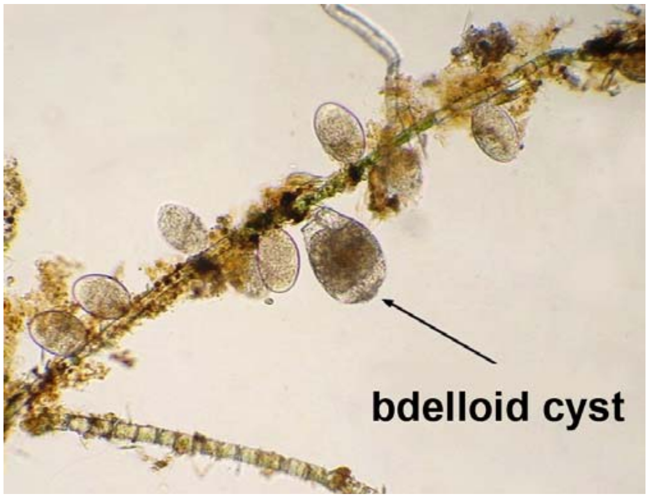

Figure 5. Bdelloid rotifer eggs on alga. Photo by Michel Verolet, with permission.

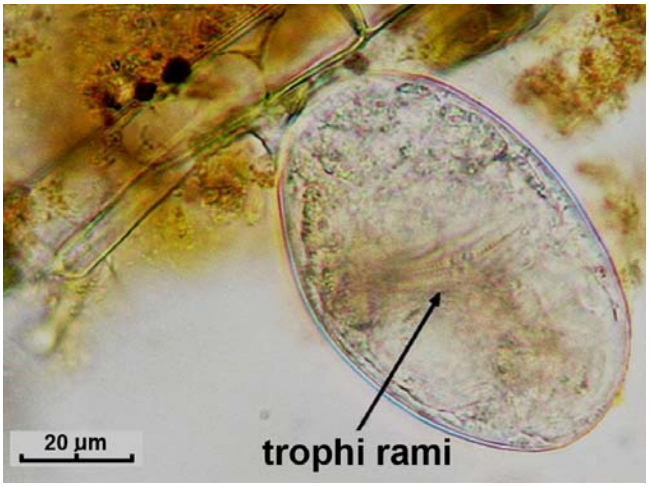

Figure 6. Egg of rotifer on an algal filament. Photo by Michel Verolet, with permission.

Figure 7. ***Brachionus*** with 3 eggs. Photo by Jean-Marie Cavanihac, with permission.

The female reproductive system of rotifers consists of one (**Monogononta**) or two (**Bdelloidea**) ovaries. Each ovary has a **vitellarium gland** (Figure 9) that supplies the eggs with yolk.

Figure 8. ***Cephalodella gibba*** in copulation, male on left. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 9. ***Asplanchna girodi*** **vitellarium**. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bdelloidea

Bdelloid rotifers (class **Bdelloidea**; Figure 10-Figure 11), known as moss rotifers, are less species rich (over 450 described species) than the **Monogononta** (ca 1500 species). The **Bdelloidea** are the most common rotifers in peatlands (bogs and fens; Bielańska-Grajner *et al.* 2011) and other mosses (Sayre & Brunson 1971; Ricci *et al.* 2003b; Gilbert & Mitchell 2006). All known taxa are **parthenogenetic**, *i.e.*, they have only females that reproduce asexually, giving rise to more females (Hingley 1993). However, Danchin *et al.* (2011) analyzed the genome of one of these, ***Adineta vaga*** (Figure 12), a moss dweller, and found four genotype modifications that suggested rare events of sexual reproduction may have occurred.

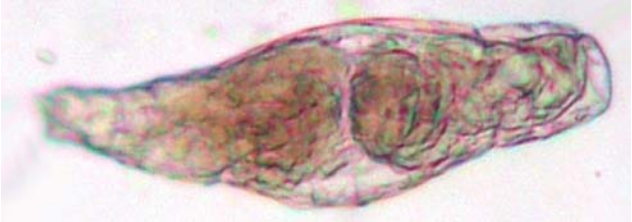

Figure 10. **Bdelloid rotifer** taken from bryophytes. Photo courtesy of Dan Spitale.

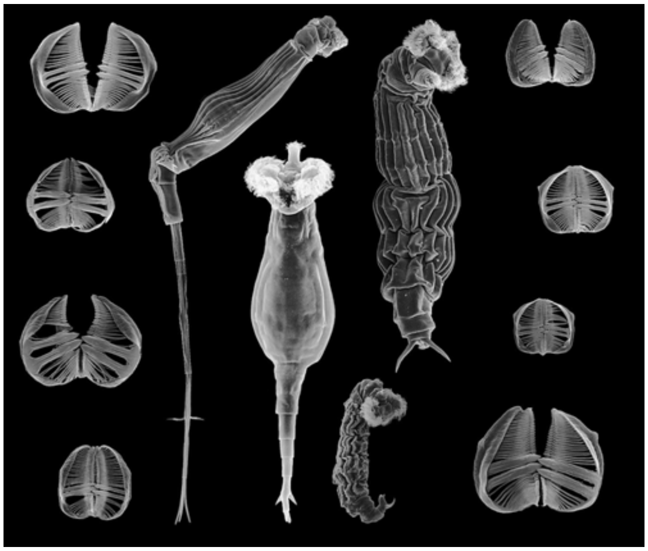

Figure 11. Examples of **bdelloid rotifers** and **trophi**, the hardened part of the **mastax**. Photos by Diego Fontaneto, through Creative Commons

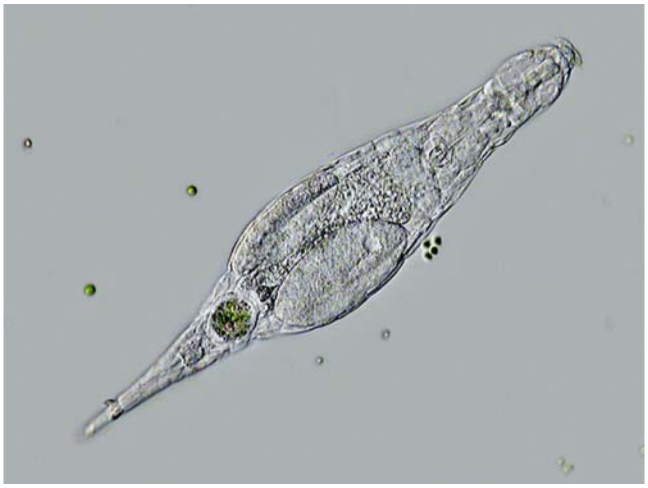

Figure 12. ***Adineta vaga***, a moss dweller that is 0.2-0.3 mm when extended. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Monogononta

The **Monogononta** is the second major class of rotifers, and by far the largest (ca 1500 species) (Wikipedia 2012a). Among these are members that have both sexual and asexual reproduction. The short-lived, uncommon males, however, serve only for reproduction and thus are much smaller than females. Some males are so reduced that they have little more than a bladder and a penis! One such monogonont is the mostly planktonic genus ***Brachionus*** (Wikipedia 2011; Figure 2, Figure 7, Figure 13-Figure 14). In this genus, with some members occurring among bryophytes, increases in population density can induce sexual reproduction. The sexually produced eggs can become resting eggs that survive unfavorable conditions (Plewka 2014). It appears that at least in ***Brachionus** calyciflorus* (Figure 13) only one allele is needed to turn off sexual reproduction and force all reproduction to be parthenogenetic. ***Brachionus urceolaris*** (Figure 14) sometimes lives among bryophytes (Figure 7; Hingley 1993), but it is primarily a cosmopolitan planktonic species like the other ***Brachionus*** species (EOL 2016). It is mostly parthenogenetic, but it occasionally produces males.

Figure 13. ***Brachionus calyciflorus***, a species that needs only one allele to turn off sexual reproduction. Academy of Natural Sciences in Philadelphia, through Creative Commons.

Figure 14. ***Brachionus urceolaris***, a bryophyte dweller. Photo courtesy of Emily Toscana Guerra from Rotifer World Catalog, through Creative Commons.

In the **Monogononta**, two types of reproduction occur. In one type, females produce unfertilized eggs that develop into females, just as in the bdelloids (Hingley 1993). But in the second type, sexual females appear only when environmental conditions are unfavorable, such as drought or cold. These females produce a sexual egg that forms a thick-walled resting "egg" when fertilized (Figure 15). That resting egg develops into a female. If the egg is not fertilized, it develops into a male.

Figure 15. ***Euchlanis triquetra*** with expelled resting egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bryophytes as Habitat

Moss-dwelling **rotifers** have attracted the attention of rotifer specialists for some time (Burger 1948). The family **Habrotrochidae** (see Lobule Dwellers below) seems to occur mostly on mosses but is also **benthic** (living on the bottom of a water body) (Wallace & Snell 1991). There are two species in the genus ***Elosa*** (Figure 16) that are common on ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), and these are considered bog specialists (Pejler & Bērziņš 1993b).

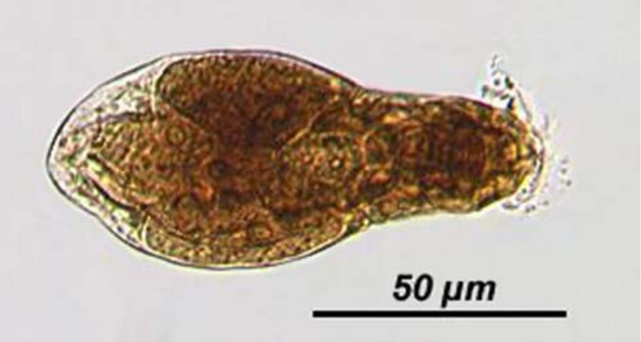

Figure 16. ***Elosa worrallii***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003 from Rotifer World Catalog, through Creative Commons.

Rotifers occur with bryophytes in both aquatic and terrestrial habitats, with bryophytes often providing a water space in the latter. Duggan (2001) points out that the **periphytic** (living on plant surfaces) species of rotifers have received little attention compared to the **planktonic** (drifting in open water) species. Bryophytes are among these **macrophytic** (referring to plants that are visible without a microscope) substrates that support the periphyton, but Duggan did not include them in his study, considering bryophytes to be a separate habitat. **Periphytic** rotifers seem to have preferences among macrophyte species based on differences in physical structure or complexity, food concentration or composition, chemical factors, macrophyte age, and differences in protection from predation they provide (Duggan 2001). The same factors are likely to control bryophyte choices as well.

Terrestrial and wetland rotifers crawl through the spaces among leaves and branches of bryophytes, living in the water film surrounding the plant (Hingley 1993). In her website on rotifers, Jean-Marie Cavanihac (2016) considers ***Rotaria rotatoria*** (formerly ***Rotifer vulgaris***; Figure 17) to be one of the most frequent rotifers on mosses, and as a free-living (unattached) rotifer, it moves like a caterpillar.

Figure 17. ***Rotaria rotatoria***, a bdelloid rotifer from moss. Photo by Christian D. Jersabek, through Creative Commons.

The bryophyte dwellers feed on the bacterial and protozoan inhabitants, swim among the leaves, or nestle between the leaves and branches where they gain more protection against their predators (Hingley 1993). The same is true for those living in terrestrial habitats as well as in ponds, lakes, and waterways.

Habitat Characteristics

Although not restricted to these habitats, rotifers are common on mosses in alpine ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) bogs and in wetlands. Bryophytes may be particularly useful to stream and other aquatic rotifers as a substrate. Pejler and Bērziņš (1989) contend that rather than any chemical attraction for a substrate, some substrates might be avoided, perhaps due to lack of periphyton. The genus ***Lecane*** (Figure 122) is a very large, widespread genus that has little preference for any particular substrate (Pejler & Bērziņš 1994). In fact, it furthermore seems to have good dispersal, as indicated by its rapid ease of colonization on an artificial substrate of cotton. Fontaneto and Ricci (2006) consider that rotifers are probably best dispersed in their dormant state (allowing them to be dispersed along with their bryophytic substrate).

The species on various macrophytes differ, even when a different species of macrophyte is growing in close proximity (Pontin & Shiel 1995; Duggin *et al.* 2001). Likewise, bryophyte species composition explains most of the variation in monogonont rotifers in springs and fens

(Hájková *et al*. 2011). Bryophytes form four functional groups, supporting the importance of plant form in their selection of the bryophyte substrate. Species composition of monogonont rotifers differs significantly (P <0.01) among crawling dense [***Cratoneuron filicinum*** (Figure 18), ***Palustriella commutata*** (Figure 19), ***P. decipiens*** (Figure 20)], crawling loose [***Brachythecium rivulare*** (Figure 21), ***Calliergonella cuspidata*** (Figure 22), ***Plagiomnium affine*** agg. (***P. ellipticum*** – Figure 23, ***P. elatum*** – Figure 24)], and ***Sphagnum*** tufts [***S. fallax*** (Figure 25), ***S. flexuosum*** (Figure 26), ***S. palustre*** (Figure 109), ***S. papillosum*** (Figure 27)]. The fourth group is erect (mostly acrocarpous) species: ***Bryum pseudotriquetrum*** (Figure 28), ***Fissidens adianthoides*** (Figure 29), ***Philonotis caespitosa*** (Figure 30).

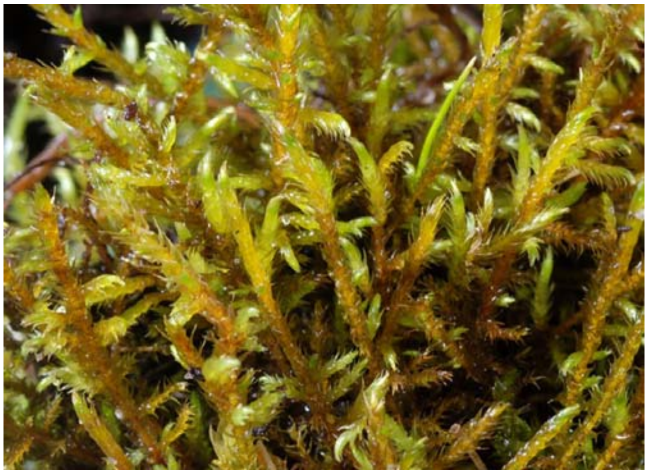

Figure 18. ***Cratoneuron filicinum***, a "crawling dense bryophyte" that serves as home for one group of rotifers. Photo by J. C. Schou, with permission.

Figure 19. ***Palustriella commutata***, a "crawling dense bryophyte" that serves as home for one group of rotifers. Photo by David T. Holyoak, with permission.

Figure 20. ***Palustriella decipiens***, a "crawling dense bryophyte" that serves as home for one group of rotifers. Photo by Michael Lüth, with permission.

Figure 21. ***Brachythecium rivulare***, a "crawling loose bryophyte" that serves as home for one group of rotifers. Photo by Michael Lüth, with permission.

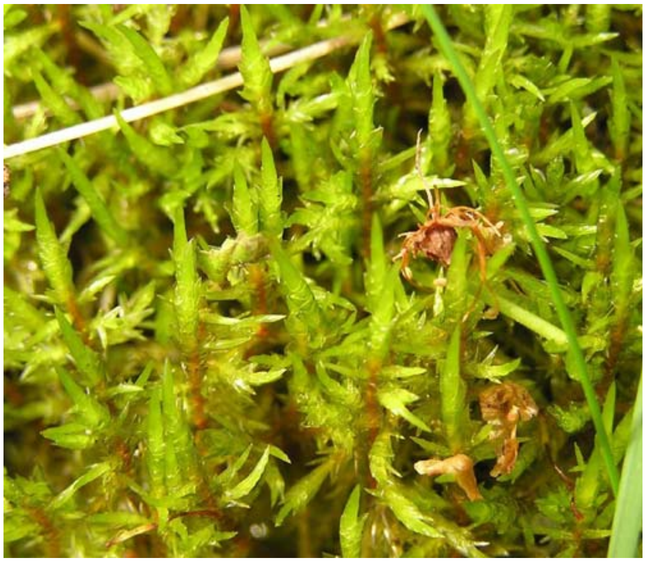

Figure 22. ***Calliergonella cuspidata***, a "crawling loose bryophyte" that serves as home for one group of rotifers. Photo by Michael Becker, through Creative Commons.

Figure 23. ***Plagiomnium ellipticum***, a "crawling loose bryophyte" that serves as home for one group of rotifers. Photo from Biopix, through Creative Commons.

Figure 24. ***Plagiomnium elatum***, a "crawling loose bryophyte" that serves as home for one group of rotifers. Photo by Michael Lüth, with permission.

Figure 25. ***Sphagnum fallax***, home of "***Sphagnum*** tuft" rotifers. Photo from <www.aphotofauna.com>, with permission.

Figure 26. ***Sphagnum flexuosum***, home of "***Sphagnum*** tuft" rotifers. Photo by Michael Lüth, with permission.

Figure 27. ***Sphagnum papillosum***, home of "***Sphagnum*** tuft" rotifers. Photo by Dale H. Vitt, with permission.

Figure 28. ***Bryum pseudotriquetrum***, home of "erect species" rotifers. Photo by Michael Lüth, with permission.

Figure 29. ***Fissidens adiantoides*** with capsules, home of "erect species" rotifers. Photo by Bob Klips, with permission.

Figure 30. ***Philonotis caespitosa***, home of "erect species" rotifers. Photo by Kristian Peters, with permission.

Hájková *et al*. (2011) demonstrated bryophyte-dwelling monogonont rotifers in springs and fens form communities that are strongly correlated with water *p*H and conductivity, Ca concentration, and ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) dominance. The rotifers did not respond to silica, iron, or nutrients, despite the effects of these factors on amoebae, algae, and other microscopic food organisms. Rotifer species composition does not depend on water chemistry, except *p*H and calcium, at least in part because their ***Sphagnum*** substrate selects for these factors. For shell-forming species, these latter chemical factors are often more important.

Aquatic bryophytes may provide a refuge during particularly heavy stream flow. The number of rotifer species among bryophytes in Tatra streams increased during spring runoff from 18 in winter to 24 during runoff (Madaliński 1961). Other factors that contribute to substrate choice include temperature, oxygen content, trophic levels, chemistry, food availability, and predators (Pejler & Bērziņš 1989).

Abundance

An average of 700 **rotifers** can exist per gram on the soil-dwelling mosses ***Ceratodon purpureus*** (Figure 31) and ***Polytrichum juniperinum*** (Figure 32), rock-dwelling moss ***Schistidium apocarpum*** (Figure 33), and bog/fen species of ***Sphagnum*** (Gerson 1982). Consider that a rough estimate for a handful of moss is about 10 grams.

Figure 31. ***Ceratodon purpureus***, a common moss on roofs, roadsides, and other open places. It typically has a large population of **rotifers**. Photo courtesy of Geralyn Merkey.

Figure 32. ***Polytrichum juniperinum***, a common **rotifer** home. Photo by Michael Lüth, with permission.

Figure 33. ***Schistidium apocarpum***, a common moss that can house 700 **rotifers** per gram. Photo by Michael Lüth, with permission.

Aquatic rotifers can occupy a significant portion of the **meiofauna** (minute organisms living in soil and aquatic sediments) of aquatic mosses such as ***Fontinalis antipyretica*** (Figure 34) (Vlčková *et al*. 2002). Out of 20 taxa, **Bdelloidea** formed the dominant group with about 76% of the total meiofauna numbers. Linhart (2000) found that clumps of ***Fontinalis antipyretica*** was inhabited by 151 times the densities of meiofaunal invertebrates compared to adjacent mineral substrate. During winter in two streams in the Czech Republic, Linhart found 182,672-390,057 individuals per 100 mL of ***F. antipyretica***. That's about a handful of moss. Rotifers (**Bdelloidea**) were the dominant organisms, occupying up to 74% of the meiofauna. The rotifers seemed to be reduced by high amounts of organic matter, whereas **Chironomidae** (Figure 35) benefitted. These differences account for the dominance of rotifers (**Bdelloidea**) in Mlýnský náhon (76% of the community), whereas in Bystřice, the dominant group was **Chironomidae** (34%) (Vlčková *et al.* 2002).

Figure 34. ***Fontinalis antipyretica***, home for a dense fauna of **rotifers**. Photo by Michael Lüth, with permission.

Figure 35. ***Propsilocerus saetheri*** larva, a member of **Chironomidae**. **Chironomidae** benefit from increased detritus, whereas rotifers are reduced in numbers. Photo by NTNU Museum of Natural History and Archaeology, through Creative Commons.

Although the aquatic moss ***Fontinalis antipyretica*** (Figure 34) often lives in relatively rapid water, it can house huge numbers of temporary and permanent meiofauna. In samples taken in October and November, Vlčková *et al.* (2002) found 261,660 individuals per 100 mL of this moss in Bystřice and 498,948 in Mlýnský náhon. More permanent residents contribute approximately 62% and 95% in these locations, respectively. At Mlýnský náhon, the **Bdelloid** rotifers form 76% of the community as permanent residents.

Aquatic mosses can contribute significantly to biodiversity by providing a 3-d habitat. Linhart *et al.* (2002a) and Vlčková *et al.* (2002) found that rock rip-rap overgrown by aquatic mosses (***Fontinalis antipyretica***; Figure 34) in a side channel of the Morava River, Czech Republic, contributed both habitat and food source for the meiofauna. Both the habitat and the food source were realized through the fine particulate matter trapped by the mosses. In this habitat, **Bdelloid** rotifers dominated as 76% of the organisms among 18 meiofaunal taxonomic groups.

Sampling

When comparing numbers of nematodes, tardigrades, mites, and annelids to rotifers among bryophytes, Merrifield and Ingham (1998) found low numbers of rotifers, with no seasonal variation. They suggested that the low numbers of rotifers in moss samples may be due to the use of the Baermann funnel for sampling. This technique is not suitable for immobile organisms like periphytic rotifers, as indicated by comparison with subsequent squeezings and agitation of the moss.

Before we explore this group of organisms, we need to consider potential sampling bias and the effects it may have on the numbers of rotifers in various studies. Because of their tendency to attach, rotifers require different sampling techniques from tardigrades and worms. They do not extract well with the Baermann funnel used so commonly for other invertebrates (Merrifield & Ingham 1998). Merrifield and Ingham tested the efficiency of this funnel technique on the moss ***Eurhynchium oreganum*** (Figure 36) on the Oregon Coast Range, USA, by squeezing and agitating the moss after the funnel extraction and suggested that the sedentary habit of the rotifers might cause them to be under sampled.

Figure 36. ***Eurhynchium oreganum***, a moss where the funnel technique might under-sample the rotifers. Photo by Blanka Shaw, with permission.

Fussmann *et al.* (2000) discussed the problems with using sedimentation chambers of **fixed** (preserved) organisms. These must be analyzed with an inverted microscope and the amount of work required becomes prohibitive. Even for **non-sessile** (unattached) rotifers, using a transparent filtering funnel with appropriate mesh screening misses a large portion of the population (Likens & Gilbert 1970). It is most likely worse for bryophyte dwellers living in the small interstitial spaces.

May (1986) suggests that sampling sediments can be done in one day and the dormant individuals or resting eggs cultured to permit identification. But this method is not only time-consuming, it may not enable one to see those individuals hiding among the bryophytes, especially in pockets, folds, and cells.

Pennak (1962) reported results from a littoral sampling tube, but cautioned that this method was less effective in sampling rotifers from macrophytes than the use of nets (Pennak 1966). Others (Goddard & McDiffett 1983; Duggan *et al.* 2001) used removal of the macrophytes, a method also appropriate for bryophytes, but the sorting process is tedious and time consuming. For example, removing the rotifers from the surfaces can be accomplished with a syringe (Pontin & Shiel 1995), but for a quantitative study this can be a large project, considering the numbers cited above. It is also a destructive method, and the patchiness of rotifer species would require a large number of samples.

Artificial substrata are a possible alternative (Duggan *et al.* 1998; Duggan 2001), but that method presumes that the bryophyte is being used only as a substrate and that shape of substrate and other organisms in the community don't matter. And this does not seem to be the case – preferred food organisms may be absent and high densities occur in leaf axils and other restricted spaces that are not mimicked by the artificial substrate.

Green (2003) sampled periphytic rotifers with Hydrobios plankton nets, mesh 55 µm. These samples were preserved in formaldehyde, then thoroughly mixed and sub-sampled with a wide-mouthed pipette. The subsamples were mixed with a small volume of lactic acid and mounted on a glass slide for examination. But once again, I question how effective this is for rotifers hiding in pockets, lobules, cells, or attached.

The closest macrophytes to use as models for bryophytes might be sampling of the alga *Chara* and the flowering plant *Utricularia vulgaris* (Figure 38). Kuczyńska-Kippen & Nagengast (2006) sampled periphyton (adhering algae, protozoa, microinvertebrates) on these and other macrophytes by removing a 0.25 x 0.25 m square of the plants. These were first rinsed in distilled water. Then the periphyton remaining was removed manually with a knife and small brush and number of rotifers calculated per volume of water above the sampled area. This is another destructive technique and would be prohibitively costly in time.

Figure 37. ***Chara vulgaris***, a potential model for bryophyte faunal communities. Photo by Mnolf, through Creative Commons.

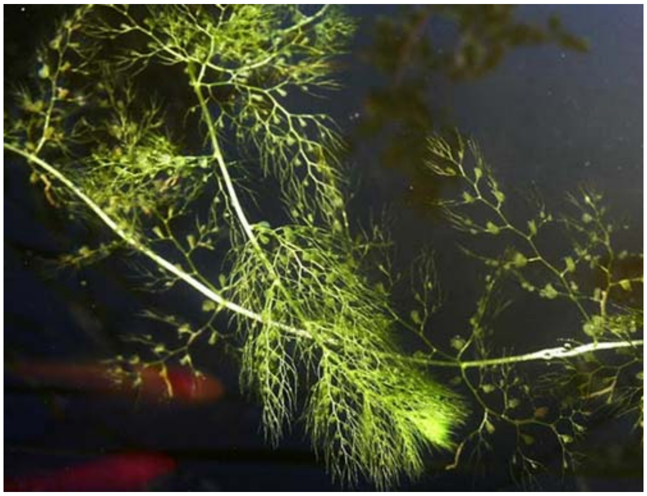

Figure 38. ***Utricularia vulgaris***, a potential structural model for bryophyte rotifer communities. Photo by Erastos Kampouropoulos, through Creative Commons.

Vlčková *et al.* (2002) attempted to sample the aquatic moss ***Fontinalis*** (Figure 34) quantitatively. They removed the moss and its associated fauna with a 30 µm mesh hand net. The associated fauna and detritus were then washed from the moss and sieved through a 1 mm mesh to remove the larger organisms and debris. The organisms that went through the net were retained on a 30 µm mesh filter. The sediment retained by this filter was diluted in a graduated cylinder and 1 ml samples were observed with a dissecting microscope and counted in a Sedgwick Rafter counting chamber. But even this extensive (and destructive) method can fail to sample attached or pocketed fauna.

These difficulties help to explain the paucity of quantitative ecological studies on bryophyte dwellers.

Extraction Techniques

To further complicate finding rotifers even under the dissecting microscope, rotifers respond to disturbance by retracting their corona and toes, appearing like a ball. In this condition, they are difficult to locate, even with a dissecting microscope. And imagine trying to identify these balls! You can place a branch of bryophyte in a Petri dish or watch glass and cover it with water (Fox 2001). Then let it sit quietly, preferably on the stage of a dissecting microscope, for 15-30 minutes until the rotifers become active again. They can then be removed with microforceps by removing several leaves on which you have observed rotifers. If they are placed on a glass slide or hanging drop slide, you can observe these with the compound microscope at 40X.

But some rotifers are too small for this technique and are likely to be missed. Peters *et al.* (1993) suggest a different method that appears to be a somewhat reliable quantitative technique. They tested it on 74 samples of mixed ***Brachythecium rutabulum*** (Figure 39) and ***Ceratodon purpureus*** (Figure 31), both terrestrial mosses. Their criteria for establishing a method were that it should not kill the organisms because some must be alive to be identified, it must be equally effective for all species, it must be quantifiable, and it should be economical in both equipment cost and time. Bryophyte samples 1 cm^2 should be shaken vigorously in a 70 ml vial with 20 ml rainwater for 15 seconds. If the sample is dry, it should soak for 24 hours in rainwater first. After shaking, put the sample and water in a Petri dish with a grid. Then put the moss back in the vial. Rotifers can be counted with a dissecting microscope at 40-50X. This should be repeated nine more times with material from the same sample, using a new Petri dish each time. From each of these samples, take 50 rotifers at random and make a separate slide for each. These can be stored for weeks in a moist chamber. This method needs more testing to check for attached species, species bias, and reliability of quantitative measures.

Figure 39. ***Brachythecium rutabulum***, a moss used for extracting rotifers by a shaking technique. Photo by J. C. Schou, with permission.

Sakuma *et al.* (2002) tested two methods (covering method; picking-up method) of obtaining epiphytic rotifers from lake vegetation (Figure 40). Their "covering method" involved shaking a vegetation sample in a 2-L jar of filtered lake water (40 µm mesh). The jar lid (cap) is placed on the jar and the jar is placed upside-down in the lake water. The lid is then removed under water and the submerged part of the bryophyte is gently covered from above. The bryophyte is cut with scissors near the lip of the jar and the jar lid is returned to cover the jar. The covered jar is shaken vigorously 50 times, which in testing recovered 90% of the rotifers. Shaking only 10 times recovered only 80%. The water in the jar is then filtered through a 40 µm filter and fixed with sugar formalin (see Haney & Hall 1973).

In the "picking-up method" the jar of lake water is prepared as above (Sakuma *et al.* 2002). It differs in cutting the bryophyte in the lake and picking it up above the water surface. This bryophyte sample is then put in the jar. The epiphytic rotifers are then treated as for the "covering method."

The authors consider the "covering method" to be superior in estimating the abundance, but it requires both hard work in a boat and more time (Sakuma *et al.* 2002). The "picking-up method" (Figure 40) introduces errors in the abundance estimates. The rotifers ***Lecane*** (Figure 41), ***Euchlanis*** (Figure 42), and ***Trichocerca*** (Figure 43) are underestimated, whereas ***Brachionus*** (Figure 13-Figure 14), ***Mytilina*** (Figure 44), ***Lepadella*** (Figure 45), and ***Colurella*** (Figure 46) seem to be accurately estimated. Such differences provide misleading information on community structure. The shaking part of the "covering method" is not without its own creation of bias. ***Lecane*** (Figure 47) and ***Collotheca*** (Figure 48) remained on the plants (*Potamogeton* – Figure 49) at ca. 50% and 70%, respectively.

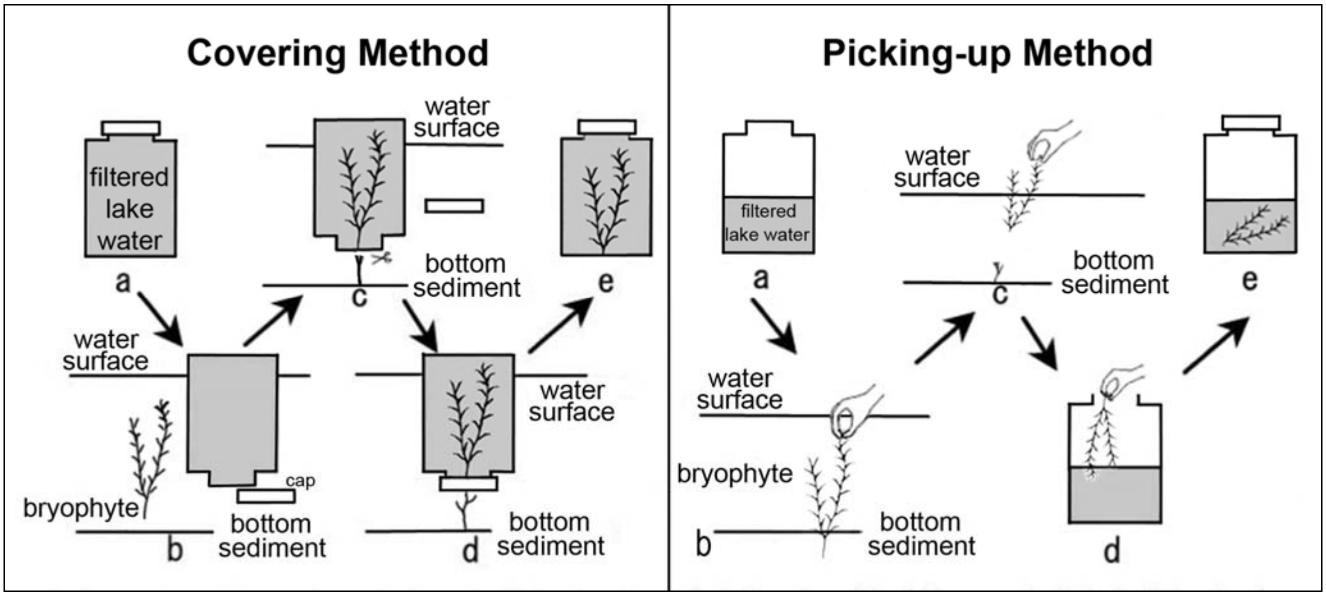

Figure 40. Methodology for the "covering method" and "picking-up method." Modified from Sakuma *et al.* (2002).

Figure 41. ***Lecane crenata***, a genus that is underestimated in the "picking-up method." Photo by Yuuji Tsukii, with permission.

Figure 42. ***Euchlanis***, a genus that is underestimated in the "picking-up method." Photo by Jean-Marie Cavanihac, with permission.

Figure 43. ***Trichocerca rattus carinata***, representing a genus that is underestimated in the "picking-up method." Photo from Jersabek *et al*. 2003, with permission.

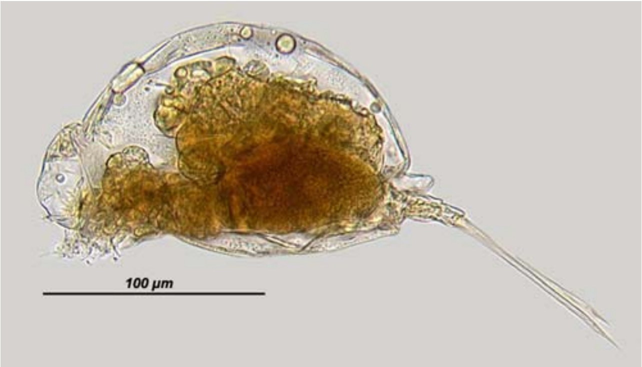

Figure 44. ***Mytilina acanthophora*** ssp. ***trigona***, a genus that seems to be adequately represented by the "picking-up" method. Photo by Jersabek *et al.* 2003, with permission.

Figure 45. ***Lepadella acuminata***, member of a genus that seems to be adequately represented by the "picking-up" method. Photo by Yuuji Tsukii, with permission.

Figure 46. ***Colurella uncinata***, a genus that seems to be adequately represented by the "picking-up" method. Photo by Jersabek *et al*. 2003, through Creative Commons.

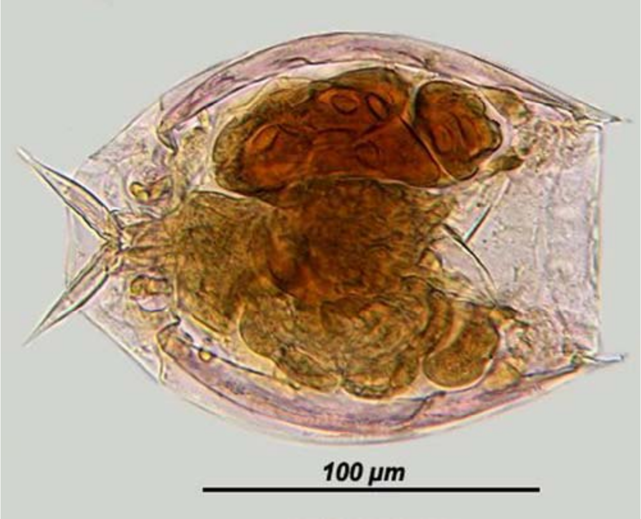

Figure 47. ***Lecane depressa*** subsp ***brachydactyla***. ***Lecane*** is a genus that remains mostly with the substrate when plants are shaken in water. Photo by Jersabek *et al*. 2003, with permission

Figure 48. ***Collotheca*** sp., a genus that does not detach well in shaking techniques. Look carefully to see the cilia. Photo by Yuuji Tsukii, with permission.

Figure 49. ***Potamogeton nodosus***. Shaking ***Potamogeton*** is an ineffective method for removing most individuals of ***Lecane*** and ***Collotheca*** species, suggesting they would likewise not be dislodged from bryophytes. Photo by Jim Conrad, through public domain.

Adaptations

The **Rotifera** are cosmopolitan, including both tropical and polar environments. There is a large number of species, permitting them to occupy a wide range of habitats. This indicates that ecological barriers are more important than geographical barriers in determining their distribution (Pejler 1995). However, many of the species are **euryoecious** (able to live in a variety of conditions), whereas few have strong restrictions on their environments. When an environment has a large number of rotifer species, the species typically differ greatly in their morphology. Therefore, it is difficult to characterize adaptations for a given environment. It is thus not surprising that published literature provides little information about adaptations of **rotifers** to the bryophyte habitat.

Particle Feeders

Rotifers among bryophytes can feed on detrital matter and algae collected by the bryophytes.

Spines

Kellicottia longispina (Figure 50) is a common plankton species that may be well adapted for bryophyte living. It has very long spines on its case (**lorica**) that Madaliński (1961) considered helpful in attaching to bryophytes. Others understand them as serving as a flotation device (De Smet, pers. comm. 3 November 2016), certainly not an adaptation to bryophyte living.

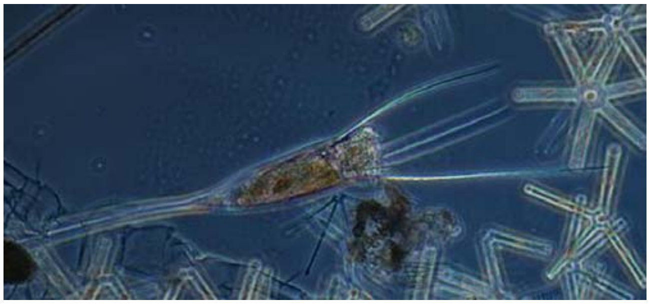

Figure 50. ***Kellicottia longispina*** showing its long spines that permit it to attach to bryophytes. Photo by Philipp Trummer, through Creative Commons.

But Pejler & Bērziņš (1989) have somewhat different ideas about long spines. They claim these are generally found in clear water as a protection against visual predators. This is consistent with defense against predation by small fish as shown by Barnhisel (1991) for *Bythotrephes*, a cladoceran. Rather, Pejler and Bērziņš suggest that adaptations to bryophytic living involve the suitability of the foot, egg-carrying protrusions, and other lorical structures. Certainly diet plays a role, with some bryophytes being suitable food for detrital feeders, but mostly because of the collected detritus and other planktonic and periphyton organisms among the bryophytes.

Small Size

If you are tiny and soft-bodied, you certainly need some sort of protection or a place to hide. Otherwise, you will be somebody's dinner. Wilts *et al.* (2010) discovered one of the smallest rotifers known, ***Bryceella perpusilla***, a new species, concealed on terrestrial mosses in Germany. It is likely that many other small bryophyte-dwelling species remain unknown.

Some rotifers, for example ***Cupelopagis vorax*** (Figure 51), are too large to live among bryophytes (Cavanihac 2004). Cavanihac (2004) considered that this size limitation may be, in part, because the bryophytes cannot house enough detritus and bacteria to meet the food needs of the large rotifers. For ***Cupelopagis vorax***, a consumer of ciliates and smaller rotifers, this may not be the case. This species lacks prominent cilia to draw food toward its mouth (Edmondson 1940, 1949). Therefore, it benefits when it settles on larger leaves where smaller ciliate rotifers bring food into the vicinity of its mouth. On the other hand, Dumont *et al.* (1975) found that the rotifers among the periphyton (which includes most of those associated with bryophytes) tended to be smaller than those living as plankton (see also Ricci *et al.* 2003a).

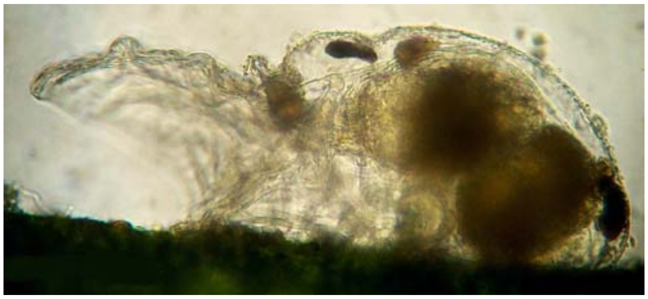

Figure 51. ***Cupelopagis vorax***, a rotifer that finds a **moss** leaf too small for its feeding needs. Photo by Jean-Marie Cavanihac at Micscape, with permission.

Mobility vs Attachment?

Epp and Lewis (1984) demonstrated that speed of motion was related to size in rotifers. Using ***Brachionus*** (Figure 2, Figure 13-Figure 14) and ***Asplanchna*** (Figure 52), they demonstrated that ***Brachionus*** has little size variation during its development, whereas ***Asplanchna*** increases significantly in size as it develops. Nevertheless, both genera decrease their speed of movement significantly as their size increases. ***Brachionus*** uses 62% of its energy for ciliary movement. This is a very inefficient activity, so we might consider one bryophyte adaptation to be attachment instead by crawling, thus saving energy. To observe the rotifers in motion, let the wet moss sit for 30 minutes before observation to provide the rotifers sufficient time to become active.

Figure 52. ***Asplanchna*** sp., a species that increases in size as it develops. Photo by Wim von Egmond, with permission.

Living in tune with their mossy environment, **limnoterrestrial** (in habitat providing tiny water reservoirs in a terrestrial environment) rotifers exhibit a seasonal dynamic that depends on water availability and air quality (Kukhta *et al*. 1990; Steiner 1994a, b, 1995a, b). Not only is water important for hydration, but it is necessary for locomotion. The bdelloid rotifers (Figure 11) have a contractile body that permits them to creep around on the moss (Sayre & Brunson 1971). And the cilia that form the corona create currents as they beat (Figure 53), directing food particles into the mouth while thrusting the rotifer forward (Hingley 1993). Thus, the corona also contributes to movement.

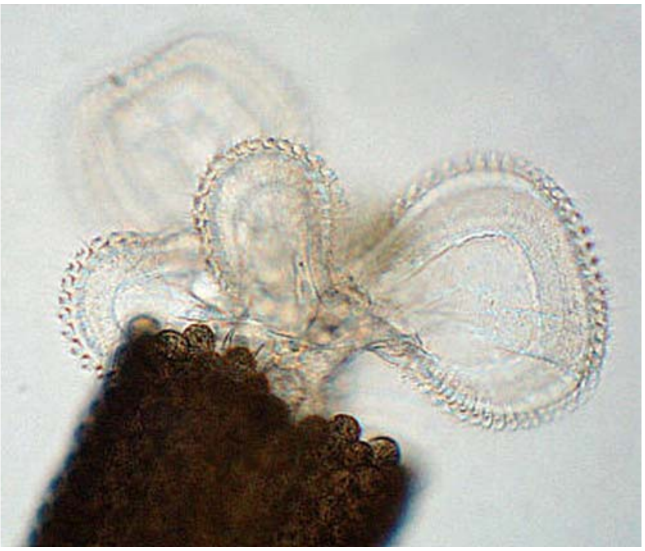

Figure 53. Wheels of cilia (**corona**) on ***Floscularia*** sp. Photo by Martin Mach, with permission.

Members of the periphyton often remain firmly attached to the substrate, be it rock, bryophyte, or other macrophyte. This attachment may use a cement, produced by the toes that have a cement gland (Baqai *et al*. 2000).

Protection

Habrotrocha sp. (Figure 54) secretes a mucus that makes it appear much larger (Figure 54). Wallace and Snell (1991) considered mucus to be an adaptation against predation in the rotifers ***Conochilus*** (Figure 55) and ***Lacinularia*** (Figure 56), but it would seem it would likewise contribute to protection of rotifers such as ***Habrotrocha*** against desiccation in a mossy habitat where some members of the genus are known to live. However, this has not been clearly demonstrated. Others, such as ***Keratella*** (Figure 57-Figure 58), are protected from both desiccation and predation by armor (Figure 57-Figure 58), with spines that may help against predation.

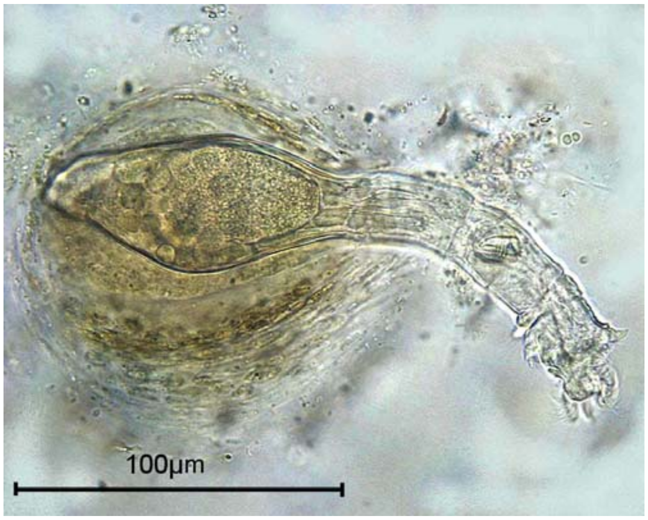

Figure 54. ***Habrotrocha*** sp. surrounded with mucus it has secreted, presumably providing it with protection against desiccation. Photo by Michel Verolet, with permission.

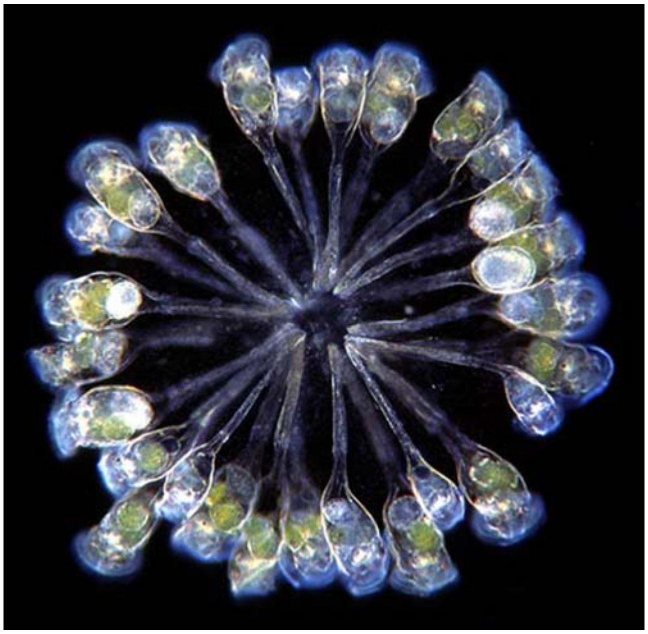

Figure 55. Colonial species of ***Conochilus***, a genus that uses mucus as protection. Photo by Wim van Egmond, with permission.

Figure 56. ***Lacinularia flosculosa***; this genus secretes mucus as protection against predators. Photo courtesy of Phuripong Meksuwan, through Rotifer World Catalog.

Figure 57. ***Keratella serrulata***, showing armor and spines. Photo by Wim van Egmond, with permission.

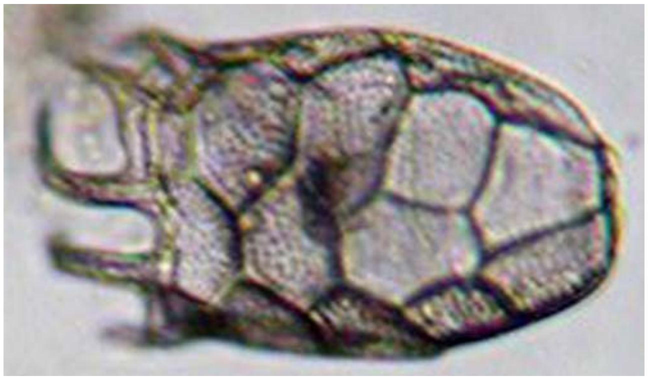

Figure 58. Armor of the rotifer ***Keratella*** sp. Photo by Paul Davison, with permission.

The genus ***Floscularia*** (**Monogononta**; Figure 59) is a tube builder, using tiny pellets, and is known to live on ***Sphagnum*** (Figure 25) (Hingley 1993).

Figure 59. ***Floscularia ringens***, member of a bryophyte-inhabiting genus. Photo by Paul Davison, with permission.

Having parthenogenesis is an advantage for rotifers that travel with a moss fragment and are likely to land where there is no male partner. This advantage is further assured by the predominance of females in the population. In addition to the reproductive adaptations, many adaptations may be physiological.

Dormant States

Of course, a major need for terrestrial moss dwellers is the ability to survive dry periods. The actual mechanisms that permit this survival have been elusive. Some early ideas lack sufficient support and have been discarded as a general mechanism. One such mechanism is the ability to secrete a mucus, as in *Macrotrachela natans* (Bryce 1929). But there is inconclusive evidence that the ability to produce this mucus actually protects the rotifer from the effects of water loss (Tunnacliffe & Lapinski 2003). Rather, it appears that most rely on physiological changes that occur during dehydration.

Physiological Adaptations

Anhydrobiosis

One reason for the abundance of bdelloid rotifers on bryophytes is that they share with the bryophytes the ability to enter dormancy (Gilbert 1974). In the **Bdelloidea**, the most common group of terrestrial rotifers, including those among bryophytes, this dormancy permits the adults to survive when frozen or desiccated. In **Monogononta**, dormancy is restricted to the fertilized resting egg. Hence, the predominant group of moss dwellers (**Bdelloidea**) has two methods of surviving desiccation.

The concept of **anhydrobiosis** was introduced by Giard in 1894 as a highly stable state of suspended animation that an organism enters as a culmination of desiccation (Tunnacliffe & Lapinski 2003). It differs from **desiccation tolerance**, which refers to the ability of a cell or organism to tolerate loss of water, although not necessarily reaching a resting state.

Cryptobiosis (**anhydrobiosis**) is one type of dormancy (Wallace & Snell 1991; Fontaneto & Ricci 2004). **Anhydrobiosis**, a dormant state caused by loss of water, permits some rotifers to live with the same water stresses to which bryophytes are subjected.

Van Leeuwenhoek was the first to recognize the state of anhydrobiosis in a rotifer, the bdelloid ***Philodina roseola*** (Figure 60) (Tunnacliffe & Lapinski 2003). Tunnacliffe and Lapinski (2003) argue that the term **anhydrobiosis** is inappropriate because the organism in not devoid of all water and that it has shut down to a state of suspended animation. They suggested the term **anhydrous cryptobiosis** because it implies the living but inactive state. Nevertheless, the term **anhydrobiosis** has been used for a long time and its intended definition is understood. Hence, I prefer not to introduce a new term and agree with Tunnacliffe and Lapinski that "as 'anhydrobiosis' is firmly established in the literature, it is unlikely that it can now be replaced."

Figure 60. ***Philodina roseola***, a species that is able to regulate its net water balance during dehydration. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Changes During Anhydrobiosis

Desiccation Stages: **Rotifers** enter this state of anhydrobiosis in stages (Ricci & Melone 1984). First they contract into the compact shape known as a **tun** (Figure 61) (Marotta *et al.* 2010). During this contraction, the cephalic and caudal extremities are withdrawn into the trunk. Presumably, this reduces the rate of water loss and minimizes water loss in the dormant state. The tissues and cells become packed, preserving their integrity (Ricci 2001). This preparation requires several hours, and a shorter period can reduce the recovery success (Caprioli & Ricci 2001).

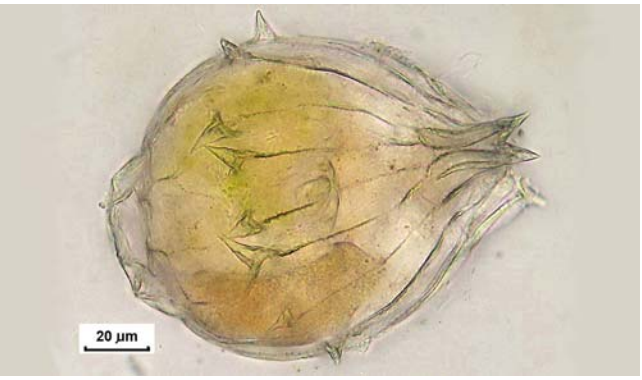

Figure 61. Tun of a **rotifer**, ***Pleuretra brycei***, a moss dweller. Photo by Michel Verolet, with permission.

Ability to contract and fold seems important to the survival of ***Macrotrachela quadricornifera*** (Figure 62) (Ricci *et al.* 2004). Upon drying, the rotifer contracts, drawing its foot and head into the body trunk (Figure 63) (Ricci & Melone 1984). Starved **rotifers** of this species survive better than those fed on concentrated food, with food remaining in the gut when the latter form the **tun** (Figure 64) (Ricci *et al.* 2004). This is in contrast to the loss of survival in ***Philodina roseola*** (Figure 60) when dried after starvation (Jacobs 1909). It is possible that the reason for the reduced survivorship of well-fed ***M. quadricornifera*** is that the food interferes with the necessary folding and contraction.

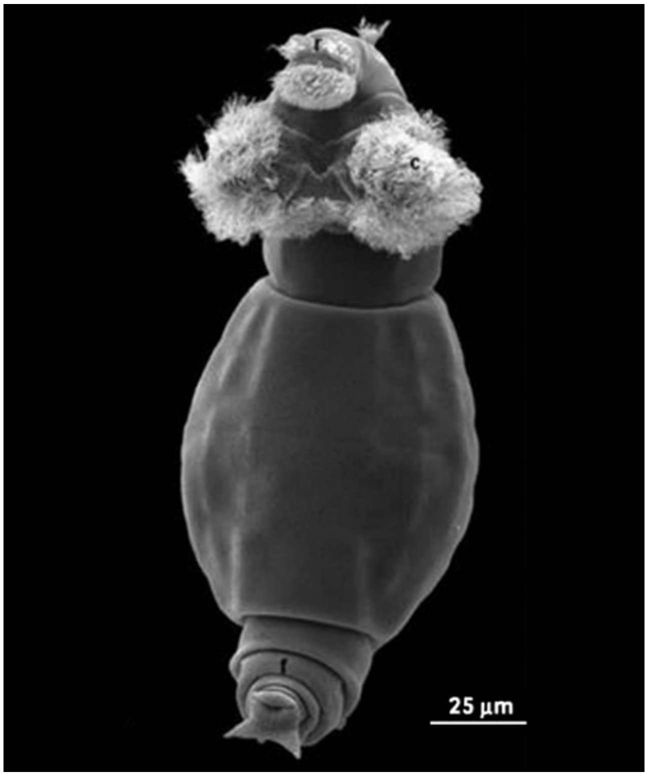

Figure 62. ***Macrotrachela quadricornifera***. Photo by Diego Fontaneto and Giulio Melone, with permission.

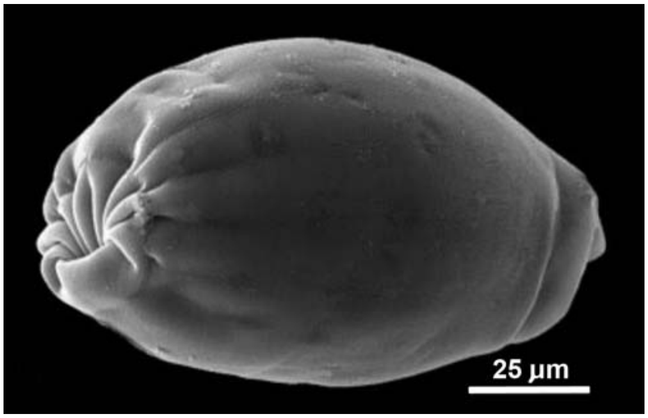

Figure 63. ***Macrotrachela quadricornifera*** contracting as it dries. Photo by Claudia Ricci, with permission.

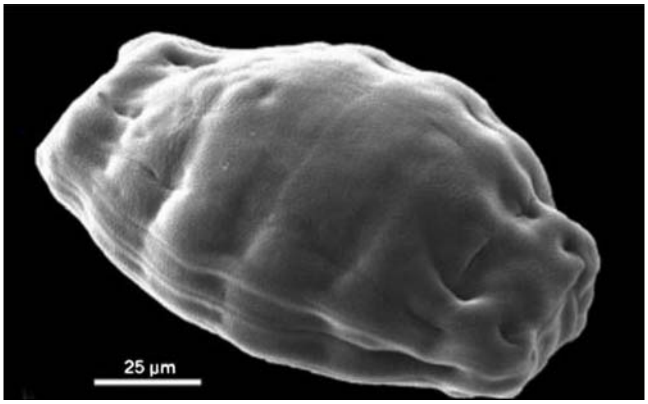

Figure 64. ***Macrotrachela quadricornifera*** tun. Photo by Diego Fontaneto & Giulio Melone, with permission.

Macrotrachela quadricornifera shrinks considerably in size during dehydration, with the anhydrobiotic animal having only about 60% of the volume of the hydrated form (Ricci *et al.* 2008; see also Marotta *et al.* 2010). The internal organization changes drastically, with body cavities becoming indistinguishable. Even more extreme is its loss of more than 95% of its weight when anhydrobiotic, mostly as water. This water loss is inconsistent with a 60% volume loss and Ricci and coworkers suggest that it may indicate presence of space-filling molecular species in the dehydrated animal.

Dehydration Conditions: Caprioli and Ricci (2001) found that ***Macrotrachela quadricornifera*** (Figure 62) was able to survive rapid desiccation, whereas ***Philodina roseola*** (Figure 60) only survived best when subjected to a slower desiccation rate. Both of these are bdelloid rotifers. Nevertheless, when Caprioli and Ricci (2001) experimented with ***Macrotrachela quadricornifera***, ***Philodina roseola***, and ***Adineta oculata***, they found that these bdelloids are able to somewhat regulate the net water balance during the onset and termination of anhydrobiosis. This would be particularly helpful in a terrestrial environment, even among bryophytes that are in an exposed habitat such as boulders in the sun.

Jacobs (1909) provided an early explanation of the dehydration process that affects the survival rate in ***Philodina roseola*** (Figure 60). He found that when rotifers were dried slowly, their survival rate was higher (75% survival) than those dried rapidly in a desiccator (12%). At 40°C they actually had a slightly higher survival rate (94%) than those dried at 20°C (82%). However, longevity during dry storage was greater in those dried at 20°C. He supported the importance of **anhydrobiosis** by showing that dry storage produced a higher survival rate than storage at high relative humidity.

Jacobs (1909) found that 82% of ***Philodina roseola*** (Figure 60) had no survival after he dried starved individuals, but 82% of the well-fed individuals survived the same treatment. This is in contrast to some macroinvertebrates that survive best when the gut is empty (see terrestrial insect chapters), including the rotifer ***Macrotrachela quadricornifera***.

The rotifer desiccation process is in some ways similar to that of bryophytes. Both require a lag time between periods of desiccation. Schramm and Becker (1987) found that ***Habrotrocha rosa*** (Figure 65), a bryophyte dweller, required a recovery period of at least one day before it could survive another period of desiccation.

Biochemical Changes: In nematodes and tardigrades, **trehalose** is produced and stored during desiccation. This molecule helps to stabilize cellular structures and preserve molecular integrity. In more modern studies, researchers have identified the non-reducing disaccharides trehalose and sucrose as playing critical roles in anhydrobiotic survival (Tunnacliffe & Lapinski 2003). One or the other of these sugars is typically present in high concentrations as many types of organisms undergo desiccation, leading to the anhydrobiotic state. These sugars seem to act as water replacement molecules, acting as "thermodynamic and kinetic stabilizers of biomolecules and membranes."

Figure 65. ***Habrotrocha rosa***, a bryophyte dweller that requires at least one day of recovery before another desiccation event. Photo by Rkitko at Wikipedia Commons.

But rotifers seem to contradict this wisdom. Protection by trehalose is not the case in the rotifers ***Philodina roseola*** (Figure 60) or ***Adineta vaga*** (Figure 12) (Tunnacliffe & Lapinski 2003). No simple sugars seem to increase at all. Contrary to the high non-reducing disaccharide concentrations found during dehydration in nematodes, brine shrimp cysts, bakers' yeast, resurrection plants, and plant seeds, the rotifers lack these high intracellular sugar concentrations in preparation for desiccation, yet have excellent desiccation tolerance (Tunnacliffe & Lapinski 2003).

Among the **Bdelloidea**, species are either desiccation tolerant or not; the difference is not a matter of degree (Örstan 1998; Ricci 1998). Lacking trehalose, they must have something that permits them to survive. That "something" continued to be elusive. Next, Tunnacliffe *et al*. (2005) found a hydrophilic protein in ***Philodina rosea*** (Figure 60) upon dehydration. This is an LEA protein that also is associated with desiccation tolerance in plants. Furthermore, this protein appears in desiccation-tolerant nematodes and micro-organisms and appears to have a role in desiccation tolerance (Denekamp *et al.* 2010; Hand *et al*. 2011). Hand and coworkers found that these LEA protein genes are expressed in the resting eggs of rotifers such as ***Brachionus plicatilis*** (Figure 66) and the female adults that formed these resting eggs.

Figure 66. ***Brachionus plicatilis*** with egg. Eggs of this species are known to have LEA proteins that are expressed during dormancy. Photo by Sofdrakou, through Creative Commons.

Longevity during Anhydrobiosis

The record for survival after the longest period of anhydrobiosis is that of ***Macrotrachela quadricornifera*** (Figure 62). It survived 59 years on a moss on a herbarium sheet, becoming active when it was rewet (Rahm 1923). But even Rahm questioned his own record, suggesting it may have been the result of more recent contamination from windborne dust carrying dormant rotifers. Furthermore, even in this species the success of recovery decreases with time (Caprioli & Ricci 2001).

Pennak (1953) cites one bdelloid rotifer that was revived from moss after 27 years of dry storage. Unfortunately, no reference is cited and we cannot evaluate whether the moss might have had rotifers introduced from dust or nearby more recently dried mosses.

To determine survival time, Guidetti & Jönsson (2002) examined rotifers that had been kept dry for 9-138 years. The adult stage may have a limited cryptobiotic lifespan in the presence of oxygen, but the rotifer ***Mniobia*** (Figure 67) survived live as eggs for nine years on bryophytes, suggesting that the egg stage (see Figure 68) might have greater longevity than the cryptobiotic adult stage. This appears to be the longest record for **rotifer** survival in anhydrobiosis other than the possible 59 years for an adult ***Macrotrachela quadricornifera*** (Figure 62-Figure 64) reported by Rahm (1923) from a herbarium moss or the undocumented record from Pennak (1953).

Figure 67. ***Mniobia*** sp. with egg. Photo by Walter Dioni, with permission.

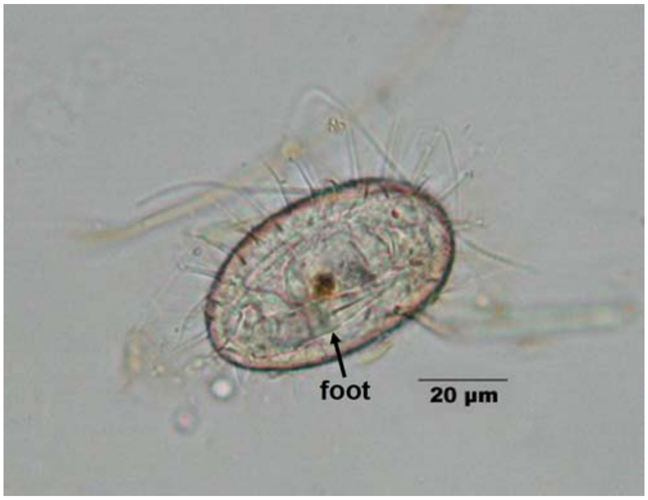

Figure 68. Egg stage of ***Squatinella lamellaris*** showing developing parts. Photo by Ralf Wagner, with permission.

Age Differences

Age affects recovery rate from desiccation but has no effect on the subsequent longevity of ***Macrotrachela quadricornifera*** (Figure 62) that do recover (Ricci *et al.* 1987). In experiments, fertility of 5-day-old stressed **rotifers** had significantly decreased, whereas 14-day-old stressed individuals had decreased life spans. Age also affected ability to survive drying. The highest recovery rate occurred for 8-day-old **rotifers** stressed for 4 days, whereas no rotifers aged 5 days survived 30 days of drying.

Size Differences – Aquatic vs Terrestrial

The moss-dwelling rotifer strains differ slightly in size, with terrestrial moss dwellers being smaller than the aquatic strains of the same species (Ricci 1991). This smaller size may permit them to take advantage of adhering moss water for a longer period of time. Among the ***Macrotrachela quadricornifera*** (Figure 62), eggs and juveniles are less able to recover from desiccation than are mature animals. This species is a good **bet-hedger**, encompassing multiple strategies for survival in a variety of habitats. The moss habitat undoubtedly offers the advantage of slow drying, which increases survivorship upon rewetting (Ricci *et al.* 2003a).

Reproductive Effects

In a study of nine species of **bdelloid rotifers**, Ricci (1983) found that those moss-dwelling terrestrial rotifers living in unpredictable environments had less likelihood of reproducing than aquatic species with a more predictable environment. Thus, it is not surprising that they reproduced less, but lived longer. Moss-dwelling species tend to reproduce throughout their mature lives and never senesce, whereas the aquatic species have a greater reproductive output and are more likely to die after reproduction, having a senescent period at the end of their lives. The strategy of the aquatic species would not serve the terrestrial moss-dwelling taxa well due to the unpredictable nature of the habitat. The terrestrial moss-dwellers, on the other hand, can enter the state of **anhydrobiosis** when the conditions become unfavorable. During this state they can tolerate extremes of temperature and desiccation and do not need food. Frequent reproduction could be detrimental to these animals if they do not have sufficient resources to sustain them during the anhydrobiotic state. Success is further supported by a delay in maturity that reduces reproductive cost. On the other hand, in the water, large adults may be easy prey, favoring a shorter time to maturity.

Furthermore, the aquatic (non-moss) strains of ***Macrotrachela quadricornifera*** invested maximum resources in reproduction (**r strategists**), consequently reducing their survival, whereas the moss-dwelling strains were long-lived and invested fewer resources in their reproduction (**K strategists**) (Ricci 1991). Ricci points out that the moss habitat experiences a much greater temperature fluctuation in a shorter period of time than would occur in the aquatic non-moss habitats. Ricci suggests that the terrestrial moss habitat has much more important limiting factors – availability of food and moisture, whereas a wide temperature range with sudden changes must be tolerated.

Temperature Protection

Despite all the preparation for anhydrobiosis, these dormant beings are not as well protected as we once thought. On the other hand, Rahm (1923) found that once dry, at least some rotifers can survive 151°C for 35 minutes. Broca (1860) revived rotifers with water after they remained dry in a vacuum for 82 days, then were immediately heated to 100°C for 30 minutes.

The temperature relationships of the moss-dwelling rotifers are interesting. Compared to the non-moss populations, those of ***Macrotrachela quadricornifera*** (Figure 62) living among mosses exhibit an irregular response to increasing temperature in the range of 16-24°C (Ricci 1991).

Recovery Rate

As one might expect, terrestrial rotifers have the greatest desiccation recovery rates compared to aquatic rotifers. When fifteen bdelloid species (6 genera) were collected from water and terrestrial moss environments, the highest recovery rates following anhydrobiosis for seven days were for the adults from terrestrial mosses (Ricci 1998). Activity generally resumed in about one hour after rehydration. Ricci suggests that evolutionarily all bdelloid rotifers originally had the ability to enter anhydrobiosis, but that some species have subsequently lost it. Aquatic species had only 20-50% recovery among young, pre-reproductive individuals, whereas moss-dwelling species had 50-100% recovery among these juveniles. This improved in adults of both groups. Could it be that this group evolved originally in a moss habitat? On the other hand, ***Otostephanos macrantennus***, a moss and soil dweller (Ricci 1998), did not survive desiccation at any life stage, except for one individual older adult. Furthermore, its eggs collapsed and were unable to survive desiccation, whereas the overall viability among these fifteen species was 40-60%. Ricci considered ***Otostephanos macrantennus*** to have "an anomalously low desiccation survival rate."

The Bryophyte Connection

The data for ***Macrotrachela quadricornifera*** (Figure 62) and other species raise the question of how these animals survive on bryophytes. To partially answer this question, Ricci *et al.* (1987) collected mosses from a spring-fed pond in Italy. Hence, it is likely that the humidity remained higher than that of the laboratory. Furthermore, the mosses themselves provide capillary spaces that can lock in water for a longer period of time than that of the surroundings. Unlike the rotifers that depend on eggs for reproduction, bdelloid rotifers in this study had a much lower hatching rate (19%) compared to 40-100% (Pourriot & Snell 1983) reported for those species that depend on resting eggs to colonize new environments. ***Macrotrachela quadricornifera*** (Figure 62) is a parthenogenetic rotifer, requiring no partner to reproduce. Therefore, its life on a moss leaf is not dependent on finding a partner in what can be an isolated habitat. The ability of the moss leaf to disperse in the wind provides a means for the rotifer likewise to disperse.

Certainly one of the most important adaptations of bryophyte dwellers is this ability to withstand drying.

Bdelloid rotifers in particular are common among bryophytes and humus-containing soil (Sládeček 1983). Many of these are able to desiccate for long periods of time and become active again. Pennak (1953) reports that one bdelloid rotifer revived after 27 years of desiccation.

Other Protections during Anhydrobiosis

Once in the state of anhydrobiosis, the rotifer gains protections not available to it in the active state. Among these is the ability to survive strong ultraviolet light (Rahm 1923, 1926, 1937). In its normal hydrated state, strong UV light kills the rotifers "almost instantly." This dehydrated state also confers a high tolerance to low temperatures (-190°C) (Rahm 1923), and Becquerel (1950) showed survival of ***Habrotrocha constricta*** (Figure 69) and ***Philodina roseola*** (Figure 60) at 0.05K (-273.1°C, or close to absolute zero)! Anhydrobiosis also stops the internal clock of the rotifers so that they do not age unless they are in the active state (Ricci *et al*. 1987). This is an advantage for those living among bryophytes that dry periodically.

Figure 69. ***Habrotrocha constricta***, a species of both aquatic and epiphytic mosses that is able to survive at 0.05K. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Gladyshev and Meselson (2008) demonstrated that bdelloid rotifers have extreme resistance to ionizing radiation. Using bryophyte dwellers ***Adineta vaga*** (Figure 12) and ***Philodina roseola*** (Figure 60), they were able to show that the reproduction is much more resistant to ionizing radiation than that of the monogonont ***Euchlanis dilatata*** (Figure 70). They suggest that this resistance is due to the same evolutionary adaptation that permits these rotifers to survive desiccation in their natural habitats. They consider the mechanism to involve DNA breakage that is repaired following rehydration. This breakage/repair sequence may be the mechanism that kept their load of transposable genetic elements low, thus contributing to the success of the asexual species for such a long time rather than suffering from the early extinction suffered by so many other asexual taxa. This connection should be explored in bryophytes that also have survived for a very long time as asexual organisms. Kamisugi *et al*. (2016) found indications of the possibility in ***Physcomitrella patens***, a moss that demonstrates repair genes for damaged chromosomes.

Figure 70. ***Euchlanis dilatata***, a monogonont moss dweller that has poor resistance to ionizing radiation. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Surviving Fungi

Wilson (2011) found yet another advantage to having anhydrobiosis in the life cycle. He pointed out that organisms that lack sexual reproduction usually do not survive evolutionary time. The **Red Queen hypothesis** is that the limited capacity to create new genetic makeup leads to extermination due to rapidly evolving parasites and pathogens. But the asexual **Bdelloidea** have indeed survived under these conditions. Wilson explains this survival of bdelloid rotifers as a result of their ability to disperse while in a desiccated state, arriving in a new location parasite free.

In experiments, wind dispersal during seven days of desiccation successfully removed a fungal parasite from populations of one species and permitted them to disperse independent of their fungal parasite (Wilson 2011). Wilson desiccated a "heavily infected" population of ***Habrotrocha elusa*** on a moss, placed it in a wind chamber, and collected those that landed on target dishes. These were rehydrated after 7 days. In 70% of the dishes, new populations became established and two-thirds of these were free of parasites. However, if the rotifers were "dispersed" while wet, all the new populations were infected and were killed by the fungus.

Wilson (2011) made an additional observation on ***Adineta vaga*** (Figure 12) collected from an **epiphytic** moss. In bryological literature, **epiphytic** moss refers to those mosses living on trees or shrubs; these are often referred to as "tree mosses" in the rotifer literature. Following anhydrobiosis this species had enhanced **fecundity** (reproductive rate) compared to those that had not been dehydrated, even when they were infected with fungal parasites. This suggests that the desiccation-rehydration cycle may serve as a cue to invest heavily in reproduction.

Food

Rotifers obtain their food by rotating **cilia** in the **corona** (Figure 71) that directs the food into the mouth. This enables them to eat small particles of organic matter, bacteria, algae, protozoa, and even other rotifers (Wikipedia 2012b). [These same cilia can be used for swimming (Fontaneto & Ricci 2004)]. The food is directed to the mouth and the modified pharynx called a **mastax** (Figure 72-Figure 73), the latter consisting of the **trophus** and its musculature. Their menu usually consists of food items that are up to 10 µm in size (Wikipedia 2012b). This ability to filter such small particles from their environment makes them useful in maintaining clean water in aquaria. Clément *et al*. (1980) described the muscle structure and method of controlling the cilia to obtain food for the moss dweller ***Philodina roseola*** (Figure 60, Figure 71) and planktonic *Brachionus calyciflorus* (Figure 74) and their ability to reject some foods.

Figure 71. ***Rotaria*** sp. showing cilia that direct food into the mouth. Photo by Wim van Egmond, with permission.

Figure 72. ***Dissotrocha scutellata*** showing **mastax**. This species has been collected on the moss ***Andreaea rupestris*** growing on a rock in the open. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 73. Mastax, showing the **trophi** of a **rotifer** from the liverwort ***Frullania eboracensis***. This structure is used for crushing food items. Photo courtesy of Mark Pokorski.

Figure 74. *Brachionus calyciflorus*, a species that can reject some foods. Photo from Academy of Natural Sciences in Philadelphia, through Creative Commons.

Food choices differ with habitat, even within the same species. The bdelloid rotifer ***Macrotrachela quadricornifera*** (Figure 62) is a filter feeder whose food preference and survivorship both differ among the habitat strains (Ricci 1991). Moss dwellers were unable to survive on yeast (*Saccharomyces cerevisiae*) alone, whereas the two aquatic strains survived and grew. One of the moss-dwelling strains was unable to eat the one-celled green alga *Chlorella pyrenoidosa* (see Figure 75). The other moss strain did best on the bacterium *Escherichia coli*, which resulted in poor growth of all the other strains. It appears that the habitat may influence the types of enzymes available for digestion of food. We cannot, however, say if this is an environmental response during development or a genetic one that has persisted through a number of moss-dwelling generations.

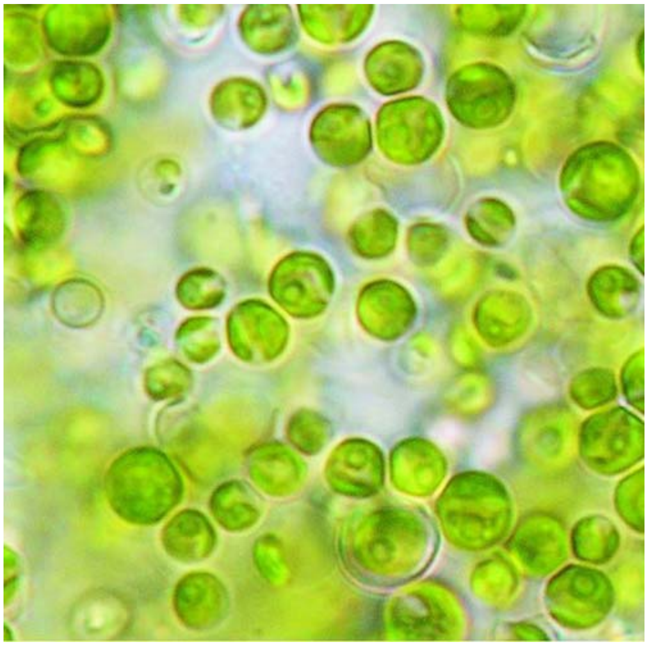

Figure 75. ***Chlorella vulgaris***; ***C. pyrenoidosa*** a rejected food for moss-dwelling ***Macrotrachela quadricornifera***. Photo by Sarah Duff, through Creative Commons.

Most of the **rotifer** inhabitants of ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) feed on small particles of food directed to them by their wheel cilia (Figure 76) (Hingley 1993). They mash their food with their **mastax** (Figure 72-Figure 73, Figure 3), thus modifying these in the ecosystem.

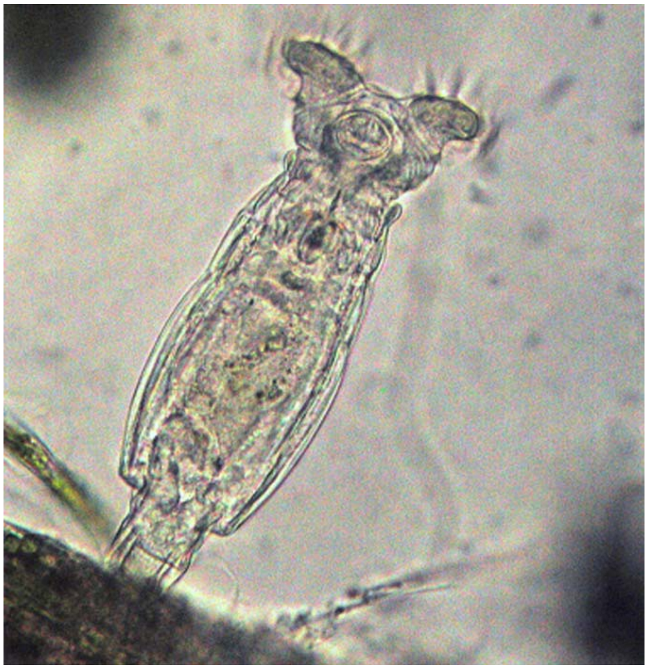

Figure 76. The two "wheels" of cilia on this moss-dwelling rotifer are in full motion. Photo courtesy of Andi Cairns.

A few rotifers actually bite their food. For example, among the moss dwellers, this method is used by ***Lindia torulosa*** (Figure 77-Figure 78) and ***Notommata groenlandica*** (Figure 79), but there are many others as well (Plewka 2016).

Figure 77. ***Lindia torulosa*** biting ***Oscillatoria***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 78. ***Lindia torulosa*** consuming ***Oscillatoria***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 79. ***Notommata groenlandica*** ready to penetrate and eat the desmid ***Netrium*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Role in the Food Web

Tiny animals usually have bigger animals that eat them. The rotifers fall prey to copepods, fish, and Bryozoa, but small rotifers are also eaten by bigger rotifers (Wallace *et al*. 2006). For example, members of the rotifer genus ***Lecane*** (Figure 122, Figure 128) are eaten by the rotifer ***Dicranophorus robustus*** (Figure 80) (Jersabek *et al*. 2003), both known from bryophytes. On the other hand, when the ***Asplanchna*** ate too much ***Keratella*** (Figure 81), the ***Asplanchna*** died, possibly due to the spines and hard lorica of the ***Keratella*** (Figure 57).

Figure 80. ***Dicranophorus robustus***, a bryophyte dweller that eats smaller rotifers on bryophytes. Photo from Jersabek *et al*. 2003, through Creative Commons.

Figure 81. ***Asplanchna*** sp. overfed on ***Keratella*** sp. This large rotifer died after eating a large quantity of the smaller ***Keratella*** (van Egmond 2003). Photo by Wim van Egmond, with permission.

Some rotifers, especially **sessile** (attached) rotifers, are easy prey for larger invertebrates. For example, Antarctic tardigrades appear to be important predators on rotifers (Sohlenius & Boström 2006). Some rotifers make tubes in which to hide. ***Ptygura velata*** (Figure 82-Figure 83) solves the problem of becoming someone else's dinner by making a tube from its own fecal pellets (Figure 82-Figure 83), where it withdraws from danger (Edmondson 1940).

Figure 82. ***Ptygura*** sp. with its case made of its own fecal pellets, attached to a ***Sphagnum*** leaf. Photo by Wim van Egmond, with permission.

Figure 83. Close view of ***Ptygura*** sp. showing fecal pellets in the case. Photo by Wim van Egmond, with permission.

Rotifers participate in a food web within the moss habitat. Therefore, things that hurt their food items indirectly impact the rotifers. For example, rotifer biomass on ***Sphagnum fallax*** (Figure 25) decreased in response to experimentally added lead (Nguyen-Viet *et al*. 2007). The mechanism, however, appeared to be indirect due to the loss of microbial biomass and not due to the direct effects of lead on the rotifers. The biomass of bacteria, microalgae, testate amoebae, and ciliates decreased significantly and "dramatically." The linkage appears to be that bacteria provided food for the ciliate and testate protozoa, and these in turn provided food for the rotifers. Rotifers do have preferences, and these preferences affect the species composition of algae in their ecosystems (Wikipedia 2012b). They also affect the species composition through competition for food with Cladocera and Copepoda.

Specific Habitats

We would probably make some very interesting discoveries if bryologists and rotifer biologists would join forces. But rotifer folks rarely name the bryophytes where their rotifers dwell, and most bryologists can't name the rotifers they find and are likely to miss the dormant ones. Some rotifers may have very specific habitats, particularly among bryophytes that offer unusual conditions.

Lobule Dwellers

Claudine Ah-Peng expressed surprise to find invertebrates in the lobules of some species of **Lejeuneaceae**, notably in the lobules of the leafy liverwort ***Acrolejeunea emergens*** (Figure 84-Figure 85). These occurred on plants at the Piton de la Fournaise volcano (Réunion in the Indian Ocean) collected on a 1986 lava flow.

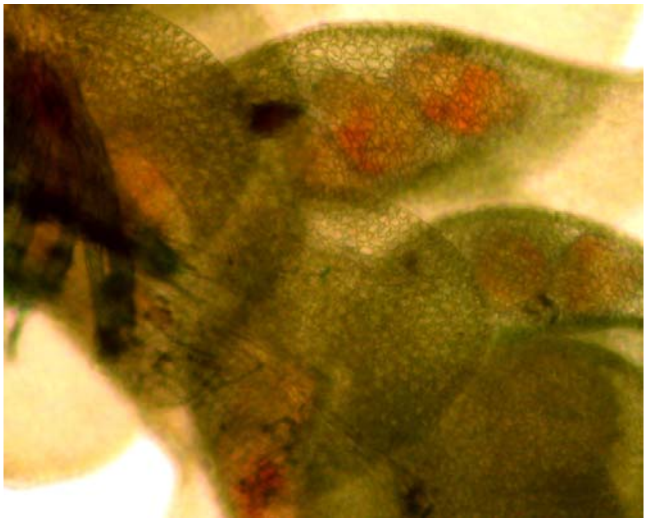

Figure 84. ***Acrolejeunea emergens*** with several orange invertebrates in the lobules. These appear to be resting stages of rotifers. Photo courtesy of Claudine Ah-Peng.

Figure 85. ***Acrolejeunea emergens*** with an emerging invertebrate, apparently a **rotifer**, in a lobule. Photo courtesy of Claudine Ah-Peng.

Bdelloid rotifers seem to be common in lobules, even in the tiny leafy liverwort ***Microlejeunea*** (Figure 86). Blanka Shaw has provided me with pictures of the tiny leafy liverwort ***Microlejeunea ulicina*** (Figure 87) from Whitewater Falls in Transylvania County, North Carolina, USA, with rotifer inhabitants, again in lobules. These initially motionless animals began moving their "wheels" when the warmth of the microscope light activated them.

Figure 86. ***Microlejeunea*** sp. showing lobules. Photo by Paul Davison, with permission.

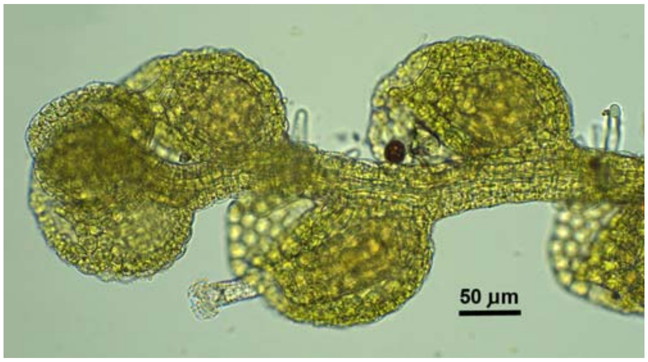

Figure 87. ***Microlejeunea ulicina*** with a rotifer emergent from a lobule. Scale is 50 µm. Photo courtesy of Blanka Shaw.

In North America, Puterbaugh *et al.* (2004) found that rotifers were common in the lobules of the leafy liverwort ***Frullania eboracensis*** (Figure 88-Figure 92). The younger outer portions of the plants had more rotifers in the lobules than did the interior lobules. Sterile plants had a mean ratio of 0.83±0.15 rotifers per lobule. Male and female plants had a mean ratio of 0.38±0.04 rotifers per lobule. Sterile plants likewise tend to be younger. Since we would expect older lobules to have more rotifers due their greater time available for colonization, these findings suggest that older portions may have something, perhaps a chemical exudate, that discourages the colonization by rotifers, or it could be due to lobule size difference, microhabitat differences, or accessibility.

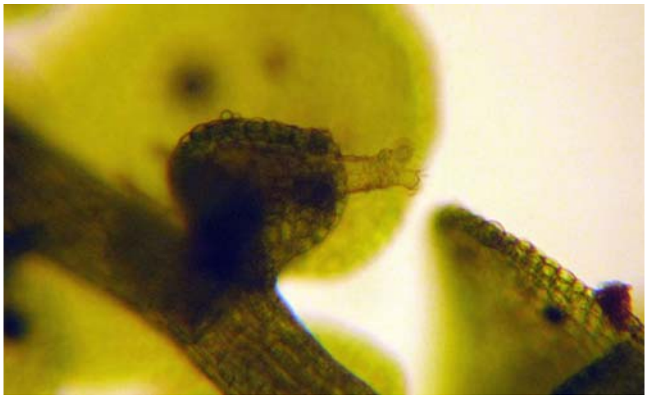

Figure 88. ***Frullania eboracensis*** with a rotifer in its **lobule**. Photo by Robert Klips, with permission.

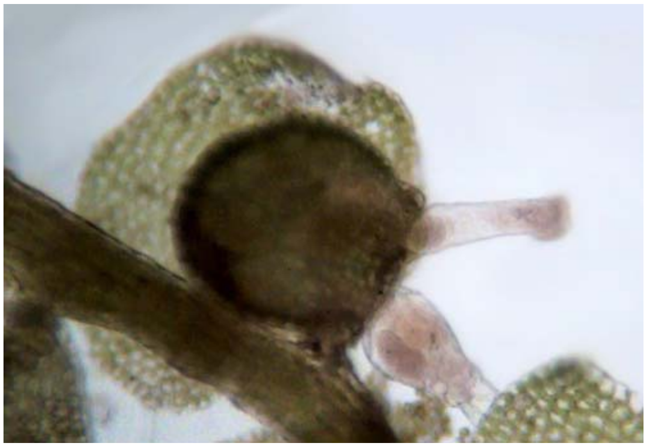

Figure 89. Bdelloid rotifers in lobules of ***Frullania eboracensis***. Photo courtesy of Mark Pokorski.

Figure 90. Bdelloid rotifer on lobule of ***Frullania eboracensis***. Photo courtesy of Mark Pokorski.

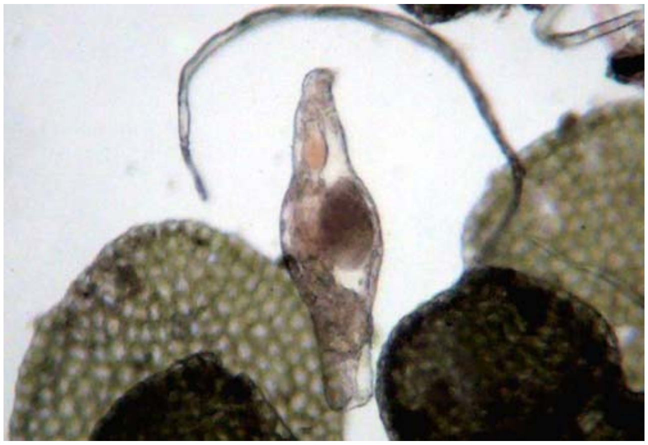

Figure 91. ***Frullania eboracensis*** with bdelloid rotifers as inhabitants. Photo courtesy of Mark Pokorski.

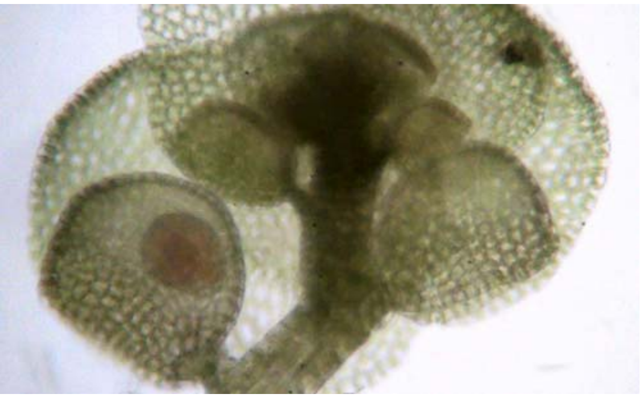

Figure 92. Lobules of ***Frullania eboracensis*** with dormant rotifers. These dormant stages could be resting eggs or cysts. Photo courtesy of Mark Pokorski.

Hess *et al.* (2005) found rotifers in lobules of ***Colura*** sp. (Figure 93-Figure 95) and ***Pleurozia purpurea*** (Figure 96-Figure 100). These liverworts have a trap lid on the lobules, and it appears that the inhabitants might not be able to escape, dying in the lobule (trap) and contributing organic matter that could break down and provide nutrients to the liverworts. However, there does not seem to be any evidence that ***Microlejeunea*** (Figure 86-Figure 87) or ***Frullania*** (Figure 88-Figure 92) species have this trapping action.

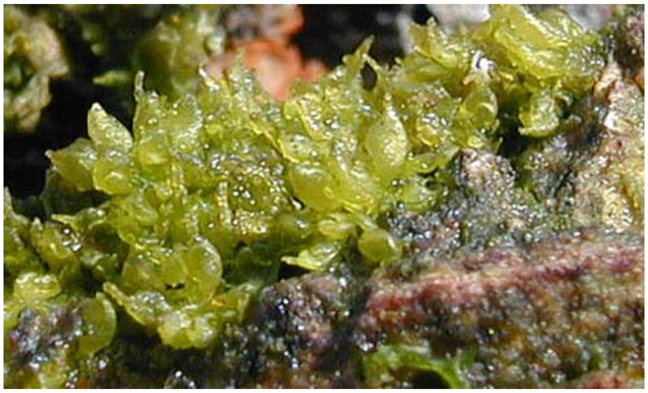

Figure 93. ***Colura calyptrifolia***, a leafy liverwort with lobules where **rotifers** can live. Photo by Michael Lüth, with permission.

Figure 94. ***Colura*** leaf with lobule where rotifers often live. Photo courtesy of Jan-Peter Frahm.

Figure 95. SEM of ***Colura*** leaf lobule where rotifers often live. Photo courtesy of Jan-Peter Frahm.

Figure 96. ***Pleurozia purpurea***, a leafy liverwort with lobules that house, and possibly trap, rotifers and other fauna. Photo by Janice Glime.

Figure 97. Branch of ***Pleurozia purpurea***. Photo courtesy of Sebastian Hess.

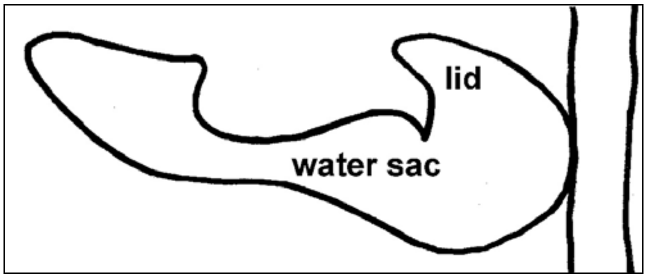

Figure 98. Lobule of ***Pleurozia purpurea*** showing the trap and lid. Redrawn from Hess *et al*. 2005.

Figure 99. Leaf of ***Pleurozia purpurea*** showing lobule and lid. Photo courtesy of Sebastian Hess.

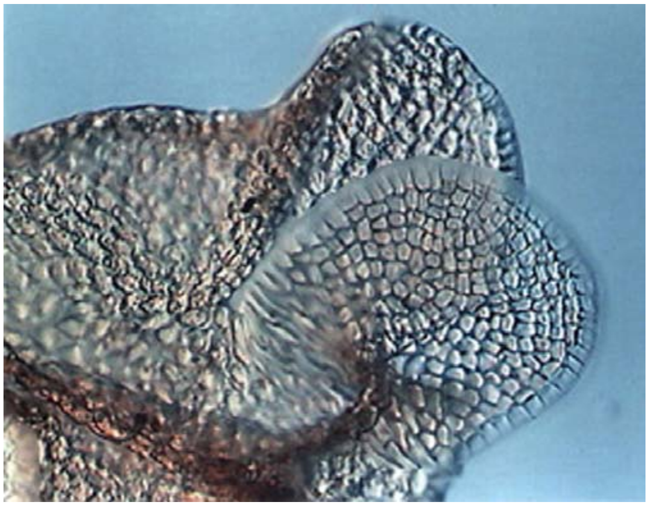

Figure 100. Lobule of ***Pleurozia purpurea*** showing lid. Photo courtesy of Sebastian Hess.

Lobules are not necessary for rotifer habitation of the leafy liverworts. ***Jungermannia cordifolia*** (Figure 101), with only a flat leaf surface to offer, likewise has its fauna of these interesting invertebrates (Javier Martínez Abaigar, pers. comm. 2008), as do mosses that lack similar structures.

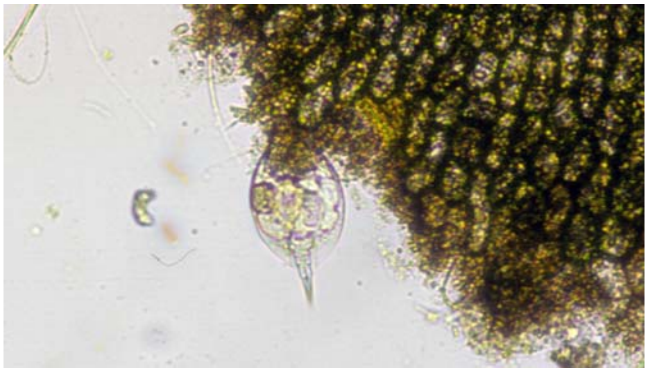

Figure 101. This ***Lepadella*** species, with its "wheels" hidden and its toes showing, is feeding on detrital material associated with the liverwort ***Jungermannia cordifolia***. Photo courtesy of Javier Martínez Abaigar.

Des Callaghan (Bryonet 10 November 2012) kindly provided us with a YouTube video <http://youtu.be/kHhBBppqh_Y> of rotifers feeding from the lobules of the tiny ***Lejeunea patens*** (Figure 102-Figure 103) in Wales and another of rotifers in lobules of ***Harpalejeunea molleri*** (Figure 104). I knew that the ciliated "wheels" directed food into the mouth, but I never realized the speed or the distance of that effect. The particles started outside the field of view and travelled farther than the extended length of the rotifer. Some particles came from near the foot and others shot in like a meteor from the height of the cilia or a little above, but from some distance.

Figure 102. ***Lejeunea patens*** on rocks near Swallow Falls stream, Wales. Photo by Janice Glime.

Figure 103. ***Lejeunea patens***, home of rotifers in Wales. Photo by Michael Lüth, with permission.

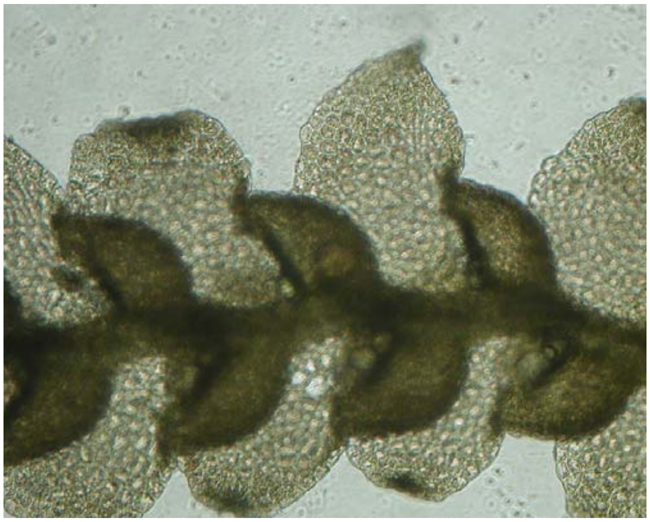

Figure 104. ***Harpalejeunea molleri*** with lobules that are home for rotifers. Photo by Jan-Peter Frahm, with permission.

Retort Cells

Curiously, two species of ***Habrotrocha*** (Figure 105) (***Habrotrocha roeperi***, Figure 106; ***Habrotrocha reclusa***, Figure 107) choose to live in the **retort** cells (Figure 106, Figure 108) of the stems of some species of ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), entering through the subterminal pore. **Retort** cells differ from other ***Sphagnum*** outer stem (Figure 110) and branch cells by having a terminal neck that terminates in a pore, somewhat like the neck of a leather wine flask. Hingley (1993) found it interesting that these rotifer species seemed to avoid the stem cells of ***Sphagnum palustre*** (Figure 109), ***S. papillosum*** (Figure 27, Figure 110), and ***S. magellanicum*** (Figure 111-Figure 112), all species of the subgenus ***Sphagnum*** that has spiral thickenings in the **cortical** (outer stem) cell walls (Figure 110).

Figure 105. ***Habrotrocha bidens*** from moss on ground; ***Habrotrocha*** is a genus known from retort cells of ***Sphagnum*** and lobules of ***Frullania***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

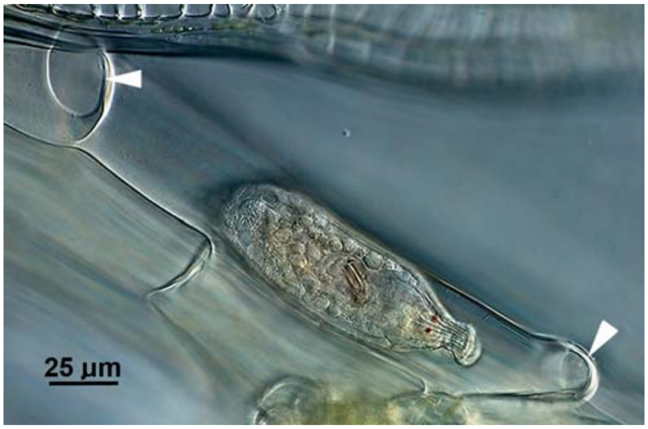

Figure 106. ***Habrotrocha roeperi*** in **retort** cell. Arrows indicate protruding pores. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 107. ***Habrotrocha*** *cf* ***reclusa***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

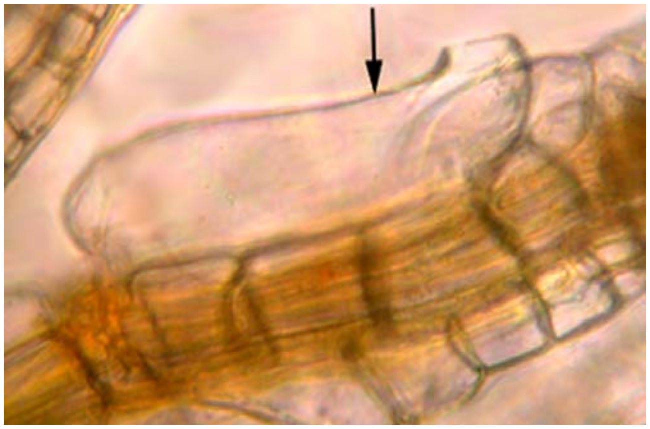

Figure 108. Retort cell of ***Sphagnum***, lacking spiral thickenings. Picture with permission from Wilf Schofield, University of British Columbia botany web site.

Figure 109. ***Sphagnum palustre***, a species with retort cells on the stem that rotifers seem to avoid. Photo by Michael Lüth, with permission.

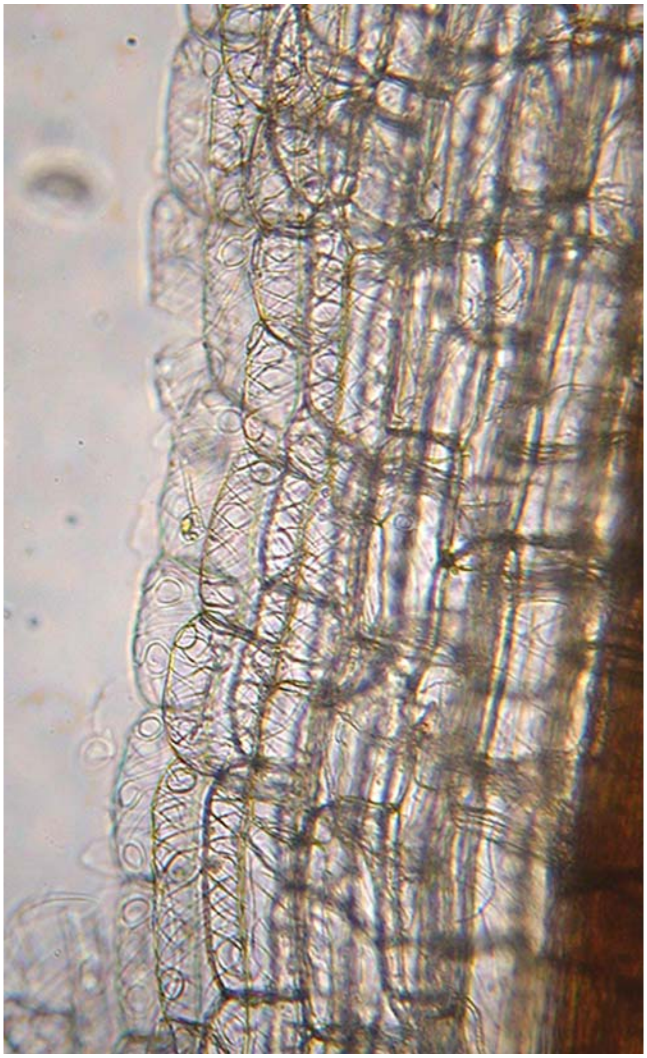

Figure 110. ***Sphagnum papillosum*** outer stem cells in longitudinal view showing fibrils and pores that are flat against the cell surface. Rotifers do not inhabit these. Photo from UBC Botany website, with permission from Shona Ellis.

Figure 111. ***Sphagnum magellanicum*** hummock, a species whose retort cells are avoided by the retort-inhabiting ***Habrotrocha*** species. Photo by James K. Lindsey, through Creative Commons.

Figure 112. ***Sphagnum magellanicum***, a species whose stem cells lack retort cells and are avoided by retort-cell species of ***Habrotrocha***. Photo by Michael Lüth, with permission.

In addition to living in ***Sphagnum*** retort cells, ***Habrotrocha roeperi*** (Figure 106) and ***Habrotrocha reclusa*** (Figure 107) live inside the outer cells of ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) branches (May 1989). May states that these rotifers could be considered as parasites. I have to question what nutrition they get from the ***Sphagnum*** by living in those outer cells. It is more likely that they feed on associated micro-organisms.

Roofs

Colonization of mosses on roofs permitted Hirschfelder *et al.* (1993) to compare species of rotifers on an upright acrocarpous moss (***Ceratodon purpureus***; Figure 31) and a mat-forming pleurocarpous moss (***Brachythecium glareosum***; Figure 113). They collected mosses every two weeks from roofs aged 3-92 years, dried them at 20ºC, and cut them into small pieces. The pieces were re-wet in deionized water and examined for awakening rotifers. The mat-forming moss had significantly more species and greater numbers of rotifers than did the upright moss, but species on ***C. purpureus*** differed little from those that could be found on ***B. glareosum***. They found that rotifer colonization of the mosses continued for decades and that the colonization of the mosses was rapid. Nevertheless, the numbers of rotifer species increased with time (Figure 114).

Figure 113. ***Brachythecium glareosum***, a rotifer habitat on roofs. Photo by Des Callaghan, with permission.

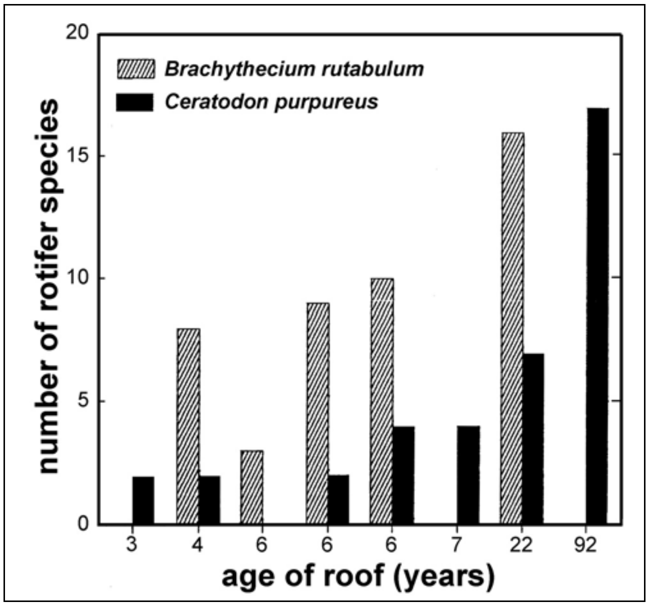

Figure 114. Succession of rotifer species that increase in number with age of roof. Redrawn from Hirschfelder *et al.* 1993.

Arctic and High Altitude

De Smet and Beyens (1995) considered rotifers to be one of the dominant bryophyte dwellers on Devon Island. In the Arctic Spitsbergen, the bdelloid rotifers among mosses had an unexpectedly high species richness – 52 taxa (Kaya *et al.* 2010). Kaya and coworkers concluded that the moisture regime and geographic localization of the mosses were the most important ecological factors in affecting the differences in species composition between samples. (See also De Smet 1988).

Fontaneto and Ricci (2006) examined elevational effects on the rotifer fauna of lichens and mosses across the Italian, French, and Swiss Alps. Distances among the 47 sample sites ranged from 1 m to 420 km. Low elevation sites ranged 850-1810 m asl; high elevation sites were 2984-4527 m asl. They found significant differences in both species richness and species composition between the mosses and lichens at high elevations. Nevertheless, there was no significant difference in the heterogeneity of the species assemblages. High-elevation **alpha diversity** (diversity of each site, *i.e.* local species diversity) was significantly lower than that at lower elevations. On the other hand, when comparing only species richness, there was no difference between higher and lower elevations.

Alpha diversity in these Alp rotifers was significantly lower at high-elevation than at low-elevation sites, but the estimated number of species was not reduced when compared with sites at low elevations (Fontaneto & Ricci 2006). Geographical distance between sites had no effect on species composition of rotifers in either mosses or lichens. The high elevation sites did not simply represent a reduction in number of species represented at lower elevations. Rather, they indicated that low density of favorable habitat patches, coupled with the low number of available propagules (moss riders), accounts for the heterogeneity of rotifers among the moss patches and the lower richness in individual patches at higher elevations.

Antarctic

In the Antarctic, rotifers share the mosses with tardigrades and nematodes among the microinvertebrates. Early explorations of de Beauchamp (1913) in the Antarctic revealed the bdelloid ***Mniobia*** (Figure 67) among mosses. Most of the bdelloids he located were contracted and could not be identified. In addition, he found the monogononts ***Lindia torulosa*** (Figure 115), ***Colurella adriatica*** (Figure 3), and ***C. colurus***.

Figure 115. ***Lindia torulosa*** head, a species that lives among mosses in the Antarctic. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Petz (1997) found that 95% of the samples from Wilkes Land, East Antarctica, had rotifers, with the highest numbers in mosses (1,311/g), although it was tardigrades that dominated. Water and organic matter seemed to be the most important controlling factors for these invertebrate numbers.

The Antarctic mosses sport an active community of invertebrates that move among the stems and branches. Priddle and Dartnall (1978) showed experimentally that wind caused mixing in summer, resulting in the transport of larval rotifers from shallow portions of the lake. Priddle and Dartnall found six rotifer species along the stems of aquatic mosses [***Warnstorfia sarmentosa*** (Figure 116), ***Drepanocladus*** sp. (probably ***Sanionia uncinata***; Figure 117)]. Two of these rotifers were bdelloids and four were sessile monogonont species. These rotifers preferred the middle stem zones of mosses where the highest growths of epiphytic algae and other epiphytic organisms occurred. Of these, four species chose leaf axils, whereas the other two settled on the bare underside of the leaf.

Figure 116. ***Warnstorfia sarmentosa***, home for a variety of Antarctic rotifers. Photo by David T. Holyoak, with permission.

Figure 117. ***Sanionia uncinatus***, a suitable substrate for Antarctic rotifers. Photo by Michael Lüth, with permission.

These studies were followed by those of Dartnall and Hollowday (1985), Hansson *et al.* (1996), Dartnall (1980, 1995, 1997, 2000, 2005a,b (flooded moss carpets), all providing records of Antarctic bryophytes.

Dartnall and Hollowday (1985) found that ***Macrotrachela concinna*** was most often encountered in terrestrial mosses. An unidentified species of ***Philodina*** (Figure 60) occurred on growing tips of mosses in the lake. ***Notholca salina*** and ***Resticula gelida*** (Figure 118) were most common in the flooded moss carpet. ***Adineta barbata*** (Figure 119) was collected from drying mosses.

Figure 118. ***Resticula gelida***, a plankton species that is common in flooded moss carpets in the Antarctic. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 119. ***Adineta barbata*** from epiphytic moss, a species that occurs among mosses that dry out in the Antarctic. Photo by Michael Plewka <www.pllingfactory.de>, with permission.

Hansson *et al*. (1996) found that rotifers in the Antarctic (South Georgia) were rare in the open water and were restricted mostly to mosses in shallow areas, as well as sediment surfaces. These taxa were varied, including ***Cephalodella auriculata*** [Figure 120; a cold-water species (Segers 2001)], ***C. gibba*** [Figure 121; (see also De Smet 2001)], a cold-water species (Segers 2001) known from habitats with *p*H <3.0 in Germany (Deneke 2000), ***Lecane closterocerca*** (Figure 122; see also Hingley 1993), ***L. lunaris*** (Figure 123), ***Lepadella patella*** (Figure 124; see also Hingley 1993), ***Resticula*** sp. (Figure 125), ***Testudinella*** sp. [perhaps ***Testudinella patina*** (Figure 126) found by Hingley (1993)], ***Tricocerca brachyura*** (Figure 127), and several bdelloid rotifers among the more common ones.

Figure 120. ***Cephalodella auriculata*** (**Notommatidae**), a cold-water benthic and epiphytic moss-dwelling rotifer. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 121. ***Cephalodella gibba***, an aquatic rotifer (Segers 2001), typically occurring in the sediments (Hingley 1993; Schmid-Araya 1995), that is found among the Antarctic mosses (De Smet 2001). Photo from Jersabek *et al*. 2003, through Creative Commons.

Figure 122. ***Lecane closterocerca***, a species primarily on mosses in the Antarctic. Photo by Jersabek *et al*. 2003 from Rotifer World Catalog, through Creative Commons.

Figure 123. ***Lecane lunaris***, a bryophyte dweller in the Antarctic. Photo from Jersabek *et al.* 2003, with permission.

Figure 124. ***Lepadella patella***, an Antarctic moss dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 125. ***Resticula nyssa***; this genus is a common moss dweller in the Antarctic. Photo by Jersabek *et al.* 2003 from Rotifer World Catalog, through Creative Commons.

Figure 126. ***Testudinella patina***, an Antarctic moss dweller. Photo by Yuuji Tsukii, with permission.

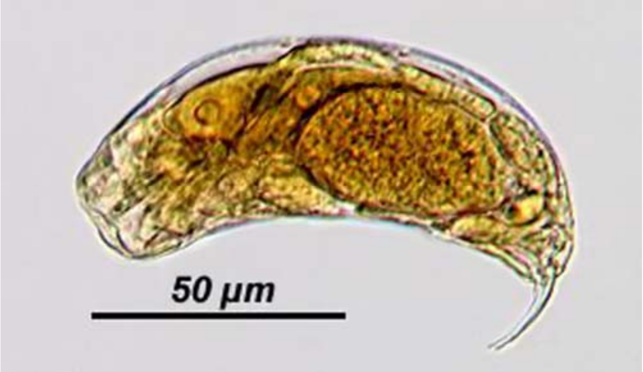

Figure 127. ***Trichocerca brachyura***, an Antarctic moss dweller. Photo by Jersabek *et al.* 2003, with permission.

Hansson *et al*. (1996) found the genus ***Lecane*** (Figure 128), to be one of the more common rotifers on Antarctic bryophytes. This is a widespread genus with one of the largest numbers of species. It includes several endemic species (Segers 1996) and members that are able to live in the contrasting warm climates of southeast Asia (Segers 2001) and Brazil (Turner & Da Silva 1992).

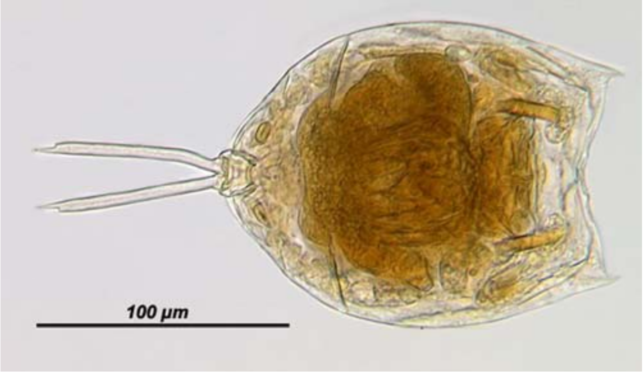

Figure 128. ***Lecane curvicornis***, member of a genus that has several species living on mosses in the Antarctic. Photo by Jersabek *et al*. 2003, with permission.

One of the common habitats for Antarctic rotifers is the moss ***Sanionia uncinata*** (Figure 129). In this habitat, the rotifers (Figure 130) are subject to predation by nematodes (Newsham 2004).

Figure 129. ***Sanionia uncinata***, a common moss in higher latitudes, including the Antarctic, and home for rotifers. Photo by Hermann Schachner, through Creative Commons.

Figure 130. Moss-dwelling ***Adineta*** sp. from the moss ***Sanionia uncinata*** on the Barton Peninsula of King George Island, Antarctica. Photo by Takeshi Ueno, with permission.

Fontaneto *et al.* (2015) determined that the number of monogonont rotifer species decreases toward the poles. The number of bdelloid species, on the other hand, increases toward the poles. Bryophytes play an important role in providing habitats for them farther north and south. The **Bdelloidea** are most common in limnoterrestrial environments – mosses, lichens, and soils (Wallace *et al.* 2006; Fontaneto & De Smet 2015). The **Monogononta**, although sometimes present in limnoterrestrial habitats, including mosses, are mostly aquatic. Hansson *et al.* (1996) found that rotifers were rare in the open water of the Antarctic region, being restricted to the vegetation (mainly mosses) in shallow areas as well as the sediment surface.

Sudzuki (1964) enumerated the moss-water community at Langhovde in the Antarctic region and found that it was "not so unusual." He identified 13 rotifer species in the Antarctic region. These included ***Adineta gracilis*** (Figure 131), ***Adineta*** sp., *Encentrum antarcticum* (invalid species), ***Habrotrocha*** (Figure 105-Figure 107), *Lepadella patella matsuda* (invalid subspecies, ***Macrotrachela*** sp. from Langhovde. However, some of these species are now invalid. Sudzuki (1979) also sampled mosses using polyurethane foam in a variety of Antarctic sites. These added ***Habrotrocha cf. gulosa*** and ***Macrotrachela nixa*** to the moss rotifer fauna.

Figure 131. ***Adineta gracilis***, a moss dweller that lives among Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Freshwater plankton and submerged mosses supported 13 species of monogonont rotifers in the South Shetland Islands (Janiec 1993, 1996a, b; Janiec & Salwicka 1996).

In their studies of southern Victoria Land, Schwarz *et al.* (1993) found that the protozoa, rotifers, nematodes, and tardigrades dominate the invertebrate fauna of the moss-dominated flushes. These invertebrates, including rotifers, were concentrated at 5-10.83 mm depth in the moss carpets. In post-melt cores, the upper 5 mm of the moss mats had more rotifers (and other invertebrates) than in pre-melt samples.

Nevertheless, whereas the rotifers are common on terrestrial mosses, few studies have gone farther than identifying them as rotifers. It is likely that new species, or at least cryptic species, remain to be described there.

Nunataks

Sohlenius and Boström (1996, 2005) examined samples from **nunataks** (Figure 132; exposed, often rocky portions of ridges, mountains, or peaks that escape snow and glaciation, typically vegetated by algae, mosses, and lichens). Among these samples, 67% contained rotifers, with the most frequent and diverse microfauna group being bdelloid rotifers (19 species).

Figure 132. **Nunatak** in Antarctica. Photo by Stephen Bannister, through Creative Commons.

In moss cushions alone from Antarctic nunataks, Sohlenius and Boström (2006) found that 82% of their 91 samples had rotifers, the highest, above the nematodes (64%) and tardigrades (32%). Jennings (1976) studied the ecology of bdelloid rotifers in moss carpets on Signy Island. He found bdelloid and two monogonont rotifer species. These included ***Adineta gracilis*** (Figure 131), ***A. steineri*** (Figure 133), ***A. vaga*** (Figure 12), ***Habrotrocha constricta*** (Figure 69), ***H. crenata*** (Figure 134, ***H. pulchra***, ***Macrotrachela concinna***, ***M. kallosoma***, ***Mniobia burgeri***, and ***Philodina plena*** (Figure 135-Figure 136; see also Donner 1980).

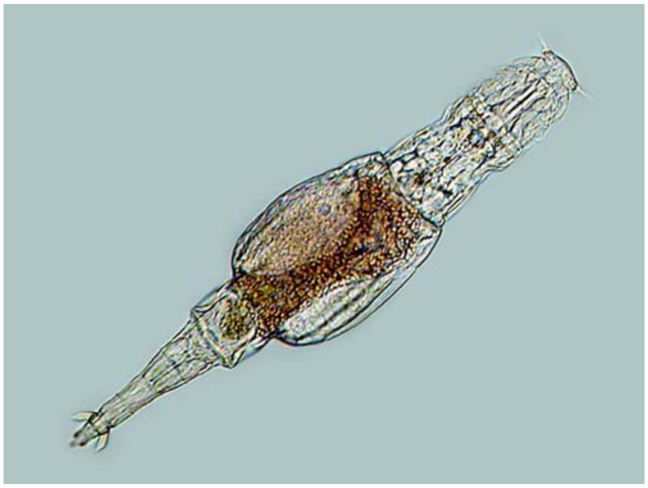

Figure 133. ***Adineta steineri***, an epiphytic moss dweller that also lives in Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 134. ***Habrotrocha crenata***, a beech litter species that is also known from Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 135. ***Philodina plena***, a ***Sphagnum*** dweller that lives in Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission

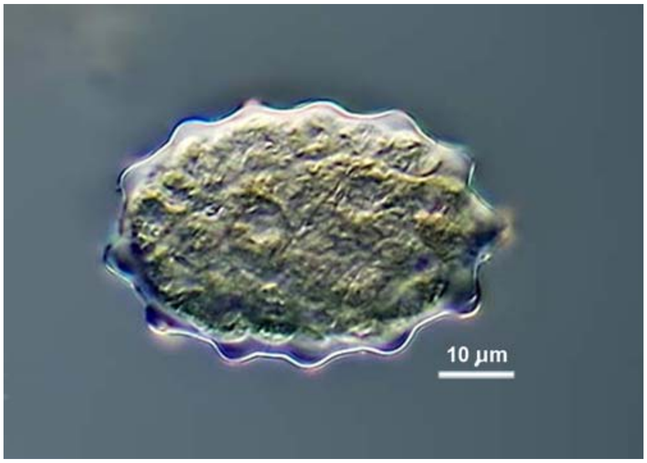

Figure 136. Egg, probably from ***Philodina plena***, a species that occurs in Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission

Bog and Fen Habitats

The terminology of bog and fen has differed between North America and Europe, with North Americans tending to refer to any habit with dominant ***Sphagnum*** as a bog, whereas the Europeans have considered bogs to be defined by their water sources as only precipitation (*i.e.*, raised bogs or other peatland with no source of mineral-rich water) (Rydin & Jeglum 2013). Those low-nutrient sites with groundwater sources are considered by the Europeans to be poor fens. Other differences in nomenclature exist, making the habitat discussion in this chapter a little fuzzy since I had no way to know which definition the researcher might be using. Fortunately, the rotifers seem to care more about the species of bryophytes than the source of the water, most likely liking the same habitat types as their bryophyte substrates.

The diversity of habitats in bogs and fens results in a number of species preferring these ecosystems. Halsey *et al*. (2000) considered ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) to be a suitable habitat for rotifers due to its large water-holding capacity. Unique communities characterize the various stages in the peatland ecosystem (Francez & Dévaux 1985).

Sayre and Brunson (1971) considered rotifers to be excellent tools for research on the periphyton/epiphyte organisms on mosses in peatlands. Although ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) seems to be important for many species of rotifers, many rotifers are missed during casual observance because their size is less than 200 µm (Gilbert & Mitchell 2006). Some are missed because they hide inside hyaline cells of ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) leaves and stems, entering through the pores (Hingley 1999), or in outer branch cells (May 1989).

Nevertheless, an important deterrent for many rotifers is that ***Sphagnum*** acidifies its surroundings (Clymo 1963, 1964; Williams *et al*. 1998) and may account for a higher species diversity in rich fens than in ***Sphagnum*** peatlands. Since many rotifer species are intolerant of a low *p*H, especially loricate species, the low *p*H limits the rotifer diversity (Nogrady *et al*. 1993) (see Acidity below.) On the other hand, ***Sphagnum*** is important in the phosphorus and nitrogen cycling in bog ecosystems, with the help of the rotifers that process the detritus (Błedzki & Ellison 1998, 2002).

Some rare species can be common among ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112). For example, the ***Tetrasiphon hydrocora*** (Figure 137) was not uncommon in association with ***Sphagnum*** in Lac des Femmes, Quebec, Canada, yet seemed to be rare on a more general scale (Nogrady 1980). It likewise was one of the rotifers reported in the peatland study by Hingley (1993). One reason for the occurrence of rare species among ***Sphagnum*** may be its ability to serve as a safe site/refugium against predators (Kuczyńska-Kippen 2008). ***Sphagnum*** also provides a source of food such as the desmids seen in the gut of ***Tetrasiphon hydrocora*** (Figure 137). Desmids are common in ***Sphagnum*** peatland pools and among the ***Sphagnum*** plants (personal observation), providing food for many kinds of rotifers. Others may require the alternating wet and dry cycles.

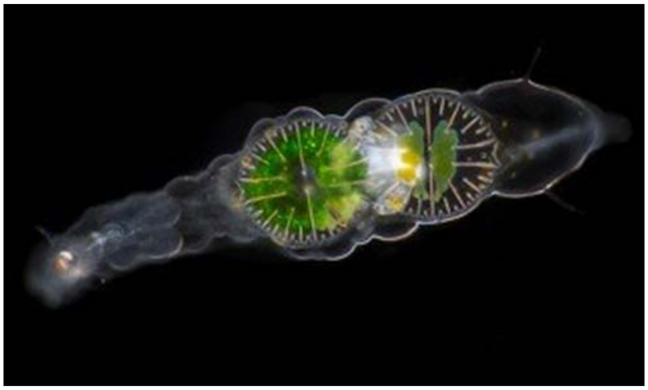

Figure 137. ***Tetrasiphon hydrocora*** with the desmid ***Micrasterias rotata*** in its gut. Photo by Wim von Egmond, with permission.

Species Richness

The abundant peatlands of the Scandinavian countries has resulted in most of our basic knowledge of peatlands arising there.

Pejler and Bērziņš (1993a) found that species richness of rotifers associated with the ***Sphagnum*** (Figure 157) in Swedish peatlands ranged from 33 to 59, including both **Bdelloidea** and **Monogononta**. In an extensive study of peatlands in Poland, Bielańska-Grajner *et al.* (2011) examined the rotifers in eight sampling locations in peatlands, including 2 raised bogs, 2 poor fens, 1 intermediate fen, and 1 rich fen. They found 42 taxa of **Monogononta** and 26 of **Bdelloidea**. **Monogononta** comprised only 4-18% of the numbers among the eight sites sampled. On the other hand, bdelloids were dominant and contributed 80% overall to the number of individuals, ranging 56-85%. Among the **Bdelloidea**, the most abundant rotifers were ***Habrotrocha angusticollis*** (Figure 4), ***H. lata*** (Figure 138), ***H. roeperi*** (Figure 106), ***Macrotrachela quadricornifera*** (Figure 62-Figure 64), ***Rotaria rotatoria*** (Figure 17), ***Lecane elasma*** (Figure 139), ***L. lunaris*** (Figure 123), ***L. scutata*** (Figure 140).

Figure 138. ***Habrotrocha lata*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

The large genus ***Lecane*** (Figure 139-Figure 140) enjoys widespread distribution, including the Antarctic. Nevertheless, there are species in this genus restricted to ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) bogs (Pejler & Bērziņš 1994). ***Lecane elasma*** (Figure 139) is considered characteristic of ***Sphagnum*** (Francez & Dévaux 1985).

Figure 139. ***Lecane elasma***, a peatland species. Photo by Jersabek *et al.* 2003, with permission.

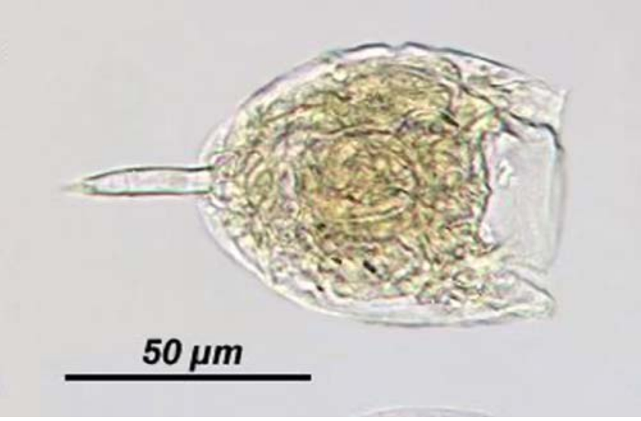

Figure 140. ***Lecane scutata***, one of the abundant bdelloid rotifers in Polish peatlands. Photo by Jersabek *et al.* 2003, with permission.

Bielańska-Grajner *et al*. (2011) selected ***Habrotrocha angusticollis***, ***Dicranophorus capucinus*** (Figure 141), ***Keratella serrulata*** (Figure 142), and ***Lepadella elliptica*** for further analysis and found that abiotic factors were important determinants of distribution. Nevertheless, the researchers found that the highest density of rotifers occurred in a raised bog dominated by ***Sphagnum angustifolium*** (Figure 157), but this might suggest that a number of rotifer species may prefer the same abiotic conditions as this moss. Francez and Dévaux (1985) similarly found the highest proportion of characteristic rotifer species in a low moor where ***Sphagnum angustifolium*** was dominant.

Figure 141. ***Dicranophorus capucinus*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 142. ***Keratella serrulata***, an abundant ***Sphagnum*** associate in Sweden. Photo by Michael Plewka <www.plingfactory.de>, with permission.

As noted, the **Bdelloidea** are the dominant group, in peatlands mostly represented by the genera ***Philodina*** (Figure 143-Figure 144) and ***Habrotrocha*** (Figure 145) (Gilbert & Mitchell 2006). Among the **Monogononta**, peatlands are occupied mostly by ***Colurella*** (Figure 3), ***Euchlanis*** (Figure 146-Figure 148), ***Lecane*** (Figure 139-Figure 140), and ***Trichocerca*** (Figure 149) (Gilbert & Mitchell 2006). Francez (1981), who identified 142 species in peatlands, found that in France both abundance and average size were greater in fens than in bogs. Many kinds of rotifers are unable to live among peat mosses because of the high degree of acidity (Hingley 1993).

Figure 143. ***Philodina*** on the alga *Spirogyra*. Photo by Yuuji Tsukii, with permission.

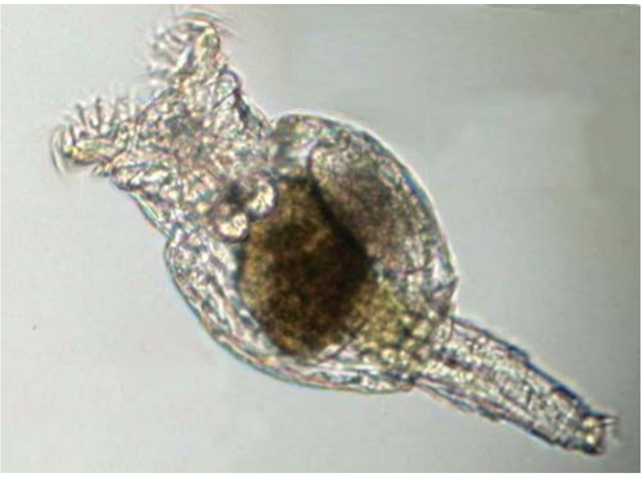

Figure 144. Extended ***Philodina.*** Photo by Jean-Marie Cavanihac at Micscape, with permission.

Figure 145. ***Habrotrocha rosa*** (**Bdelloidea**). Photo by Rkitko from Wikipedia Commons.

Figure 146. ***Euchlanis***, a genus having species of peatland rotifers. Photo by Yuuji Tsukii, with permission.

Figure 147. ***Euchlanis***. Photo by Jean-Marie Cavanihac at Micscape, with permission.

Figure 148. ***Euchlanis.*** Photo by Jean-Marie Cavanihac at Micscape., with permission.

Figure 149. ***Trichocerca longiseta***, an alpine species but not typically a moss dweller. Photo by Yuuji Tsukii, with permission.

In Australia, Koste and Shiel (1989) identified members of the **Euchlanidae**, **Mytilinidae**, **Trichotriidae**, all members of **Monogononta**. In ***Sphagnum*** pools (Figure 150) they found ***Diplois daviesiae*** and ***Euchlanis meneta*** (Figure 151) in acid water and on submerged ***Sphagnum*** (Figure 150). ***Trichotria truncata*** (Figure 152), an acidophile, occurred among ***Sphagnum***.

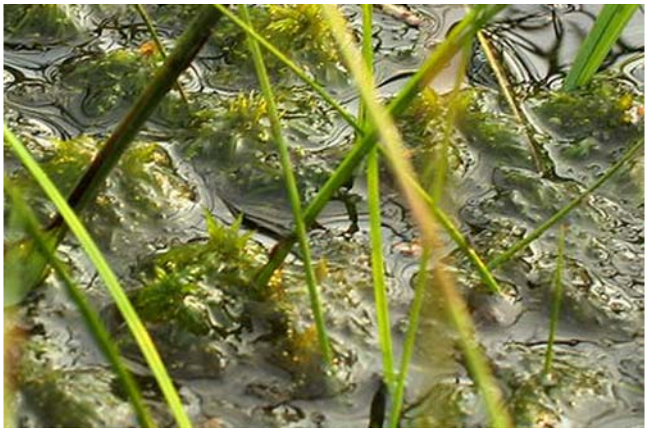

Figure 150. Submersed ***Sphagnum cuspidatum***, potential home for the rotifers ***Diplois daviesiae***, ***Euchlanis meneta***, and ***Trichotria truncata***. Photo by Andrew Spink, with permission.

Figure 151. ***Euchlanis meneta*** female, an inhabitant of acid ***Sphagnum*** pools. Photo by Jersabek *et al.* 2003, with permission.

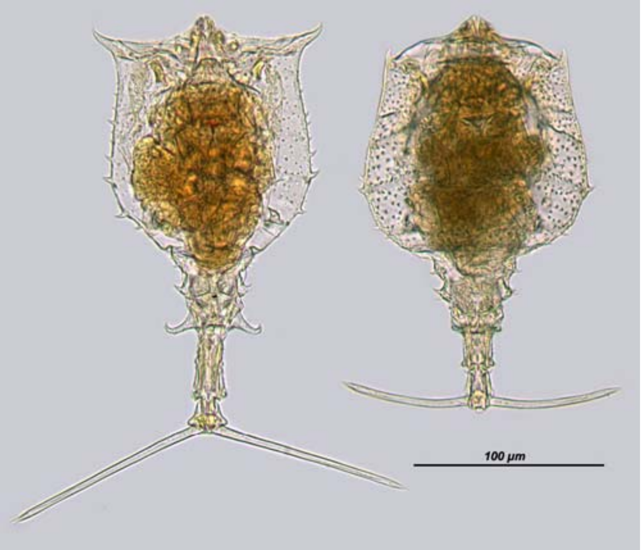

Figure 152. ***Trichotria truncata***, a ***Sphagnum***-dwelling acidophile. Photo by Jersabek *et al.* 2003, with permission.

Rotifer studies in North American bogs have been somewhat limited compared to the number of bogs present in the northern part of the continent. We can safely say that the **Bdelloidea** are the most abundant rotifers among the mosses in peatland habitats (Sayre & Brunson 1971). Some species of rotifers are **tyrphobionts**, restricted to peatlands, but many are also known from other types of habitats (Warner & Asada 2006). Few species seem to be restricted to peatlands, conforming to the typical widespread nature of rotifers.

Most Canadian peatland studies concentrated on the plants and vertebrates. Warner and Asada (2006) were among the first to include invertebrates in an extensive survey. In a **poor fen** (similar to a bog in bryophyte species composition) in Newfoundland, Canada, Bateman and Davis (2007) found 25 **bdelloid** and 39 **monogonont** rotifers. Among these, 27 were new records for Canada and 13 new for North America. They found an average of 354 rotifers per cm^2 and 17 species per formation. These were seasonal, with the **monogononts** almost vanishing in winter. The **bdelloids** decreased, but not so dramatically.

The first extensive study of New England, USA, included 31 bogs from Vermont, Massachusetts, and northwestern Connecticut (Błedzki & Ellison 2003). Błedzki and Ellison collected from **interstitial spaces** (pore water), bog pools, and pitcher plants (see below). These three habitats yielded 38 rotifer species among more than 50,000 individuals. These bogs had a rotifer density that ranged 150-51,250 individuals dm^{-3} (Błedzki & Ellison 2002).

The bog ponds had 16 species; the interstitial spaces had 14 (Błedzki & Ellison 2003). The rotifer species richness increased significantly with bog elevation. On the other hand, latitude, longitude, and bog area made no significant difference in richness. The most frequent species was ***Habrotrocha rosa*** (Figure 65), present in pore water of 30 out of 31 bogs, but never in the bog pools. This species comprised 31% of the collected rotifers (Błedzki & Ellison 2002). The other abundant species were ***Lecane pyriformis*** (Figure 153), ***L. lunaris*** (Figure 123), ***Cephalodella gibba*** (Figure 121), and ***Polyarthra vulgaris*** (Figure 154). The sampling methods involved 50 ml plastic centrifuge tubes pressed into the ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) mat (Błedzki & Ellison 2003). These tubes readily filled with water. While this method may have been effective for those rotifers that swam in the pore water, their methodology most likely missed attached species that rarely enter open water, such as ***Collotheca*** (Figure 48) and ***Lecane*** (Sakuma *et al*. 2002).

Edmondson (1940) explored the rotifers in bogs in Wisconsin, USA. Although he found no species to be restricted to ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), the rotifer ***Collotheca heptabrachiata*** was known only from ***Sphagnum*** in Wisconsin. In his studies, both ***Ptygura pilula*** (Figure 155) and ***P. velata*** (Figure 156) occurred in "enormous numbers" in one ***Sphagnum*** peatland during the latter part of July and all through August.

For more species associated with ***Sphagnum*** or peatlands, see individual families in the following subchapters.

Figure 153. ***Lecane pyriformis***, a common bog species in association with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

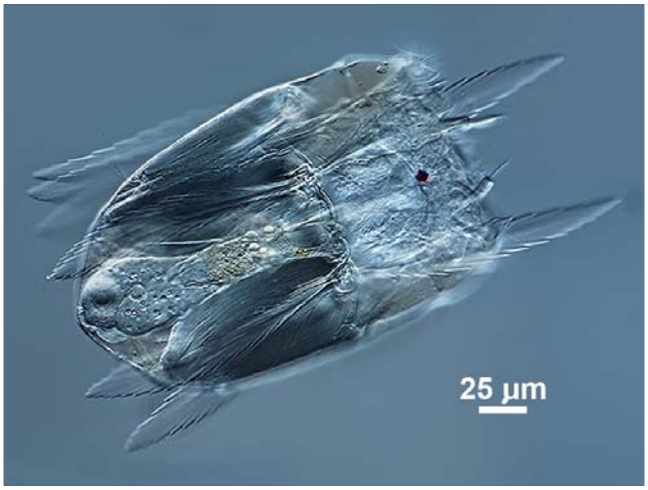

Figure 154. ***Polyarthra vulgaris***, a common bog species in association with ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 155. ***Ptygura pilula***, a species that can reach large numbers on ***Sphagnum***. Photo by Jersabek *et al*. 2003 from Rotifer World Catalog, through Creative Commons.

Figure 156. ***Ptygura velata*** shown here on the macrophyte *Ceratophyllum*, but it can reach large numbers in peatlands. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Abiotic Factors

The hummocks and hollows of bogs and fens present very different moisture and temperature regimes, and this is represented by differences in rotifer species (Bateman & Davis 2007). The summits of the hummocks in a poor (**mesotrophic**) fen (a habitat similar to a bog) in Newfoundland, Canada, house predominately bdelloid rotifers, although these never become desiccated. They found that position on the hummock was important in determining species composition. The **Bdelloidea** were the main rotifers on the tops of the hummocks. The **Monogononta**, on the other hand, increased in number of species and individuals from top to bottom, reaching their greatest number of species in the hollows. Nevertheless, the total numbers of rotifers was greatest at the tops of the hummocks. They determined that desiccation did not occur and that predation was not an important factor in determining distribution.

As the peatland water content decreases, the fauna become less like that of open water. Among peat mosses, the species with the highest percentage of characteristic rotifer species is the **oligotrophic** (low nutrient) ***Sphagnum angustifolium*** (Figure 157) of low moors (Francez & Dévaux 1985). Pejler and Bērziņš (1993a) found most bdelloids need lots of oxygen, commensurate with their limnoterrestrial environment, but some survive in soft bottom sediments.

Figure 157. ***Sphagnum angustifolium***, a commonly dominant peat moss that provides a home for species of ***Habrotrocha***, ***Macrotrachela***, ***Rotaria rotatoria***, and ***Lecane***. Photo by Michael Lüth, with permission.

Acidity

The acidity of the water may play a role in distribution, but it is difficult to determine if it is a direct or indirect effect. Bērziņš and Pejler (1987) found that **oligotrophic** (low nutrient) species occur at a *p*H optimum at or below 7.0, whereas **eutrophic** (rich in nutrients and so supporting a dense population) species are generally at or above this level. The rotifers may be there because of a suitable *p*H and absent elsewhere because the *p*H is too high or too low, or they may be there because they are limited to a particular substrate such as ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), which is itself limited to that same *p*H range (Edmondson 1940). Edmondson considers the rotifers ***Lecane satyrus*** (Figure 158), ***Notommata falcinella*** (Figure 159), ***Lindia pallida*** (Figure 160), among others, to be limited to ***Sphagnum***. Jersabek *et al.* (2003) also reported ***Notommata falcinella*** from submerged ***Sphagnum*** in Maryland, USA. In these cases, it appears to be the substrate that is important, as these species are not found on other substrates at the same *p*H.

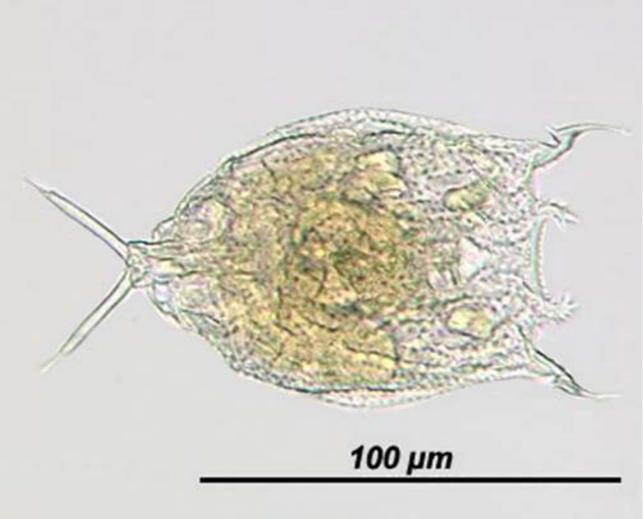

Figure 158. ***Lecane satyrus***, a species that seems to be limited to ***Sphagnum***. Photo by Jersabek *et al.* 2003 from Rotifer World Catalog, through Creative Commons.

Figure 159. ***Notommata falcinella***, a species that seems to be restricted to ***Sphagnum***. Photo by Jersabek *et al.* 2003 from Rotifer World Catalog, through Creative Commons.

Figure 160. ***Lindia pallida***, a species that seems to be limited to ***Sphagnum***. Photo by Christian Jersabek, through Creative Commons.

Lecane lunaris (Figure 123) is tolerant of a broad *p*H range (Pejler & Bērziņš 1993b). This widespread species furthermore occurs in peatlands in both New England, USA (Błedzki & Ellison 2003), and Poland (Bielańska-Grajner *et al*. 2011). ***Habrotrocha angusticollis*** (Figure 4), a characteristic species for peatlands, particularly ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112), generally occurs in a *p*H range of 3.8-6.4 (Warner & Asada 2006). **Bdelloidea** dominate in peatlands. This group is typically dominant in acidified water (Bateman & Davis 1980; Bielańska-Grajner *et al*. 2011), but it has a broad *p*H tolerance range (Bērziņš & Pejler 1987; Bateman & Davis 1980). Their reliance on parthenogenesis makes colonization easier, often evoking the **founder principle** (loss of genetic variation in new population established elsewhere by very small number of individuals from larger population), and may account for this wider range of *p*H tolerance among populations (Bērziņš & Pejler 1987; Ricci 1987).

In the Wisconsin study of Edmondson (1940), ***Ptygura mucicola socialis*** (Figure 161-Figure 162) was found amid a colony of the **Cyanobacterium *Gloeotrichia*** sp. (Figure 163) at the low *p*H of 3.5 in a ***Sphagnum*** peatland. It is interesting that these rotifers are often associated with algae on the mosses, presumably using them as a food source, although it might be other organisms associated with the algae that provide the food.

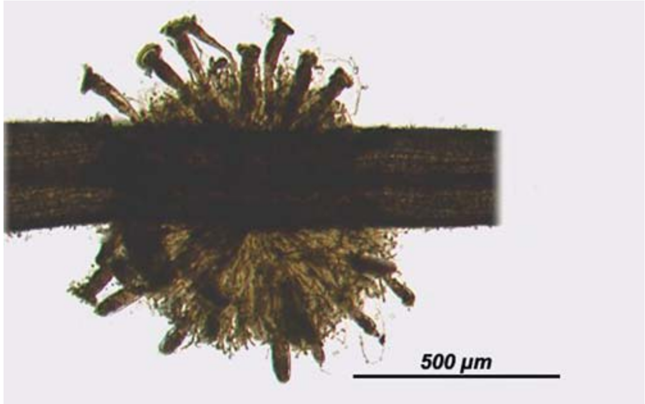

Figure 161. ***Ptygura mucicola***, a species that lives in colonies of ***Gloeotrichia*** amid ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

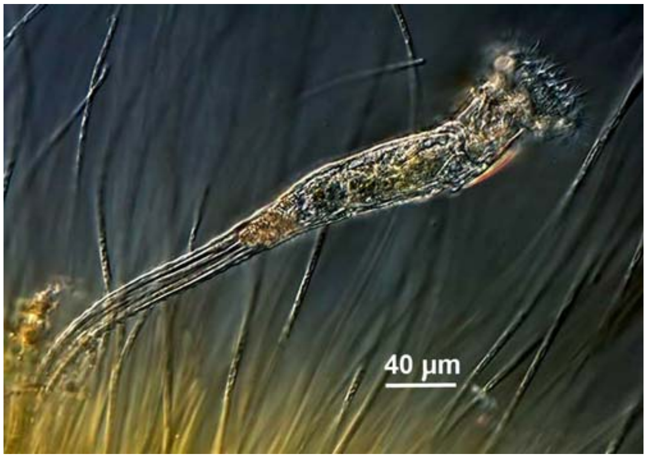

Figure 162. ***Ptygura melicerta*** var. ***melicerta*** with ***Gloeotrichia***. ***Ptygura mucicola***, a moss dweller, is considered by some to be a variety of ***P. melicerta***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

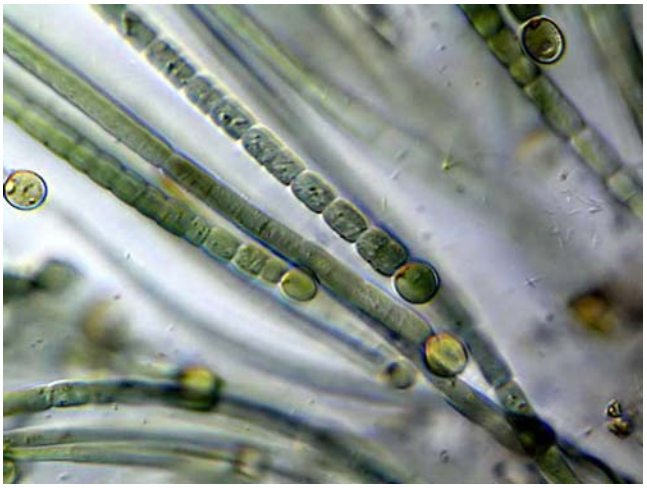

Figure 163. ***Gloeotrichia*** sp. with heterocysts, home for ***Ptygura mucicola socialis*** in peatlands. Photo from <www.diatom.org>, through Creative Commons.

Surface Configuration

Flat, broad surfaces do not seem to be suitable for most sessile rotifers, something to consider when using an artificial substrate. Edmondson (1940) suggested this may relate to their method of feeding. But it could also relate to capillary water.

Sphagnum (Figure 25-Figure 27, Figure 109-Figure 112, Figure 150) leaf morphology seems to play a role in the location of the rotifers. The rotifer ***Collotheca gracilipes*** lived on the concave side of a submerged moss leaf along with the green algae ***Bulbochaete*** (Figure 164) and ***Oedogonium*** (Figure 165) (Edmondson 1940). And ***Collotheca cucullata*** occurred on the concave side of a ***Sphagnum*** leaf (Figure 166) in a different peatland at *p*H 5.6. ***Ptygura velata*** (Figure 156) likewise is found on the concave side of the leaf, suggesting the importance of water held there by capillarity in the interstitial spaces. On ***Sphagnum perichaetiale*** (syn. ***Sphagnum erythrocalyx***; Figure 167-Figure 168), the rolled tip of the leaf provides a similar protection, and Edmondson found more than 200 rotifers residing there!

Figure 164. ***Bulbochaete***, a green alga that shares the ***Sphagnum*** spaces and leaves with the rotifer ***Collotheca gracilipes***. Photo from Proyecto Agua, through Creative Commons.

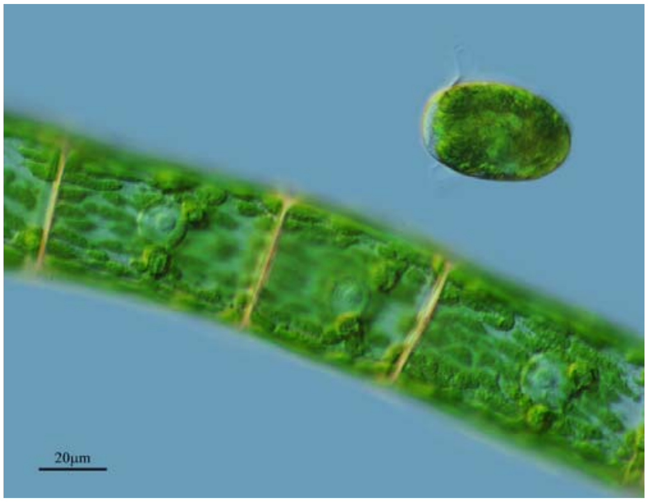

Figure 165. ***Oedogonium***, a green alga that shares the ***Sphagnum*** leaf with the rotifer ***Collotheca gracilipes***. Photo from Proyecto Agua, through Creative Commons.

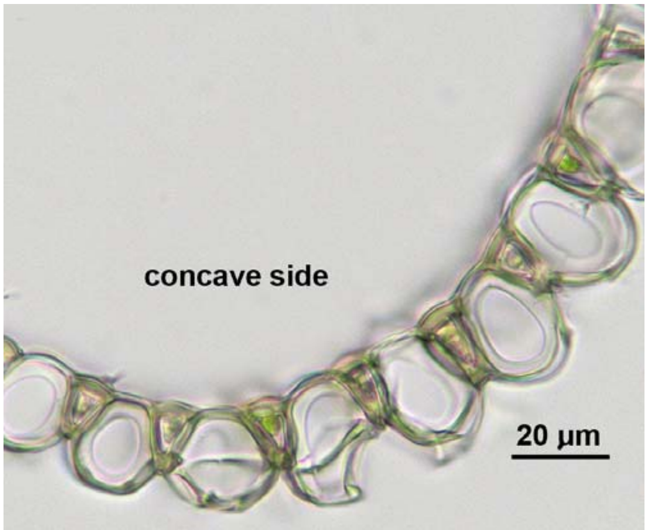

Figure 166. ***Sphagnum subnitens*** leaf cross section showing concave side where some species of ***Collotheca*** live. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

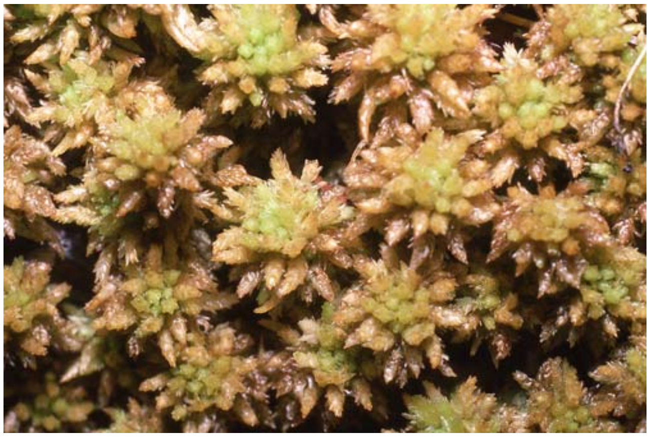

Figure 167. ***Sphagnum perichaetiale***, a species known to house 200 rotifers. Photo by Janice Glime.

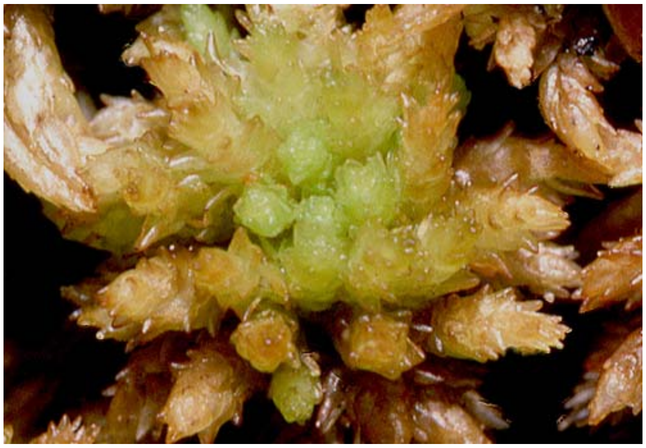

Figure 168. ***Sphagnum perichaetiale***. Note the rolled leaf tip where the rotifers attach. Photo by Janice Glime.

Rotifer and other invertebrate species assemblages change as the peatland develops so that specific associations can be described for each stage (Francez & Dévaux 1985). Likewise, communities differ with position in the hummock-hollow complex (Bateman & Davis 1980). The oligotrophic ***Sphagnum angustifolium*** (Figure 157), a species typical of mineral-rich sites (Hale 2012), seems to have one of the most unique and consistent assemblages of rotifer taxa (Francez & Dévaux 1985). Water content of the moss environment is the major factor determining the fauna, with the wettest mosses having communities most similar to those of the water. This is further supported by changes in protozoa species arising as a result of drainage (Warner & Chmielewski 1992).

Like the **Protozoa** (**Rhizopoda**), rotifers have both horizontal and vertical distribution patterns among the ***Sphagnum*** (Figure 25-Figure 27, Figure 109-Figure 112) (Meisterfeld 1977) and this may account for some variation in the distribution patterns of animals that prey upon them. But this vertical zonation also reflects the food available to the microfauna (Strüder-Kypke 1999). Differences in light and nutrients result in a denser colonization in the upper part where photosynthetic cryptomonads can provide food and mobile ciliate protozoa can take advantage of these food sources. Lower in the mat, but within the upper 30 cm, sessile ciliates and heterotrophic flagellates predominate. Moisture seems to be the dominant determiner of species assemblages, with *p*H being secondary (Charman & Warner 1992). As Bērziņš and Pejler (1987) indicated, *p*H may not in itself be a strong determinant of rotifer assemblages in peatlands, but rather may create an environment that supports oligotrophy or eutrophy as determining factors.

Pitcher Plants

The pitcher plants, especially ***Sarracenia purpurea*** (Figure 169), are interesting habitats for rotifers. These plants require the moist habitat of peatlands to become established and grow, growing upward as the moss grows upward. Hence, rotifers that live in the water of their pitcher-like leaves are indirectly dependent on the peat mosses (***Sphagnum***).

Figure 169. ***Sarracenia purpurea*** with water in leaves, home for several rotifer species. Photo by David Midgley, through Creative Commons.

Rotifers in the pitcher plant leaves are important in the cycling of nitrogen and phosphorus (Błedzki & Ellison 1998, 2002). By eating the detritus, they convert these two nutrients into forms usable by the pitcher plants. In their study of Massachusetts, USA, pitcher plants (***Sarracenia purpurea***; Figure 169), Błedzki and Ellison (1998) found that ***Habrotrocha rosa*** (Figure 65) could provide a pitcher plant leaf with 8.8-43 mg of N and 18.2-88 mg of P in a single growing season, far exceeding that supplied by insects and rainfall. The rotifers accomplish this by having populations of ca. 400 individuals per leaf pitcher. These rotifers can excrete ~5.2 µg NO_3-N, ~3.91 µg NH_4-N, and ~18.4 µg PO_4-P per day into a single leaf.

Błedzki and Ellison (2003) compared the rotifers in the pitcher plant leaves [***Sarracenia purpurea*** (Figure 169)] to those of pore water and bog ponds. These three habitats had low species similarity (Jaccard indices of similarity <0.25). The most common species was ***Habrotrocha rosa*** (Figure 65). This species had its highest production at *p*H 4 in culture (Błedzki & Ellison 1998). The pitcher plant water had a *p*H range of 3.5-6.3, dropping from the higher *p*H as the dying trapped insects decompose (Fish & Hall 1978). The ***H. rosa*** is subject to severe predation by the **Diptera** larvae that also live in the pitchers, including several mosquito species (Błedzki & Ellison 1998). Numbers of ***H. rosa*** are inversely related to numbers of these larvae.

Lecane lunaris (Figure 123) and ***Notholca acuminata*** (Figure 170) occurred in water-filled leaves in a Vermont bog. In that same bog ***Cephalodella anebodica*** occurred in a water-filled leaf (Błedzki & Ellison 2003).

Figure 170. ***Notholca acuminata***, a species that lives in water-filled leaves of the northern pitcher plant in bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Aquatic Bryophytes

Most of the studies on rotifers of **lentic** bryophytes are in peatlands. Several studies on littoral species have also been described above because they involved peat mosses. However, there have been a number of studies on the rotifers of stream bryophytes.

Drazina *et al.* (2011) studied both lakes and streams and found that rotifers were the dominant group of meiofauna among aquatic bryophytes, with 52 species among bryophytes in Europe (National Park Plitvice Lakes). In fast water, they averaged 219 individuals per cm^3. Several researchers have found the **Bdelloidea** to be dominant among rotifers associated with submerged mosses (Badcock 1949; Madaliński 1961; Donner 1972).

Streams

In his study of rotifers in German streams, Donner (1964) found that the rotifers were the most numerous as inhabitants of mosses. Fontaneto *et al.* (2005) analyzed an 80-m stretch of a stream in NW Italy to describe the **meta-community** (set of interacting communities linked by dispersal of multiple, potentially interacting species) structure of rotifers that colonized mosses. Mosses were absent in the riffles, but the shoreline was almost continuously covered with submerged mosses (***Brachythecium*** sp. – Figure 171). The same species of moss also occurred in the pools. The researchers concluded that rotifers in pools most likely arrived from other pools by travelling with their moss substrate, whereas within the pool they could move about by themselves. Different movement capabilities of the species within pools could account for small scale differences in communities. The species occupying these habitats in this stream segment were ***Adineta vaga minor*** (Figure 12), ***Embata hamata***, ***Habrotrocha bidens*** (Figure 172), ***H. constricta*** (Figure 69), ***H. gracilis***, ***H. pulchra***, ***Macrotrachela quadricornifera*** (Figure 62-Figure 64), ***Philodina acuticomis odiosa***, ***P. flaviceps*** (Figure 173), ***P. plena*** (Figure 135-Figure 136), ***P. rugosa*** (Figure 174), ***P. vorax*** (Figure 175), ***Pleuretra brycei*** (Figure 61, Figure 176), and ***Rotaria rotatoria*** (Figure 17). There was only a slight trend of differences in species composition from upstream to downstream (Figure 177).

Figure 171. ***Brachythecium rivulare***, potential streamside and in-stream habitat of several rotifer species. Photo by David T. Holyoak, with permission.

Figure 172. ***Habrotrocha bidens*** from moss on ground; a species that also occurs on mosses in streams. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 173. ***Philodina flaviceps*** from detritus, a stream bryophyte dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 174. ***Philodina rugosa*** from epiphytic moss, a rotifer that also occurs on streamside mosses, especially ***Brachythecium*** sp. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 175. ***Philodina vorax***, a species that lives on epiphytic mosses, ***Sphagnum***, and streambank mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

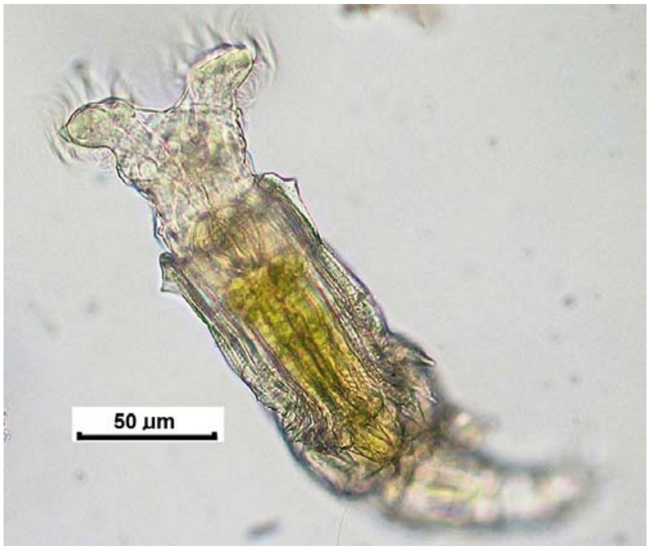

Figure 176. ***Pleuretra** cf **brycei***, a species that lives among ***Brachythecium***. Photo by Michel Verolet, with permission

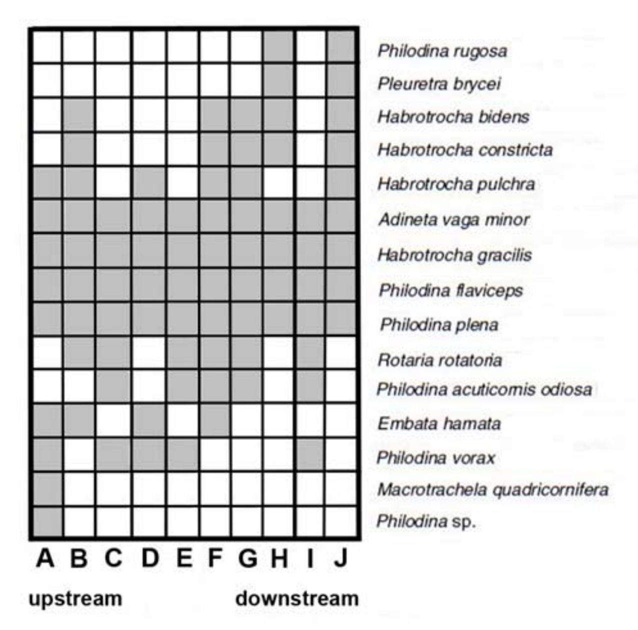

Figure 177. Distribution of moss-dwelling rotifers in a stretch of an Italian stream, arranged from upstream to downstream. Based on Fontaneto *et al.* 2005.

Suren (1992) suggested that the high densities of meiofaunal communities, including rotifers, associated with the bryophytes in New Zealand alpine streams may result from the food value of the large periphyton component and the shelter from fast water currents. In the stream bed, these organisms move into interstitial spaces in the substrate to avoid fast flow. Among the bryophytes, where they occur in high densities, they live among the stems and leaf axils where they are less exposed.

Bryophytes in streams provide a safe harbor within a tumultuous habitat and a substrate for food organisms (Suren 1992). Although the stream has an ameliorated temperature compared to terrestrial systems, its constantly changing water levels and flow rates make it a challenging environment for small organisms, especially attached species. Bryophytes offer a place where flow rate reaches virtually zero at the base, providing a range of flow rates. Furthermore, current can affect where rotifers occur within the moss mat, with some species remaining in lower layers where the current is reduced to zero. Hence, it appears that flow rate has little effect on bryophyte fauna in different parts of mountain streams (Madaliński 1961). However, this ignores the fact that bryophytes themselves may be limited by current.

Linhart *et al.* (2002b) considered the stream bryophyte-rotifer association to result from the exposure of the stream bryophytes to water current (Wulfhorst 1994). Historically, the bryophytes have been considered to be refuge sites from flow (Madaliński 1961; Elliot 1967; Gurtz & Wallace 1984; Suren 1992) due to the reduction of flow within the moss mat (Gregg & Rose 1982; Madsen & Warncke 1983; Sand-Jensen & Mebus 1996). But for small invertebrates, this argument is questionable because the flow rates at the surface layer of gravel or bedrock sediments are similar to those within the moss mats (Williams & Hynes 1974; Gregg & Rose 1982; Angradi & Hood 1998). On the other hand, the **Monogononta** do seem to be affected by the flow within the mats of ***Fontinalis antipyretica*** (Figure 34). Could it be ease of food capture rather than protection from flow that determines where they are able to live? Or refuge from predators?

Some rotifers are able to withstand the flow of a stream, whereas others in streams hide among the bryophytes or other protected areas. Linhart *et al.* (2002b) collected data to compare the **Bdelloidea** and **Monogononta** relative to flow velocity amid the moss ***Fontinalis antipyretica*** (Figure 34) and on the surrounding mineral substrate. The **Monogononta** were unable to withstand the high flow velocities, whereas the **Bdelloidea** did not seem to have a preference. Therefore, the ratio of **Bdelloidea** to **Monogononta** had a strong positive relationship to the flow velocity within the moss with the ratio of **Bdelloidea** to **Monogononta** reaching as high as 13:1 in high flow areas in these streams. A similar relationship did not exist on the mineral substrate. Linhart and coworkers concluded that this does not support the concept of the mosses serving as a refugium from flow.

Bryophytes also serve as traps for drifting rotifers. Madaliński (1961) found that bryophytes in streams that flow out of lakes have a richer fauna than those in torrents arising from springs. Hence, numbers can vary widely between streams, perhaps due to available food and flow rate, as well as differences in sources for new or replacement fauna. Rotifers on the moss ***Fontinalis antipyretica*** (Figure 34) reached over 100,000 per mL in one stream in the Czech Republic and over 400,000 per mL in another (Vlčková *et al.* 2002).

Suren (1992) investigated the role of shade in determining the meiofaunal communities of bryophytes in New Zealand alpine streams. He found that the unshaded site had higher meiofaunal densities than did the shaded site and that bryophytes had higher faunal densities than did gravel habitats. Furthermore, the meiofaunal communities differed between bryophytes and gravel. He suggested that food value within the bryophyte habitat may account for the higher densities of rotifers and other meiofauna there.

In a Wisconsin, USA, study, ***Ptygura linguata*** occurred only on the bladderwort (*Utricularia* sp.; Figure 38) and the brook moss ***Fontinalis*** sp. (Figure 34) (Edmondson 1940). ***Ptygura cristata*** (Figure 178), a species known previously only from Australia, likewise was found on ***Fontinalis*** in the inlet to a Wisconsin lake! Molecular studies may tell us that these long-distance variants are actually different species, or at least microspecies. Or did some limnologist wear the same boots in both places?

Figure 178. ***Ptygura cristata***, a species known from ***Fontinalis***. Drawing by Murray (1913) from Rotifer World Catalog, through Creative Commons.

Waterfalls

Savatenalinton and Segers (2008) examined the rotifers among the wet mosses of a waterfall in Thailand. Among these, they found the new species ***Lecane martensi*** (Figure 179). They located twelve species in their single day of collection, December 2004. ***Lepadella minuta*** and ***Lecane agilis*** (Figure 180-Figure 181) were new to Thailand. The other species were ***Brachionus angularis*** (Figure 182-Figure 183), ***B. forficula*** (Figure 184), ***Colurella adriatica*** (Figure 3), ***Keratella cochlearis*** (Figure 185), ***K. tropica*** (Figure 186), ***Lecane arcuata***, ***L. lunaris*** (Figure 123), ***L. paxiana***, and ***Trichocerca pusilla*** (Figure 187) among the waterfall mosses.

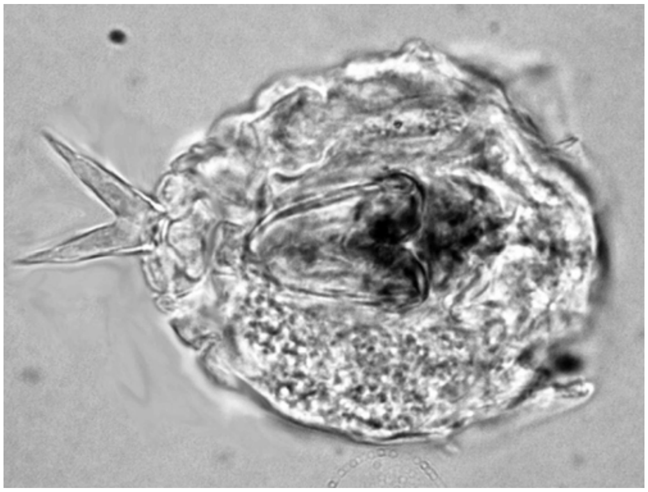

Figure 179. ***Lecane martensi***, a species that was discovered among mosses in a waterfall. Photo by Savatenalinton & Segers 2008, through Creative Commons.

Figure 180. ***Lecane agilis*** from submerged ***Sphagnum***, a rotifer that also occurs among mosses in a waterfall. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 181. ***Lecane agilis*** contracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 182. ***Brachionus angularis***, a planktonic species that can occur in waterfalls, perhaps trapped by the mosses of the waterfall. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 183. **Brachionus angularis** lateral view showing its armored lorica. This is a planktonic species that can occur in waterfalls. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 184. **Brachionus forficula**, a planktonic species known from mosses in waterfalls where they may have been trapped by the mosses. Photo by Jersabek *et al.* 2003, with permission.

Figure 185. **Keratella cochlearis** with two eggs; this planktonic species can occur among mosses in waterfalls. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 186. **Keratella tropica**, a planktonic species that can occur among mosses in waterfalls. Photo by Jersabek *et al.* 2003, with permission.

Figure 187. **Trichocerca pusilla**, a planktonic species that can occur among waterfall mosses. Photo by Jersabek *et al.* 2003, with permission.

Krakatau

Krakatau is a volcanic island west of Java and south of Sumatra. Heinis (1928) examined the moss fauna of the island. Rotifers were identified on the moss ***Philonotis*** sp. (Figure 30). Heinis found ***Rotaria montana***, ***Habrotrocha angusticollis*** (Figure 188), ***Macrotrachela ehrenbergi*** (Figure 189), ***Macrotrachela papillosa*** (Figure 190), and ***Adineta gracilis*** (Figure 191).

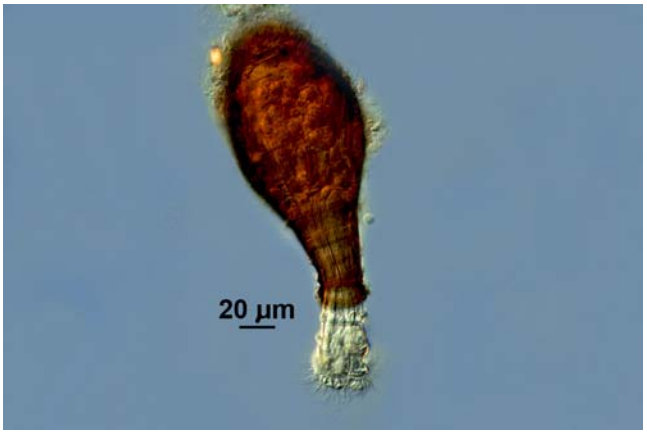

Figure 188. **Habrotrocha angusticollis**, a moss dweller. Photo by Proyecto Agua, through Creative Commons.

Figure 189. ***Macrotrachela ehrenbergii***, a moss resident on Krakatau. Photo by Jersabek *et al* 2003, with permission.

Figure 190. ***Macrotrachela papillosa***, a moss resident on Krakatau. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 191. ***Adineta gracilis***, a moss resident on Krakatau. Photo by Jersabek *et al*. 2003, with permission.

Seasons

In Oregon, USA, densities of rotifers did not vary by season in the moss ***Eurhynchium oreganum*** (Figure 36), a tree trunk and log dweller, whereas those of nematodes, tardigrades, mites, and some annelids did (Merrifield & Ingham 1998). They suggested that the low numbers of rotifers in moss samples may be due to the use of the Baermann funnel for sampling. This technique is not suitable for immobile organisms like rotifers, as indicated by their comparison with subsequent squeezings and agitation of the moss.

Periphytic rotifers living on non-bryophytic macrophytes must find a way to survive the winter season in parts of the world where these macrophytes disappear as winter approaches. On the other hand, life is possible on bryophytes because they are present year-round. There are insufficient detailed studies to make any generalizations about differences in life cycles of bryophyte dwellers vs periphyton on other macrophytes and algae.

Bielańska-Grajner *et al.* (2011) assessed the numbers (density) of rotifers in spring, summer, and autumn in peatland types in eastern Poland. They found considerable differences among sites. For example, in one raised bog (DB1) the greatest density of rotifer individuals was in summer, whereas in another (DB2), the greatest density was in autumn (Figure 192).

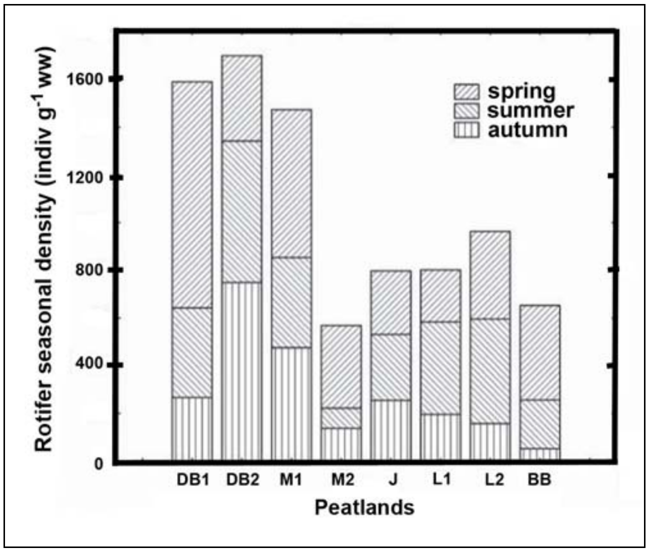

Figure 192. Seasonal changes in moss-dwelling rotifers from eight peatlands in eastern Poland. DB1, DB2, & M1 = raised bogs; M1 & J = poor fens; L1 & L2 = intermediate fen; BB = rich fen. Modified from Bielańska-Grajner *et al.* 2011.

Bateman and Davis (1980) examined the seasonal differences among rotifers in a hummock-hollow complex in a poor fen in Newfoundland, Canada. The **Monogononta** all but disappeared in winter. **Bdelloidea** decreased but still maintained relatively good numbers.

Ricci *et al.* (1989) found no seasonal replacement of clones of ***Macrotrachela quadricornifera*** (Figure 62-Figure 64) from a terrestrial moss in northern Italy. Likewise, the isozyme variant composition was unaffected by temperature changes. Instead, relative humidity seemed to regulate the number of isozyme morphs.

Danger amidst the Bryophytes

The fungi ***Lecophagus longispora*** (Figure 194-Figure 195) and ***L. musicola*** (Figure 196-Figure 199) use adhesive pegs that attract rotifers (George Barron, pers. comm. 25 January 2010). But the rotifers are lured to the fungus, only to be attacked themselves. Once the rotifers are attached, the pegs adhere, using lectin/carbohydrate bonding, and the fungus penetrates the rotifer, ultimately parasitizing it.

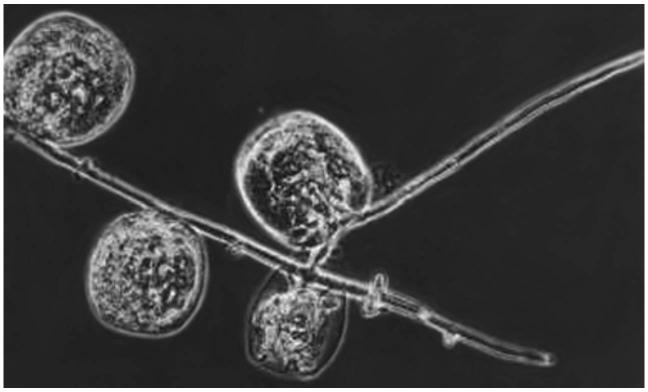

Figure 193. ***Lecophagus longispora*** infecting four rotifers. Photo by George Barron, with permission.

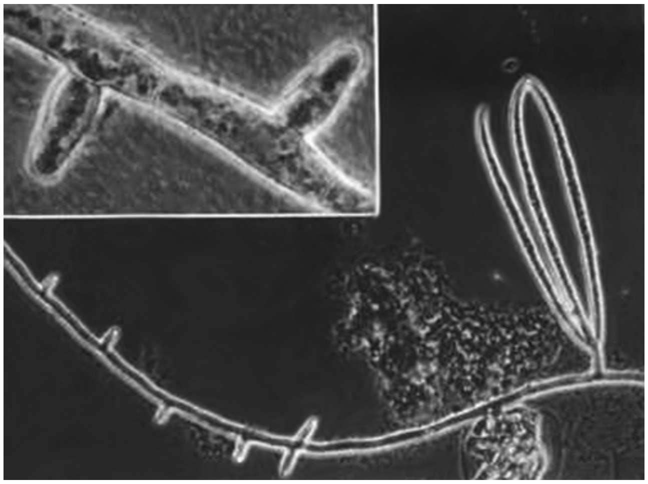

Figure 194. ***Lecophagus longispora***, fungus that traps **tardigrades** and **rotifers** and may be a threat in mosses. Lower image is hypha of fungus with cluster of conidia and adhesive pegs. Inset shows adhesive pegs. Photos by George Barron, with permission.

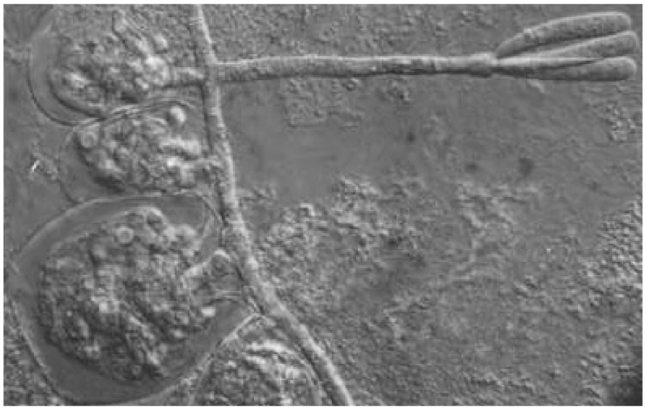

Figure 195. ***Lecophagus longispora*** infecting rotifers and showing an elongate branch with terminal conidiogenous cell bearing a cluster of developing conidia. (X450). Photo by George Barron, with permission.

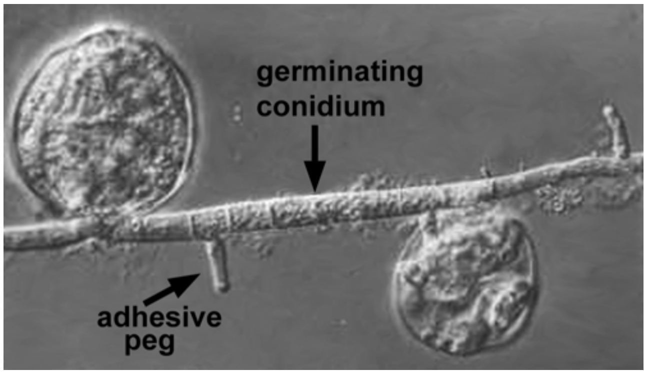

Figure 196. ***Lecophagus muscicola*** that has captured two rotifers and two adhesive pegs. Photo by George Barron, with permission.

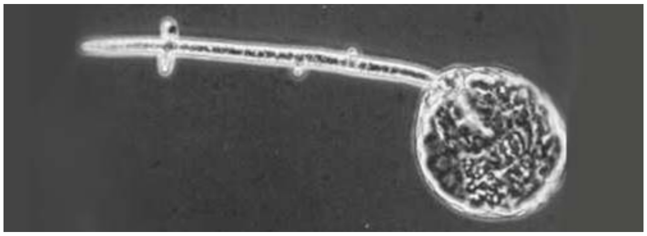

Figure 197. ***Lecophagus longispora*** infecting a rotifer; hypha shows adhering pegs. Such infections are also known for tardigrades. Photo by George Barron, with permission.

Figure 198. **Rotifer** with hyphae of ***Lecophagus muscicola*** inside. Photo by George Barron, with permission.

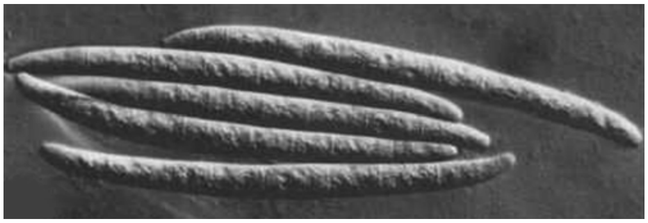

Figure 199. Conidia (X600) of ***Lecophagus muscicola***. Photo by George Barron, with permission.

Another fungus dangerous to some bryophyte-dwelling species is ***Zoophagus insidians*** (Figure 200). Aquatic rotifers attempt to feed on its branch tips, but the adhesive tips bond (possibly lectin/carbohydrate bonding) to the rotifer mouth and inside the oral cavity (Barron 2012). The tip grows there and assimilative hyphae penetrate the body cavity of the rotifer, releasing digestive enzymes that ultimately digest the rotifer from the inside. This attack on the rotifer mouth permits this fungal species to select loricate rotifers (Prowse 1954).

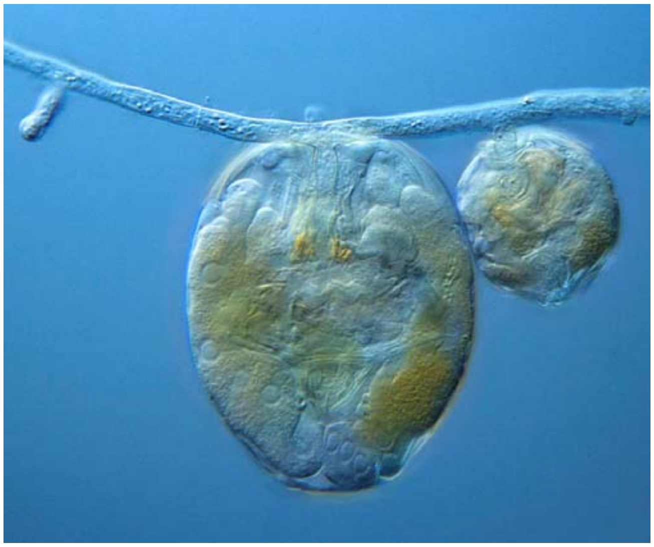

Figure 200. ***Philodina roseola***, sometimes a bryophyte dweller, caught by the fungus ***Zoophagus insidians***. Photo by Wim van Egmond, with permission.

Whisler and Travland (1974) refer to the fungus as "wily" because of its sneak attack on the rotifers. When the **adhesive peg** of the fungus contacts the rotifer (Figure 201), the fungus is stimulated to release a glue from its trap. The traps are branches that are packed with vesicles containing an electron-dense glue, and upon contact the two layers of the fungal wall separate and the vesicles fuse with the cell membrane. The cilia of the rotifer are stuck to the fungal trap by this glue. Growth of the fungal **haustorium** [slender projection from fungal thread (hypha) of parasitic fungus that enables it to penetrate host] proceeds rapidly, digesting the rotifer within a few hours.

Zoophagus (Figure 200-Figure 201) apparently does not produce zoospores, with those few zoospores reported apparently belonging to contaminants (Dick 1990; Powell *et al.* 1990). Instead it reproduces by **fusiform conidiospores** (asexual fungal spores; see Figure 199), and it has been placed in the **Zygomycetes** (Powell *et al.* 1990) due to its reproductive differences. These conidiospores are sometimes referred to as gemmae.

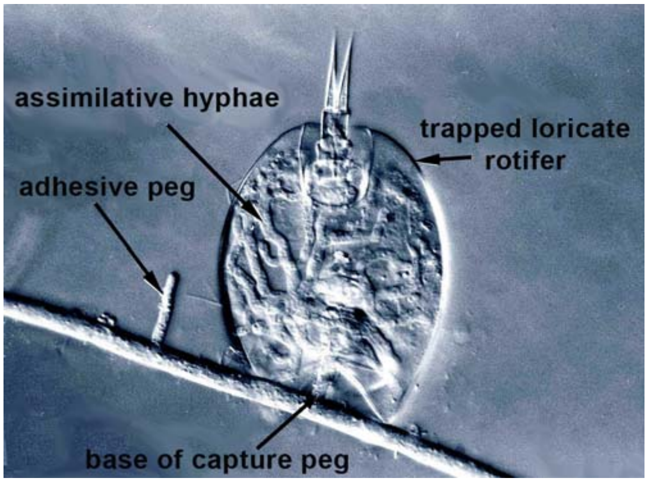

Figure 201. The rotifer ***Lepadella*** caught by the fungus ***Zoophagus insidians***. Photo by Wim van Egmond, with permission.

Ozone Hole and Pollution Dangers?

A number of researchers have chosen the microfauna of terrestrial bryophytes as indicators of air pollution effects (Steiner 1994a, b). Meyer *et al.* (2010) compared the microfauna on transplanted mosses (***Pseudoscleropodium purum*** – Figure 202) in rural, urban, and industrial areas of France. The mosses were placed in jars in open shelters that prevented contamination carried by rain. They found that the biomasses for microalgae, bacteria, rotifers, and testate amoebae were greatest in the rural area. However, at the end of the study there were no significant differences for nematodes or rotifers. Although the mosses absorbed Al, Cr, Cu, Fe, Pb, Sr, and Zn, only Cu and Pb had a significant effect on the biomass of rotifers.

Figure 202. ***Pseudoscleropodium purum***, the moss used in transplant experiments to assess effects of pollution on microfauna, including rotifers. Photo by Hermann Schachner, through Creative Commons.

Responses of functional groups to air pollution is often ignored in favor of simpler studies on single species. Nguyen-Viet *et al.* (2007) examined the effects of simulated lead pollution by experimenting in controlled laboratory conditions on the microbial communities associated with ***Sphagnum fallax*** (Figure 203). But in this case, the biomass of rotifers was not significantly affected by lead addition. However, the biomass decreased in all treatments (including controls) during the experiment (20 weeks). On the other hand, biomasses of bacteria, microalgae, testate amoebae, and ciliates were dramatically and significantly decreased in both Pb addition treatments (625 & 2,500 µg L^{-1} of Pb^{2+}) compared to the controls. This decrease in microbial food source unbalanced the microcosms, causing significant differences in microfaunal community structure. Trophic links were changed because the testate amoebae and ciliates had strongly reduced biomass, whereas the bacteria had a relatively stable contribution to the microbial biomass. These changes affected the rotifer biomass through the food web.

Figure 203. ***Sphagnum fallax***, a species that absorbs lead but houses rotifers that are not harmed directly by lead additions. Photo by Christian Fischer, through Creative Commons.

Although there seemed to be no differences in growth of ***Sphagnum magellanicum*** (Figure 111-Figure 112) under the ambient UV-B radiation in the ozone hole and reduced UV-B under filters in Tierra del Fuego, southern Argentina, the rotifer fauna of this moss seems to prefer the greater UV-B under ambient conditions (Searles *et al.* 1999). The rotifers were actually more numerous under the ambient conditions of UV-B in the ozone hole than under the reduced UV-B created by the filters.

Summary

Rotifers (**Rotifera**) can enter a state of **cryptobiosis** (dormant state) and survive desiccation right along with bryophytes, also getting dispersed with the fragments of mosses. The **bdelloid rotifers** are the most common among bryophytes and are **parthenogenetic**, hence are all female. In the **Monogononta**, unfertilized eggs develop into a male. In unfavorable conditions, monogononts form thick-walled resting "eggs" (really zygotes and embryos). They depend on water not only for hydration, but for locomotion and directing food to the mouth using cilia in the corona.

The dehydrated state (**anhydrobiosis**) helps to protect them from UV light, high temperatures, cold temperatures, and fungal infection. When confronted with drying conditions, bdelloid rotifers form a compact structure known as a **tun**. Slow drying produces the greatest survival and production of the disaccharide sugar **trehalose** maintains membrane integrity. Activity generally resumes within one hour of rehydration, but they need about a day of active state before they go into another dehydrated state. The record survival for an egg appears to be nine years, whereas an adult of ***Macrotrachela quadricornifera*** mya have survived dry on a moss on a herbarium sheet for 59 years. Mucus appears to deter predation, but it could also protect against or slow dehydration.

Bryophyte-dwelling rotifers tend to be smaller than those in open water. Terrestrial bryophytes provide slow but unpredictable and frequent drying. Adaptations to bryophyte living include small size, ability to attach or crawl in small spaces, parthenogenesis, dormancy by egg and tun, detritus as a food source, and structures such as tubes, mucus, and loricas for protection. Bryophytes contribute cover, water film, slow drying, and periphytic and detrital food sources.

Tardigrades may be significant predators, but rotifers such as ***Ptygura velata*** construct a tube from their own feces for protection. Some rotifers in epiphytic sites live in lobules of leafy liverwort leaves (***Frullania***, ***Microlejeunea***, ***Colura***, ***Pleurozia purpurea***, ***Acrolejeunea***) where desiccation is less frequent and there is a modicum of protection.

Rotifers are common on bryophytes. In the Antarctic the terrestrial species are largely restricted to mosses. Peatland habitats have the highest diversity among the bryophyte habitats, with the **Bdelloidea** predominating. ***Habrotrocha roeperi*** and ***Habrotrocha reclusa*** seem to be restricted to the **retort** cells of some ***Sphagnum*** species. Bog and fen rotifers are mostly widespread species with wide habitat tolerances. A few are restricted to bryophytes in bogs. In ***Sphagnum*** peatlands, acidity seems to discourage many species, with more species and greater abundance in fens. Rotifers in pitcher plants contribute to decomposition and nutrient cycling in the leaves, especially for nitrogen and phosphorus. In aquatic habitats, those occupying ***Fontinalis antipyretica*** can reach densities 151 times that of adjacent mineral substrate. Hundreds of thousands of rotifers can exist in 100 mL of this moss. Unique species can occur among bryophytes in waterfalls. Fine particulate matter trapped by mosses can serve as food. In the Antarctic, many **rotifers** prefer the middle stem zone where epiphytic algae are most abundant.

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CHAPTER 4-6

INVERTEBRATES: ROTIFER TAXA – BDELLOIDEA

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Figure 1. **Rotifer** on a ***Sphagnum*** leaf. Photo by Marek Miś at <http://www.mismicrophoto.com/>, with permission.

Taxa on Bryophytes

With about 2200 species, rotifers are a group with a wide range of aquatic, marine, and **limnoterrestrial** (requiring watery matrix in terrestrial habitats, but also subject to desiccation) species, permitting us to analyze habitat relations. This analysis is limited with respect to bryophytes because few studies describe those in the bryophyte habitat, and those that do typically simply indicate "moss." This is demonstrated by the delineation of rotifer habitats in the comprehensive study on the relationship of rotifers to habitat, using only **macrophytes** (housing periphytic rotifers), open water (with planktonic forms), **minerogenous** sediments (with **psammon** and **hyporheos**), **organogenous** sediments, and other organisms (*i.e.* parasites and epizoans) (Pejler 1995). Bryophytes are not given separate attention. Pejler (1995) pointed out that rotifers are mostly cosmopolitan, hence suggesting that ecological barriers are more important in determining their distribution. Nevertheless, Pejler considers rotifers to lack strong restrictions of habitat. Extreme environments do support few species, but can support large numbers of individuals, typically primary consumers. On the other hand, when rotifer species are numerous the differences in their morphology are so great that patterns of adaptations are difficult to define.

Pejler (1995) considered that adaptations to chemical and physical environments may develop rapidly in geologic time, whereas those changes that are more fundamental occur over a longer time period. Differences in structure of **trophi** (tiny, calcified, jaw-like structures in the pharynx) seem to facilitate differences in food type and these differences are most apparent among **Bdelloidea**, but even in extreme environments, differences don't seem to correlate with habitat and closest relatives seem to occur in "normal" habitats.

Although many taxa can be found on bryophytes, few have been studied relative to the role of the bryophytes, and finding the existing studies among published literature can be a bit hit or miss. I am unable to summarize adaptations except to suggest that being small (which applies to the entire phylum) and being able to attach may be advantages. Movement among bryophytes is mostly inchworm style rather than being accomplished by the cilia. The trophi need to be adapted to the available food, with detritus being abundant among the bryophytes. The species included here most likely provide a very incomplete list, and the ecological information included with the images is likewise very incomplete. Furthermore, the distribution of species is poorly known, although many are considered cosmopolitan. Due to these limitations, these chapters are organized first by classification rather than ecology.

CLASS BDELLOIDEA

The name **Bdelloidea** (the "B" is silent) refers to the method of movement and means "leech-like." The **Bdelloidea** have a **corona** that is split into two, creating two "wheels" to direct food to the mouth (Figure 1). It is the smaller in number of species of the two classes and has only four families (Melone & Ricci 1995), all of which are represented on bryophytes. In fact, Donner (1956, 1975) reported that 95% of the rotifers living on terrestrial mosses, soil, and lichens are in the **Bdelloidea**. The most species on soil and moss are in the genus ***Habrotrocha***, whereas 30% of the overall species in **Bdelloidea** are in ***Macrotrachela***.

This group is comprised of ~460 species, only one of which Segers (2008) considered to be marine, but Fontaneto (2006) reported several strictly marine species. They are distinguished from the **Monogononta** by the presence of two ovaries (**Monogononta** have only one). This class of rotifers is comprised entirely of females and is exclusively **parthenogenetic** (having offspring from unfertilized eggs), negating the need for males to complete the life cycle.

The bdelloid rotifers are characterized by an elongated body with a telescopically retractable foot, single dorsal antenna, and apical rostrum (Melone & Ricci 1995). The ciliatory apparatus is used for both locomotion and collecting food, making it adaptive based on the animal's life style. The moss dwellers typically have a narrower wheel apparatus, a more rigid cuticle that has cuticular spines or knobs, and smaller toes (Donner 1953, 1956).

The **bdelloids** are known from freshwater and soil, and are common on **bryophytes**. They have a retractable head with a well-developed **corona** that is divided into two parts. Movement includes both swimming and crawling, but they seldom venture into the plankton (Fontaneto & Ricci 2004). Crawling is similar to the movement of inchworms, or some leeches, using the toes and head while arching the mid body, then elongating again forward.

Burger (1948) suggested three regulatory mechanisms to determine the suitability of mosses for the **Bdelloidea**:

1. The age of the moss at the site affects the time during which colonization has been possible, and that in turn affects the number of species present.
2. Water presence and resultant osmotic potential affect activity of the rotifers.
3. Availability of suitable food is important. This includes both size of potential food and food quality (Ricci 1984).

Kutikova (2003) considered their morphological structures, obligate parthenogenesis, and **anhydrobiosis** to be important adaptations to living among mosses and other terrestrial substrata that have sharp environmental fluctuations. Most of the **bdelloids** survive unfavorable periods, particularly drought, by entering a type of dormancy known as **anhydrobiosis,** *i.e.* dry dormancy (Gilbert 1974; Ricci 1987, 1998, 2001). All the bdelloids that live among bryophytes are able to secrete mucus as they dry (Figure 2) and create a case-like structure with adhering particles. It is their ability to withstand drying, along with their parthenogenetic reproduction (Ricci 1992), that fosters their cosmopolitan distribution (Fontaneto *et al.* 2006, 2007, 2008). And this ability of anhydrobiosis may also be the reason that Horkan (1981), in his report on Irish rotifers, found only this group on mosses other than those in bogs. Furthermore, no **Bdelloidea** were present in the Irish bogs, on bog moss, or in bog pools, suggesting they may require those dry periods. On the other hand, Diego Fontaneto (pers. comm. 2 November 2016) finds **Bdelloidea** to be common among mosses in bogs. It could be that hydrology plays an important role, but Fontaneto also finds **Bdelloidea** in habitats that never dry.

Figure 2. ***Habrotrocha pusilla textris*** in mucilaginous nest with 2 eggs, a condition that permits them to survive drought. Photo by Michael Plewka <www.plingfactory.de>, with permission.

In addition to the ability of anhydrobiosis and the addition of mucus, those **Bdelloidea** living in habitats that dry frequently may have thicker integuments that include distinct outgrowths, granules, and spines (***Macrotrachela multispinosa***, ***Dissotrocha aculeata***) (Kutikova 2003). However, the value of these thick integuments is unknown (Diego Fontaneto, pers. comm. 2 November 2016).

Richters (1907) described six bdelloid rotifers from mosses in the Kerguelen Islands in the Antarctic. On the other hand, **Bdelloidea** were conspicuously absent from the littoral mosses on Svalbard (De Smet 1988).

Only one carnivorous **bdelloid** is known, and it is not known from **bryophytes**. Rather, the **bdelloids** filter or scrape or browse their diet of bacteria, one-celled algae, yeast, or particulate organic matter (Ricci 1984).

Adinetidae

Ricci and Covino (2005) demonstrated various aspects of anhydrobiosis in the **Adinetidae**, using ***Adineta ricciae***. Rotifers that recovered from anhydrobiosis had similar longevity and significantly higher **fecundity** (reproductive rate of an organism or population) than did the hydrated controls. Lines of offspring produced after the anhydrobiosis dormancy likewise had significantly higher fecundity and longevity than controls from mothers of the same age. The name ***A. ricciae*** led me on a search to find its connection to the thallose liverwort genus ***Riccia***, one that has several members that are dormant in muds and revive when the area is flooded. But of course, the genus is not named for the liverwort, but for the rotifer biologist, Claudia Ricci.

Adineta

The genus ***Adineta*** has many **cryptic species** (species that look alike but can't interbreed), as demonstrated by DNA and a diversity of narrow ecological niches (Fontaneto *et al*. 2011). This diversity has led to superfluous names in many of the rotifer genera. This text follows the nomenclature of Segers (2007).

Several species of ***Adineta*** are known from bryophytes. ***Adineta barbata*** (Figure 3), ***A. gracilis*** (Figure 4), and ***A. vaga*** (Figure 5) occur in bogs or among ***Sphagnum*** (Figure 6) (Myers 1942; Hingley 1993; Bielańska-Grajner *et al*. 2011). ***Adineta barbata***, in particular, is associated with ***Sphagnum subsecundum*** (Figure 7) (Horkan 1981; Hingley 1993; Jersabek *et al.* 2003). ***Adineta vaga*** is more widespread, occurring on sandstone, roof, and **epiphytic** (in this case growing on trees) mosses as well. ***Adineta vaga rhomboidea*** occurs on the terrestrial weedy moss ***Ceratodon purpureus*** (Figure 8) (Yakovenko 2000).

Figure 3. ***Adineta barbata***, a species known to live on ***Sphagnum subsecundum*** (Figure 7) and other mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 4. ***Adineta gracilis***, a species known from ***Sphagnum*** and other mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 5. ***Adineta vaga***, a **moss** dweller that is 0.2-0.3 mm when extended. It is known from mosses on tree (*Salix*), roof, and sandstone substrates. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 6. ***Sphagnum*** sp., home for a variety of rotifers. Photo by Bernd Haynold, through Creative Commons.

Figure 7. ***Sphagnum subsecundum***. Photo by Michael Lüth, with permission.

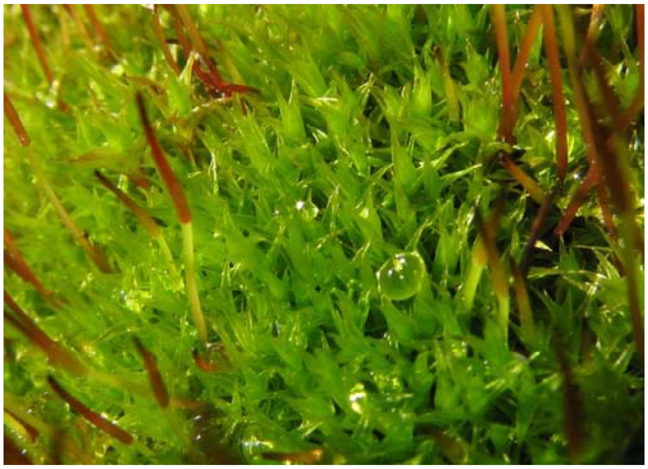

Figure 8. ***Ceratodon purpureus***, home for ***Adineta vaga*** *var*. ***rhomboidea***. Photo by Jiří Kameníček, with permission.

Other species occur on bryophytes in various habitats. In most cases, the habitat is simply listed as moss, or some other non-bryophyte habitat and moss. These include ***Adineta cuneata*** (Figure 9) on moss (Plewka 2016), ***A. steineri*** (Figure 10) on epiphytic mosses (Hirschfelder *et al*. 1993; Plewka 2016), and ***A. tuberculosa*** (Figure 11) on moss (Horkan 1981; Plewka 2016).

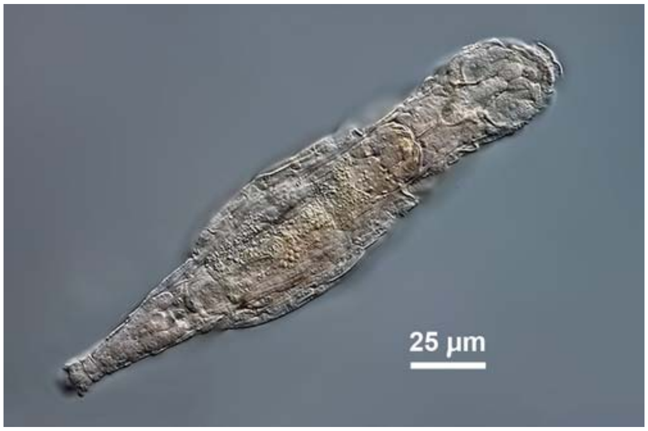

Figure 9. ***Adineta cuneata*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

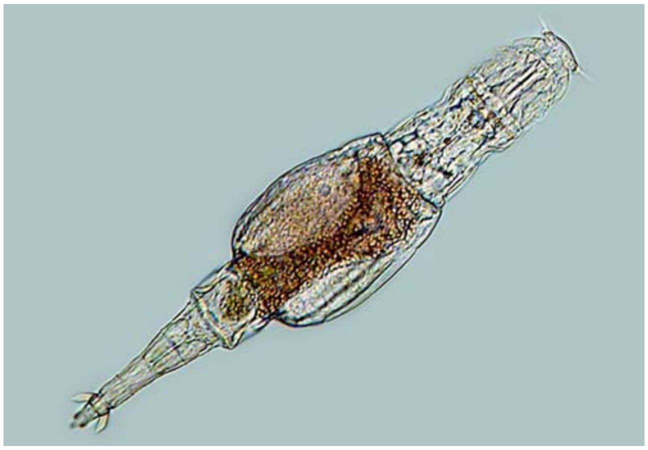

Figure 10. ***Adineta steineri***, a species that lives on epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 11. ***Adineta tuberculosa***, a moss inhabitant. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bradyscela

In addition to the ***Adineta*** species, ***Bradyscela clauda*** (Figure 12) occurs on the terrestrial moss ***Brachythecium rutabulum*** (Figure 13) (Madaliński 1961; Plewka 2016).

Figure 12. ***Bradyscela clauda*** with retracted cilia, from ***Brachythecium rutabulum.*** Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 13. ***Brachythecium rutabulum***, home for ***Bradyscela clauda*** in Europe. Photo by Michael Lüth, with permission.

Habrotrochidae

The **Habrotrochidae** is a family with three genera, all of which occur among mosses.

Habrotrocha

Habrotrocha species are common inhabitants among ***Sphagnum*** (Figure 6) (Bateman 1987; Peterson *et al*. 1997; Błedzki & Ellison 1998) as well as other mosses. ***Habrotrocha*** is able to survive decreasing moisture with the protection of a mucous matrix (Kutikova 2003). This is particularly helpful when mosses are drying. The members of ***Habrotrocha*** accumulate various small adhering particles, thus further providing them a shelter to protect them while they are dry.

Habrotrocha ampulla (Figure 14), ***H. angusticollis*** (Figure 15-Figure 16), ***H. collaris*** (Figure 37-Figure 38), ***H. constricta*** (Figure 28-Figure 29), and ***H. lata*** (Figure 17-Figure 18) live among or on ***Sphagnum*** in ***Sphagnum*** ponds (Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016).

Figure 14. ***Habrotrocha ampulla*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 15. ***Habrotrocha angusticollis***, a bryophyte dweller. Photo by Yuuji Tsukii, with permission.

Figure 16. ***Habrotrocha angusticollis*** from ***Sphagnum*** ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 17. ***Habrotrocha lata***, a species collected from **bryophytes** in more than one location. Photo through Proyecto Agua, with permission.

Figure 18. ***Habrotrocha lata*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Some species of ***Habrotrocha*** use the protection of ***Sphagnum*** **retort** cells (Figure 19-Figure 21) for their homes (Plewka 2016). These are special cells that have a pore in a flask-like neck at the end of the stem epidermal cell. The rotifers that live there extend outward from the pore to feed. This is particularly true for ***Habrotrocha reclusa*** (Figure 22), known from ***Sphagnum subsecundum*** (Figure 7) (Myers 1942) and ***H. roeperi*** (Figure 23; Bielańska-Grajner *et al.* 2011; Plewka 2016).

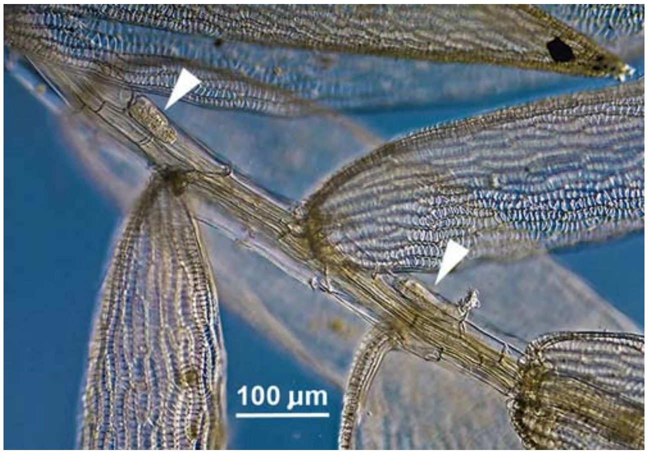

Figure 19. ***Sphagnum*** showing retort cells with ***Habrotrocha roeperi*** (arrows), a retort cell dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

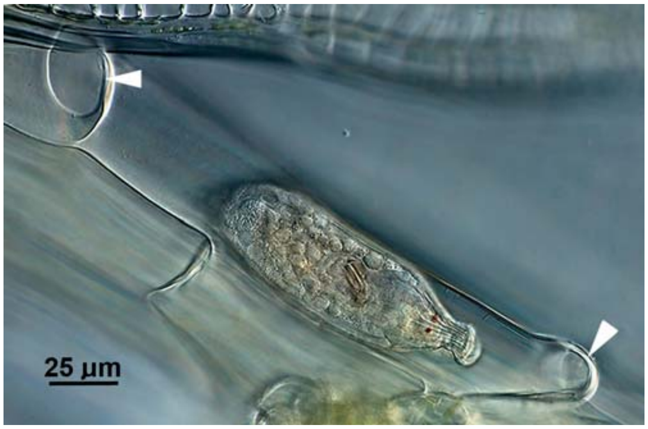

Figure 20. ***Habrotrocha roeperi*** in a retort cell. Arrows indicate the pores. Photo by Michael Plewka <www.plingfactory.de>, with permission.

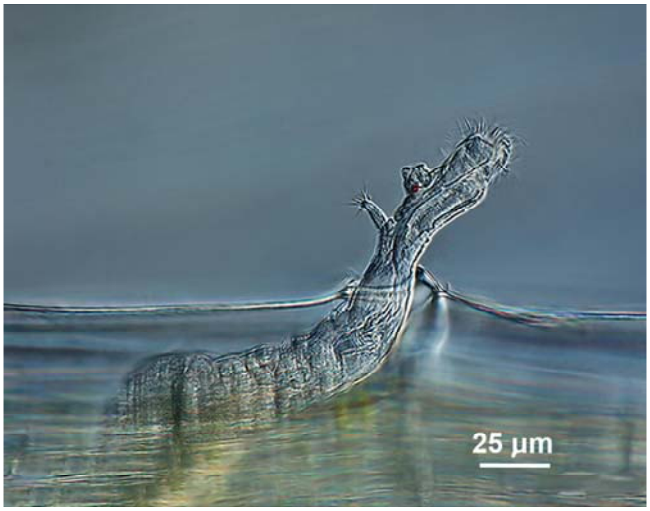

Figure 21. ***Habrotrocha roeperi*** extending out of a retort cell, a position in which it can attempt to trap food. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 22. ***Habrotrocha*** *cf.* ***reclusa***, a retort cell dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 23. ***Habrotrocha roeperi***, a retort cell dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bog habitats for ***Habrotrocha*** (Figure 24), in particular ***H. rosa*** (Figure 25), include pitcher plants (***Sarracenia purpurea***, Figure 26), where the rotifers are a major food source for co-habiting members of the **Culicidae** (mosquitoes) (Bateman 1987), causing the mosquito population numbers to rise (Błedzki & Ellison 1998). The pitcher plants are common plants among the ***Sphagnum*** (Figure 6) in bogs and provide a pool of water in their leaves. The rotifers are an important source of N and P in the bog/fen-dwelling pitcher plants.

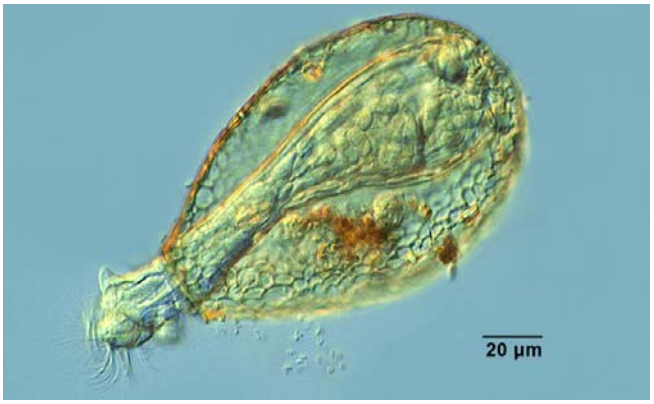

Figure 24. ***Habrotrocha***, a genus with many species that occur on **bryophytes**. Photo by Proyecto Agua Water Project through Creative Commons, with permission.

Figure 25. ***Habrotrocha rosa***, a species that lives in pitcher plants. Photo by Rkitko at Wikipedia Commons.

Figure 26. ***Sarracenia purpurea***, a bog plant that provides a watery home for ***Habrotrocha rosa***. Photo by Pouzin Oliver, through Creative Commons.

There are many species in ***Habrotrocha*** that live among bryophytes. These include ***H. bidens*** (Figure 27) on mosses on the ground (Hingley 1993; Plewka 2016), ***H. constricta*** (Figure 28-Figure 29) on ***Sphagnum***, water mosses, and **epiphytic** bryophytes (those growing on trees) (Myers 1942; Horkan 1981; Hingley 1993; Plewka 2016), ***H*. *novemdens*** (Figure 30) on mosses (Plewka 2016), ***Habrotrocha pavida*** on the mosses ***Ceratodon purpureus*** (Figure 8) and ***Bryum argenteum*** (Figure 31) (Yakovenko 2000), ***H. pusilla*** (Figure 32) in mucilage on moss (Horkan 1981; Plewka 2016), and ***H. quinquedens*** (Figure 33) on both wet and dry mosses (Plewka 2016). Some species also occur in the lobules of the leafy liverwort ***Frullania*** (Figure 34-Figure 35; Michel Verolet).

Figure 27. ***Habrotrocha bidens*** from moss on ground. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 28. ***Habrotrocha constricta***, a species that lives on both water moss and epiphytic moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 29. ***Habrotrocha constricta***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 30. ***Habrotrocha novemdens*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 31. ***Bryum argenteum***, home of ***Habrotrocha pavida***. Photo by Manju Nair, through Creative Commons.

Figure 32. ***Habrotrocha pusilla***, a species that lives in mucilage on moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Hirschfelder *et al*. (1993) examined the rotifers among epiphytic bryophytes and added ***Habrotrocha flava***, ***H. fusca***, and ***H. insignis***.

Figure 33. ***Habrotrocha quinquedens***, a species that lives on both wet and dry mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

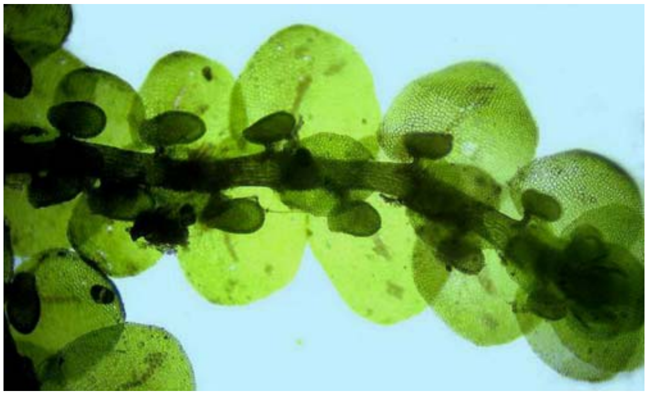

Figure 34. ***Habrotrocha*** on ***Frullania***, peeking out of the hood-shaped lobules. Photo by Michel Verolet, with permission.

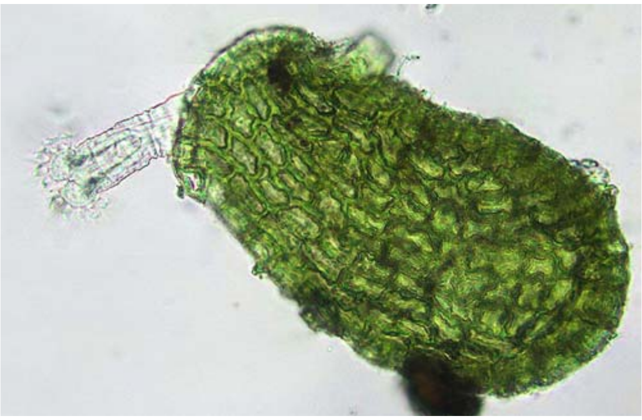

Figure 35. ***Habrotrocha*** in ***Frullania*** lobule. Photo by Michel Verolet, with permission.

A number of additional species are known from bryophytes, but with no additional details. Madaliński (1961) reported ***H. microcephala*** and ***H. tridens*** (see also Bielańska-Grajner *et al*. 2011) from the environs of Tatra streams. Horkan (1981) reported ***Habrotrocha aspera*** (Figure 36; see also Plewka 2016); see also Hingley 1993 for bog mosses), and ***H. pulchra***. Hingley (1993) added ***H. longula***, and ***H. minuta***; Peters *et al*. (1993) added ***H. eremita***. It appears that 1993 was a good year for bryophyte rotifer studies.

Figure 36. ***Habrotrocha aspera***, a moss inhabitant. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 37. ***Habrotrocha collaris***, a species known from bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

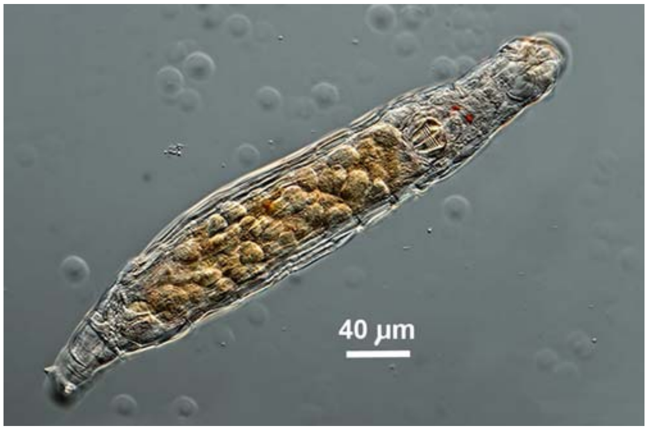

Figure 38. ***Habrotrocha collaris*** with two red eyespots, a bryophyte dweller, including ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Otostephanos

The genus ***Otostephanos*** has species on ***Sphagnum*** (Figure 6), but others occur on terrestrial mosses. ***Otostephanos auriculatus*** (Figure 39-Figure 40) occurs on ***Sphagnum*** and ***O. jolantae*** (Figure 41) occurs in ***Sphagnum*** ponds (Plewka 2016). ***Otostephanos monteti*** (Figure 42) lives on the emergent moss ***Drepanocladus aduncus*** (Figure 43) (Yakovenko 2000). ***Otostephanos cuspidilabris*** is known from "soggy" plants of the moss ***Atrichum*** sp. (Figure 44-Figure 45) (Yakovenko 2000). ***Otostephanos macrantennus*** is a bryophyte dweller (Ricci 1998). Two species live among dry mosses, ***O. regalis*** (Figure 46) on roof mosses (Hirschfelder *et al*. 1993; Plewka 2016) and ***O. torquatus*** (Figure 47) on mosses on concrete (Peters *et al*. 1993; Plewka 2016).

Figure 39. ***Otostephanos auriculatus*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 40. ***Otostephanos auriculatus***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

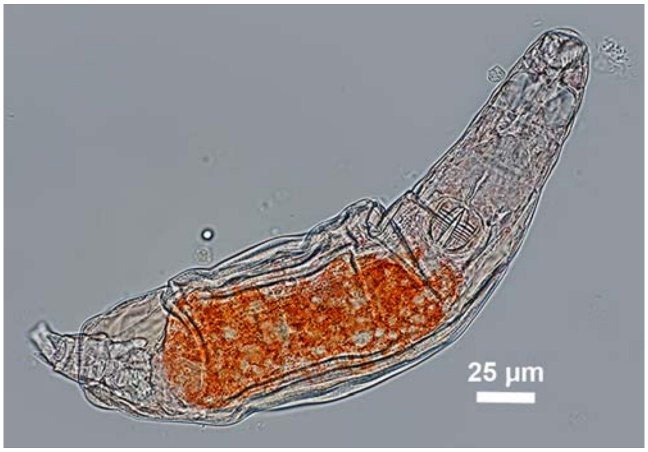

Figure 41. ***Otostephanos jolantae*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 42. ***Otostephanos monteti***, a species that lives on the emergent moss ***Drepanocladus aduncus***. Photo by Michael Plewka <www.plingfactory.de>., with permission.

Figure 43. ***Drepanocladus aduncus***, home for ***Otostephanos monteti***. Photo by Bob Klips, with permission.

Figure 44. ***Atrichum angustatum*** streamside habitat and home of ***Otostephanos cuspidilabris***. Photo by Bob Klips, with permission.

Figure 45. ***Atrichum angustatum***, home of ***Otostephanos cuspidilabris***. Photo by Bob Klips, with permission.

Figure 46. ***Otostephanos*** *cf.* ***regalis*** from dry moss on roof. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 47. ***Otostephanos torquatus*** from dry moss on concrete. Michael Plewka <www.plingfactory.de>, with permission.

Scepanotrocha

Some members of a second genus seem also to find the retort cells of ***Sphagnum*** to be a suitable home. ***Scepanotrocha rubra*** (Figure 48-Figure 49) lives in these cells, extending out of them to feed (Figure 48) (Myers 1942; Plewka 2012).

Figure 48. ***Scepanotrocha rubra*** in a retort cell of a ***Sphagnum*** stem. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 49. ***Scepanotrocha rubra***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

In addition to the retort dwellers, ***Scepanotrocha corniculata*** (Figure 50) lives on mosses, ***S. semitecta*** (Figure 51) is a ***Sphagnum*** (Figure 6) dweller, and ***S. simplex*** (Figure 52) lives on epiphytic mosses as well as ***Sphagnum***, once again demonstrating the seemingly wide range of microhabitats used by a single rotifer species (Plewka 2016).

Figure 50. ***Scepanotrocha*** *cf.* ***corniculata*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 51. ***Scepanotrocha semitecta*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 52. ***Scepanotrocha simplex***, a species that lives on both epiphytic mosses and ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Philodinavidae

Only two species from this family seem to be moss dwellers. ***Philodinavus paradoxus*** (Figure 53) lives in lakes, rivers, and streams (Madaliński 1961; Ricci & Melone 1998; Plewka 2016) and is preyed upon by flatworms, larger moss-dwelling rotifers, and nematodes (Schmid-Araya & Schmid 1995). It is tiny (200 µm long) and creeps with leech-like movements, being unable to swim (Ricci & Melone 1998). Instead, its strong foot anchors it to its substrate, a feature of importance in streams and rivers. Its corona is poorly developed and it obtains its food by browsing, facilitated by the ciliated buccal field and trophi protruding throughout the mouth. Its disjunct distribution in Europe and New Zealand may indicate a lack of collecting and lack of experts on this group.

Figure 53. ***Philodinavus paradoxus***, a species from stream mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Within its short lifetime of only 20 days, ***Philodinavus paradoxus*** can produce 6-7 eggs (Ricci & Melone 1998). These seem to have about the same resistance to desiccation damage as adults, with only 10% of each surviving 7 days of desiccation, a desiccation intolerance that is typical of aquatic rotifer taxa.

Henoceros falcatus is commonly found in the same mosses in running waters with ***Philodinavus paradoxus*** (Diego Fontaneto, pers. comm. 2 November 2016). Ricci and Melone (1998) reported this species from mosses. They noted that ***H. falcatus*** was first found in mosses submerged in streams in South Africa (Milne 1916). Later ***H. falcatus*** was found in similar habitats in Europe, South America, Asia, and Hawaii (Schmid-Araya 1995; Turner 1996). The two species co-occur in Austria (Schmid-Araya 1995) and in Valle Argentina, Italy. It seems to be common for these two species to co-occur, suggesting similar ecological requirements. In fact, rather than being rare (Schmid-Araya 1995; Ricci & Melone 1998), Fontaneto *et al*. (2007) consider them to be fairly common in their specialized habitat of stream mosses.

Figure 54. ***Henoceros falcatus***, a stream moss dweller. Photo by Michel Verolet, with permission.

Philodinidae

The philodinids use their cilia or foot and rostrum (Figure 55) to facilitate swimming (Hickernell 1917). At high temperatures these rotifers engage in active swimming, but in cold water they creep like a leech with the cilia retracted. During feeding, they attach themselves by the foot and use the cilia to direct food to the pharynx. When drying occurs, the animal forms a ball and dries up. The ball is formed by retracting both the head and the foot into the trunk of the rotifer and losing all the water, pulling the organs together and eliminating spaces. When they get water again, they resume their normal shape in ten minutes or less.

Ceratotrocha and *Didymodactylos*

This family has many bryophyte-dwelling species. ***Ceratotrocha cornigera*** is the only member of its genus documented from bryophytes, including bogs (Horkan 1981; Hingley 1993). ***Didymodactylos carnosus*** (Figure 55) likewise is known from mosses (Ricci & Melone 2000; Plewka 2016).

Figure 55. ***Didymodactylos carnosus***, common in moss. Note the two rings of cilia. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Dissotrocha

Dissotrocha has several known bryophyte-dwelling species. ***Dissotrocha aculeata*** (Figure 56), ***D. macrostyla*** (Figure 57), and ***D. spinosa*** occur on or among ***Sphagnum*** (Figure 6) (Horkan 1981; Hingley 1993; Bielańska-Grajner *et al.* 2011; Plewka 2016). ***Dissotrocha scutellata*** (Figure 58-Figure 59) is known from the moss ***Andreaea rupestris*** (Figure 60-Figure 61), a rock dweller that dries out frequently (Plewka 2016).

Figure 56. ***Dissotrocha aculeata***, a species known from ***Sphagnum*** and **other mosses**. Photo by Jersabek *et al.* 2003, with permission.

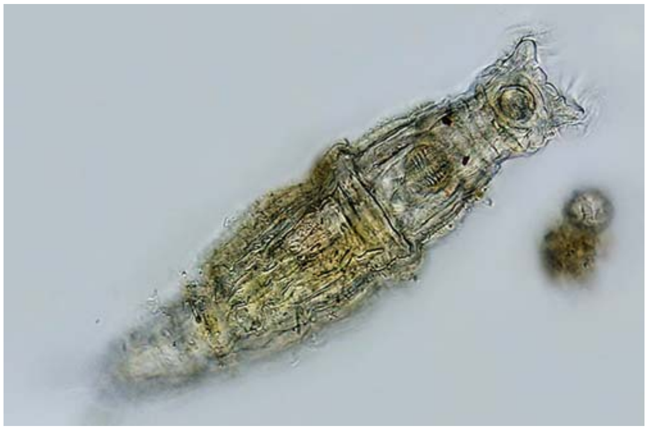

Figure 57. ***Dissotrocha macrostyla*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 58. ***Dissotrocha scutellata***, a dweller on ***Andreaea rupestris***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 59. ***Dissotrocha scutellata***, a species that lives on the exposed rock-dwelling moss ***Andreaea rupestris***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 60. ***Andreaea rupestris***, home for ***Dissotrocha scutellata***. Photo by Michael Lüth, with permission.

Figure 61. ***Andreaea rupestris***, home for ***Dissotrocha scutellata***. Photo by Michael Lüth, with permission.

Macrotrachela

A number of species of the large genus ***Macrotrachela*** occur on mosses. Some of these are from ***Sphagnum*** (Figure 6), including ***Macrotrachela concinna*** (Myers 1942; Hingley 1993), ***M. crucicornis*** (Myers 1942), ***M. decora*** (Figure 62) (Plewka 2016), and ***M. papillosa*** (Figure 63) (Horkan 1981; Hingley 1993).

Figure 62. ***Macrotrachela*** *cf.* ***decora*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 63. ***Macrotrachela papillosa***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Other species occur in contrasting habitats of both ***Sphagnum*** (Figure 6) and mosses growing on trees. These include ***M. multispinosa*** (Figure 64-Figure 65; Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003), ***M. nana*** in stream environs (Figure 67; Madaliński 1961; Bielańska-Grajner *et al*. 2011; Plewka 2016), ***M. plicata*** (Figure 66; Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016), and ***M. quadricornifera*** (Figure 68; Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al.* 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016).

Figure 64. ***Macrotrachela multispinosa brevispinosa***, a species that occurs on submerged mosses and mosses on limestone and trees. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 65. ***Macrotrachela multispinosa*** from among epiphytic mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 66. ***Macrotrachela plicata*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 67. ***Macrotrachela nana*** from ***Sphagnum***, tree moss, and other mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 68. ***Macrotrachela quadricornifera***, a species from ***Sphagnum*** and epiphytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Others are known only as epiphytes, including ***M. aculeata*** (Figure 69; Plewka 2016), ***M. magna*** (Figure 70; Plewka 2016), and ***M. tuberilabris*** (Figure 71; Plewka 2016).

Figure 69. ***Macrotrachela aculeata*** from mosses on trees. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 70. ***Macrotrachela magna*** from epiphytic moss, showing its extended position. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 71. ***Macrotrachela tuberilabris*** from moss on tree. Michael Plewka <www.plingfactory.de>, with permission.

Additional members of the genus occurred on various mossy substrates, including ***Macrotrachela ehrenbergii*** (Figure 72) on ***Sphagnum*** (Figure 6), mosses on walls, and epiphytes (Peters *et al*. 1993; Jersabek *et al.* 2003; Plewka 2016), ***M. habita*** (Figure 74) on ***Sphagnum***, moss on trees, rocks, and ground (Myers 1942; Horkan 1981; Hirschfelder *et al*. 1993; Jersabek *et al*. 2003; Plewka 2016), ***M. insolita*** (Figure 75) on mosses submerged in pond (Hirschfelder *et al*. 1993; Plewka 2016) and in peatlands (Bielańska-Grajner *et al*. 2011), ***M. musculosa*** (Figure 76) on ***Sphagnum***, ground mosses, and epiphytic mosses (Myers 1942; Hirschfelder *et al*. 1993; Plewka 2016), ***M. punctata*** (Figure 77-Figure 78) on dry mosses on rocks (Hirschfelder *et al.* 1993; Plewka 2016); ***M. zickendrahti*** (Figure 79) on ***Sphagnum*** and other mosses (Jersabek *et al.* 2003; Plewka 2016). For ***M. muricata***, I have found little information except it occurs on mosses (Horkan 1981).

Figure 72. ***Macrotrachela ehrenbergii***, a species that lives among mosses on walls and trees as well as on ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

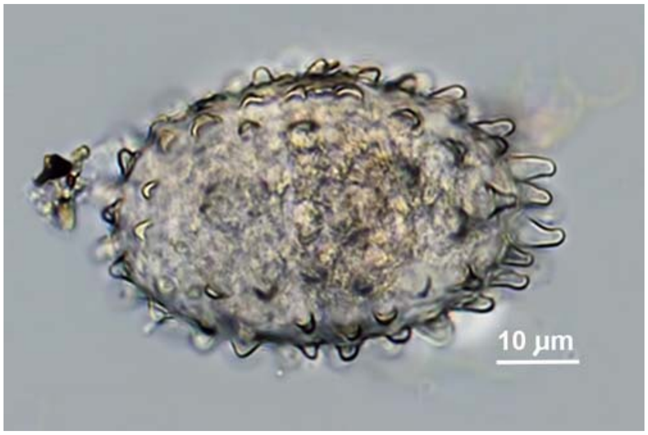

Figure 73. ***Macrotrachela ehrenbergii*** egg. The projections may help to preserve it during drought. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 74. ***Macrotrachela habita***, a species from moss on trees, rocks, and ground. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 75. ***Macrotrachela insolita***, s species that lives in ponds with submerged moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

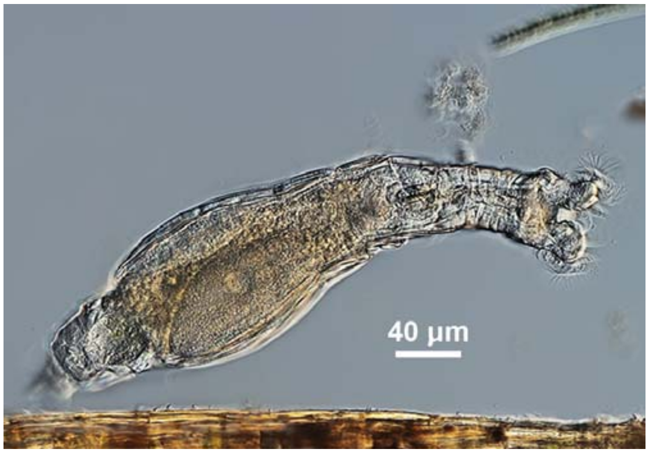

Figure 76. ***Macrotrachela musculosa***, a species from mosses on ground and trees. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 77. ***Macrotrachela punctata***, a species from dry moss on rocks. Here it is contracted with cilia out. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 78. ***Macrotrachela punctata***, a species of dry moss on rocks. Here it is extended with cilia contracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 79. ***Macrotrachela zickendrahti***, a species from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

The absence of records for moss dwellers may be common. For example, Ricci (1980) found ***Macrotrachela plicatula*** (Figure 80) among mosses in Uganda. This was the first time it had been found since its 1911 description as a new species.

Figure 80. ***Macrotrachela plicatula*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Mniobia

Mniobia likewise has its ***Sphagnum*** (Figure 6) dwellers, including those found by Hingley (1993): ***M. incrassata*** (Figure 81-Figure 82), ***M. magna*** (Figure 84), ***M. obtusicornis*** (Figure 85), ***M. symbiotica*** (see also Hudson 1889; Horkan 1981). Among these, ***M. incrassata*** is known from other mosses as well (Plewka 2016). ***Mniobia scarlatina*** (Figure 83; Jersabek *et al.* 2003) and ***M. tetraodon*** (Myers 1942; Horkan 1981) occur on epiphytic mosses. ***Mniobia symbiotica*** also occurs in the lobules of the leafy liverwort ***Frullania eboracensis*** (Figure 86-Figure 88), an epiphyte in eastern USA (Biechele 2014).

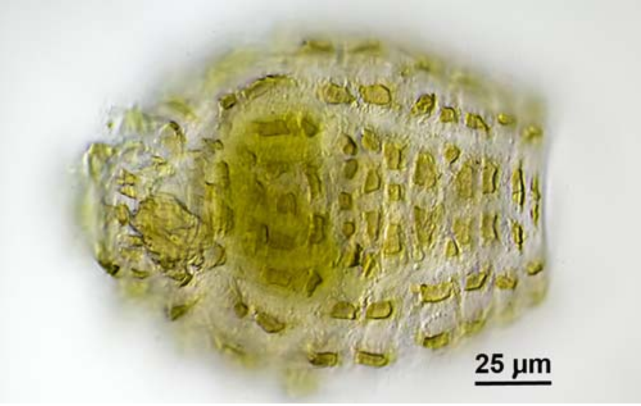

Figure 81. ***Mniobia incrassata*** from moss, showing exterior of lorica. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 82. ***Mniobia incrassata*** from moss, showing rotifer inside lorica. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 83. ***Mniobia scarlatina*** from among epiphytic mosses. Photo by Jersabek *et al.* 2003, with permission.

Figure 84. ***Mniobia magna***, a moss inhabitant, including epiphytes, with its body shortened and cilia out. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 85. ***Mniobia** cf.* ***obtusicornis***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 86. ***Frullania eboracensis*** on bark – home for ***Mniobia symbiotica***. Photo by Janice Glime

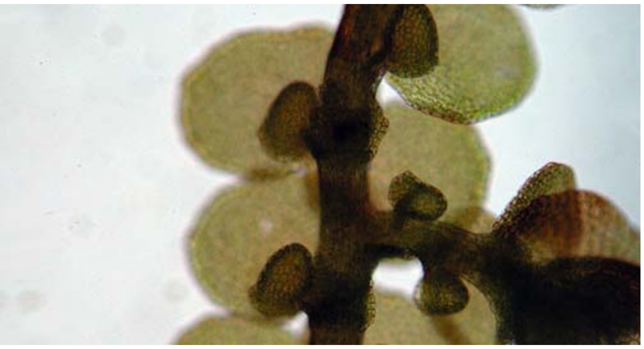

Figure 87. ***Frullania eboracensis*** showing lobules that serve as home for ***Mniobia symbiotica***. Photo by Bob Klips, with permission.

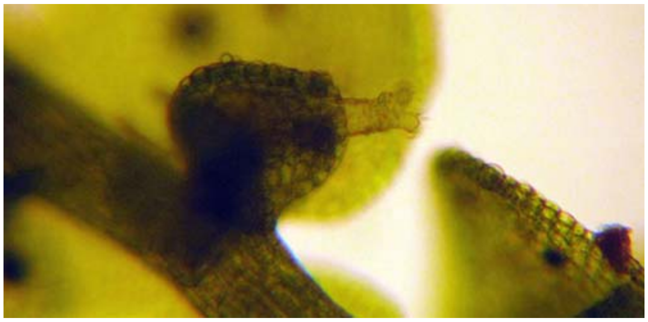

Figure 88. ***Frullania eboracensis*** from Ohio, USA, with a rotifer in a lobule – possibly ***Mniobia symbiotica***. Photo by Bob Klips, with permission.

Mniobia orta (Peters *et al*. 1993) and ***M. russeola*** (Horkan 1981; Hirschfelder *et al*. 1993) are also bryophyte dwellers.

Pleuretra

The genus ***Pleuretra*** seems to prefer habitats that dry out. ***Pleuretra humerosa*** (Figure 89-Figure 90) occurs on dry mosses on granite (Plewka 2016). ***Pleuretra lineata*** (Figure 91-Figure 93) occurs on the mosses ***Andreaea rupestris*** (Figure 60-Figure 61) and ***Grimmia pulvinata*** (Figure 94) (Hirschfelder *et al*. 1993; Plewka 2016), both species of exposed rocks. ***Pleuretra brycei*** (Figure 95-Figure 96) is also a bryophyte dweller, but among ***Sphagnum*** (Figure 6-Figure 7) and demonstrates the spines that help to protect it among the bryophytes (Madaliński 1961).

Figure 89. ***Pleuretra humerosa***, a species of dry mosses on granite. It is shown here in its extended position that is used during its inchworm movement. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 90. ***Pleuretra humerosa***, a species of dry moss on granite, shown here in its contracted shape with cilia out. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 91. ***Pleuretra lineata***, a species that lives on ***Andreaea rupestris*** and ***Grimmia pulvinata***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 92. ***Pleuretra lineata***, a species that lives on the mosses ***Andreaea rupestris*** and ***Grimmia pulvinata***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

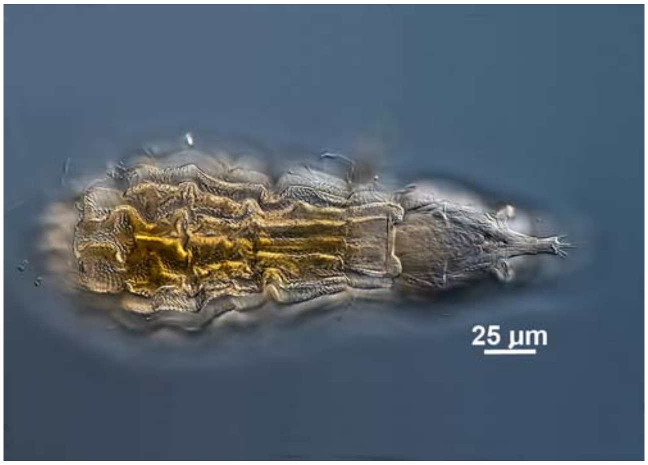

Figure 93. ***Pleuretra lineata***, inhabitant of ***Andreaea rupestris*** and ***Grimmia pulvinata***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 94. ***Grimmia pulvinata***, home of ***Pleuretra lineata***. Photo by Michael Lüth, with permission.

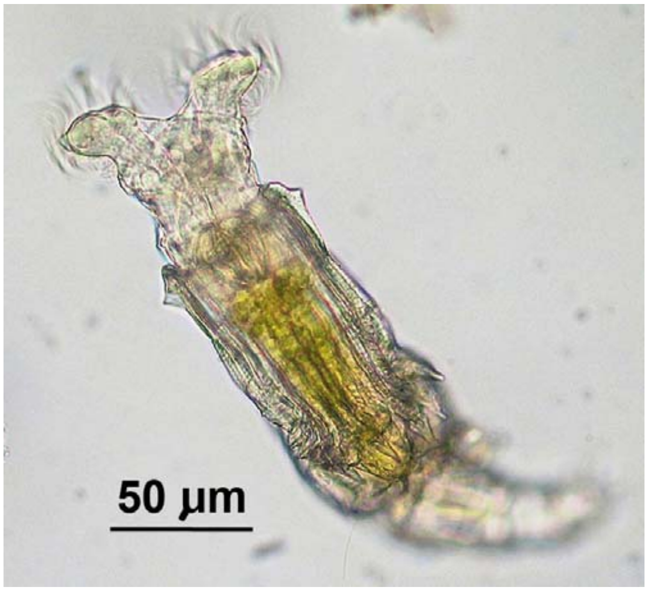

Figure 95. ***Pleuretra** cf **brycei***, a bryophyte dweller. Photo by Michel Verolet, with permission.

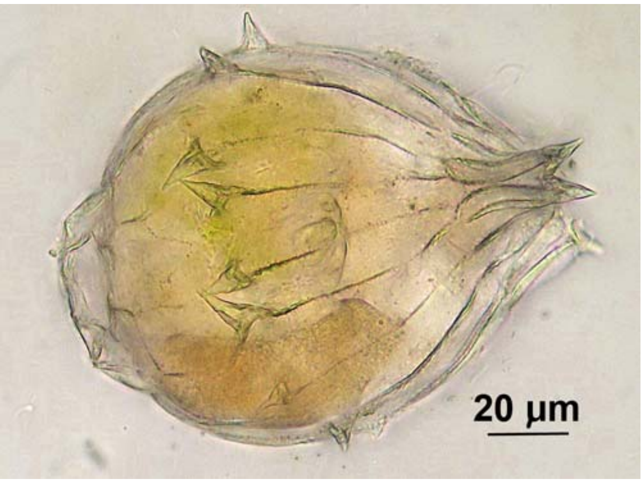

Figure 96. ***Pleuretra*** *cf* ***brycei*** tun, demonstrating the spines that help to protect it. Photo by Michel Verolet, with permission.

Philodina

Philodina acuticornis (Figure 97), ***P. nemoralis*** (Figure 98), and ***P. brevipes*** live on ***Sphagnum*** (Figure 6) (Hingley 1993). ***Philodina citrina*** (Figure 99-Figure 100), ***P. plena*** (Figure 101), ***P. proterva***, and ***P. vorax*** (Figure 102) all occur on ***Sphagnum*** (Figure 6) (Hirschfelder *et al.* 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016). But ***P. plena*** also occurs on epiphytes (Myers 1942) and ***P. citrina*** and ***P. vorax*** live on epiphytic mosses and mosses on rock or concrete. ***Philodina nemoralis*** (Figure 103; Plewka 2016) and ***P. rugosa*** (Figure 105; Horkan 1981; Hingley 1993; Fontaneto *et al*. 2007; Plewka 2016) live in contrasting submersed and dry habitats, including on epiphytic mosses. Other rotifers on epiphytic mosses include ***Philodina childi*** (Figure 104; Horkan 1981; Hingley 1993; Plewka 2016). Other members of the genus that are associated with bryophytes include ***P. erythrophthalma***, ***P. flaviceps*** (Figure 106), and ***P. roseola*** (Figure 107-Figure 111) (Horkan 1981; Hirschfelder *et al*. 1993; Madaliński 1961; Plewka 2016).

Figure 97. ***Philodina acuticornis***, a species that likes green algae among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 98. ***Philodina nemoralis***, a species of submersed, dry, and epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 99. ***Philodina citrina*** from ***Sphagnum*** bogs and mosses on stones. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 100. ***Philodina citrina***, a species known from ***Sphagnum*** bogs and epiphytic mosses. Photo by Jersabek *et al.* 2003.

Figure 101. ***Philodina plena*** occurs on ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 102. ***Philodina vorax***, a species that occurs on ***Sphagnum***, epiphytic mosses, and mosses on concrete. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 103. ***Philodina nemoralis***, a species that occurs on submersed, dry, and epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 104. ***Philodina childi*** occurs on epiphytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 105. ***Philodina rugosa***, a species that lives on epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 106. ***Philodina flaviceps***, a species that occurs on moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 107. ***Philodina roseola***, a species that can be found on bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

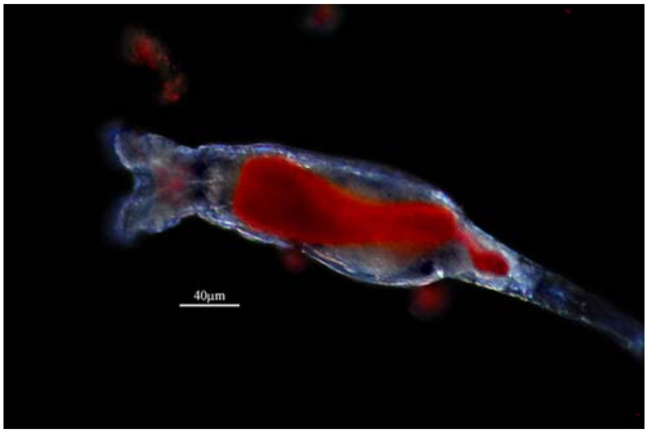

Figure 108. ***Philodina roseola***, a species that can be found on bryophytes. Photo from Proyecto Agua, with permission.

Figure 109. ***Philodina roseola*** with eggs, a species known to inhabit **bryophytes**. Photo by Jersabek *et al.* 2003, with permission.

Rotaria

Rotaria (Figure 110) is a genus that moves like a leech, permitting it to move among bryophytes. The genus ***Rotaria*** is able to move among mosses and other substrata by creeping with its head and foot (van Egmond 1999). The foot is sticky, enabling it to attach to a surface while it feeds (Dickson & Mercer 1966; Schmid-Araya 1998). The anterior cilia (Figure 111) make a current that directs the food toward the pharynx for ingestion.

Figure 110. ***Rotaria***, fully extended as it would be for its leech-like movement. This is a genus with several bryophyte-dwelling species that can move about the bryophytes in this manner. Photo by Wim van Egmond, with permission.

Figure 111. ***Rotaria***, showing the two wheels that direct the food into the gullet. Photo by Yuuji Tsukii, with permission.

Several species of ***Rotaria*** live in association with ***Sphagnum*** (Figure 6). These include ***R. citrina*** (Figure 112-Figure 113), ***R. haptica***, ***R. macroceros*** (Figure 114), ***R. macrura*** (Figure 115-Figure 116; see also Horkan 1981; Bielańska-Grajner *et al.* 2011), ***R. magnacalcarata***, ***R. neptunia*** (Figure 117-Figure 118), ***R. neptunoida*** (Figure 119), ***R. quadrioculata***, ***R. socialis*** (Figure 120), ***R. spicata***, and ***R. tardigrada*** (Figure 121; see also Bielańska-Grajner *et al.* 2011) (Hingley 1993; Plewka 2016). In addition to the ***Sphagnum*** dwellers, ***R. rotatoria*** (Figure 122) and ***R. macrura*** live on mosses (Madaliński 1961; Horkan 1981; Plewka 2016) as well as living in peatlands (Bielańska-Grajner *et al.* 2011). ***Rotaria sordida*** (Figure 123) is unusual in living not only on mosses on limestone, but also in living on the thallose liverwort ***Marchantia polymorpha*** (Figure 124; Horkan 1981; Hirschfelder *et al.* 1993; Plewka 2016) and in peatlands (Bielańska-Grajner *et al.* 2011).

Figure 112. ***Rotaria citrina*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 113. ***Rotaria citrina*** with 2 daughters (see the two mastax), from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 114. ***Rotaria macroceros***, known from **bog pools**. Note the long antenna in the middle of the head. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 115. ***Rotaria macrura***, a ***Sphagnum*** associate. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 116. ***Rotaria macrura*** from among ***Sphagnum*** and other mosses, showing fully extended foot. Photo by Jersabek *et al.* 2003, with permission.

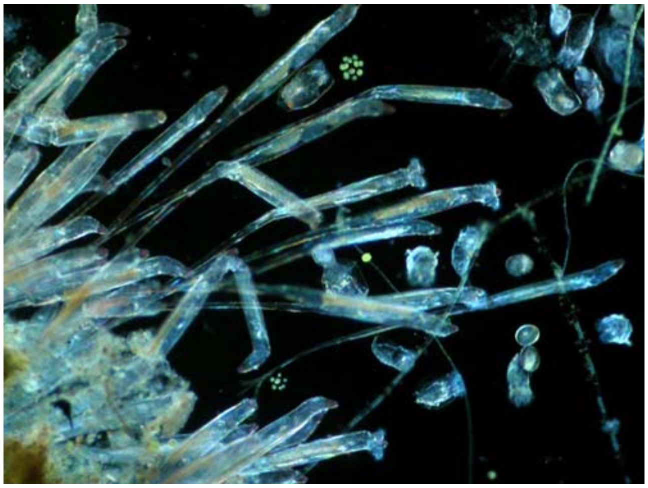

Figure 117. ***Rotaria neptunia*** colony. Photo by Michael Plewka <www.plingfactory.de>, with pernission.

Figure 118. ***Rotaria neptunia*** anterior. Photo by Michael Plewka <www.plingfactory.de>, with pernission.

Figure 119. ***Rotaria neptunoida***, a ***Sphagnum*** dweller, extended while creeping. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 120. ***Rotaria socialis***, an inhabitant of ***Sphagnum*** and other mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 121. ***Rotaria tardigrada*** creeping, with its corona retracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 122. ***Rotaria rotatoria***, a species known from bryophytes in more than one location. Photo by Jersabek *et al.* 2003, with permission.

Figure 123. ***Rotaria sordida sordida***, a species that lives on the thallose liverwort ***Marchantia polymorpha*** and moss on limestone. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 124. ***Marchantia polymorpha***, home for ***Rotifera sordida***. Photo by David T. Holyoak, with permission.

Desiccation Tolerance

Ricci (1998) compared the desiccation survival percentage of rotifers in the **Philodinidae** from water vs those from terrestrial mosses. The rotifers from terrestrial mosses survived seven days of desiccation better than did those from the water (Figure 125). The 2-day-old rotifers (juveniles) had poor resistance to desiccation. ***Rotaria rotatoria***, *R. neptunia*, and ***Otostephanos macrantennus***, all from bodies of water that do not dry out, did not recover from desiccation at any life stage. On the other hand, ***Philodina acuticornis*** and ***R. neptunoida*** likewise live in permanent bodies of water (including among mosses) and do withstand desiccation. Ricci also summarized indications of desiccation tolerance of **Bdelloidea** reported in the literature and from her own studies (Table 1).

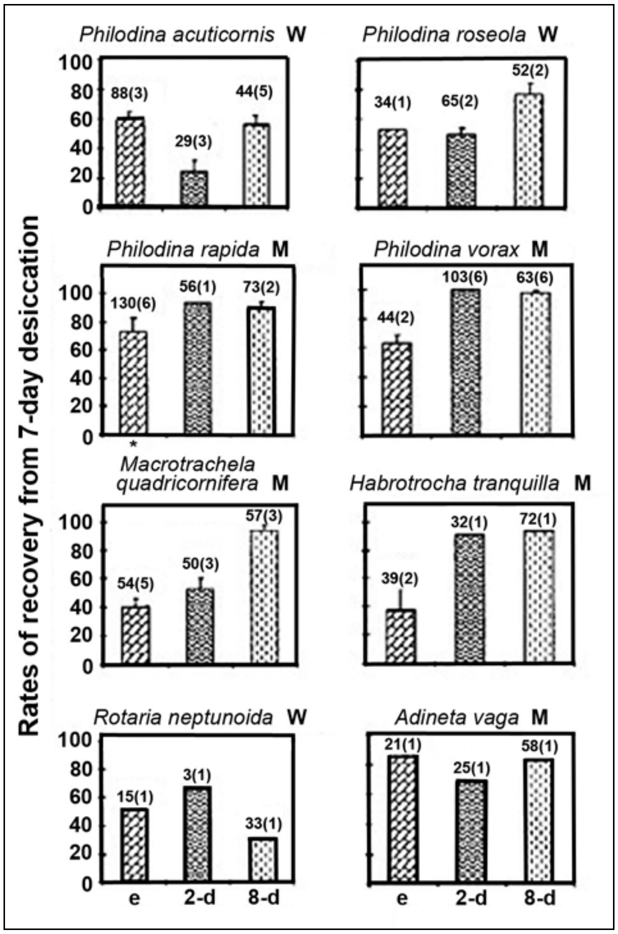

Figure 125. Recovery rates of rotifers collected from terrestrial mosses (**M**) and from water bodies (**W**). Life stages are **e** = newly laid eggs or embryos; **2-d** = 2-day-old juveniles; **8-d** = 8-day-old adults. Numbers above bars = sample size; (number) = number of replicates. Bars represent mean recovery rates among replicates; vertical lines = standard error. *Percentage viability adjusted to control. Redrawn from Ricci (1998).

Table 1. Genera of **Bdelloidea** that inhabit mosses compared to those from water, among genera for which desiccation tolerance is known. Adapted from Ricci (1998). Habitats are based on Donner (1965).

Adinetidae			
Adineta	moss, water	+	Dobers 1915; Örstan 1995
Bradyscela	moss	(+)	Donner 1976
Habrotrochidae			
Habrotrocha	mainly moss & soil	+	Schramm & Becker 1987
Otostephanos	moss, *Sphagnum*	(+)	Murray 1911
Scepanotrocha	moss, soil	(+)	Donner 1976
Philodinavidae			
Abrochtha	water	+	Ricci 1998
Henoceros	water	+	Ricci 1998
Philodinavus	water	+	Ricci 1998
Philodinidae			
Didymodactylos	moss	(+)	Donner 1976
Macrotrachela	moss, water	+	Dobers 1915; Ricci *et al.*1987
Mniobia	moss, soil	+	Dobers 1915
Pleuretra	moss	(+)	Murray 1911
Philodina	moss, water	+	Jacobs 1909; Ricci 1998
Rotaria	mainly water, soil	+	Ricci 1998

Summary

The rotifers in **Bdelloidea** are the most frequently represented rotifers on bryophytes.The bryophyte dwellers are usually not also planktonic and typically attach to the bryophytes by their toes. They move like an inchworm or use their cilia. They obtain their food from the microscopic organisms and detritus among the mosses. Only females exist and the eggs can typically survive desiccation. Mucus helps these rotifers to survive desiccating conditions.

Bryophyte-dwelling **Bdelloidea** include four families known from bryophytes: **Adinetidae**, **Habrotrochidae**, **Philodinavidae**, **Philodinidae**. The **Adinetidae** are known from bogs and other bryophytes. The **Habrotrochidae** have a number of species from bogs and from other bryophytes. Many of the species live in such small niches as ***Sphagnum*** retort cells and liverwort lobules. The **Philodinavidae** has two moss dwelling species that often occur together in streams. The **Philodinidae** creep in cold water and live attached on plants; a number of species occur on bryophytes. The **Philodinidae** terrestrial moss dwellers tested have greater desiccation tolerance than do the aquatic species. Adults are more desiccation tolerant than juveniles.

Acknowledgments

Claudia Ricci has generously answered my questions. Bryonetters have been wonderful in making their photographs available to me and seeking photographs from others. Tom Powers and Walter Dioni helped me obtain images and permission from others. Christian D. Jersabek very generously gave me permission to use the wealth of images from the Online Catalog of Rotifers. Tom Thekathyil and Des Callaghan helped me in finding and gaining permission from Marek Miś for the beautiful image in the frontispiece and others. Aydin Orstan helped me find email addresses and reviewed an earlier version of the chapter. Diego Fontaneto reviewed this sub-chapter and offered many suggestions and corrections. Many photographers have been generous with permission for the use of their images and others have provided them online through Creative Commons and other public domain sources. Antonio Guillén provided me with credit information on images from Proyecto Agua. My special thanks go to Michael Plewka for his generous permission to use so many of his beautiful online images.

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CHAPTER 4-7a

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

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CHAPTER 4-7a

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

Figure 1. ***Keratella*** sp. among ***Sphagnum*** leaves. Photo by Marek Mis <www.mismicrophoto.com>, with permission.

CLASS MONOGONONTA

This is the largest of the two classes of rotifers, comprised of ~1570 species, ~1488 of which are free-living in fresh water of limnoterrestrial habitats (Segers 2008). It differs from the **Bdelloidea** in having two sexes and having only one ovary. Nevertheless, asexual reproduction occurs over and over until environmental conditions, often related to crowding, trigger the reproduction to become sexual (Welch 2008). At this time, the eggs of the **amictic** (non-sexual) females hatch into **mictic** females that produce their eggs by meiosis. The **haploid** eggs that are not fertilized develop into much smaller males and fertilization of a female by these males produces **diploid** eggs that become resting eggs.

The monogonont rotifers mostly eat small particles and organisms by filtering them, some actually seize them, and some are parasitic.

ORDER COLLOTHECACEA

Many members of this order are **sessile** (attached) and some are colonial. These rotifers have a foot that lacks toes, but they possess many foot glands that are used for adhesion. The females are predominantly sessile, but males and immature rotifers are free-living.. The rotary apparatus surrounds a funnel-like **invagination**. Many are surrounded with a jelly sheath.

Collothecidae

Many members of the Collothecidae are plant and algal inhabitants. The **Collothecidae** provide us with evidence of adaptive strategies embodied in reproduction. An examination of 65 species of rotifers, including this family, revealed that egg volume of rotifers increased as body volume increased, but the relative size of eggs actually decreased as body size increased (Wallace *et al.*

1998). This means that smaller species, typical among planktonic species and bryophytes, invest the most in egg production. The **Flosculariidae** (**Flosculariacea**) species are of intermediate size and their relative investment in egg mass is likewise intermediate. The **Collothecidae** family has the largest species and the lowest relative biomass of egg production among those examined by Wallace *et al*.

Collotheca

Collotheca (Figure 2-Figure 8) is a common genus in peatlands, living in ***Sphagnum*** pools (Figure 5) and on ***Sphagnum*** (Figure 2, Figure 21, Figure 61-Figure 62).

Figure 2. ***Collotheca*** on ***Sphagnum***. Photo by Marek Mis <www.mismicrophoto.com>, with permission.

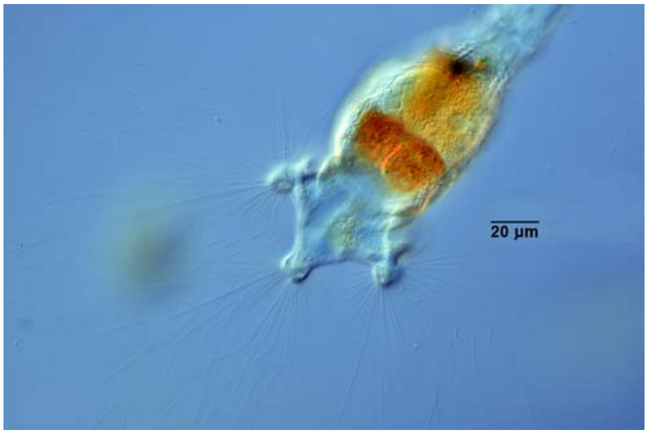

Figure 3. ***Collotheca***, a common genus on ***Sphagnum***. Photo by Proyecto Agua Water Project through Creative Commons.

Figure 4. ***Collotheca*** sp., a common genus on ***Sphagnum***. Photo by Yuuji Tsukii, with permission.

Figure 5. ***Sphagnum*** pond, home for rotifers. Photo by Michael Luth.

Collotheca campanulata occurs on wet mosses as well as in the plankton on Svalbard (De Smet 1993). The relationships of this species to aquatic flowering plants can instruct us on relationships to look for among bryophytes. ***Collotheca campanulata*** (***gracilipes***) (Figure 6) is selective in its location on its aquatic plant substrate (Wallace & Edmondson 1986). On plants such as *Elodea canadensis*, it selected (98%) the lower (**abaxial**) surfaces of the leaves. When given equal opportunities for four plant species, it selected *Lemna minor* over *Elodea canadensis*, but in the field more were found on *Elodea canadensis*, with densities reaching more than six individuals per mm^2. Light made a difference, with 91% of the rotifers selecting the **adaxial** (upper) surface in continuous light, but showing no preference in continuous darkness. **Alpha amylase** appears to be the chemical that helps them to identify a plant substrate. Those rotifers that were induced to settle on the abaxial surface produced more eggs than those that were induced to settle on the adaxial surface. It would be interesting to see if these relationships persist on liverworts like ***Riccia fluitans*** (Figure 9) and ***Ricciocarpos natans*** (Figure 10). But what would they do on mosses like ***Fontinalis*** (Figure 11)? They are also known from bog pools where they attach to ***Sphagnum*** (Figure 2, Figure 21, Figure 61-Figure 62) and algae (Figure 8).

Figure 6. ***Collotheca campanulata***, a rotifer that takes up residence on aquatic plants, ***Sphagnum***, and algae. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 7. ***Collotheca campanulata***, a species that is known as sessile on ***Sphagnum*** and occurs in bog pools. Photo by Yuuji Tsukii, with permission.

Figure 8. ***Collotheca campanulata***, a species that is known as sessile on ***Sphagnum*** in bogs and occurs in bog pools. Photo by Jersabek *et al.* 2003, with permission.

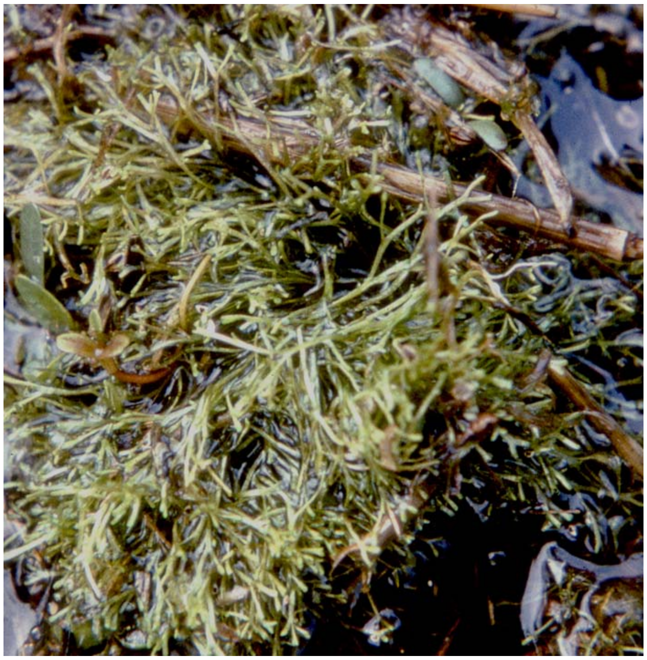

Figure 9. ***Riccia fluitans***, a substrate for rotifers, stranded here above water. Photo by Janice Glime.

Figure 10. ***Ricciocarpos natans***, potential home for rotifers. Photo by Janice Glime.

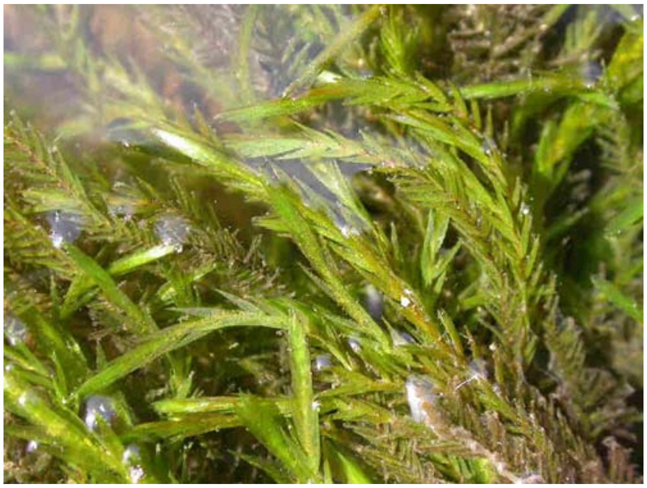

Figure 11. ***Fontinalis antipyretica*** var. ***gracilis***, home for rotifers that are able to feed on the associated detritus. Photo by David T. Holyoak, with permission.

Sphagnum peatlands (Figure 61) are home to several species of ***Collotheca***. ***Collotheca coronetta*** (Figure 12-Figure 13) and ***Collotheca ornata*** (Figure 14) live sessile on ***Sphagnum*** (Figure 21, Figure 62) (Jersabek *et al*. 2003). ***Collotheca ornata*** also occurs on wet mosses and in plankton on Svalbard. ***Collotheca crateriformis*** (Figure 15-Figure 16) and ***C. trilobata*** (Figure 17) live among ***Sphagnum*** (Figure 21). Bielańska-Grajner *et al*. (2011) reported ***C. wiszniewski*** from bogs and fens in Poland.

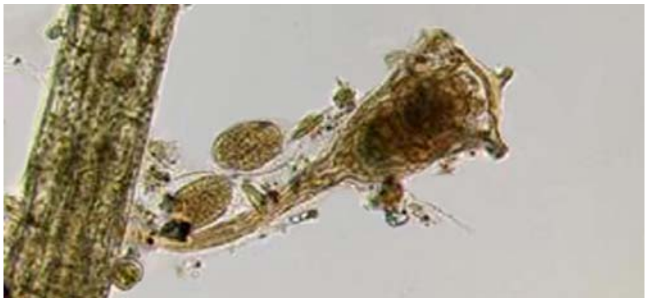

Figure 12. ***Collotheca coronetta***, a species that occurs sessile on ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 13. ***Collotheca coronetta***, a species that lives sessile on ***Sphagnum***, shown here with mucilage and resting eggs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 14. ***Collotheca ornata***, a species that lives in bogs and is sessile on ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Figure 15. ***Collotheca crateriformis*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

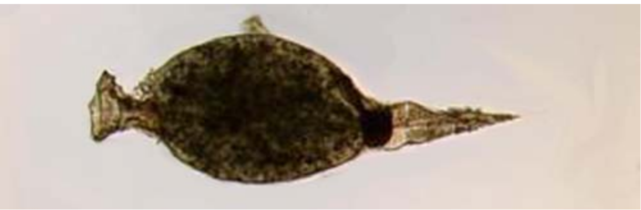

Figure 16. ***Collotheca crateriformis*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

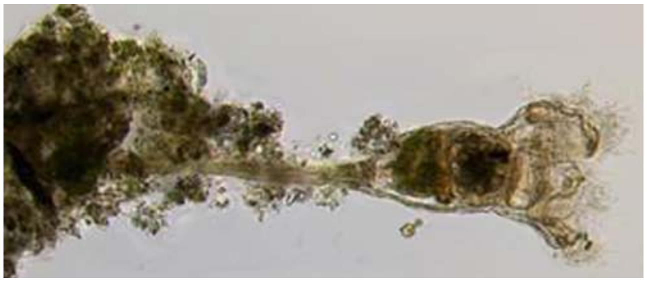

Figure 17. ***Collotheca trilobata*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Stephanoceros

So far I have found few reports on ***Stephanoceros*** from bryophytes, but then, it is a genus with only two species (Meksuwan *et al*. 2013), both of which occur on bryophytes. And even the taxonomy is questionable, with the genus arguably belonging to ***Collotheca***. ***Stephanoceros fimbriatus*** (Figure 18-Figure 20) is a sessile species that lives on ***Sphagnum*** (Figure 21) as one of its substrates (Jersabek *et al*. 2003). ***Stephanoceros millsii*** (Figure 22) is known from bryophytes.

Figure 18. ***Stephanoceros fimbriatus***, a sessile species that can occur ln ***Sphagnum***. Photo by Wim van Egmond, with permission.

Figure 19. ***Stephanoceros fimbriatus*** with ***Sphagnum***. Photo by Marek Mis <www.mismicrophoto.com>, with permission.

Figure 20. ***Stephanoceros fimbriatus*** female, a species that occurs sessile on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 21. ***Sphagnum cuspidatum***, potential home for a variety of rotifers. Photo by David T. Holyoak, with permission.

Figure 22. ***Stephanoceros millsii***, a species known from bryophytes. Note the eggs. Photo by Jersabek *et al.* 2003.

ORDER FLOSCULARIACEA

Not only do the members of this order lack toes; some of the planktonic species lack feet as well. Nevertheless, they have multiple foot glands to secrete glue. The rotary organ has a double ring of cilia that surrounds the anterior of its lobe-like appendages. Species may be either free-living or sessile and are suspension feeders.

Conochilidae

The species ***Conochilus hippocrepis*** (Figure 23-Figure 24) is typically planktonic in both ponds and large bodies of water, but among these habitats you can find it associated with ***Sphagnum*** (Figure 21) (Jersabek *et al.* 2003). It generally lives in a habitat with a *p*H of 6.3-8.3 and temperature range of 6.4-15.4°C (de Manuel Barrabin 2000). Its colonies can reach 30-60 members that are joined in a gelatinous case (Figure 25). Detritus and bacteria, generally abundant in the habitat, serve as food (Pourriot 1977).

Figure 23. ***Conochilus hippocrepis*** female, member of a genus known on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 24. ***Conochilus unicornis*** female, member of a genus known to associate with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

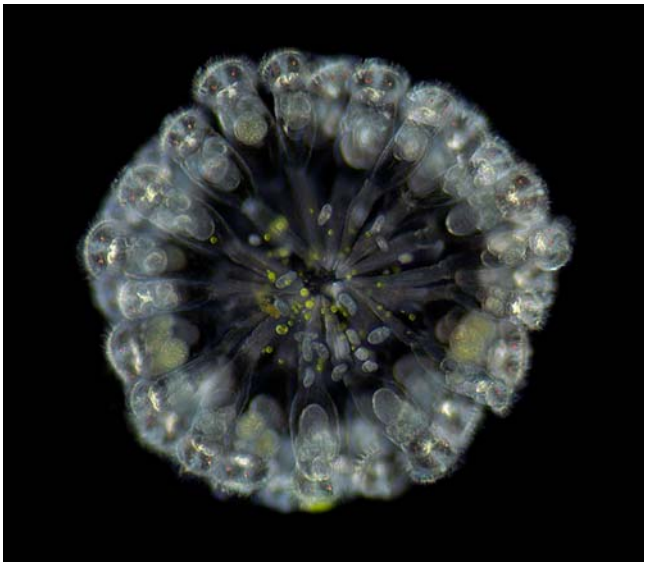

Figure 25. ***Conochilus*** sp. colony. This genus has species that are sessile on ***Sphagnum***. Photo by Wim van Egmond, with permission.

Conochilus hippocrepis (Figure 23-Figure 24) is sensitive to increasing predator pressure from the copepod ***Parabroteas sarsi*** (Figure 26) (Diéguez & Balseiro 1998). As the predator increases in size and begins to prey on the ***C. hippocrepis***, this rotifer responds by increasing its colony size (Figure 25). This seems to be the only member of this family known to associate with bryophytes, in particular ***Sphagnum*** (Figure 21).

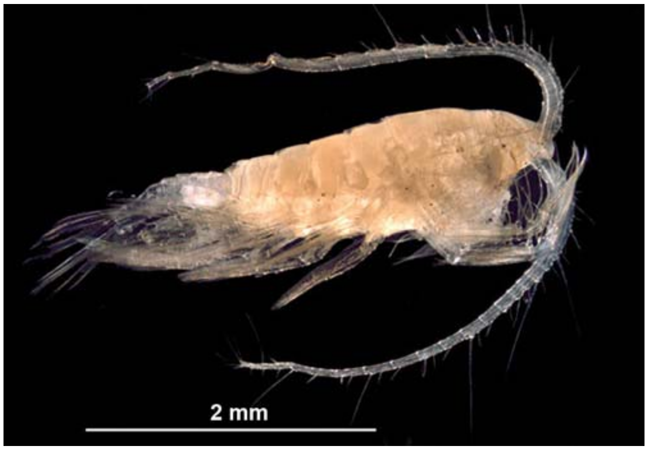

Figure 26. ***Parabroteas sarsi*** male, predator on ***Conochilus hippocrepis***. Photo by Cristián Correa Guzmán, with permission.

Flosculariidae

In this family the male is small and free-swimming, whereas the female lives in a tube and usually attaches by its modified foot. Some of these females (*e.g.* ***Ptygura linguata***) live on the bladders of species of the bladderwort ***Utricularia***. But, sadly for the rotifers, they also constitute part of the diet of these same bladderworts (Mette *et al.* 2000). This habitat affords the rotifers a special aid in getting food as it is sucked into the bladder. Bryophytes can offer no such aid, and although the genera on bryophytes are often the same because they are sessile, species differ.

Floscularia

The genus ***Floscularia*** (Figure 27-Figure 29) is a tube builder and is known to live on ***Sphagnum*** (Figure 66) (Hingley 1993). Jabez Hogg described this tube-building behavior in 1883 (*In* Rotifers 2012). The case is composed of tiny pellets. Gosse, in 1851 (*In* Rotifers 2012), reported a specimen attached to a submerged moss in a pond and observed its case-building behavior. I cannot improve upon the text provided by Hogg (1854, *In* Rotifers 2012): "In November, 1850, Mr. Gosse found a fine specimen of a ***Floscularia*** (Figure 27-Figure 29) attached to a submerged moss from a pond at Hackney; this he watched as it engaged in building its case, and at the same time discovered the use of the curious little rotatory organ on the neck. When fully expanded, the head is bent back at nearly a right angle to the body, so that the [rotary] disc (Figure 29) is placed nearly perpendicularly, instead of horizontally; the larger petals, which are the frontal ones, being above the smaller pair." The terminology has changed, but the observations still provide us with a clear picture of this rotifer on a moss. He discovered the role of these wheels of cilia by adding carmine to the water and observing its pathway.

Figure 27. ***Floscularia conifera*** female, a species that occurs sessile on ***Sphagnum*** and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

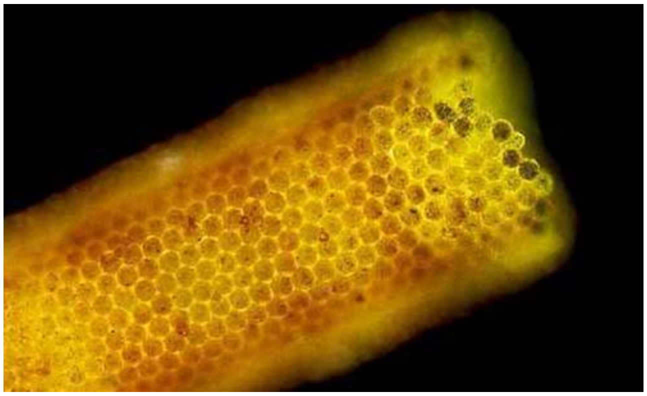

Figure 28. ***Floscularia ringens*** tube. Photo with online permission from <http://www.micrographia.com/>.

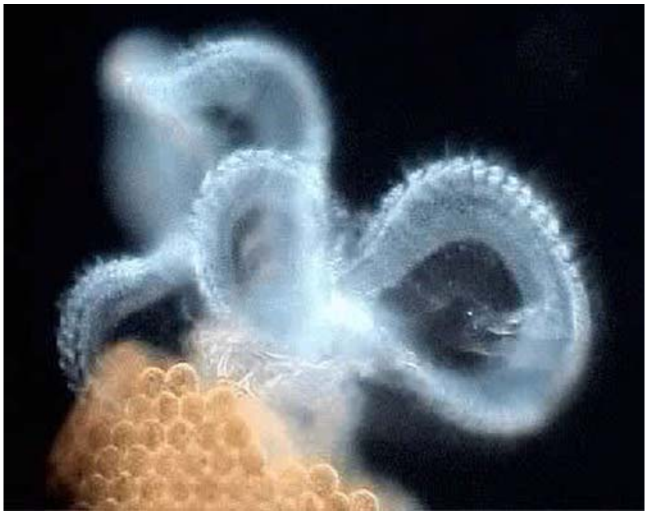

Figure 29. Tip of case of ***Floscularia ringens***, showing the geometric arrangement of pellets and the rotary apparatus. Photo by Martin Mach, with permission.

Gosse (1851 *In* Rotifers 2012) provided a charming description of the feeding as well: "If the atoms be few, we see them swiftly glide along the facial surface, following the irregularities of outline with beautiful precision, dash round the projecting chin like a fleet of boats doubling a bold headland, and lodge themselves, one after another, in the little cup-like receptacle beneath." But these were not used as food. Rather, they were eventually emptied from the cup, which was bent down to the margin of the case and the pellet, mixed with "salivary secretion," added to the margin of the case (Figure 29). Each pellet required 2-3 minutes to be gathered and deposited.

Fontaneto *et al.* (2003) added detail to tube building in ***Floscularia***. They observed that each pellet in the tube has a hole in the middle. The pellets are cemented together with "glue bundles" and the tube is lined with mucus.

Ptygura

As I read through account after account of rotifer sampling, I can't help but wonder if more attention should be given to the bryophyte habitat for locating new rotifer species, especially for sessile groups like this one. A number of these species are sessile on ***Sphagnum*** (Figure 66) and feed on associated algae. De Smet (1990) reported an unidentified species from wet mosses on Svalbard.

Ptygura rotifer (Figure 30) is a free-swimming rotifer (Michael Plewka, pers. comm. 6 August 2016), but Hingley (1993) collected them among ***Sphagnum*** (Figure 66) as well and reported them as sessile there.

Ptygura brachiata (Figure 31-Figure 32) and ***P. velata*** (Figure 33) likewise are species that live on ***Sphagnum*** (Figure 66) (Jersabek *et al*. 2003; Opitz 2016). In addition, a number of species live on other bryophytes as well as living in bogs. For example, ***Ptygura crystallina*** (Figure 34) lives on bryophytes and in bogs in the Pocono Mountains, Pennsylvania, USA. ***Ptygura melicerta*** (Figure 35-Figure 38) forms colonies (Figure 35) in a lake in Wisconsin, USA, but it is also present on bryophytes and in bog pools. It is common among colonies of the **Cyanobacterium *Gloeotrichia*** (Figure 38) (Plewka 2016).

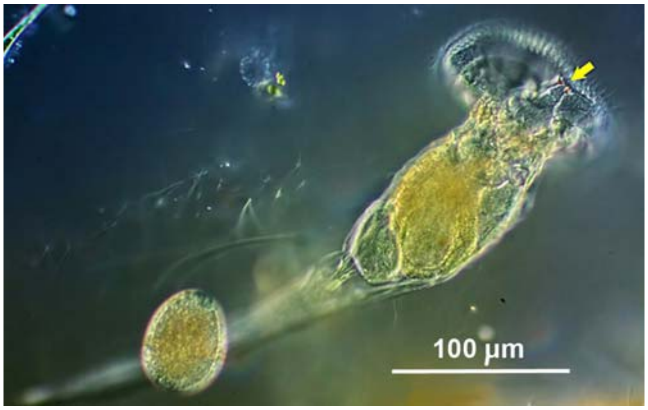

Figure 30. ***Ptygura rotifer***, a species of submersed moss in ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 31. ***Ptygura brachiata*** female, known to be sessile on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 32. ***Ptygura brachiata***, a species known to be sessile on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 33. ***Ptygura velata***, typically living on ***Ceratophyllum***, occurs in bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 34. ***Ptygura crystallina*** female, a species from bryophytes and can occur in bogs. Photo by Jersabek *et al.* 2003, with permission.

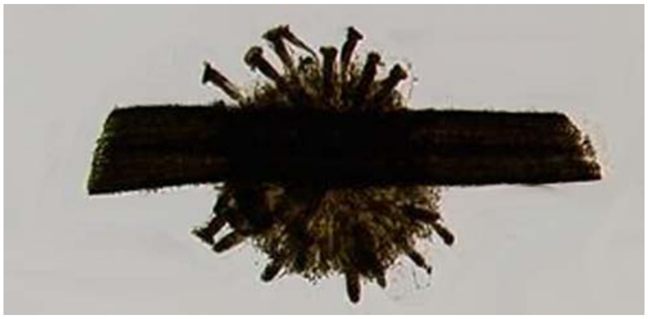

Figure 35. ***Ptygura melicerta*** colony in a lake in Wisconsin, USA. This species can occur among bryophytes and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 36. ***Ptygura melicerta*** female from a lake in Connecticut, USA. Here it is among **Cyanobacteria**; it can occur among bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 37. ***Ptygura melicerta*** colony in a lake in Wisconsin, USA. This species is known from bryophytes and bog pools. Photo by Jersabek *et al.* 2003, with permission.

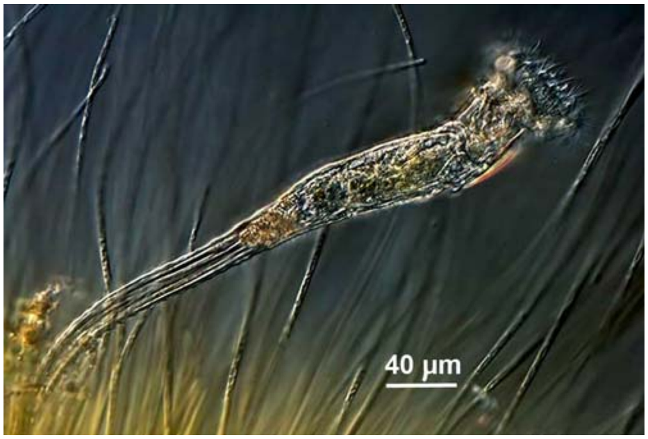

Figure 38. ***Ptygura melicerta*** with ***Gloeotrichia***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Ptygura pilula (Figure 39) seems to be more commonly a moss dweller, including ***Sphagnum*** (Figure 40), where it passes dry periods with a gelatinous covering (Plewka 2016). It incorporates feces (Figure 39-Figure 41) into this tubular housing, further adding to its protection. It also produces resting eggs (Figure 42) that help it to survive dry periods. ***Ptygura stygis*** is also known from submerged mosses (Ptygura 2016).

Figure 39. ***Ptygura pilula*** with feces in gelatinous housing. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 40. ***Ptygura pilula*** female sessile on a ***Sphagnum*** leaf; it also occurs in bog pools. Photo by Jersabek *et al.* 2003, with permission.

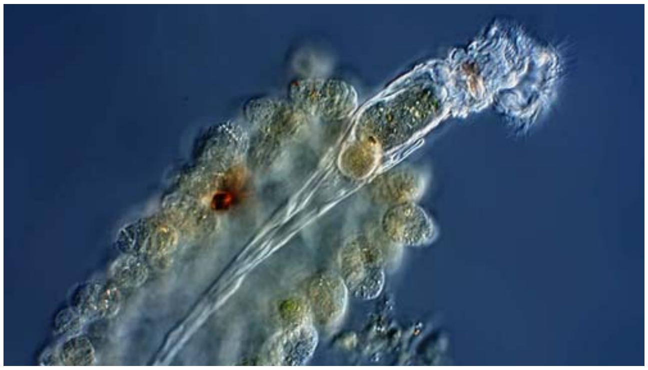

Figure 41. ***Ptygura pilula*** in case, an aquatic moss inhabitant. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 42. ***Ptygura pilula*** resting egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Hexarthridae

In a study of a Turkish lake, Gülle *et al*. (2010) found that rotifers were most abundant from June through August and disappeared from November through April. It was a member of the **Hexarthridae**, *Hexarthra fennica*, that was one of the dominant taxa – 51% of the zooplankton. The rotifers were most dense at a depth of 5 m. But it seems that bryophyte dwellers are few. I found only ***Hexarthra mira*** (Figure 43-Figure 44) reported as a bog and occasional bryophyte dweller, but this species is likewise planktonic. It most likely occurred among mosses accidentally from open water. Its amictic eggs become resting eggs (Figure 45-Figure 46), helping to permit its survival as its habitat dries.

Figure 43. ***Hexarthra mira***, a typically planktonic species known from bryophytes and bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 44. ***Hexarthra mira*** female from Mexico. This planktonic species is sometimes found among bryophytes and in bogs. Photo by Jersabek *et al*. 2003, with permission.

Figure 45. ***Hexarthra mira*** with amictic egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 46. ***Hexarthra mira*** resting egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Testudinellidae

The family **Testudinellidae** includes both saltwater and freshwater species. It is characterized by having dorsal and ventral plates of the lorica that are completely fused laterally. The body is greatly flattened dorsi-ventrally (top-bottom). The foot is long and retractile (see Figure 49 and Figure 50) with a tuft of cilia at its tip. These rotifers are free swimming, typically in the littoral zone, but members of ***Testudinella*** (Figure 48-Figure 59) may also occur on bryophytes and in ***Sphagnum*** pools (Figure 5) as well as on other macrophytes. There are three genera, but only ***Testudinella*** seems to be represented on bryophytes.

Myers (1942) provided one of the more detailed texts on rotifer habitats. Among these are a number of species that live on or among ***Sphagnum*** (Figure 21) or in pools (Figure 5) among the peatlands. One such species is ***Testudinella armiger*** (Figure 47), a species that lives on the emergent species ***Sphagnum cuspidatum*** (Figure 21).

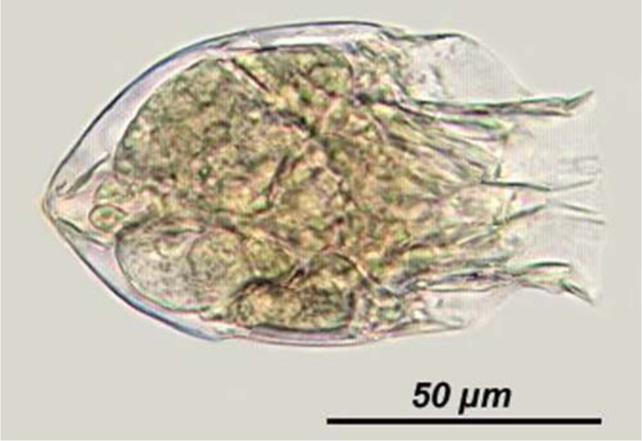

Figure 47. ***Testudinella armiger***, an inhabitant of ***Sphagnum cuspidatum***. Photo by Jersabek *et al.* 2003, with permission.

The records for ***Sphagnum*** (Figure 21) associates include ***Testudinella aspis***, ***T. emarginula*** (Figure 48), ***T. epicopta*** (Figure 49), ***T. tridentata*** (Figure 50-Figure 51), and ***T. truncata*** (Figure 52) (Myers 1942; Jersabek *et al.* 2003). ***Testudinella emarginula*** occurs in ***Sphagnum*** bogs (Figure 66) (Jersabek *et al.* 2003). This cosmopolitan species lives on plant surfaces, although it occasionally occurs in the plankton (de Manuel Barrabin 2000). It is a cold-water species (7.7-7.8°C) with a circumneutral *p*H preference (*p*H 6..8-7.5) and wide alkalinity range.

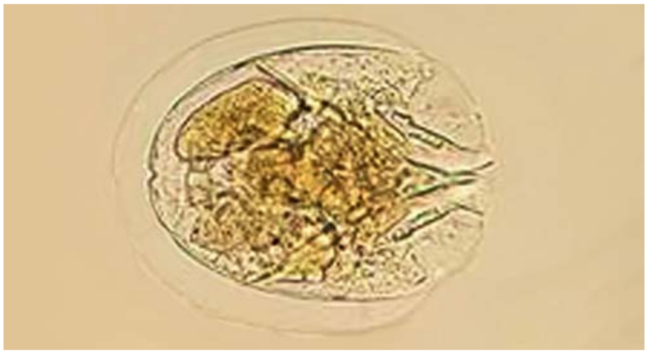

Figure 48. ***Testudinella emarginula*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 49. ***Testudinella epicopta*** from among ***Sphagnum***. Photo by Jersabek *et al. 2003*, with permission.

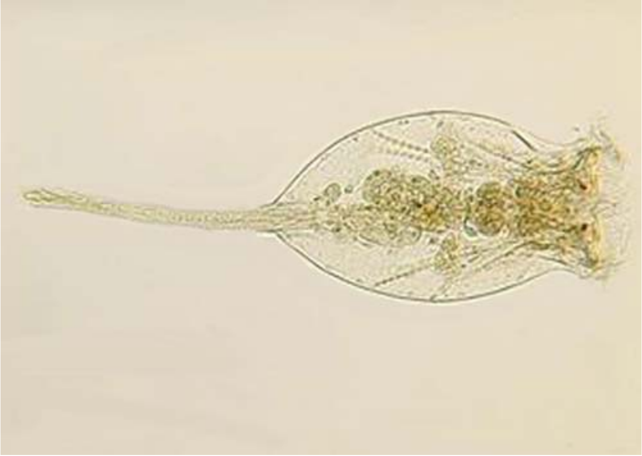

Figure 50. ***Testudinella tridentata*** subsp. ***dicella*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 51. ***Testudinella tridentata*** subsp ***dicella*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 52. ***Testudinella truncata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Testudinella incisa (Figure 53) is typically a plankton species (Plewka 2016), but it also occurs in association with ***Sphagnum*** (Figure 54) (Jersabek *et al*. 2003). The former subspecies, ***T. incisa emarginula***, is now considered a separate species, ***T. emarginula***, so it is possible that the reference to the planktonic ***T. incisa*** really belongs to ***T. emarginula***.

Figure 53. ***Testudinella incisa***, a species sometimes associated with ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 54. ***Testudinella emarginula*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Some members of ***Testudinella*** (Figure 55) are known from bryophytes outside of bogs. Others, such as ***Testudinella elliptica*** (Figure 56-Figure 57), live among both bog bryophytes and non-bog bryophytes.

Figure 55. ***Testudinella patina***, a genus that occurs on bryophytes. Note the complete retraction of the foot. Photo by Wim van Egmond, with permission.

Figure 56. ***Testudinella elliptica***, a species that lives on both ***Sphagnum*** and other bryophytes. Photo by Michael Plewka <www.plingfactory.de>.

Figure 57. ***Testudinella elliptica***, a species that lives on both ***Sphagnum*** and other bryophytes. Photo by Michael Plewka <www.plingfactory.de>.

Testudinella patina (Figure 58-Figure 59) is a planktonic species that likes small bodies of water where aquatic plants are abundant (de Manuel Barrabin 2000), but it is also known from peatlands (bogs or fens) in Poland (Bielańska-Grajner *et al*. 2011). Bryophytes are among the aquatic plants in some associations where it has been found. The aquatic plant area provides it with its preferred foods of the green alga ***Chlorella*** (Figure 64) and diatoms (Figure 60). It tolerates high salinity and lives in a *p*H range of 6.3-8.89. It enjoys a wide temperature range of 9.5-24.3°C. Some occur on mosses in Antarctica (Figure 59).

Figure 58. ***Testudinella patina*** female, a species that sometimes is associated with aquatic bryophytes. Here its cilia are withdrawn. Photo by Jersabek *et al.* 2003, with permission.

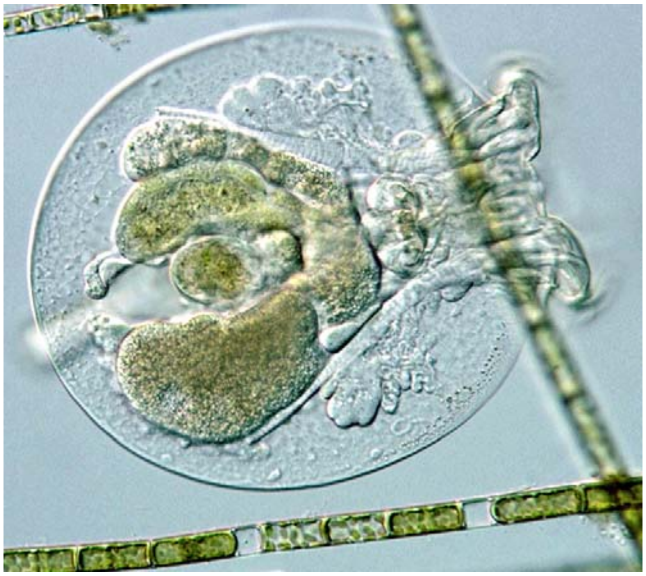

Figure 59. ***Testudinella patina***; some members of this genus are Antarctic moss dwellers. Photo by Yuuji Tsukii, with permission.

Figure 60. Diatoms that can be found among bryophytes, some serving as food for rotifers living there. Photo by Damian H. Zanette, through Public Domain.

ORDER PLOIMIDA

This order has the most families. But are these species ones likely to be on bryophytes? Myers (1942) reported 52 species of ploimate rotifers among ***Sphagnum subsecundum*** (Figure 61-Figure 62) from collections in 1941.

Figure 61. ***Sphagnum subsecundum*** in its habitat, home of ***Pedipartia gracilis***. Photo by Michael Lüth, with permission.

Figure 62. ***Sphagnum subsecundum***, home of ***Pedipartia gracilis***. Photo by Michael Lüth, with permission.

Wallace *et al.* (2008) asked if "everything is everywhere?" They answered this question in the Chihuahua Desert pools in Mexico. They found that indeed the specialized, warm-water habitat of the desert did not support "everything." The microinvertebrate fauna was dominated by rotifer families that are also common on bryophytes: **Brachionidae**, **Lecanidae**, **Lepadellidae**, and **Notommatidae**. Both habitats dry up. The full statement for "everything is everywhere" includes "but the environment selects." The desert pools are actually a similar environment to that of bryophytes that dry out between rain events.

Trochosphaeridae

Cryptic species, morphologically indistinguishable biological groups incapable of interbreeding, are not uncommon in many rotifer families. ***Filinia*** species of **Trochosphaeridae** are highly variable and likely comprise a number cryptic species (Ruttner-Kolisko 1989). This is at least in part due to the parthenogenetic reproduction that can quickly lead to a clone of genetically identical individuals in a **founder population** in a lake or other habitat. This is furthermore complicated by the absence of many good morphological characters by which to distinguish species. In the ***Filinia terminalis-longiseta*** group, ecological properties differ and suggest the existence of these microspecies, or perhaps sister species. Only two members of the **Trochosphaeridae** seem to be known from bryophytes: ***Filinia longiseta*** (Figure 63) and ***F. terminalis*** (Figure 65).

Filinia longiseta (Figure 63) is known from bryophytes in England and Ireland. This is typically a cosmopolitan planktonic species of lakes, ponds, moorland waters, and even brackish water (de Manuel Barrabin 2000). It lives in a wide range of warm temperatures (7.7-26.2°C) and *p*H (6.3-9.9). It is a filter feeder on detritus, bacteria, and small algae like ***Chlorella*** (Figure 64) in a size range of 10-12 µm (Pourriot 1965) and most likely competes for its food with members of the rotifer genus ***Conochilus*** (Figure 23-Figure 25).

Figure 63. ***Filinia longiseta***, a bryophyte dweller in lakes, ponds, and moorland waters. Photo by Jersabek *et al.* 2003, with permission.

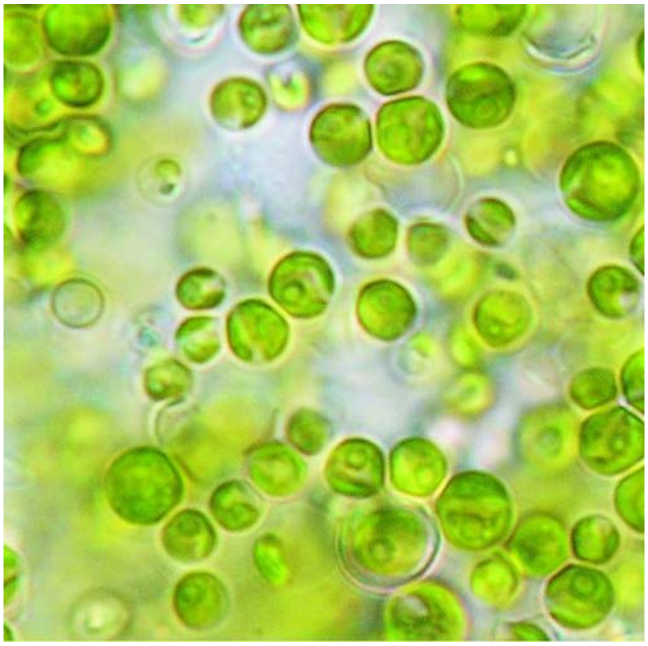

Figure 64. ***Chlorella vulgaris***, a green alga that is often associate with ***Sphagnum*** and that provides food for ***Testudinella patina***. Photo by Sarah Duff, through Creative Commons.

Filinia terminalis (Figure 65) is morphologically variable but seems to occupy a narrow and well-defined niche (Ruttner-Kolisko 1980). At an oxygen content of less than 2 mg L^{-1}, it can reach as many as 1000 individuals per liter. Not surprisingly, it is facultatively anaerobic. Its food sources include bacteria that are chemosynthetic or that decompose plankton.

Figure 65. ***Filinia terminalis*** female, Photo by Jersabek *et al.* 2003, with permission.

Although ***Filinia terminalis*** (Figure 65) is a cosmopolitan, planktonic species, it is known from bryophytes and ***Sphagnum*** bogs (Figure 66) (de Manuel Barrabin 2000). Its preferred conditions are mesotrophic to eutrophic in a *p*H range of 6.64-8.22. Its temperature range is relatively wide: 7.3-22.8°C, although de Manuel Barrabin considers it to be a species of the cool **hypolimnion** (bottom layer of deep lake; temperature never goes below 4°C). Ruttner-Kolisko (1980) found that it prefers temperatures below 12-15°C.

Figure 66. ***Sphagnum papillosum***, a bog moss. Photo by James K. Lindsey, with permission.

Brachionidae

This is a family dominated by planktonic species and was the family with the most species represented in Spanish reservoirs (de Manuel Barrabin 2000), but a few seem to spend time among bryophytes, perhaps as a place to avoid predation, or just dropped there by moving water. An interesting study by Stenson (1982) demonstrated, however, that an experimental reduction of the fish population led to an increase in larger rotifers and a decrease in the smaller filter-feeding species such as ***Keratella cochlearis*** (Figure 79), a member of the **Brachionidae**. Stenson attributed this to a change in competition for food from rotifers such as ***Polyarthra*** (**Synchaetidae**; Figure 67).

Figure 67. ***Polyarthra major***, a large rotifer that eats smaller rotifers. Note the feather-like blades that are used like paddles in swimming. Photo by Wim van Egmond, with permission.

Anuraeopsis

Anuraeopsis fissa (Figure 68-Figure 71) has been reported from a pond in Pennsylvania, USA (Jersabek *et al.* 2003). This is a planktonic rotifer that has been found among bryophytes and in bog pools. It prefers warm water and a **eutrophic** (nutrient-rich) habitat (Margalef 1955). It frequents small water bodies (de Manuel Barrabin 2000). Its food includes bacteria and detritus (Pourriot 1977) and it may become food for the rotifer ***Asplanchna*** (Figure 72) (Guiset 1977).

Figure 68. ***Anuraeopsis fissa*** with an emerging juvenile from a pond in Pennsylvania, USA. Photo by Jersabek *et al.* 2003, with permission.

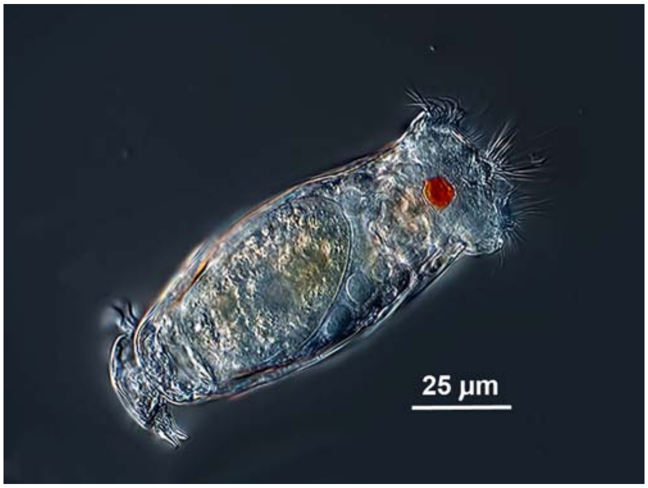

Figure 69. ***Anuraeopsis fissa*** showing toes and red eyespot. Photo by Michael Pewka <www.plingfatory.de>, with permission.

Figure 70. ***Anuraeopsis fissa*** showing a single, light-sensitive red eyespot and cilia, but with toes retracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

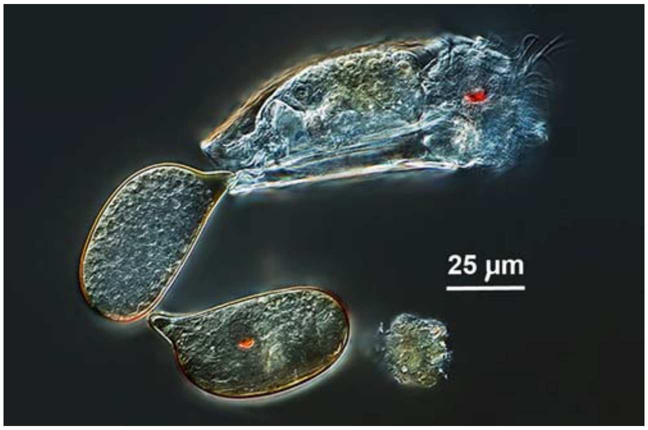

Figure 71. ***Anuraeopsis fissa*** with amictic eggs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 72. ***Asplanchna***, in this case with a gut of ***Keratella***. It is also a predator on ***Anuraeopsis fissa***. Photo by Wim van Egmond, with permission.

Brachionus

Brachionus urceolaris (Figure 73) is planktonic, common in small, alkaline bodies of water (*p*H 7.25-9) (de Manuel Barrabin 2000). It can occur in moving water and is relatively tolerant of high salinity. It is a cosmopolitan species with a wide temperature tolerance (7.35-24.3°C). Despite its alkaline preference, Hingley (1993) found it closely associated with ***Sphagnum*** (Figure 21) in a bog.

Figure 73. ***Brachionus urceolaris***, a species that is closely associated with bog ***Sphagnum***. Photo from Proyecto Agua, with permission.

Brachionus urceolaris (Figure 74), and probably others, has a survival trick against predation. The eggs survive consumption by predators such as the cladoceran *Leptodora kindtii* (Figure 75) without harm (Nagata *et al.* 2011). Often the cladocerans would eject the eggs, and they typically ejected the lorica while digesting the living contents. There was a negative correlation between the portion of unconsumed (ejected) eggs and the length of the predator. That is, longer predators ejected fewer eggs. Nevertheless, hatching success seemed to be independent of the predator's body length. As many as 75% of the undigested eggs hatched successfully.

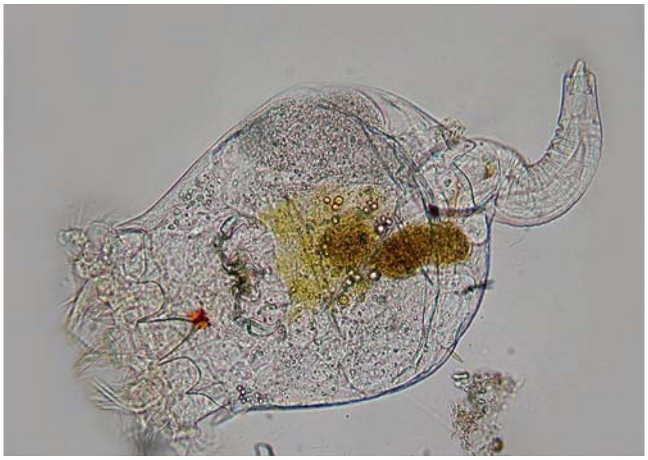

Figure 74. ***Brachionus urceolaris***, a planktonic species that can occur in a ***Sphagnum*** bog. Photo by Michael Verolet, with permission.

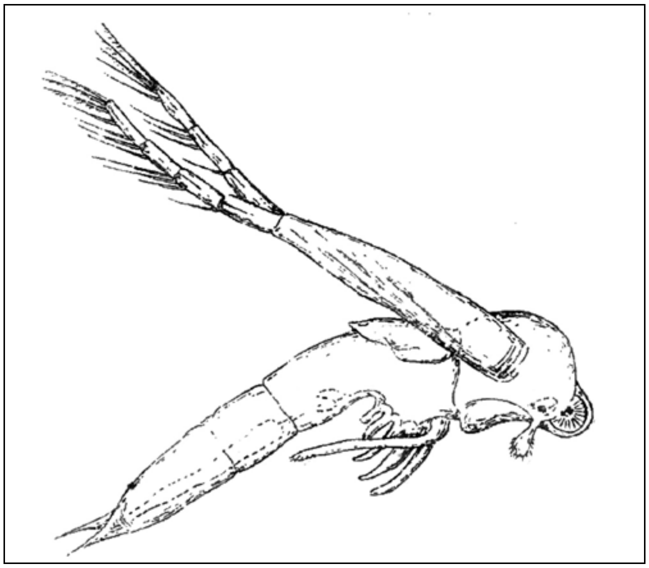

Figure 75. ***Leptodora kindtii***, a large cladoceran that is a predator on ***Brachionus urceolaris***. Drawing by A. Milnes Marshall, through Public Domain.

Kellicottia

Kellicottia is a genus with only two species (Segers 2007). ***Kellicottia longispina*** (Figure 76-Figure 77) is a central European species known from bryophytes, but it is actually typically a planktonic species (Plewka 2016). Its long spines no doubt help to protect it from predation (see Barnhisel 1991), but Madaliński (1961) suggested they may help attach it to bryophytes. It is active year-round as an inhabitant of oligotrophic lakes with a rather narrow *p*H range of 8.2-8.5, but as expected its temperature range is broad (10.6-21.8°C) and it does not occur in small bodies of water (de Manuel Barrabin 2000). Its food is primarily chrysomonads and centric diatoms (Pourriot 1977).

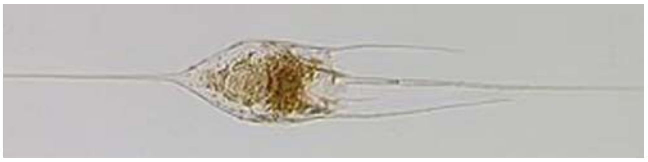

Figure 76. ***Kellicottia longispina*** female, a planktonic species that has also been found with bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 77. ***Kellicottia longispina*** demonstrating spines that may help in attaching it to bryophytes. Photos by Michael Plewka <www.plingfactory.de>, with permission.

Figure 78. ***Kellicottia longispina*** demonstrating spines that probably protect it from predation. Photos by Michael Plewka <www.plingfactory.de>, with permission.

Keratella

Feeding rates are inversely related to the density of food organisms in ***Keratella cochlearis*** (Figure 79), as well as in the planktonic, but occasional bryophyte-dweller, ***Polyarthra vulgaris*** (**Synchaetidae**), and *Polyarthra dolichoptera* (Bogdan & Gilbert 1982). ***Keratella cochlearis*** preferred the alga ***Chlamydomonas*** (Figure 80) to all other foods offered, perhaps explaining the rarity of this rotifer among mosses, where ***Chlamydomonas*** also is uncommon (pers. obs.). Nevertheless, ***K. cochlearis*** lives in bog/fen habitats (Bielańska-Grajner *et al.* 2011) where some species of ***Chlamydomonas*** occur (Struder-Kypke & Schonborn 1999).

Figure 79. ***Keratella cochlearis*** showing lorica, a species that is mostly planktonic but also occurs in bog/fen peatlands. Photo by Michael Plewka <www.plingfactory.de>, with permission.

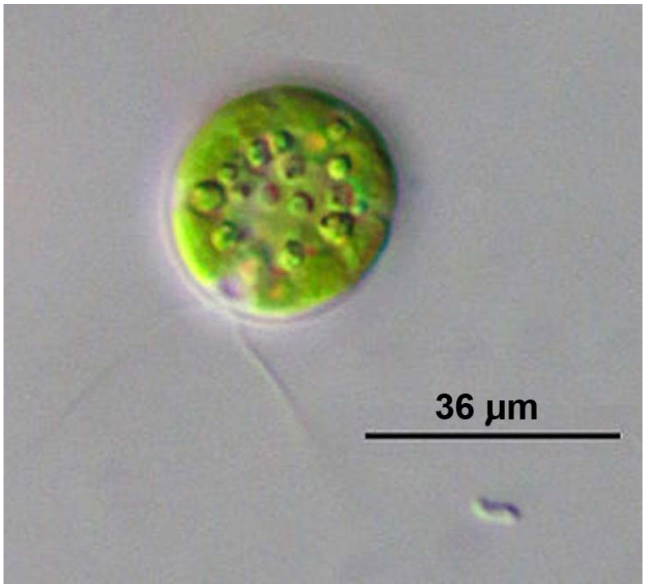

Figure 80. ***Chlamydomonas*** *globosa*, a genus that is food for ***Keratella cochlearis***. Photo by Picturepest, through Creative Commons.

Nevertheless, a number of species of ***Keratella*** live among bryophytes. ***Keratella mixta*** (Figure 81) lives among ***Sphagnum*** (Figure 62) (Jersabek *et al.* 2003). Others live in peatlands (bogs or fens), including ***K. paludosa*** (Figure 82) (Bielańska-Grajner *et al.* 2011).

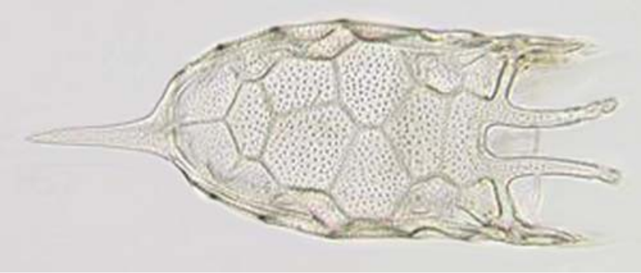

Figure 81. ***Keratella mixta*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 82. ***Keratella paludosa*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Keratella quadrata (Figure 83-Figure 85) is a species known from bryophytes. This is also a cosmopolitan species that is active all year round (de Manuel Barrabin 2000). It is tolerant of mineralization and survives a wide *p*H range of 6.64-10.19. Its temperature range is likewise wide (6.4-26.1°C), as expected for a perennial species. It has broad food preferences, including detritus, bacteria, and algae in the Chlorococcales, Volvocales, Euglenales, Chrysophyceae, and diatoms (Pourriot 1977). As is typical among rotifers, females are larger than males (Figure 84). Resting eggs (Figure 85) help it to survive in this changeable habitat.

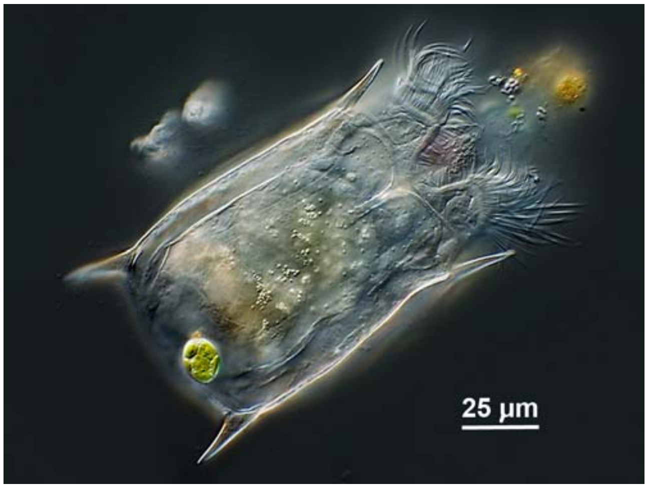

Figure 83. ***Keratella quadrata*** showing lorica and cilia. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 84. ***Keratella quadrata*** female (larger) and male (smaller), a species known from bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 85. ***Keratella quadrata*** resting eggs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Keratella serrulata (Figure 86-Figure 88) is the only planktonic brachionid that is a specialist of acid water, particularly water from bogs with ***Sphagnum*** (Figure 21) (Bērziņš & Pejler 1987; Bielańska-Grajner *et al*. 2011). Its known *p*H is around 6.6 and temperature around 18.6°C (de Manuel Barrabin 2000). It feeds on algae in the Chrysophyceae and Volvocales (Pourriot 1977). ***Sphagnum*** is important in creating its acid habitat – it lives especially in the outflow of ***Sphagnum*** bogs and poor fens (Jersabek *et al*. 2003).

Figure 86. ***Keratella serrulata***, an inhabitant of acid bog outflow water. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 87. ***Keratella serrulata***, a ***Sphagnum*** dweller, showing its ventral surface. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 88. ***Keratella serrulata***, a species known from ***Sphagnum*** bogs and poor fen waters. Photo by Jersabek *et al.* 2003, with permission.

Figure 89. ***Keratella serrulata*** showing rotary cilia. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Keratella also can occur among wet mosses in waterfalls. Savatenalinton and Segers (2008) found ***Keratella cochlearis*** (Figure 79) and ***Keratella tropica*** (Figure 90) in a waterfall in Thailand, but it is likely that these planktonic species were carried there from open water (De Smet, per. comm. 3 November 2016).

Figure 90. ***Keratella tropica***, a waterfall moss dweller. Photo by Jersabek *et al.* 2003, with permission.

Notholca

Although ***Notholca*** is a relatively large genus, only three species seem to be bryophyte dwellers. ***Notholca foliacea*** (Figure 91) occurs on mosses (Plewka 2016). ***Notholca latistyla*** is restricted to the Arctic and occurs on submerged mosses (De Smet 1990). ***Notholca squamula*** likewise occurs on submerged mosses on Svalbard.

Figure 91. ***Notholca foliacea*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Dicranophoridae

The **Dicranophoridae** are predators and are agile in pursuing and capturing their prey (Pejler & Bērziņš 1993a). Unlike many rotifers, the **Dicranophoridae** are not planktonic – other predatory rotifers exist among the plankton – and they avoid the sediments where their prey organisms are not sufficiently abundant. Unlike many rotifers, these have been documented on two species of bryophytes through a study of their substrata. ***Albertia naidis*** (Figure 92), ***Aspelta angusta*** (Figure 97), ***A. aper*** (Figure 95), ***A. circinator*** (Figure 96), ***Dicranophorus forcipatus*** (Figure 117-Figure 118), ***D. haueri***, ***D. robustus*** (Figure 113-Figure 114), ***Encentrum eurycephalum***, ***E. fluviatile***, ***E. lupus***, and ***E. mustela*** (Figure 134), and ***E. uncinatum*** (Figure 131), were all present on 1-10% of the 122 collections of ***Fontinalis*** (Figure 11). ***Aspelta aper***, ***A. circinator***, ***Dicranophorus epicharis*** (Figure 107), ***D. luetkeni*** (Figure 110-Figure 112), ***Encentrum arvicola***, ***E. elongatum***, ***E. incisum*** (Figure 127), ***E. lupus***, ***E. sutor***, ***E. sutoroides***, ***E. tyrphos***, and ***Wierzejsklella velox*** (Figure

139-Figure 140) were all present on 1-10% of the 194 collections of ***Sphagnum*** (Figure 21). The species differ, but only the genus ***Albertia*** is present exclusively on ***Fontinalis***, and only ***Wierzejsklella*** is present exclusively on ***Sphagnum*** in this comparison. Both sets of bryophyte dwellers occur on a wide variety of other plant substrata – none was specific to bryophytes.

Albertia

Only one species of this relatively small genus is associated with bryophytes. ***Albertia naidis*** (Figure 92) not only occurs among ***Sphagnum*** (Figure 5) and ***Fontinalis*** (Figure 11), but it also is parasitic on ***Stylaria lacustris*** (Figure 93), an oligochaete (segmented worm) (Jersabek 2003).

Figure 92. ***Albertia naidis*** subsp ***intrusor*** from among ***Sphagnum*** and parasitic on ***Stylaria lacustris***. This species is also known from the aquatic moss ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

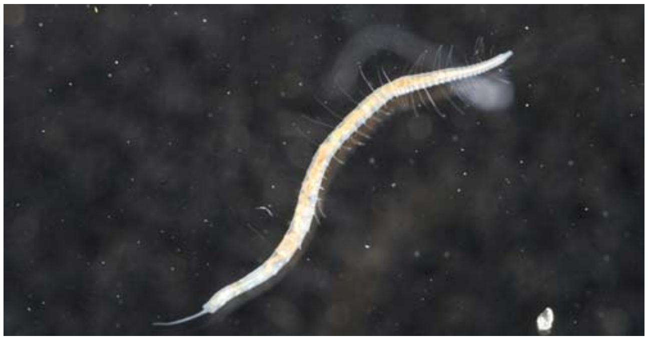

Figure 93. ***Stylaria lacustris***, an annelid that is parasitized by ***Albertia naidis***. Photo by Niels Sloth, with permission.

Aspelta

Several species of ***Aspelta*** live among ***Sphagnum*** (Figure 5) (*e.g.* ***A. beltista***, Figure 94) (Jersabek *et al.* 2003). Others occur not only with ***Sphagnum***, but also occur with the aquatic moss ***Fontinalis*** (Figure 11). These are ***Aspelta aper*** (Figure 95) (Pejler & Bērziņš 1993a) and ***A. circinator*** (Figure 96) (Plewka 2016). ***Aspelta angustus*** (Figure 97) occurs among mosses on rock and also among the periphyton on ***Sphagnum*** (Figure 21) (Plewka 2016).

Figure 94. ***Aspelta beltista*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 95. ***Aspelta aper***, a rotifer that occurs on both ***Fontinalis*** and ***Sphagnum*** species. Photo by Jersabek *et al.* 2003, with permission.

Figure 96. ***Aspelta cf circinator***, a species of ***Sphagnum*** ponds, but also occurs with ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

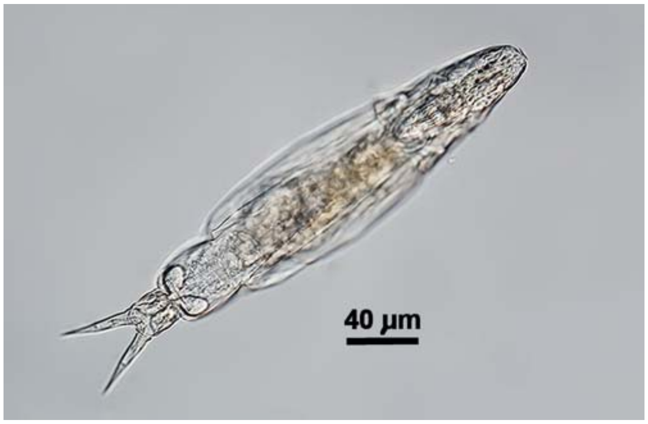

Figure 97. ***Aspelta angusta*** from among mosses on rock but also among the periphyton on ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Aspelta chorista (Figure 98) lives among the moss ***Warnstorfia exannulata*** (Figure 99-Figure 100) (Myers 1942; Jersabek *et al.* 2003).

Figure 98. ***Aspelta chorista*** from among the moss ***Warnstorfia exannulata***. Photo by Jersabek *et al.* 2003, with permission.

Figure 99. ***Warnstorfia exannulata*** habitat where one might find ***Aspelta chorista***. Photo by J. C. Schou, with permission.

One known species of ***Aspelta*** is more terrestrial. ***Aspelta secreta*** is characteristic of mosses on sandstone rocks in firewood habitats (De Smet & Verolet 2009).

Figure 100. ***Warnstorfia exannulata***, home for ***Aspelta chorista***. Photo by J. C. Schou, with permission.

Dicranophorus

Sphagnum (Figure 21) seems to be a common habitat for a number of species of ***Dicranophorus***. These include ***Dicranophorus alcimus*** (Figure 101; Jersabek *et al.* 2003), ***D. artamus*** (Figure 102; Jersabek *et al.* 2003), ***D. biastis*** (Figure 103; Jersabek *et al.* 2003), ***D. capucinus*** (Figure 104-Figure 105; Jersabek *et al.* 2003; Bielańska-Grajner *et al.* 2011), ***D. colastes*** (Figure 106; Jersabek *et al.* 2003), ***D. epicharis*** (Figure 107; Pejler & Bērziņš 1993a), ***D. facinus*** (Figure 108; Myers 1942), ***D. hercules*** (Bielańska-Grajner *et al.* 2011), ***D. isothes*** (Figure 109; Jersabek *et al.* 2003), ***D. luetkeni*** (Figure 110-Figure 112; Jersabek *et al.* 2003; Bielańska-Grajner *et al.* 2011), and ***D. proclastes*** (Myers 1942).

Figure 101. ***Dicranophorus alcimus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 102. ***Dicranophorus artamus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 103. ***Dicranophorus biastis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

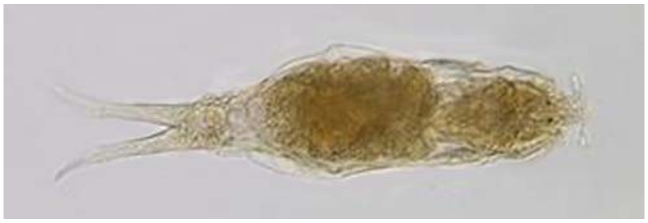

Figure 104. ***Dicranophorus capucinus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 105. ***Dicranophorus capucinus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 106. ***Dicranophorus colastes*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

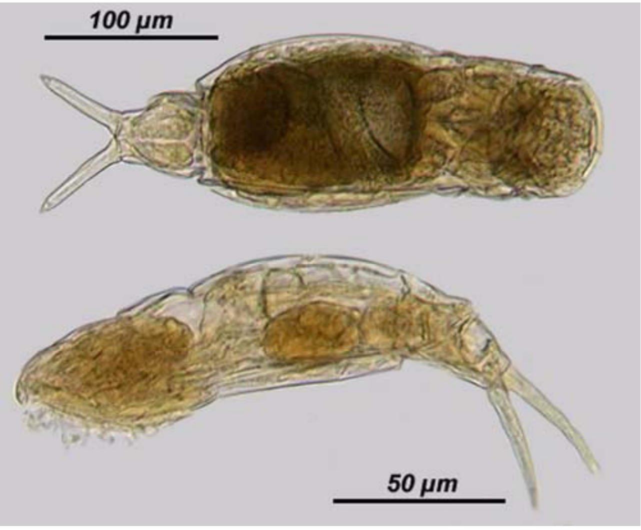

Figure 107. ***Dicranophorus epicharis***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 108. ***Dicranophorus facinus*** lives among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

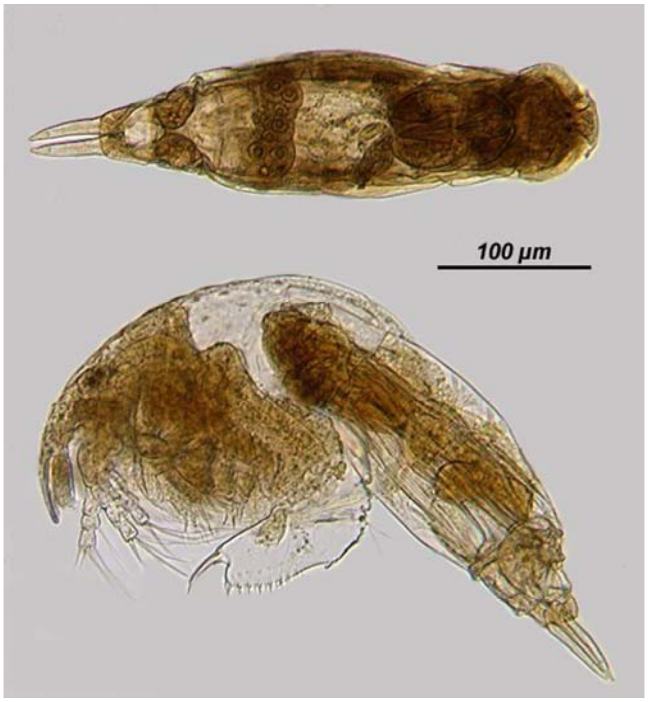

Figure 109. ***Dicranophorus isothes***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 110. ***Dicranophorus luetkeni*** female, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 111. ***Dicranophorus luetkeni*** male, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 112. ***Dicranophorus luetkeni*** female with egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Dicranophorus robustus (Figure 113-Figure 114), like several other members of the **Dicranophoridae**, occurs on both the bog moss ***Sphagnum*** (Figure 21) and the brook moss ***Fontinalis*** (Figure 11) (Hingley 1993; Pejler & Bērziņš 1993a). It commonly ingests members of the rotifer genus ***Lecane*** (Figure 115), a very large genus that is abundant on bryophytes (Jersabek *et al*. 2003). This dual habitat of ***Sphagnum*** and ***Fontinalis*** also works for ***D. rostratus*** (Figure 116; Hingley 1993; Jersabek *et al*. 2003).

Figure 113. ***Dicranophorus robustus*** from *Aufwuchs*, a species found with bryophytes, including ***Sphagnum*** and ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 114. ***Dicranophorus robustus*** female, a species that is known to live among bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 115. ***Lecane clara***, without stiffened lorica. Members of ***Lecane*** serve as food for ***Dicranophorus robustus***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 116. ***Dicranophorus rostratus*** female, a species known from ***Sphagnum*** (Myers 1942) and ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

Some species are known thus far only from ***Fontinalis*** (Figure 11). Among these is ***Dicranophorus forcipatus*** (Figure 117-Figure 118) (Pejler & Bērziņš 1993a; Plewka 2016), including its occurrence on Svalbard exclusively on submerged mosses (De Smet 1993).

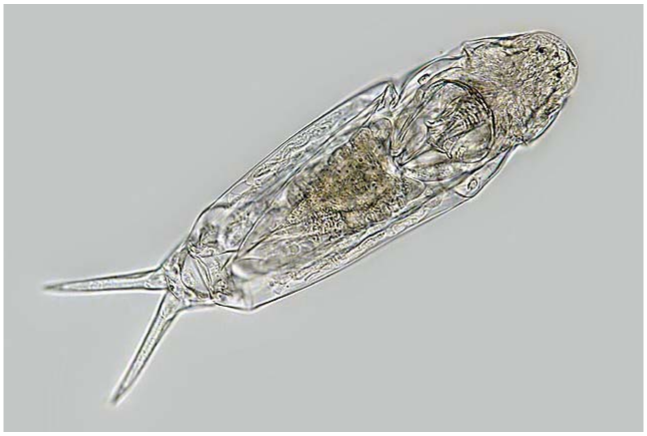

Figure 117. ***Dicranophorus forcipatus***, a rotifer found among bryophytes in several studies, including ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 118. ***Dicranophorus forcipatus***, a rotifer found among bryophytes in several studies, shown here feeding on the surfacce of ***Spirogyra*** sp. Photo by Michael Plewka <www.plingfactory.de>, with permission.

The aquatic ***Dicranophorus hercules*** (Figure 119) is known from bryophytes (Jersabek *et al*. 2003), but its typical habitat is in the **psammon** (interstitial community among sand grains in fresh water) (Ruttner-Kolisko 1954; Pejler & Bērziņš 1993b). In fact, Wizsniewski (1934, 1937) considered this species to be exclusive to the psammon. Nevertheless, Bielańska-Grajner *et al*. (2011) found it among the peatland bryophytes in Poland.

Figure 119. ***Dicranophorus hercules***, a species known from bryophytes. Photo by Jersabek *et al*. 2003, with permission.

Dorria

Dorria dalecarlica (Figure 121) is the only species in the genus (Segers 2007) and is a moss dweller in aquatic habitats, where it lives on dripping and submersed ***Fontinalis dalecarlica*** (Figure 11) (Myers 1942).

Figure 120. ***Dorria dalecarlica***, a species that can occur on submerged mosses in streams. Photos by Jersabek *et al.* 2003, with permission.

Figure 121. ***Dorria dalecarlica***, a species that can occur on submerged mosses in streams. Photos by Jersabek *et al*. 2003, with permission.

Encentrum

The genus ***Encentrum*** is a large genus with a number of species that live on bryophytes. ***Sphagnum*** (Figure 21, Figure 66) dwellers include ***E. aquilus*** (Figure 122; Jersabek *et al*. 2003), ***E. arvicola*** (Pejler & Bērziņš 1993a), ***E. carlini*** (Figure 123; Jersabek *et al*. 2003), ***E. elongatum*** (Pejler & Bērziņš 1993a), ***E. felis*** (Figure 124-Figure 125; Hingley 1993; Jersabek *et al*. 2003), ***E. glaucum*** (Figure 126; Hingley 1993), ***E. incisum*** (Figure 127; Pejler & Bērziņš 1993a), ***E. saundersiae*** (Figure 128; Myers 1942), ***E. sutor*** (Pejler & Bērziņš 1993a), ***E. sutoroides*** (Pejler & Bērziņš 1993a), ***E. tobyhannaense*** (Figure 129; Jersabek *et al*. 2003), and ***E. tyrphos*** (Pejler & Bērziņš 1993a).

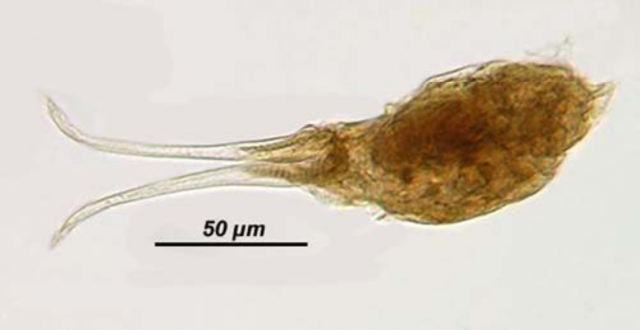

Figure 122. ***Encentrum aquilus***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

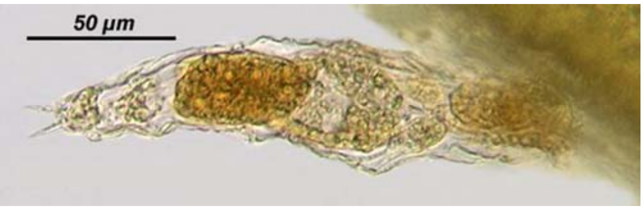

Figure 123. ***Encentrum carlini***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Figure 124. ***Encentrum felis*** with protruding forcipate trophi. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 125. ***Encentrum felis***, a species known from bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 126. ***Encentrum glaucum*** female, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 127. ***Encentrum oxyodon/E. incisum***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

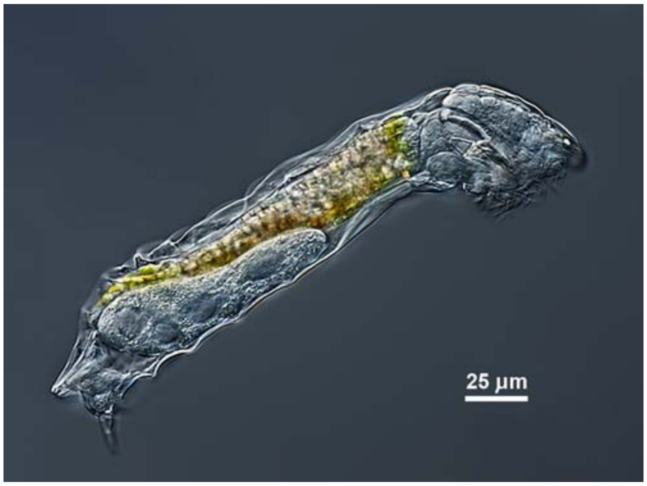

Figure 128. ***Encentrum saundersiae*** lateral view, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 129. Trophus of ***Encentrum tobyhannaensis*** from among ***Sphagnum***. Often this is the only structure that can be recognized in old collections. Photo by Jersabek *et al.* 2003, with permission.

As seems to be a common feature of this family, several species live on both ***Sphagnum*** (Figure 21, Figure 66) and ***Fontinalis*** (Figure 11). These are ***Encentrum lupus*** (Pejler & Bērziņš 1993a), ***E. mustela*** (Figure 130) (Hingley 1993; Pejler & Bērziņš 1993a), and ***E. uncinatum*** (Figure 131; Horkan 1981; Hingley 1993; Pejler & Bērziņš 1993a; Plewka 2016). ***Encentrum eurycephalum*** and ***E. fluviatile***, on the other hand, are only known from ***Fontinalis*** (Pejler & Bērziņš 1993a). ***Encentrum mucronatum*** and ***E. uncinatum*** live on submerged mosses on Svalbard, where the former is one of the most frequent species (De Smet 1990); ***E.*** cf. ***marinum*** (Figure 132) lives exclusively among submerged mosses on Svalbard, whereas ***E. mustela*** occurs on submerged mosses and in the plankton (De Smet 1993).

Figure 130. ***Encentrum mustela***, a species that occurs on both ***Sphagnum*** and ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 131. ***Encentrum uncinatum*** swimming. This species is known from the brook moss ***Fontinalis*** and the bog moss ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 132. ***Encentrum marinum***, a species that occurs exclusively among submerged mosses on Svalbard. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Encentrum lutra (Figure 133) also lives in the unpredictable habitat of epiphytic mosses (Plewka 2016). The habitat of ***E. permolle*** (Figure 134) is on moss (Plewka 2016) in Antarctic islands (Fontaneto *et al*. 2015).

Figure 133. ***Encentrum lutra***, a species that lives among epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

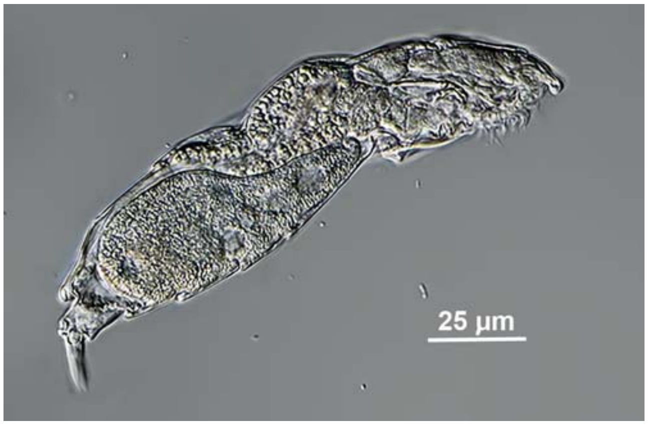

Figure 134. ***Encentrum permolle***, a moss dweller in the Antarctic. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Pedipartia

Pedipartia is a genus with only one species, ***P. gracilis*** (Figure 135) (Segers 2007). This rotifer species is known from just one species of ***Sphagnum***, ***S. subsecundum*** (Figure 61-Figure 62) (Myers 1942; Jersabek *et al*. 2003).

Figure 135. ***Pedipartia gracilis*** from among ***Sphagnum subsecundum***. Photo by Jersabek *et al.* 2003, with permission.

Streptognatha

Streptognatha is another genus known by only one species (Segers 2007). ***Streptognatha lepta*** (Figure 136-Figure 137), a species reported in Great Britain and elsewhere, occurs on ***Sphagnum*** (Figure 21, Figure 66) (Jersabek *et al*. 2003).

Figure 136. ***Streptognatha lepta*** female, lateral view, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

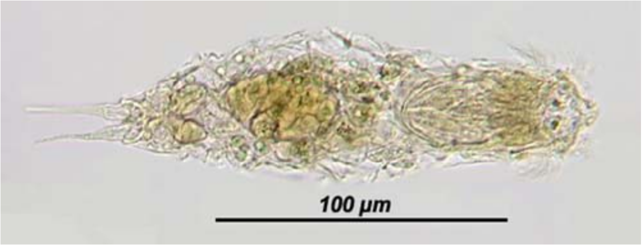

Figure 137. ***Streptognatha lepta*** female, a rotifer known to associate with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Wierzejskiella

Of the eight species (Segers 2007) of ***Wierzejskiella***, three are known bryophyte dwellers. And all three live on ***Sphagnum*** (Figure 21, Figure 66). ***Wierzejskiella elongata*** (Figure 138) lives among ***Sphagnum*** (Myers 1942). ***Wierzejskiella velox*** (Figure 139-Figure 140) occurs both among ***Sphagnum*** and in ***Sphagnum*** pools (Myers 1942).

Figure 138. ***Wierzejskiella elongata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

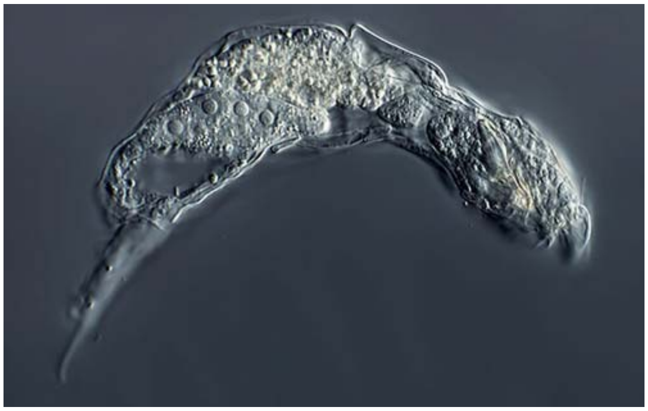

Figure 139. ***Wierzejskiella velox***, a species from ***Sphagnum*** and ***Sphagnum*** pools (Myers 1942). Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 140. ***Wierzejskiella velox*** from ***Sphagnum***, shown here with its forcipate trophi extruded as it approaches the desmid food item.. Photo by Mark Plewka <www.plingfatory.de>, with permission.

Epiphanidae

This family has rotifers that are usually planktonic, so like most of the rotifers on bryophytes, it is likely that the bryophyte is a temporary refuge. Many of the members of this family are marine (Koste 1978; Fontaneto *et al*. 2006, 2008), where no bryophytes are known.

Cyrtonia

Cyrtonia is another genus with only one species (Segers 2007), and that species is a moss dweller – ***C. tuba*** (Figure 141-Figure 142). It is known from ponds, but it has also been collected from mosses (Jersabek *et al*. 2003).

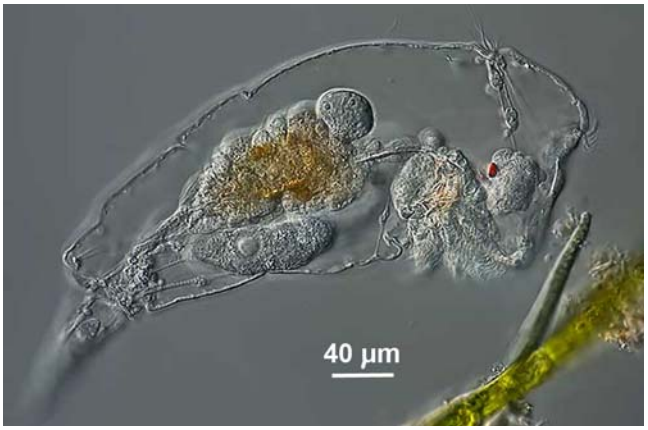

Figure 141. ***Cyrtonia tuba***, a pond and moss dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 142. ***Cyrtonia tuba*** from a pond in Ohio, USA. This species has been collected from mosses. Photo by Jersabek *et al.* 2003, with permission.

Epiphanes

This genus of nine species seems to have only one that lives with bryophytes. ***Epiphanes brachionus*** (Figure 143) lives in ***Sphagnum*** (Figure 21, Figure 66) bogs (Plewka 2016).

Figure 143. ***Epiphanes brachionus*** from a ***Sphagnum*** bog. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Mikrocodides

Mikrocodides, a genus of three species (Segers 2007), typically occurs in the plankton and among the periphyton. One species, ***Mikrocodides chlaena*** (Figure 144-Figure 146), however, lives among mosses and in bog pools (Plewka 2016).

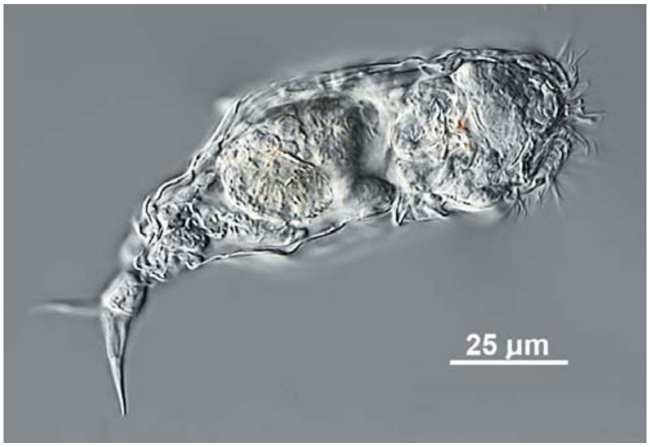

Figure 144. ***Mikrocodides chlaena***, a species that occurs among mosses and in bog pools. Photo by Michael Plewka <www.plingfactory.de>, with permission.

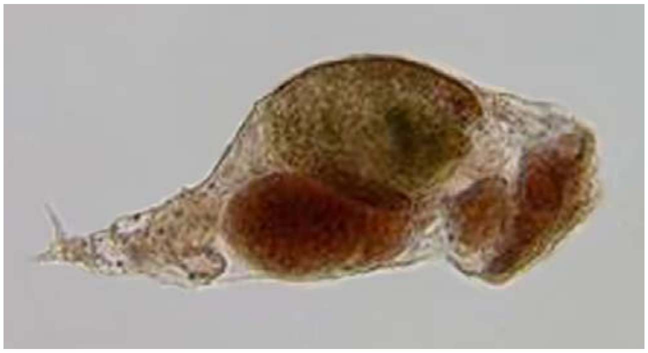

Figure 145. ***Mikrocodides chlaena*** female from New Jersey, USA. This species has been collected from mosses and from bog pools. Photos by Jersabek *et al.* 2003, with permission.

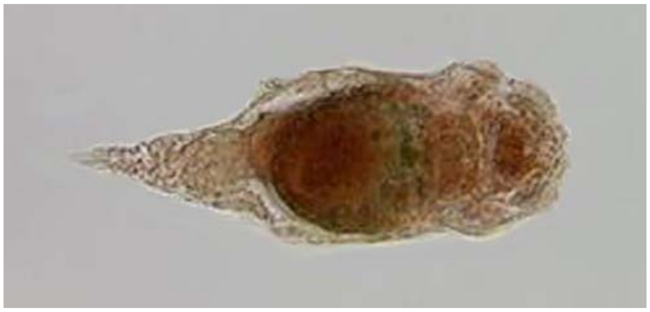

Figure 146. ***Mikrocodides chlaena*** female from New Jersey, USA. This species has been collected from mosses and from bog pools. Photos by Jersabek *et al.* 2003, with permission.

Euchlanidae

This family is characterized by a lorica consisting of connected plates (Koste & Shiel 1989). The toes are elongated. Of the five genera in the family, only ***Euchlanis*** is known from mosses.

Sphagnum (Figure 21, Figure 66), as usual, is a common substrate, with a number of species of ***Euchlanis*** associated with it. These include ***E. callysta*** (Figure 147), ***E. calpidia*** (Figure 148-Figure 149, ***E. dilatata*** (Figure 156-Figure 157), ***E. incisa*** (Figure 150) and ***E. triquetra*** (Figure 151-Figure 155) (Błedzki & Ellison 2003; Jersabek *et al*. 2003).

Figure 147. ***Euchlanis callysta*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 148. ***Euchlanis calpidia*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 149. ***Euchlanis calpidia*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

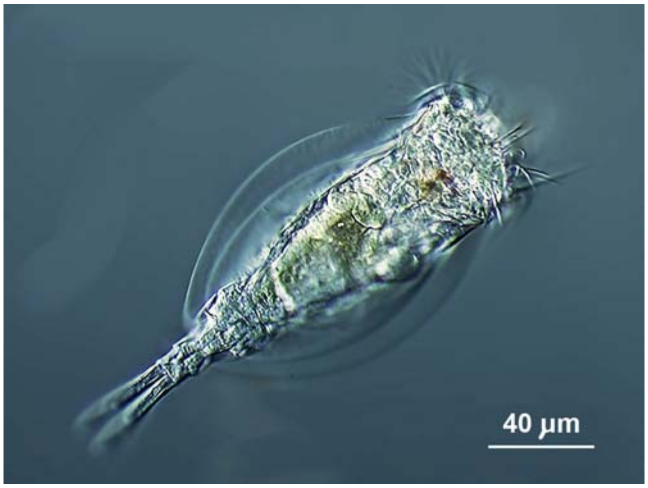

Figure 150. ***Euchlanis incisa*** from ***Fontinalis***. Photo by Michael Plewka <www. plingfactory.de>, with permission.

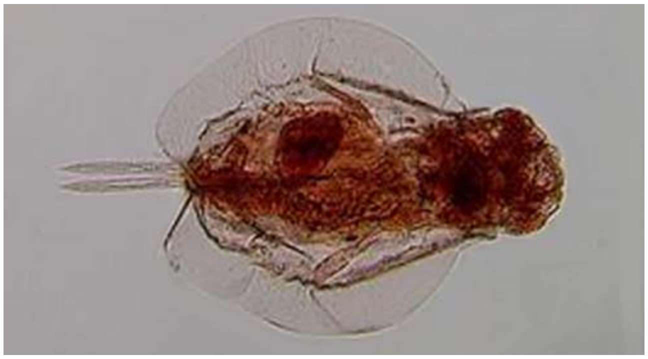

Figure 151. ***Euchlanis triquetra*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 152. ***Euchlanis triquetra*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

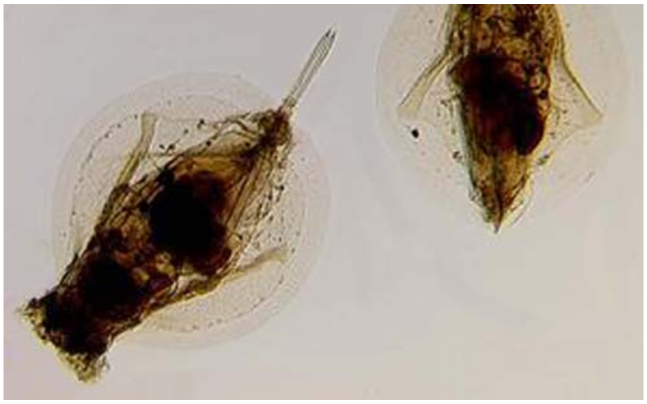

Figure 153. ***Euchlanis triquetra*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

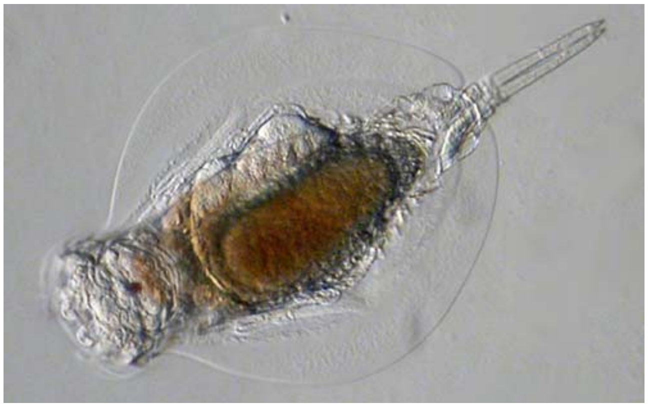

Figure 154. ***Euchlanis triquetra***, a species known from ***Sphagnum*** bogs. Photo by Mark Plewka <www.plingfactory.de>, with permission.

Figure 155. ***Euchlanis triquetra*** with expelled resting egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

There seems to be a paucity of studies on rotifers beyond listing the taxa present in various water bodies. But in the **Euchlanidae**, at least one species that is known from ***Sphagnum*** (Figure 21, Figure 66) seems to have been the subject of several kinds of biological studies. For example, ***Euchlanis dilatata*** (Figure 156-Figure 157) has proven its ability to serve as a sensitive biomonitor (Sarma *et al.*

2001). In an experiment on herbicides, this species experienced a significant reduction in population density and rate of population increase in the presence of methyl parathion. These responses were exacerbated as the concentration of methyl parathion increased, regardless of food (**Chlorella vulgaris** – Figure 64) concentration. However, higher food concentrations served to mediate the effect on the rate of population increase.

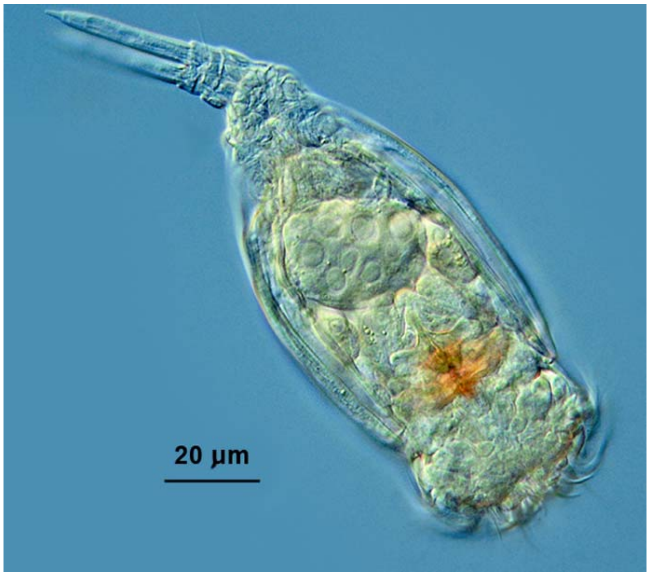

Figure 156. **Euchlanis dilatata**, a species that can occur on bryophytes and other macrophytes. Photo by Proyecto Agua Water Project, through Creative Commons.

Figure 157. **Euchlanis dilatata**, a species that has been collected from bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Euchlanis dilatata (Figure 156-Figure 157) is a benthic-periphytic species known from littoral zones of small bodies of eutrophic waters (de Manuel Barrabin 2000), but can occur on bryophytes (Jersabek 2016) and other macrophytes (Plewka 2016). On Svalbard, it occurs exclusively on submerged mosses, along with **E. deflexa** (Figure 159) and **E. meneta** (Figure 158) (De Smet 1988, 1993). **Euchlanis dilatata** occurs in both fresh water and brackish water, preferring water rich in nutrients, especially those favoring **Cyanobacteria** (de Manuel Barrabin 2000). These waters generally have a *p*H range of 6.3-9.6 and a temperature range of 6.4-24°C. Although only 200 µm long, this species is consumed by damselfly naiads (Ejsmont-Karabin *et al.* 1993). In the lab, it is able to survive on **Cyanobacteria** [***Limnothrix*** *redekei* (Figure 160), ***Oscillatoria***. *limnetica* (Figure 161), ***Aphanizomenon*** *flos-aquae* (Figure 162), ***Anabaena*** sp. (Figure 163)], all genera that can be found with ***Sphagnum***, and a prochlorophyte (*Prochlorothrix hollandica*) (Gulati *et al.* 1993). In the field ***E. dilatata*** consumes detritus, bacteria, **Cyanobacteria**, and the diatom ***Cyclotella*** (Figure 164) (Carlin 1943), all likewise present among ***Sphagnum***. It often benefits from the convenience of attaching to planktonic algae colonies (Pejler 1962).

Figure 158. **Euchlanis meneta**, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 159. **Euchlanis deflexa**, an occupier of submerged mosses on Svalbard. Photo by Jersabek *et al.*, with permission.

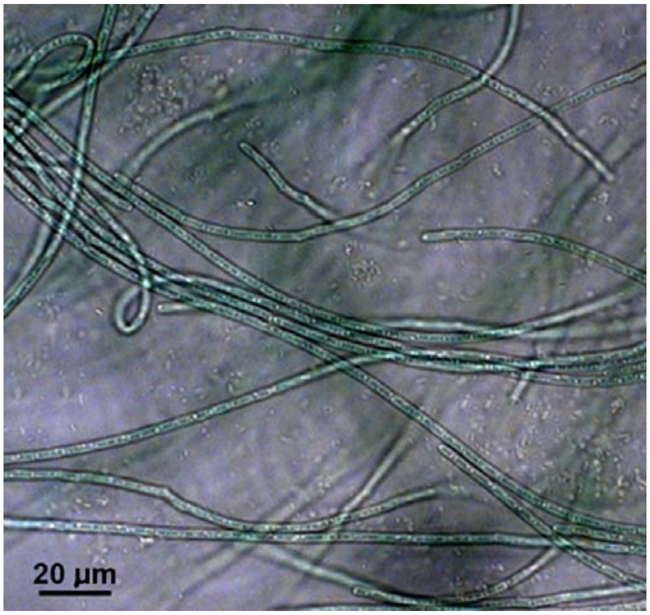

Figure 160. **Limnothrix redekei**, food for **Euchlanis dilatata**. Photo by Matt Pano, through Creative Commons.

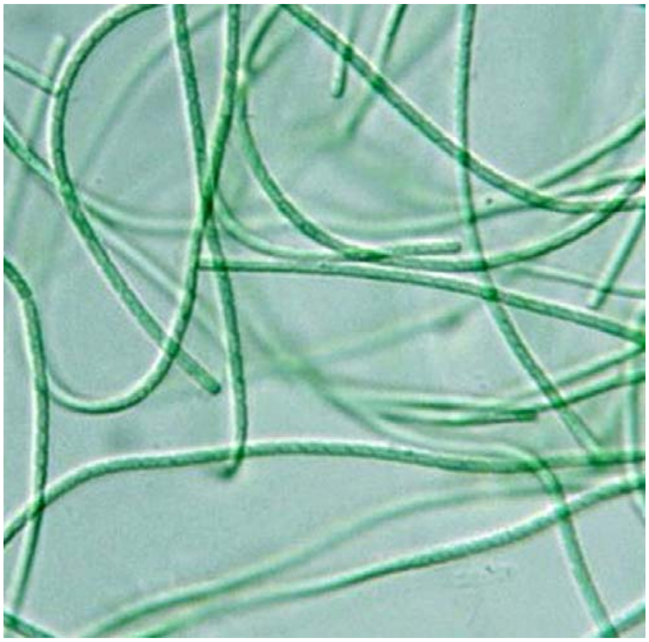

Figure 161. ***Oscillatoria limnetica***, food for ***Euchlanis dilatata***. Photo by Yuuji Tsukii, with permission.

Figure 162. ***Aphanizomenon flos-aquae***, food for ***Euchlanis dilatata***. Photo by Nordic Microalgae <www.nordicmicroalgae.org>, with online permission.

Figure 163. ***Anabaena***, food for ***Euchlanis dilatata***. Photo by Jason Oyadomari, with permission.

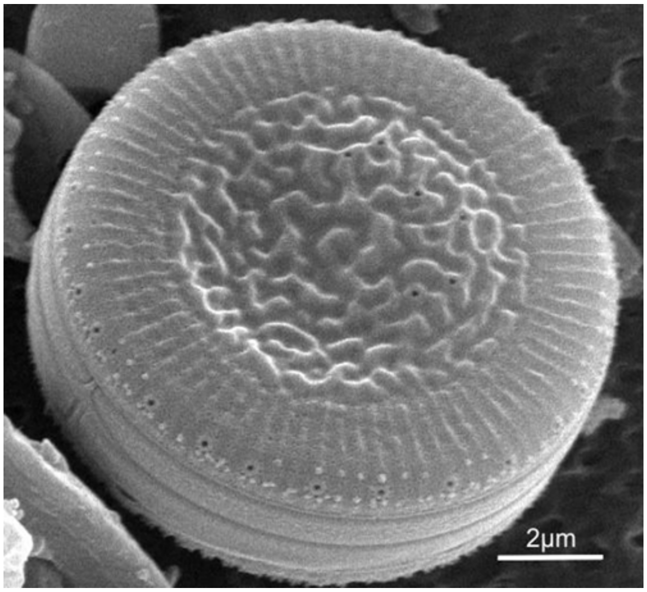

Figure 164. ***Cyclotella caspia***, food for ***Euchlanis dilatata***. Photo by Janina Kownacka, Nordic Microalgae <www.nordicmicroalgae.org>, with online permission.

Euchlanis incisa (Figure 165-Figure 167) is likewise a ***Sphagnum*** (Figure 21-Figure 66) dweller, in the northeastern USA (Błedzki & Ellison 2003), but it is also known from the non-bog aquatic moss ***Fontinalis*** (Figure 11) (Plewka 2016).

Figure 165. ***Euchlanis incisa*** female, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 166. ***Euchlanis incisa***, a species known from bryophytes, including ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 167. ***Euchlanis incisa***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

In addition to ***Sphagnum***, other bryophytes may be substrates for members of ***Euchlanis***. ***Euchlanis meneta*** (Figure 158-Figure 168) is among the dominant rotifers on mosses on Devon Island, Baffin Bay, Canada (De Smet & Beyens 1995). This species is also known from the other end of the Earth, from New Zealand (Shiel & Green 1996).

Figure 168. ***Euchlanis meneta*** female, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Euchlanis oropha (Figure 169) is a widespread **rheophilic** (loving flowing water) species that can occur on mosses, among other substrates.

Figure 169. ***Euchlanis oropha*** female, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Gastropodidae

This family is distinguished by its oval shape and sac-like or compressed body plan. It has a thin shell that surrounds the entire body with only a small opening for the head and ventrally located foot (Figure 170-Figure 173) that is sometimes absent. The family occurs primarily in fresh water, with few marine species. There are two genera, but only members of ***Gastropus*** seem to have been collected from bryophytes. Of the three species in this genus, two are known bryophyte dwellers: ***G. hyptopus*** (Figure 170-Figure 171) and ***G. minor*** (Figure 172) (Plewka 2016). ***Gastropus stylifer*** lives on submerged mosses in trenches of Alaskan polygons (Segers *et al.* 1996).

Figure 170. ***Gastropus hyptopus***, a moss dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 171. ***Gastropus hyptopus***, a species known from bryophytes and from bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 172. ***Gastropus minor*** lateral view, a bryophyte dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 173. ***Gastropus minor*** female, a species known from ***Sphagnum*** bogs. Note the ventral foot. Photo by Jersabek *et al.* 2003, with permission.

Summary

The rotifers in **Monogononta** are often represented on bryophytes, especially in peatlands. The Class **Monogononta** has three orders and is the largest class of rotifers. Many members of order **Collothecacea** are sessile. Some members of family **Collothecidae** are known from ***Riccia fluitans***, ***Sphagnum***, and other bryophytes. Members of the order **Flosculariacea** are suspension feeders, and known bryophyte dwellers include members of **Conochilidae**, **Filiniidae**, **Flosculariidae**, **Hexarthriidae**, and **Testudinellidae**. The order **Ploimida** includes both planktonic and non-planktonic families that are known from bryophytes. Those included in this subchapter are **Brachionidae**, **Dicranophoridae**, **Epiphanidae**, **Euchlanidae**, and **Gastropodidae.** Additional families are in the next sub-chapters.

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CHAPTER 4-7b

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

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CHAPTER 4-7b

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

Figure 1. Lecane stokesii, a monogonont rotifer that can be found among bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Taxa on Bryophytes, Ploimida continued

Lecanidae

The **Lecanidae** were represented by the second highest number of species among rotifers in the reservoirs in Spain (de Manuel Barrabin 2000) and their species are well represented among those rotifers collected with bryophytes as well (*e.g.* Jersabek et al. 2003). One reason for this is that the family has only one, but a very large, genus – ***Lecane***. The genus ***Lecane*** is the second largest genus of rotifers, with at least 160 species (Segers 1995).

Not surprisingly, there are a number of ***Lecane*** species living in ***Sphagnum*** (Figure 1, Figure 2). One of the early reports including ***Sphagnum*** dwellers was that of Harring (1915) in Panama. These included ***L. bifurca*** (Figure 3; see also Myers 1942), ***L. flexilis*** (Figure 4-Figure 5; see also Bielańska-Grajner *et al.* 2011), ***L. inermis*** (Figure 7-Figure 8), ***L. monostyla*** (Figure 9; see also Bielańska-Grajner *et al.* 2011), and ***L. tenuiseta*** (Figure 10; see also Bielańska-Grajner *et al.* 2011). The ***Sphagnum*** associates include those in bogs and fens. Błedzki and Ellison (2002) found ***Lecane pyriformis*** (Figure 11) and ***L. lunaris*** (Figure 44-Figure 45) to be among the abundant ***Sphagnum*** dwellers in their study. To these, Bielańska-Grajner *et al.* (2011) added ***L. bulla*** (Figure 12-Figure 13), ***L. intrasinuata*** (Figure 14), ***L. luna*** (Figure 15), and ***L. perpusilla*** as bog dwellers. But ***Sphagnum*** fauna records must be viewed with caution. Methods using pore water often miss the relatively immobile rotifers that live on mosses (Sakuma *et al.* 2002).

Figure 2. ***Sphagnum*** and ***Potentilla tridentata***, home for many kinds of rotifers. Photo by Nancy Leonard, with permission.

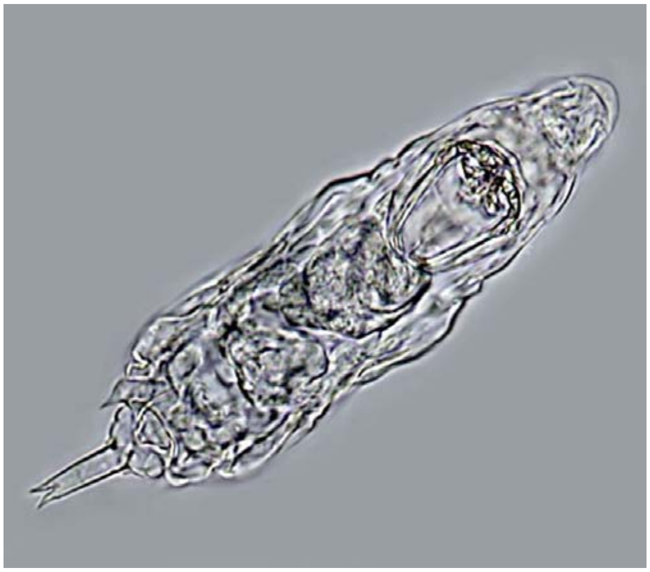

Figure 3. ***Lecane bifurca*** lives among mosses, including ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Hingley likewise found ***Lecane flexilis*** (Figure 4-Figure 5; see also Bielańska-Grajner *et al*. 2011) among ***Sphagnum*** (Figure 2), but Jersabek *et al*. (2003) further reported it from the floating thallose liverwort, ***Riccia fluitans*** (Figure 6). This rotifer species occurs infrequently in the plankton, preferring instead the littoral (near shore) zone (de Manuel Barrabin 2000). It occurs more frequently in alkaline habitats (Pejler 1962; Koste 1978) in a *p*H range of 6.64-7.87, although Koste and Shiel (1990) found it in slightly acidic water. Its wide temperature range (9.50-21.13°C) permits it to be cosmopolitan (de Manuel Barrabin 2000).

Figure 4. ***Lecane flexilis***, a species known from bogs and from the thallose liverwort ***Riccia fluitans*** in ponds. Photo by Jersabek *et al.* 2003, with permission.

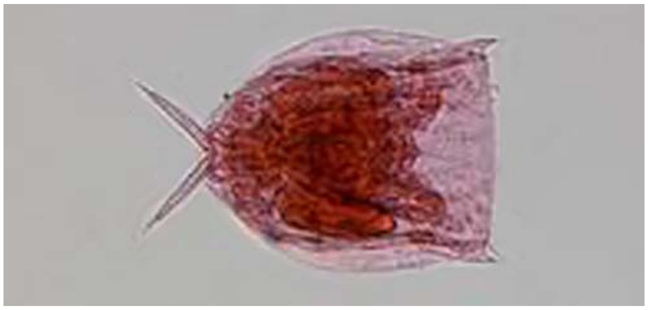

Figure 5. ***Lecane flexilis***, a species known from ***Riccia fluitans*** in ponds. Photo by Jersabek *et al.* 2003, with permission.

Figure 6. ***Riccia fluitans***, a floating liverwort that is home to ***Lecane flexilis***. Photo by Jan-Peter Frahm, with permission.

In ***Lecane inermis*** (Figure 7-Figure 8), a ***Sphagnum*** (Figure 2) dweller, **mictic** (producing eggs that without fertilization develop into males but with fertilization form resting eggs that later develop into amictic females) females have the longest lives of 11.1 ± 0.28 days, followed by amictic females with a lifespan of 8.9 ± 0.11 days, and the shortest lifespan in males at 5.7 ± 0.07 days (Miller 1931). In males, death of 83% of the population occurs in the four to six days. Sexual females lay one egg every 8.6 hours, whereas the **amictic** (producing eggs that develop without fertilization) female lays one every 7.5 hours. Amictic females usually die within 24-36 hours after laying the last egg, but among the mictic females, 19% live six more days after depositing eggs. Typically, ***Lecane inermis*** is a littoral species that also occurs in warm water such as thermal springs and geysers (de Manuel Barrabin 2000). Its typical temperature is around 19.4°C, but it can be found near geysers at temperatures up to 62.5°C. Its environmental *p*H is usually around 7.3.

Figure 7. ***Lecane inermis***, a ***Sphagnum*** dweller. The upper image is in the extended state, the lower one in the contracted state. Photo by Jersabek *et al*. 2003, with permission.

Figure 8. ***Lecane inermis***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 9. ***Lecane monostyla***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Lecane tenuiseta (Figure 10) is typically a littoral species, known from a *p*H around 7.9 and a temperature around 13.5°C (de Manuel Barrabin 2000). Although it is cosmopolitan, its restricted habitat requirements make it relatively rare.

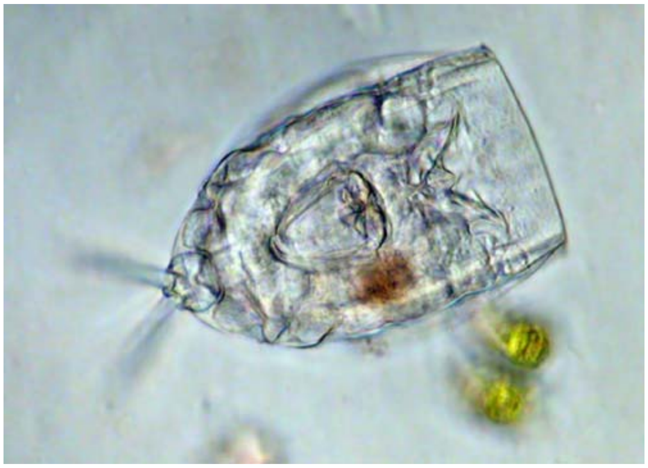

Figure 10. ***Lecane tenuiseta***, typically a littoral species, sometimes living among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 11. ***Lecane pyriformis***, an abundant bog dweller. Photo by Jersabek *et al.* 2003, with permission.

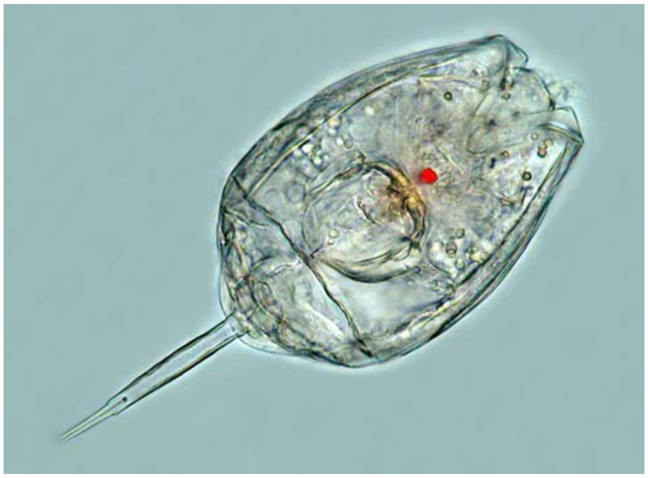

Figure 12. ***Lecane bulla*** from leaf litter, also a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 13. ***Lecane bulla*** resting egg inside its deceased mother. Photo by Michael Plewka <www.plingfactory.de>, with permission.

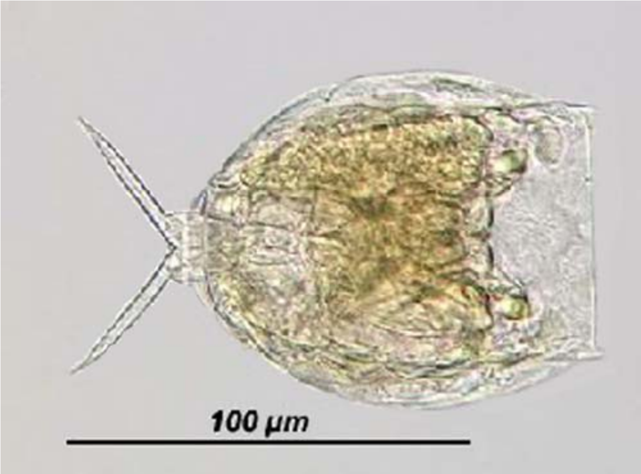

Figure 14. ***Lecane intrasinuata***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

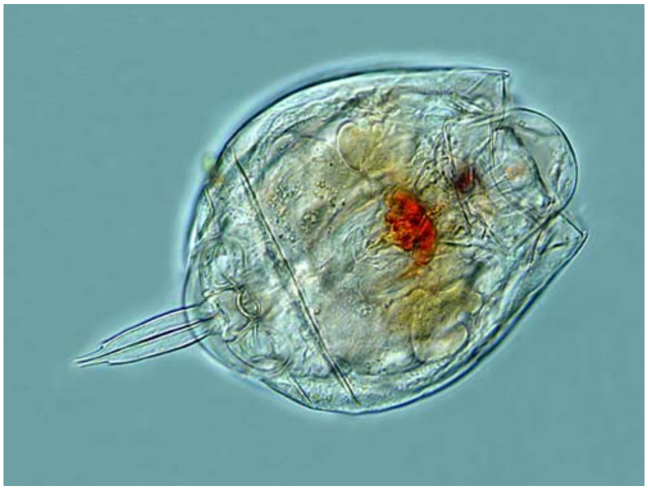

Figure 15. ***Lecane luna*** from among water plants, also a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

One of the most extensive treatments of North American rotifers is that of Myers (1942) for the Poconos in Pennsylvania, USA. He considered ***Lecane obtusa*** (Figure 16), ***L. opias*** (Figure 17; see also Bielańska-Grajner *et al.* 2011), and ***L. subulata*** (Figure 18-Figure 19) to be small species that are common among ***Sphagnum*** (Figure 2). In that same publication, he reported ***L. depressa*** (Figure 20-Figure 21; see also Hingley 1993), ***L. formosa***, ***L. furcata*** (Figure 22), ***L. niothis***, ***L. pumila*** (Figure 23), ***L. rhytida***, ***L. scutata*** (Figure 24; see also Koste & Shiel 1990; Bielańska-Grajner *et al.* 2011), ***L. subtilis*** (Figure 25; see also Bielańska-Grajner *et al.* 2011), ***L. tryphema*** (Figure 26), and ***L. verecunda*** (Figure 27) from ***Sphagnum***. He also reported ***L. dysoarata*** (Figure 28) from the emergent species ***Sphagnum cuspidatum*** (Figure 29). Horkan (1981) reported ***L. quadridentata*** (Figure 30-Figure 31) from bog pools.

Figure 16. ***Lecane obtusa***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 17. ***Lecane opias***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 18. ***Lecane subulata*** from among ***Sphagnum*** (Myers 1942). Photo by Jersabek *et al.* 2003, with permission.

Figure 19. ***Lecane subulata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 20. ***Lecane depressa***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

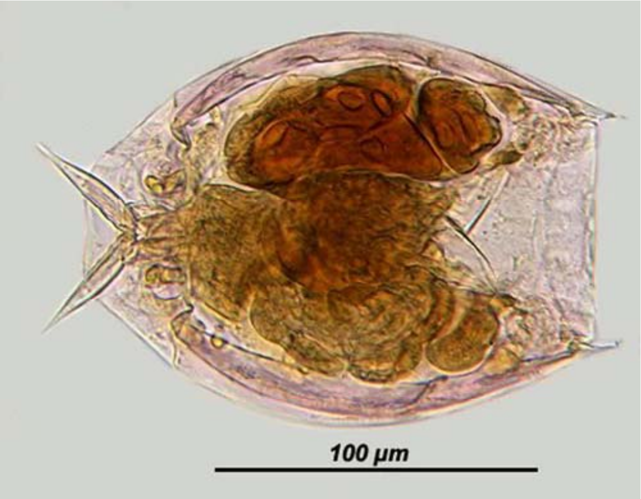

Figure 21. ***Lecane depressa***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

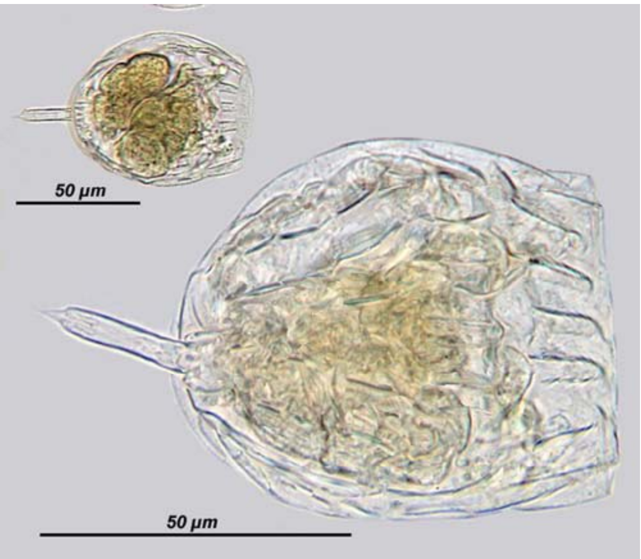

Figure 22. ***Lecane furcata***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 23. ***Lecane pumila***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Lecane scutata (Figure 24) occurs in the littoral zone of lakes where it lives on plant surfaces (de Manuel Barrabin 2000). It is an acidophile, commonly living among ***Sphagnum*** (Figure 2) (Myers 1942; Koste & Shiel 1990), but it is cosmopolitan and probably not restricted to strongly acid habitats (de Manuel Barrabin 2000).

Figure 24. ***Lecane scutata***, a ***Sphagnum*** dweller and acidophile. Photo by Jersabek *et al.* 2003, with permission.

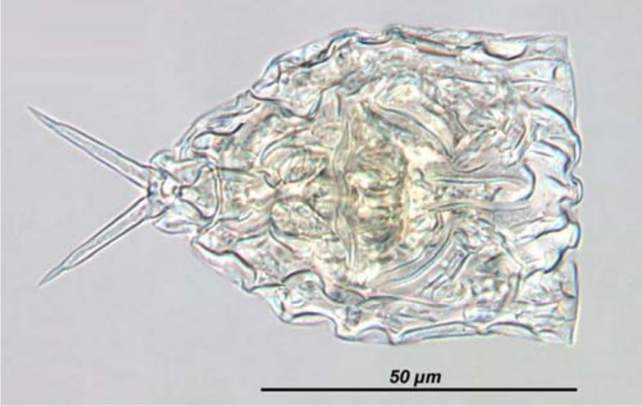

Figure 25. ***Lecane subtilis***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

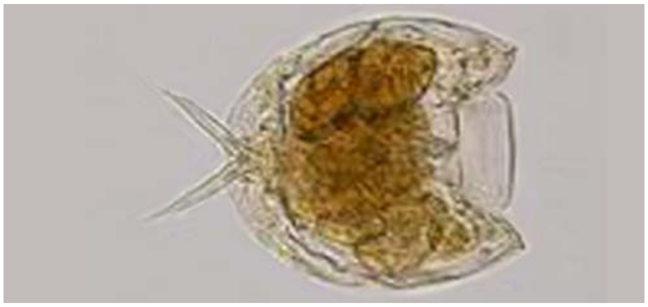

Figure 26. ***Lecane tryphema*** in a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

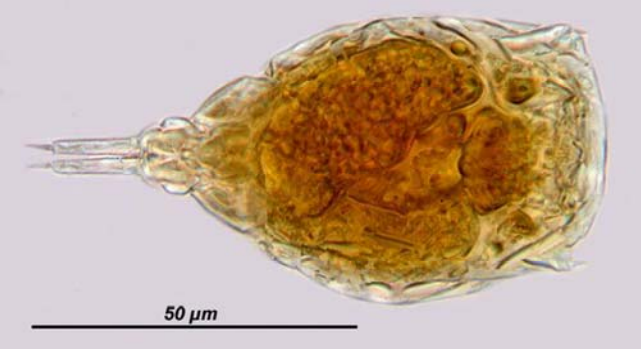

Figure 27. ***Lecane verecunda***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Figure 28. ***Lecane dysoarata***, a ***Sphagnum cuspidatum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

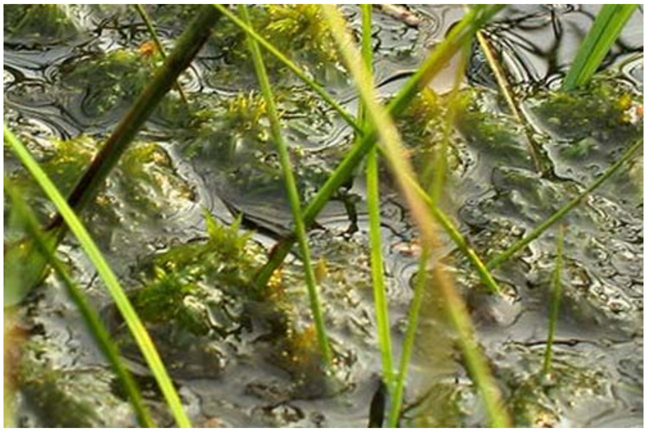

Figure 29. ***Sphagnum cuspisdatum***, home for ***Lecane quadridentata***. Photo by Andrew Spink, with permission.

Figure 30. ***Lecane quadridentata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

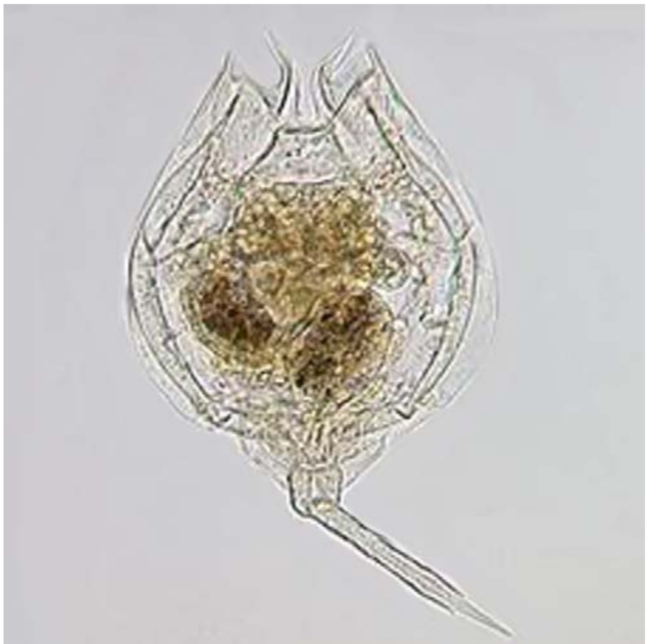

Figure 31. ***Lecane quadridentata*** from a lake in Pennsylvania, USA. This species has been collected from bryophytes and from bog pools. Photo by Jersabek *et al.* 2003, with permission.

Hingley (1993) published a manual on the microscopic life in ***Sphagnum*** (Figure 2), including the rotifer fauna. Her records included ***L. agilis*** (Figure 32), ***L. clara*** (Figure 33-Figure 34; see also Bielańska-Grajner *et al*. 2011), ***L. closterocerca*** (Figure 35-Figure 36; see also Bielańska-Grajner *et al*. 2011), ***L. cornuta*** (Figure 37-Figure 39), ***L. galeata*** [Figure 40-Figure 41; see also Jersabek *et al*. 2003 from ***Sphagnum subsecundum*** (Figure 42) and Bielańska-Grajner *et al*. 2011], ***L. hamata*** (Figure 43; see also Bielańska-Grajner *et al*. 2011), ***L. lunaris*** (Figure 44-Figure 45; see also Madaliński 1961; Bielańska-Grajner *et al*. 2011), ***L. pyrrha*** (Figure 46), ***L. signifera*** (Figure 47), ***L. signifera ploenensis*** (Figure 48), and ***L. stichaea*** (Figure 49-Figure 50).

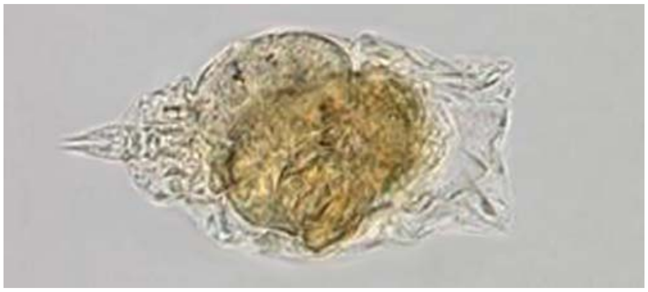

Figure 32. ***Lecane agilis***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 33. ***Lecane clara***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

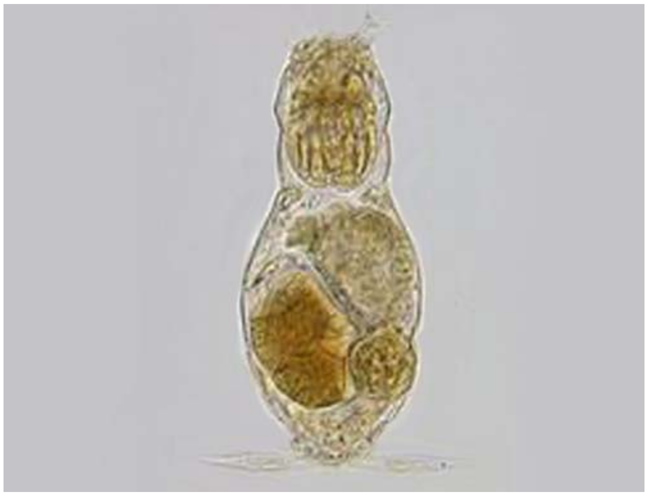

Figure 34. ***Lecane clara***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Lecane closterocerca (Figure 35-Figure 36) is a species known from bryophytes, including ***Sphagnum*** (Figure 2). This cosmopolitan littoral species is common in the plankton in a *p*H range of 6.7-9.1 and temperatures of 7.8-24°C (de Manuel Barrabin 2000). Despite its common presence in freshwater, it has a wide tolerance of salinity.

Figure 35. ***Lecane closterocerca***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 36. ***Lecane closterocerca***, a ***Sphagnum*** dweller with fused toes. Photo by Jersabek *et al.* 2003, with permission.

Figure 37. ***Lecane cornuta***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

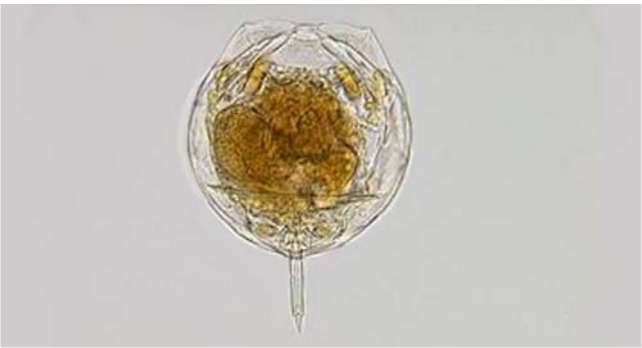

Figure 38. ***Lecane cornuta***, a species known from bryophytes**,** with foot extended. Photo by Jersabek *et al.* 2003, with permission.

Figure 39. ***Lecane cornuta***, with foot retracted. Photo by Jersabek *et al.* 2003, with permission.

Figure 40. ***Lecane*** *cf* ***galeata***, a species known from ***Sphagnum subsecundum*** (Figure 42) in bogs. Photo by Jersabek *et al.* 2003, with permission.

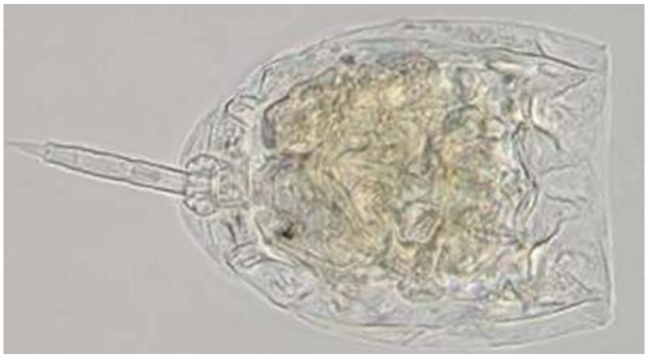

Figure 41. ***Lecane*** *cf* ***galeata***, a species known from ***Sphagnum subsecundum*** (Figure 42) in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 42. ***Sphagnum subsecudum***, home of ***Lecane galeata***. Photo by Michael Lüth, with permission.

Lecane hamata (Figure 43) is a cosmopolitan, littoral species living on plant substrata and known from bryophytes (de Manuel Barrabin 2000), including ***Sphagnum*** (Figure 2; Hingley 1993). It occurs at *p*H levels around 7.9 with a known from a temperature range of 11.9-13.5°C (de Manuel Barrabin 2000).

Figure 43. ***Lecane hamata***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Lecane lunaris (Figure 44-Figure 45) is a cosmopolitan littoral species that is frequent in the plankton (de Manuel Barrabin 2000) and is known to inhabit bryophytes, including ***Sphagnum*** (Figure 2; Hingley 1993). It is known from water that is rich in nutrients with a *p*H of 6.3-9.2 and a temperature range of 7.2-26.2°C (de Manuel Barrabin 2000).

Figure 44. ***Lecane lunaris***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 45. ***Lecane lunaris***, a species known to inhabit bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 46. ***Lecane pyrrha***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 47. ***Lecane signifera***, a species known to live among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

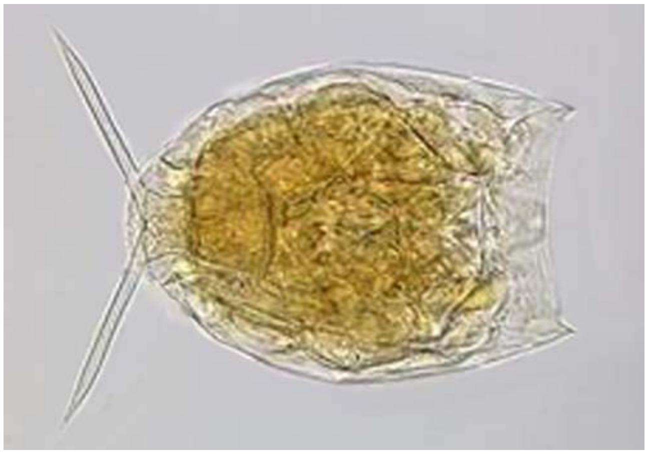

Figure 48. ***Lecane signifera ploenensis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

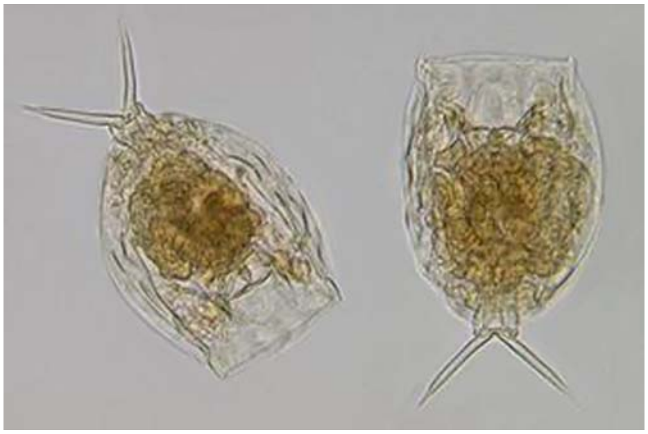

Figure 49. ***Lecane stichaea***, a species known from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 50. ***Lecane stichaea***, a rotifer associated with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

To these studies, Jersabek *et al*. (2003) added species from records at the Academy of Natural Sciences of Philadelphia. The ***Sphagnum*** (Figure 2) associates included ***Lecane calcaria*** (Figure 51), ***L. copeis*** (Figure 52), ***L. curvicornis*** (Figure 53), ***L. depressa*** (Figure 54), ***L. mira*** (Figure 55), ***L. mitis*** (Figure 56), ***L. pertica*** (Figure 57-Figure 58), ***L. psammophila*** (Figure 59), ***L. satyrus*** (Figure 60), and ***L. thalera*** (Figure 61-Figure 62). Plewka (2016) included ***L. acus*** (Figure 63) and ***L. arcula*** (Figure 64), two ***Sphagnum*** dwellers not included on the other lists here. Jersabek *et al*. (2003) reported ***L. lauterborni*** (Figure 65) from ***Sphagnum wheeleri*** in Hawaii (Figure 66).

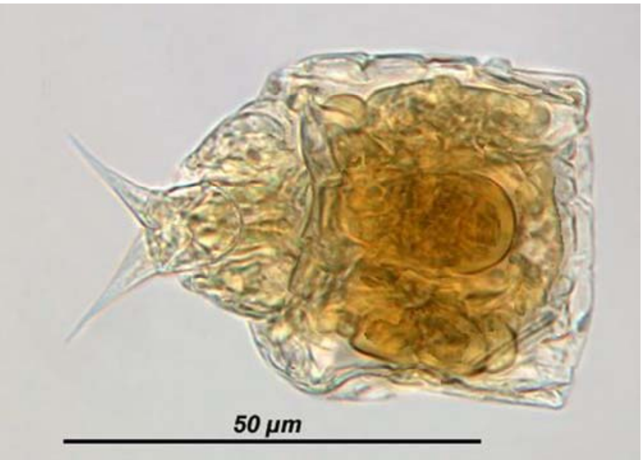

Figure 51. ***Lecane calcaria***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Figure 52. ***Lecane copeis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

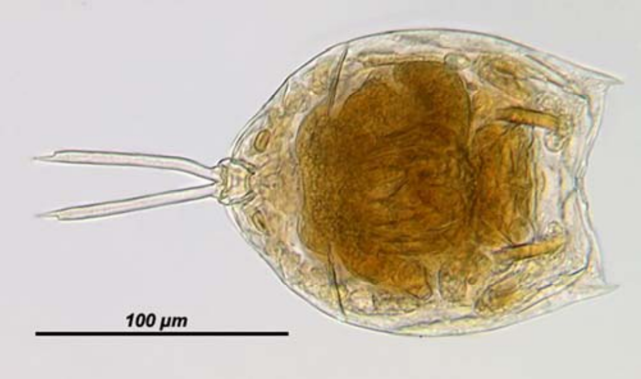

Figure 53. ***Lecane curvicornis***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 54. ***Lecane depressa*** from among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Lecane mira (Figure 55-Figure 56) is a cosmopolitan species that lives on aquatic plants, including ***Sphagnum***, and is common in somewhat acid waters, but can also be common at a *p*H around 7.2 (de Manuel Barrabin 2000). It is known from a temperature around 10.8°C.

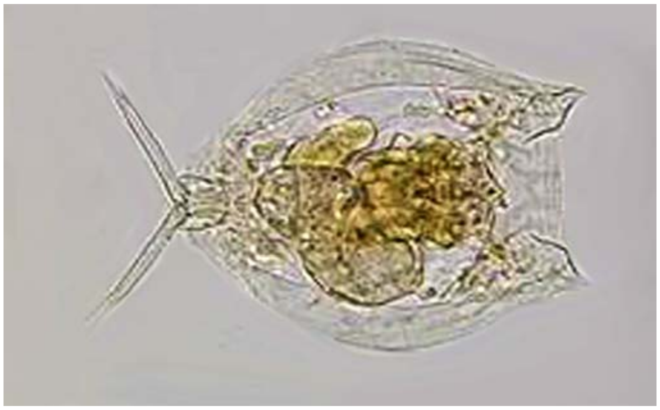

Figure 55. ***Lecane mira*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 56. ***Lecane mitis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

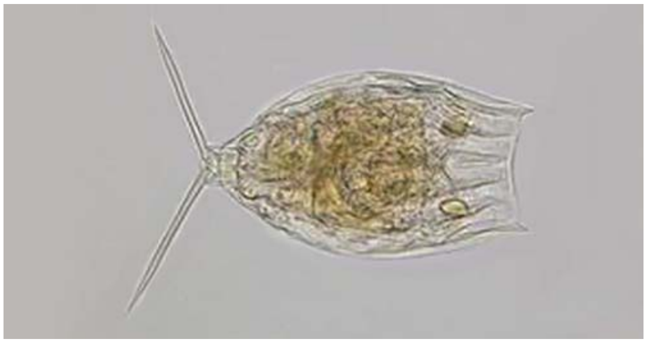

Figure 57. ***Lecane pertica*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

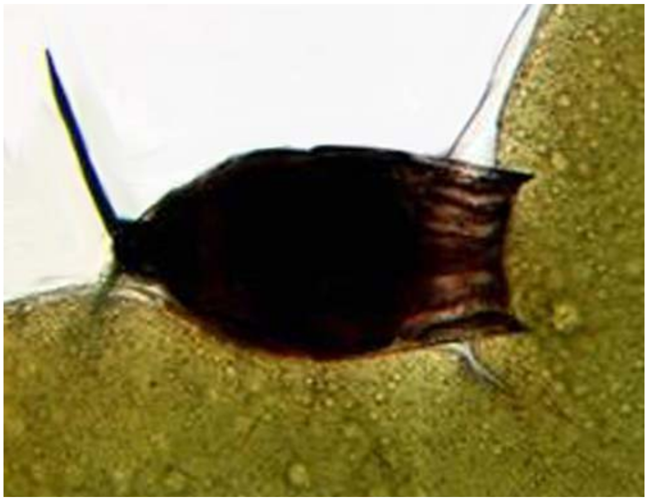

Figure 58. ***Lecane pertica***, shown here on duckweed (*Lemna*), but it also occurs among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

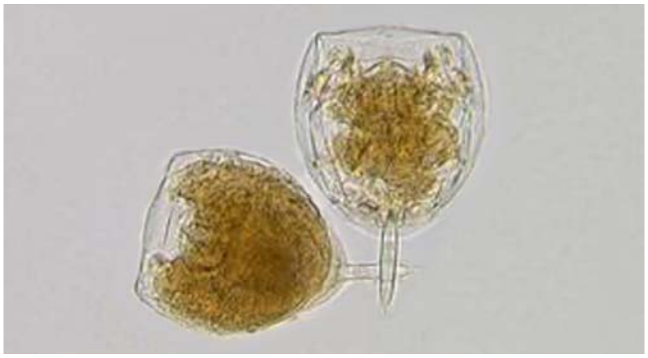

Figure 59. ***Lecane psammophila*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

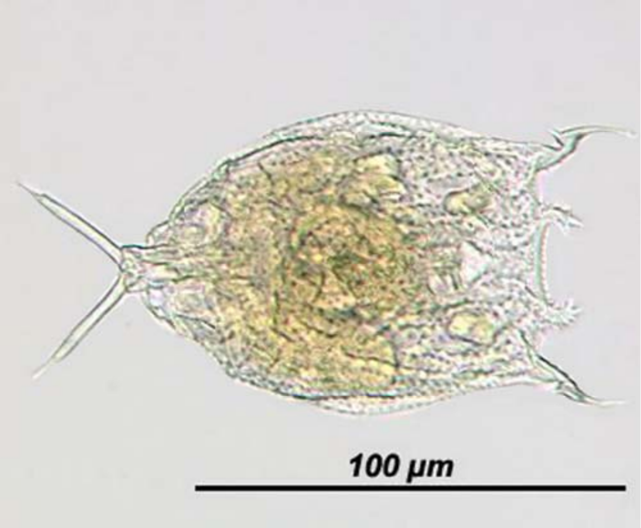

Figure 60. ***Lecane satyrus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 61. ***Lecane lamellata/thalera***, a ***Sphagnum*** dweller. These two species are difficult to distinguish and might hybridize. Photo by Jersabek *et al*. 2003, with permission.

Figure 62. ***Lecane thalera*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 63. ***Lecane acus***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 64. ***Lecane arcula***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

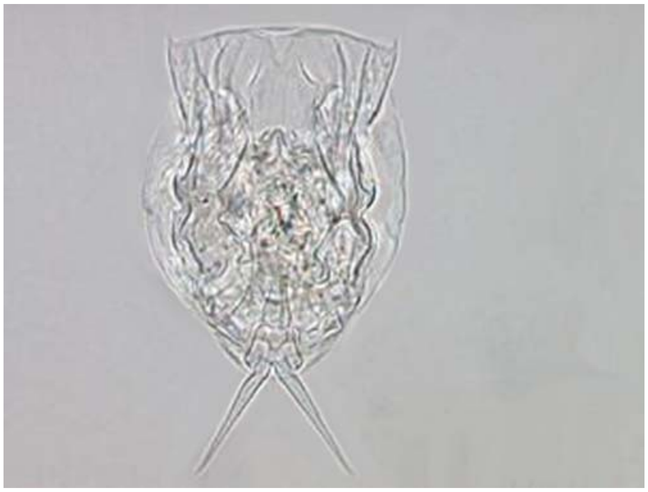

Figure 65. ***Lecane lauterborni*** from among ***Sphagnum wheeleri*** in Hawaii and ***Sphagnum*** in Pennsylvania, USA. Photo by Jersabek *et al.* 2003, with permission.

Figure 66. ***Sphagnum wheeleri***, Home for ***Lecane lauterborni*** in Hawaii. Photo by Jersabek *et al.* 2003, with permission.

Some researchers include ***Sphagnum*** (Figure 2) and "moss" (perhaps meaning ***Sphagnum***) as the rotifer habitats. Among these are ***Lecane elasma*** (Figure 67; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011), ***L. ligona*** (Figure 68; Jersabek *et al*. 2003), and ***L. stokesii*** (Figure 69) living between mosses (Plewka 2016).

Figure 67. ***Lecane elasma*** from among mosses and ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

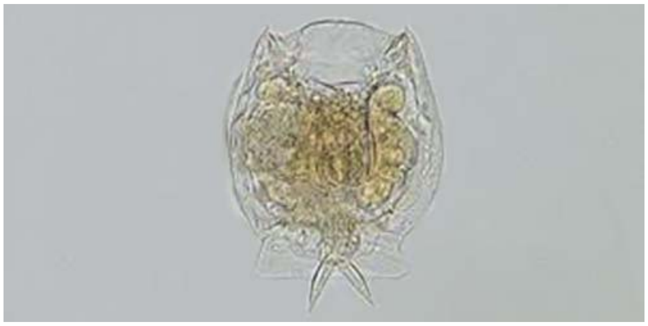

Figure 68. ***Lecane ligona*** from a ***Sphagnum*** pool. Photo by Jersabek *et al.* 2003, with permission.

A few reports simply list "moss": ***L. climacois*** (Figure 70; Myers 1942; Jersabek *et al*. 2003), ***L. rhopalura*** (Figure 71) on submerged moss (Jersabek *et al*. 2003), ***L. ungulata*** (Figure 72-Figure 74; Madaliński 1961). ***Lecane arcuata*** occurs among submerged mosses in trenches of Alaskan polygons (Segers *et al*. 1996) and wet mosses on Svalbard (De Smet 1993).

Figure 69. ***Lecane stokesii*** from between mosses, including ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 70. ***Lecane climacois*** from among mosses. Photo by Jersabek *et al.* 2003, with permission.

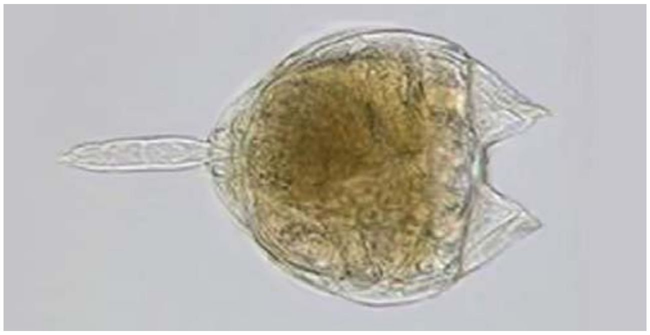

Figure 71. ***Lecane rhopalura*** from among submerged moss in a pond. Photo by Jersabek *et al.* 2003, with permission.

Figure 72. ***Lecane ungulata***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 73. ***Lecane ungulata***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

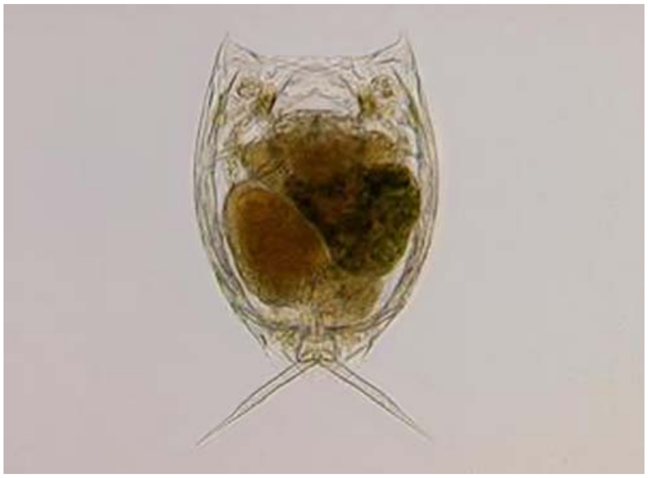

Figure 74. ***Lecane ungulata*** var. ***tenuior***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

One of the undersampled habitats seems to be waterfalls. ***Lecane martensi*** was discovered on wet mosses as a new species in this habitat by Savatenalinton and Segers in 2008. What seems to be most lacking is records of this large genus associated with terrestrial bryophytes.

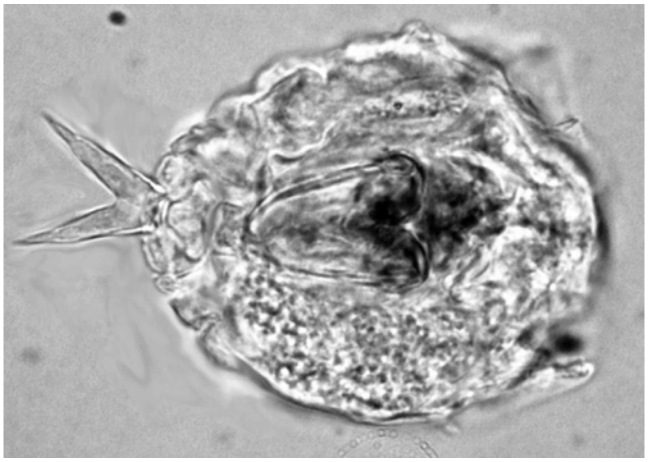

Figure 75. ***Lecane martensi***, a species that was discovered among mosses in a waterfall. Photo by Savatenalinton & Segers 2008, through Creative Commons.

Ituridae

This small family, with only one genus, seems to have little written about it beyond species lists and taxonomic distinctions. Even the map of its distribution showed nothing. I could find only one species, ***Itura aurita*** (Figure 76-Figure 77), that had been collected from mosses, including from bogs (Horkan 1981). De Smet (1993) reported it from submerged mosses on Svalbard.

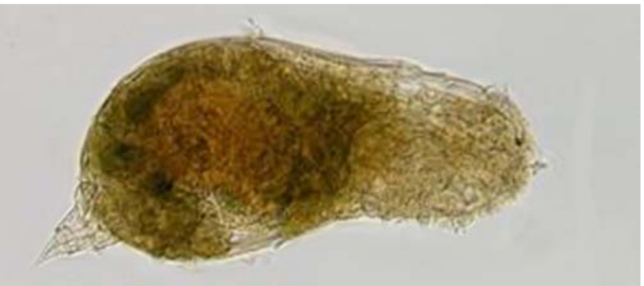

Figure 76. ***Itura aurita*** from Pocono Lake, Pennsylvania, USA. This species is known from bryophytes and from bogs. Photo by Jersabek *et al.* 2003, with permission.

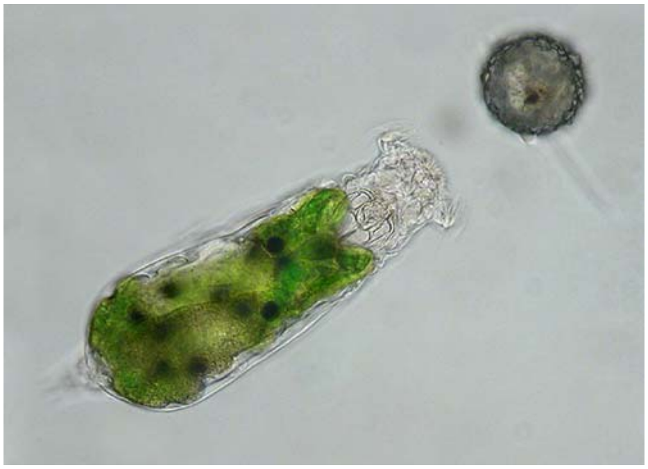

Figure 77. ***Itura aurita***, a moss dweller, with green food in its gut. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Lepadellidae

Many of the **Lepadellidae** are cosmopolitan, often occurring in freshwater habitats (Baribwegure & Segers 2001). In particular, the genera ***Colurella*** (Figure 78-Figure 86, Figure 88), ***Lepadella*** (Figure 91-Figure 112), and ***Squatinella*** (Figure 116-Figure 126) are widespread. These same three genera are well represented among bryophyte collections. A fourth genus, ***Paracolurella*** (Figure 114-Figure 115), also is known from bryophytes.

Colurella

Colurella adriatica (Figure 78-Figure 79) is an uncommon species that may be cosmopolitan (de Manuel Barrabin 2000). It is a planktonic species in small water bodies that lives among plants in the littoral zone and is known from bryophytes. It seems to prefer basic water around *p*H 8.4 and is known from temperatures around 23.5°C. It is known from bryophytes (Madaliński 1961) and occurs among submerged mosses on Svalbard (De Smet 1990, 1993). ***Colurella colurus*** has similar requirements, but is known from a *p*H level around 7.1 and temperature of 9.7°C (de Manuel Barrabin 2000). It is known from bryophytes (Madaliński 1961) and occurs among submerged mosses and in plankton on Svalbard (De Smet 1993).

Figure 78. ***Colurella adriatica***, a species known from bryophytes and bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 79. ***Colurella adriatica***, a species that lives among plants in the littoral zone and is known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Colurella clausa (Figure 80), ***C. denticauda*** (Myers 1942) and ***C. obtusa*** (Figure 81-Figure 83; Horkan 1981; Hingley 1993; Błedzki & Ellison 2003; Plewka 2016), and ***Colurella tesselata*** (Figure 84-Figure 85; Horkan 1981; Hingley 1993; Jersabek *et al.* 2003) occur with ***Sphagnum*** (Figure 2). ***Colurella obtusa*** occurs on Svalbard, where one can find it among submerged mosses and plankton (De Smet 1993). ***Colurella hindenburgi*** (Figure 86) occurs with ***Sphagnum subsecundum*** (Figure 87) (Myers 1942; Jersabek *et al.* 2003), but it also occurs among terrestrial bryophytes (Bielańska-Grajner *et al.* 2011) and in submerged mosses and plankton on Svalbard (De Smet 1993). Segers *et al.* (1996) found ***Colurella uncinata*** among submerged mosses in trenches of Alaskan polygons.

Figure 80. ***Colurella clausa*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

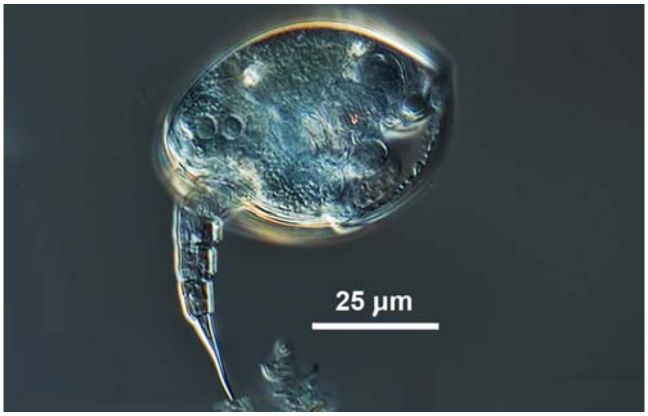

Figure 81. ***Colurella obtusa***, a bog and ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

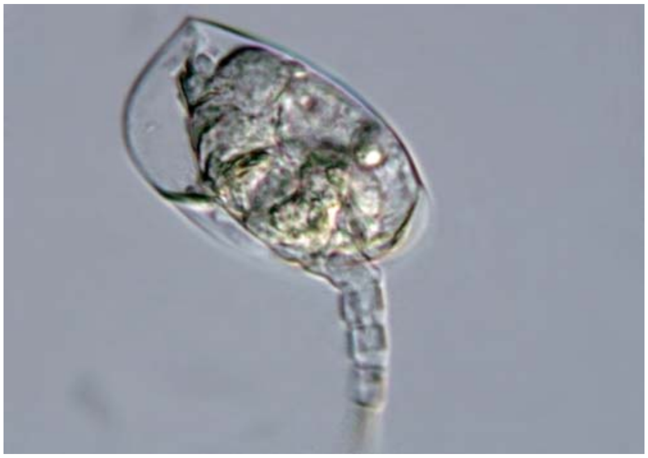

Figure 82. ***Colurella obtusa***, a bog and ***Sphagnum*** dweller. Photo by Yuuji Tsukii, with permission.

Figure 83. ***Colurella obtusa***, a species known from bryophytes and bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 84. ***Colurella tesselata*** side view, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003.

Figure 85. ***Colurella tesselata***, a species known from more than one location of ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 86. ***Colurella hindenburgi*** from among ***Sphagnum subsecundum*** (Figure 87). Photo by Jersabek *et al.* 2003, with permission.

Figure 87. ***Sphagnum subsecundum*** emersed in a fen. Photo by Michael Lüth, with permission.

The genus ***Colurella*** has several species associated with terrestrial bryophytes. ***Colurella geophila*** (Figure 88) lives on epiphytic mosses (Plewka 2016).***Colurella hindenburgi*** (Figure 89) lives on mosses on the dry habitat of granite rocks (Colurella 2016) as well as in bogs and fens (in Poland; Bielańska-Grajner *et al*. 2011). Bielańska-Grajner *et al*. (2011) likewise found ***C. adriatica*** (Figure 78-Figure 79) and ***C. colurus*** in these bogs and fens. ***Colurella paludosa*** (Figure 90) lives in ***Sphagnum*** ponds (Figure 29) (Plewka 2016).

Figure 88. ***Colurella geophila***, a species that lives on epiphytic moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 89. ***Colurella hindenburgi***, a species that lives on mosses on granite rocks. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 90. ***Colurella paludosa***, a species of ***Sphagnum*** pools. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Lepadella

Lepadella species include several that live among bryophytes. Myers (1942), working in the Poconos, Pennsylvania, USA, listed ***Lepadella apsicora*** (Figure 91), ***L. akrobeles*** (Figure 92-Figure 93), ***L. latusinus*** (Figure 94), ***L. ovalis*** (Figure 95-Figure 96; see also Bielańska-Grajner *et al*. 2011 from Poland), and ***L. zigzag*** (Figure 97) as ***Sphagnum*** (Figure 2) associates (Myers 1942).

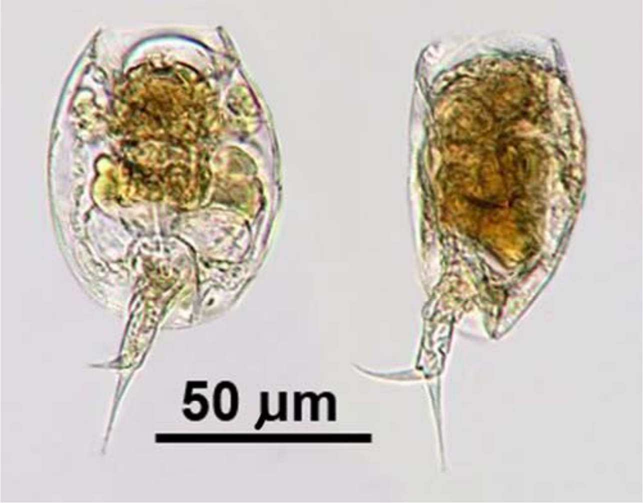

Figure 91. ***Lepadella apsicora***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Figure 92. ***Lepadella akrobeles*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 93. ***Lepadella akrobeles*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

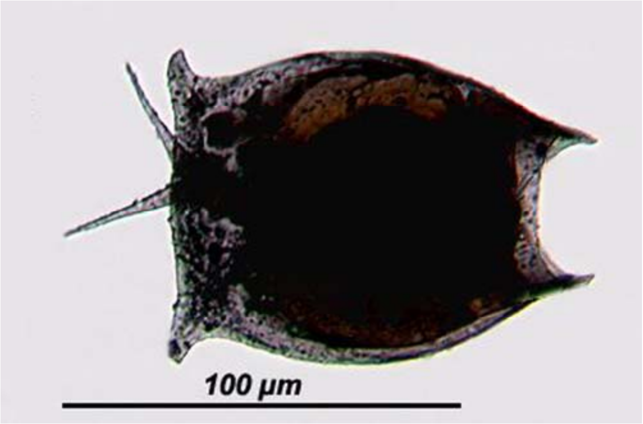

Figure 94. ***Lepadella latusinus***, a species that lives among ***Sphagnum***. Photo by Jersabek *et al*. 2003, with permission.

Lepadella ovalis (Figure 95-Figure 96) is a cosmopolitan species (de Manuel Barrabin 2000). It is a plankton species that occurs among macrophytes in the littoral zone and it can inhabit bryophytes. It is known at *p*H levels of 8.58-9.14 and from the temperature range of 23.6-24°C.

Figure 95. ***Lepadella ovalis***, a bryophyte dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

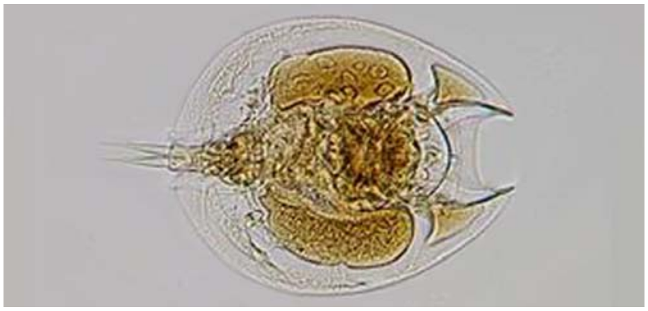

Figure 96. ***Lepadella ovalis*** is a plankton species that can inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

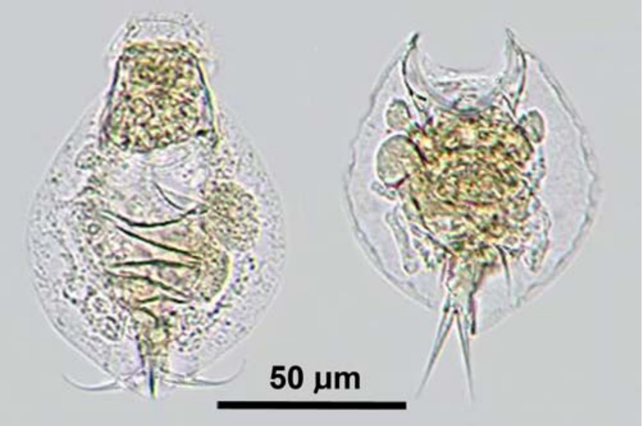

Figure 97. ***Lepadella zigzag***, from ***Sphagnum*** in a pool. Photo by Jersabek *et al*. 2003, with permission.

Lepadella patella (Figure 98-Figure 99) is a littoral species known to inhabit bryophytes (de Manuel Barrabin 2000), including submersed mosses on Svalbard (De Smet 1990, 1993) and on submerged mosses in trenches of Alaskan polygons (Segers *et al*. 1996). This cosmopolitan species lives primarily on plant substrata, but occasionally occurs in the plankton of reservoirs, rivers, and ponds. It is uncommon in large bodies of water. It is known from a *p*H of 6.7-9.3 and temperatures of 9.1-22.3. Bielańska-Grajner *et al*. (2011) and Plewka (2016) reported it from ***Sphagnum*** (Figure 2) peatlands (bogs or fens).

Figure 98. ***Lepadella patella***, a littoral species known to inhabit bryophytes, but also can be found in ***Sphagnum*** bogs Photo by Jersabek *et al.* 2003, with permission.

Plewka (2016) and others include several additional species as ***Sphagnum*** (Figure 2) associates. ***Lepadella acuminata*** (Figure 100-Figure 101; Hingley 1993; Bielańska-Grajner *et al.* 2011) [also with submerged mosses on Svalbard (De Smet 1993)], ***L. elliptica*** (Bielańska-Grajner *et al*. 2011); ***L. heterostyla*** (Figure 102; Plewka 2016), ***L. pterygoida*** (Figure 103; Hingley 1993; Jersabek *et al*. 2003), ***L. triba*** (Figure 104; Hingley 1993; Jersabek et al. 2003), ***L. triptera*** (Figure 105-Figure 108; Horkan 1981; Hingley 1993), and ***Lepadella whitfordi*** (Figure 109; Myers 1942) all are associated with ***Sphagnum*** or occur in bogs. Both ***L. triba*** and ***L. triptera*** occur among submerged mosses on Svalbard (De Smet 1993). ***Lepadella beyensi*** was described from submerged mosses in a puddle in the high Arctic (De Smet 1994). ***Lepadella deridderae*** subsp. ***alaskae*** lives on submerged mosses in trenches of Alaskan polygons (Segers *et al*. 1996). ***Lepadella minuta*** occurs among submerged mosses on Svalbard (De Smet 1993).

Figure 99. ***Lepadella patella***, a rotifer known from a ***Sphagnum*** bog. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Lepadella acuminata (Figure 100-Figure 101) is a species known to inhabit **bryophytes** as well as other plant substrata and is only occasionally found among the plankton (de Manuel Barrabin 2000). It occurs with submerged mosses on Svalbard (De Smet 1993). This species does best in water that is slightly acid (Koste 1978) [*p*H 6.8-8.3 (de Manuel Barrabin 2000)] and has a temperature range of 7.8-19°C (Koste 1978).

Figure 100. ***Lepadella acuminata*** is a species known to inhabit ***Sphagnum*** as well as other plant substrata. Photo by Jersabek *et al.* 2003, with permission.

Figure 101. ***Lepadella acuminata***, a species that sometimes occurs on bryophytes. Photo from Michael Plewka <www.plingfactory.de>, with permission.

Figure 102. ***Lepadella heterostyla***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 103. ***Lepadella pterygoida*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

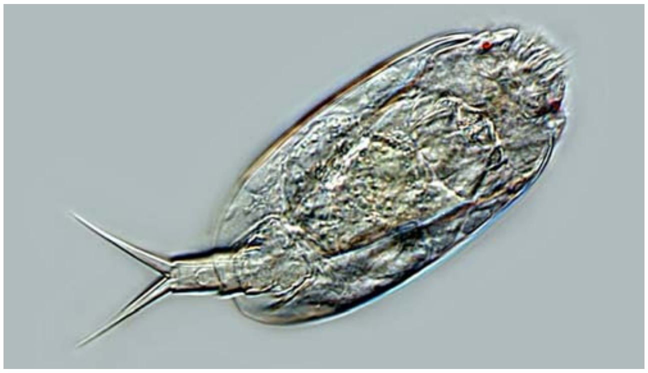

Figure 104. ***Lepadella triba***, a species known to live among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 105. ***Lepadella triptera***, a species known to inhabit bryophytes and that can occur in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 106. ***Lepadella triptera***, a species known from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 107. ***Lepadella triptera***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

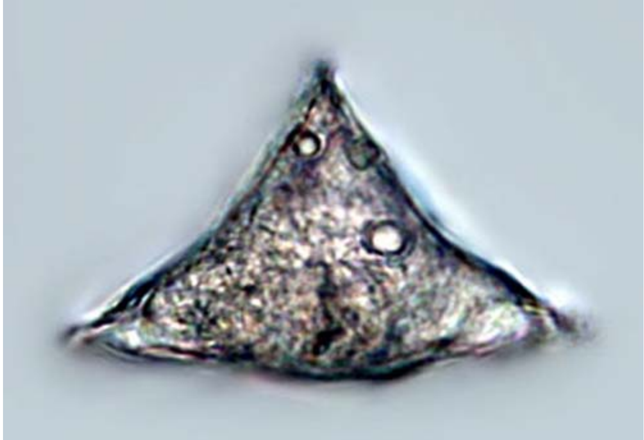

Figure 108. ***Lepadella triptera*** showing three wings of the lorica. Photo by Michael Plewka <www.plingfactory.de>, with permission.

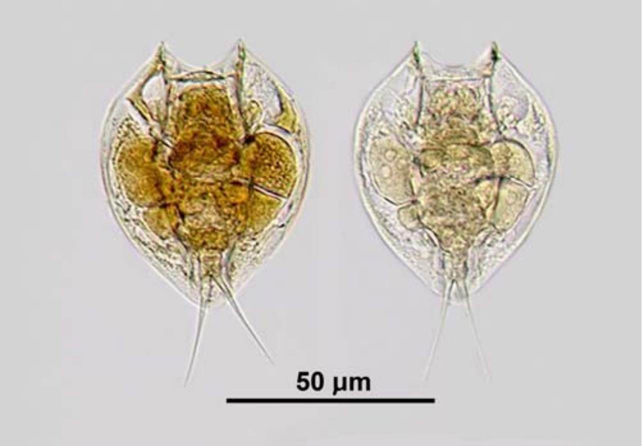

Figure 109. ***Lepadella whitfordi***, a ***Sphagnum*** dweller. Photo by Jersabek *et al*. 2003, with permission.

Lepadella venefica (Figure 110-Figure 111) lives on emersed ***Sphagnum subsecundum*** (Figure 87) and in ***Sphagnum*** (Figure 2) bogs (Jersabek *et al*. 2003).

Figure 110. ***Lepadella venefica*** from emersed ***Sphagnum subsecundum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 111. ***Lepadella venefica*** from among emersed ***Sphagnum subsecundum***. Photo by Jersabek *et al.* 2003, with permission.

Lepadella eurysterna (Figure 112) is perhaps the only ***Lepadella*** species known from the aquatic moss ***Fontinalis novae-angliae*** (Figure 113) (Myers 1942).

Figure 112. ***Lepadella eurysterna***, a species that lives among the aquatic moss ***Fontinalis novae-angliae***. Photo by Jersabek *et al.* 2003, with permission.

Figure 113. ***Fontinalis novae-angliae***, home for ***Lepadella eurysterna***. Photo by Janice Glime.

Paracolurella

Paracolurella is among the many rotifer genera represented among the ***Sphagnum*** (Figure 2). It is a genus of only two species, ***P. aemula*** (Figure 114) and ***P. logima*** (Figure 115), and both of these occur among ***Sphagnum*** (Jersabek *et al*. (2003).

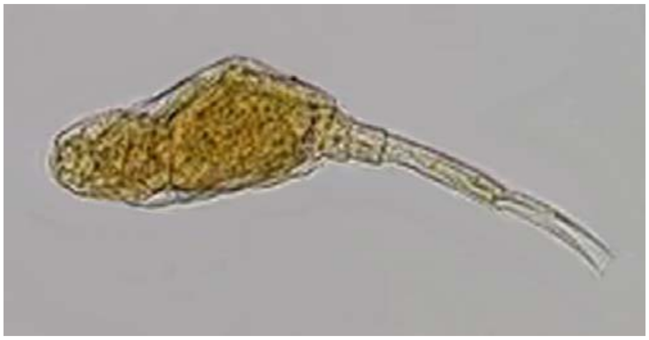

Figure 114. ***Paracolurella aemula*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 115. ***Paracolurella logima*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Squatinella

More rotifers from the genus ***Squatinella*** occur on or among ***Sphagnum*** (Figure 2). Myers (1942) reported only ***S. bifurca*** (Figure 116) as a ***Sphagnum*** associate. Hingley (1993) reported ***S. lamellaris*** [Figure 117-Figure 121, typically a periphyton species (Plewka 2016)], ***S. longispinata*** Figure 122), ***S. microdactyla*** [Figure 123; typically a plankton species (Plewka 2016)], and ***S. rostrum*** (Figure 124-Figure 125; see also Bielańska-Grajner *et al*. 2011). Jersabek *et al*. (2003) added the additional species ***S. retrospina*** (Figure 126) from a ***Sphagnum*** bog.

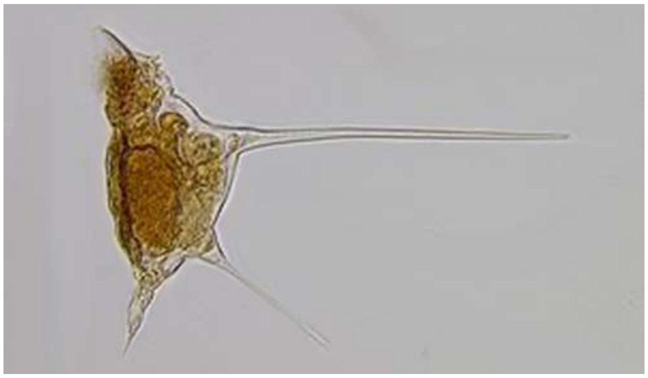

Figure 116. ***Squatinella bifurca*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 117. ***Squatinella lamellaris*** *f.* ***mutica*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 118. ***Squatinella lamellaris*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 119. Side view of ***Squatinella lamellaris*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 120. ***Squatinella lamellaris***, a member of the periphyton, including ***Sphagnum*** as a substrate. Photo by Michael Plewka <www.plingfactory.de>, with permission.

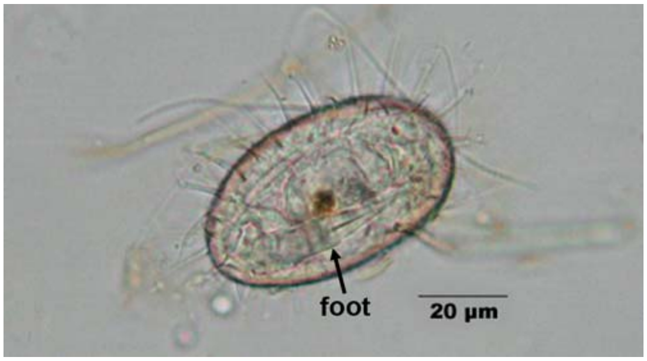

Figure 121. ***Squatinella lamellaris*** *f.* ***tridentata*** egg, showing foot and mastax, a ***Sphagnum*** dweller. Photo by Ralf Wagner, with permission.

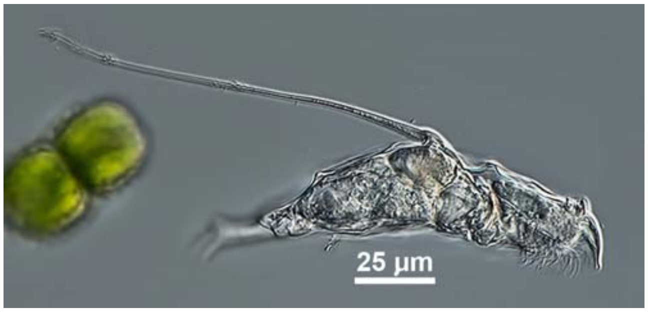

Figure 122. ***Squatinella longispinata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

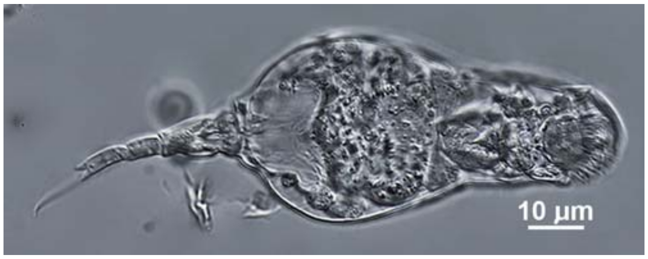

Figure 123. ***Squatinella microdactyla***, typically a plankton species, but one that also occurs among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 124. ***Squatinella rostrum***, a ***Sphagnum*** associate. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 125. ***Squatinella rostrum***, a ***Sphagnum*** associate. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 126. ***Squatinella retrospina*** from among ***Sphagnum*** in bog. Photo by Jersabek *et al.* 2003, with permission.

Lindiidae

This is a small family with only one genus and at least fifteen species (De Smet 2005). Three of these occur in salt water. Three species are known from bryophytes. ***Lindia annecta*** (Figure 127) is a periphytic species that occurs among ***Sphagnum*** in bogs (de Manuel Barrabin 2000). In reservoirs of Spain it is known at temperatures around 7.9 and a *p*H of around 6.8. Jersabek *et al*. (2003) also reported a collection of this species from a lake in the Pocono Mountains, Pennsylvania, USA.

Figure 127. ***Lindia annecta*** is a periphytic species that commonly occurs in ***Sphagnum*** bogs. Photo from Jersabek *et al*. 2003, with permission.

Lindia pallida (Figure 128) is likewise a ***Sphagnum*** (Figure 2) dweller, living anywhere that wet or partly submerged ***Sphagnum*** occurs (Harrington & Myers 1922). To quote Harrington and Myers, "in such locations it may be collected at any time and any place."

Figure 128. ***Lindia pallida*** from ***Sphagnum***. Photo by Christian Jersabek, with permission.

Lindia torulosa (Figure 129-Figure 133) is a large rotifer (>500 1 µrn) that is cosmopolitan, including records from one sub-Antarctic and four Antarctic locations (Dartnall 1995). ***Lindia torulosa*** is aquatic, but it also inhabits submersed mosses (de Beauchamp 1913) and wet terrestrial mosses (De Smet, pers. comm. 13 November 2016), where it eats the **Cyanobacteria *Oscillatoria*** (Figure 130-Figure 131) and ***Anabaena*/*Nostoc*** (Figure 132) (Koste 1979; Plewka 2016). Its trophi are specialized for eating **Cyanobacteria**.

Figure 129. ***Lindia torulosa***, a species known to inhabit bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 130. ***Lindia torulosa***, shown here preparing to eat ***Oscillatoria***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 131. ***Lindia torulosa*** consuming ***Oscillatoria***, using its specialized trophi. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 132. ***Lindia torulosa*** with ***Anabaena*** or ***Nostoc*** in its gut. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 133. ***Lindia torulosa*** showing cilia. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Microcodidae

This family has only one genus, and only a single species, ***Microcodon clavus*** (Figure 134-Figure 135), a plankton species, is also known from bryophytes (Horkan 1981; Hingley 1993; Jersabek *et al.* 2003. It has no **lorica** (shell) and is shaped like a cone with a long, ventral foot (Naberezhnomu 1984).

Figure 134. ***Microcodon clavus*** from among ***Sphagnum*** in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 135. ***Microcodon clavus***, a plankton dweller that can occur among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Mytilinidae

The **Mytilinidae** are **loricate** rotifers (Koste & Shiel 1989). That is, they have a shell. This lorica is triangular to rhombic in cross section and there is often a double keel on the dorsal side. The species are littoral bottom-dwellers, rarely occurring in the plankton. There are only two genera, but only ***Mytilina*** (Figure 136), a genus with 37 species, is represented among bryophytes, with three species thus far reported here.

Mytilina macrocera (Figure 137) is a ***Sphagnum*** (Figure 2) dweller (Jersabek *et al*. 2003). ***Mytilina mucronata*** (Figure 138-Figure 139) occurs on various substrata, including algal filaments (Figure 138; Photo by Jersabek *et al.* 2003), submerged mosses in trench of Alaskan polygons (Segers *et al*. 1996), and among ***Sphagnum*** in bogs (Horkan 1981; Hingley 1993); on Svalbard, it occurs on wet mosses, but also in the plankton (De Smet 1993). ***Mytilina brevispina*** (Figure 141-Figure 140) is a bryophyte dweller on ***Sphagnum*** (Hingley 1993; Plewka 2016).

Figure 136. ***Mytilina***, a genus with three species known from bryophytes. Note the triangular (top to bottom) shell and dorsal keel. Photo by Jean-Marie Cavanihac, with permission.

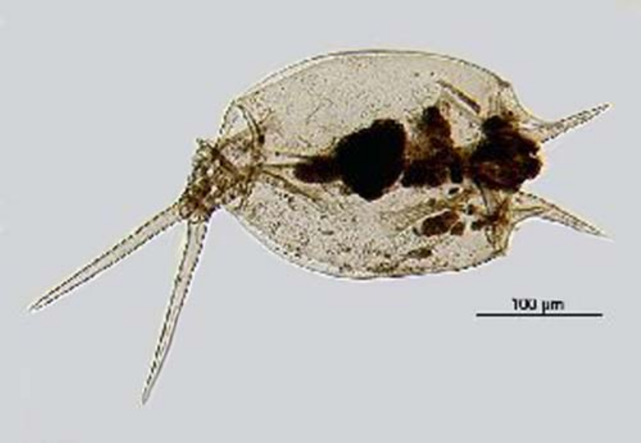

Figure 137. ***Mytilina macrocera***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 138. ***Mytilina mucronata***, a species known to inhabit bryophytes and to live in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 139. ***Mytilina mucronata*** on the filamentous alga ***Oedogonium***. It also inhabits bryophytes and lives among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

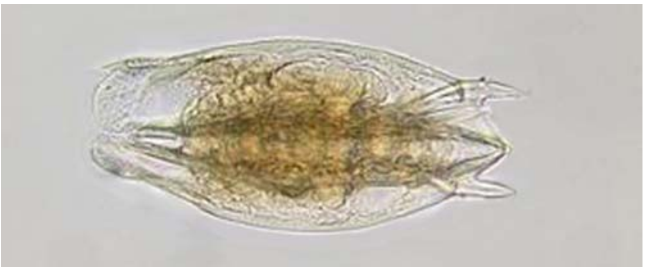

Figure 140. ***Mytilina brevispina***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 141. ***Mytilina brevispina*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Summary

The monogonont order **Ploimida** is continued here from the previous sub-chapter. The **Lecanidae** is a large family with only one genus, ***Lecane***. ***Lecane*** has many species associated with bryophytes. The **Ituridae** has one species known from bryophytes. The **Lepadellidae** is a cosmopolitan family of freshwater with four genera known from bryophytes. The **Lindiidae** is a small family with only one documented species among bryophytes. The **Microcodidae** has only one species and it occurs with bryophytes. The **Mytilinidae** are littoral species. Three species of ***Mytilina*** occur among bryophytes.

Acknowledgments

Bryonetters and rotifer photographers have been wonderful in making their photographs available to me and seeking photographs from others. Tom Powers and Walter Dioni helped me obtain images and permission from others. Christian D. Jersabek very generously gave me permission to use the wealth of images from the Online Catalog of Rotifers. My special thanks go to Michael Plewka for his generous permission to use so many of his beautiful online images. Many photographers have been generous with permission for the use of their images and others have provided them online through Creative Commons and public domain sources. Aydin Örstan helped me find email addresses and pointed out errors in an earlier version of the chapter. Claudia Ricci answered my questions and helped me with current nomenclature.

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CHAPTER 4-7c

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

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CHAPTER 4-7c

INVERTEBRATES: ROTIFER TAXA – MONOGONONTA

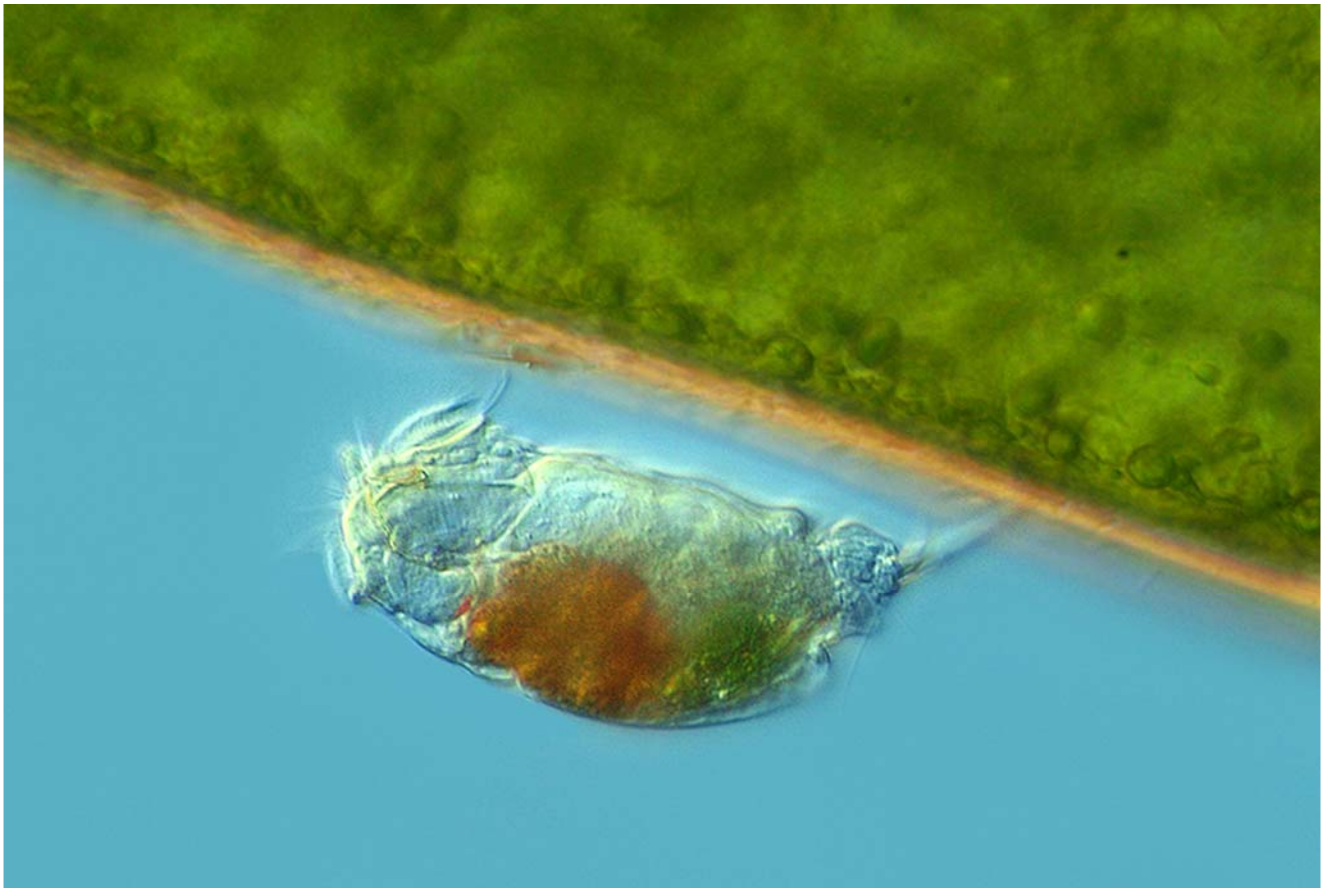

Figure 1. ***Cephalodella***, a common genus among ***Sphagnum***. Photo by Proyecto Agua Water Project Creative Commons.

Notommatidae

The name **Notommatidae** literally means "eyes on the back." The members of this family have a nearly cylindrical body with a thin foot and two toes. Many of its species are known from bryophytes.

Cephalodella

Cephalodella (Figure 1) is a large genus, with many species that occur among bryophytes. Most of these are associated with ***Sphagnum*** (Figure 2). These include ***Cephalodella abstrusa*** (Myers 1942), ***C. anebodica*** from bogs (Figure 2) (Błedzki & Ellison 2003), ***C. apocolea*** (Figure 3-Figure 5; Hingley 1993; Jersabek *et al.* 2003), ***C. auriculata*** (Figure 6-Figure 9; Hingley 1993; Jersabek *et al.* 2003), ***C. belone*** (Figure 10; Jersabek *et al.* 2003), ***C. biungulata*** (Figure 11; Jersabek *et al.* 2003), ***C. catellina*** (Figure 12-Figure 13; Horkan 1981; Hingley 1993), ***C. compressa*** (Figure 28; Jersabek *et al.* 2003), ***C. derbyi*** (Figure 29; Plewka 2016), ***C. elegans*** (Figure 30; Jersabek *et al.* 2003), ***C. forficula*** (Figure 26-Figure 25; Horkan 1981; Hingley 1993), ***C. gibba*** (Figure 15-Figure 17; Horkan 1981; Hingley 1993; De Smet 2001; Jersabek *et al.* 2003; Bielańska-Grajner, *et al.* 2011), ***C. gibboides*** (Bielańska-Grajner *et al.* 2011), ***C. gigantea*** (Figure 31; Plewka 2016), ***C. intuta*** (Figure 21-Figure 22; Hingley 1993), ***C. licinia*** (Figure 32; Jersabek *et al.* 2003), ***C. lipara*** (Figure 33-Figure 34; Jersabek *et al.* 2003), ***C. mira*** (Figure 35-Figure 36; Jersabek *et al.* 2003), ***C. mucronata*** (Figure 37; Jersabek *et al.* 2003), ***C. nana*** (Figure 38-Figure 39; plus other bryophytes; Hingley 1993), ***C. nelitis*** (Figure 40; Jersabek *et al.* 2003), ***C. pheloma*** (Hingley 1993), ***C. plicata*** (Myers 1942), ***C. rotunda*** (Figure 18; Plewka 2016), and ***C. tantilloides*** (Hingley 1993; Bielańska-Grajner *et al.* 2011).

Figure 2. ***Sphagnum*** "bog" (probably a poor fen) with pools. Photo by Boŕeal, through Creative Commons.

Figure 3. ***Cephalodella apocolea***, a ***Sphagnum*** dweller, showing curved toes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 4. ***Cephalodella apocolea*** with diatoms in its gut. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 5. ***Cephalodella apocolea***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella auriculata (Figure 6-Figure 9) is a bryophyte dweller in northern climates. In Alaska it occurs among the submerged mosses in the trenches between the polygons (Segers *et al*. 1996).

Figure 6. ***Cephalodella auriculata***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 7. ***Cephalodella auriculata***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 8. ***Cephalodella auriculata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 9. ***Cephalodella auriculata***, a ***Sphagnum*** dweller. Photo by Yuuji Tsukii, with permission.

Figure 10. ***Cephalodella belone*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

On Svalbard ***C. biungulata*** (Figure 11) lives exclusively on submerged mosses (De Smet 1993).

Figure 11. ***Cephalodella biungulata***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella catellina (Figure 12-Figure 13), ***C. evabroedae***, ***C. gibba*** (Figure 15-Figure 17), ***C. rotunda*** (Figure 18), and ***C. ventripes*** var. ***angustior*** (Figure 19) occur on submerged mosses, but also in the plankton on Svalbard (De Smet 1988, 1990, 1993). ***Cephalodella catellina*** comprised up to 20% of the rotifers on the submerged mosses (De Smet 1988). On the other hand, ***C. biungulata*** (Figure 11), ***C. glandulosa***, ***C. hoodii*** (Figure 20), ***C. intuta*** (Figure 21-Figure 22), and ***C. megalocephala*** (Figure 23) occurred exclusively on mosses (De Smet 1993). ***Cephalodella gibba*** and ***C. sterea*** (Figure 24) are among the most abundant of the submerged, moss-dwelling rotifers on Hopen, Svalbard (De Smet 1990). In Alaska, ***C. gibba*** occurred on submerged mosses in the trenches between polygons (Segers *et al*. 1993). Other species on submerged mosses on Hopen included ***Cephalodella forficula*** (Figure 26-Figure 25) and ***C. misgurnus***.

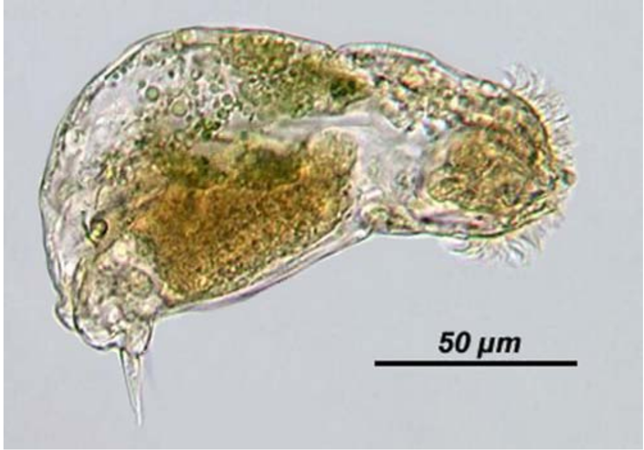

Figure 12. ***Cephalodella catellina*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

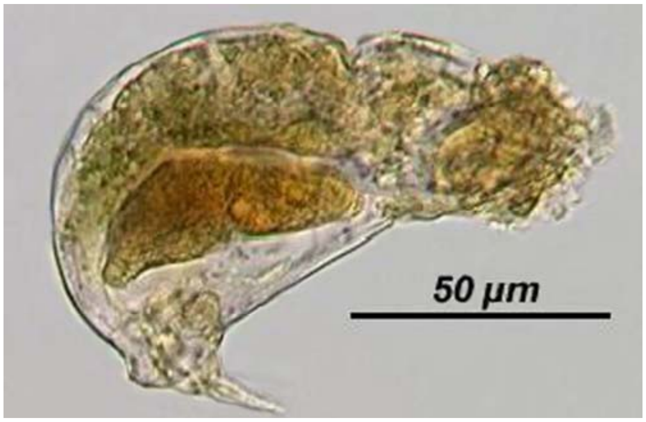

Figure 13. ***Cephalodella catellina*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella gibba (Figure 15-Figure 17) is a cosmopolitan planktonic species of small bodies of water (de Manuel Barrabin 2000). It lives in littoral areas of both fresh and brackish water and occasionally lives in branchial chambers of crustaceans. It feeds on single-celled algae, flagellates, and ciliates. It prefers cold water (Segers 2001), but is known from a range of 6.4-18.8°C (de Manuel Barrabin 2000). Its known *p*H range is 6.6-8.48. In Germany, it is known from habitats with *p*H <3.0 (Deneke 2000). It typically occurs in the sediments (Hingley 1993; Schmid-Araya 1995), but it also is found among the Antarctic mosses (De Smet 2001).

Figure 14. ***Cephalodella gibba***, a ***Sphagnum*** associate. Photo by Jersabek *et al.* 2003, through Creative Commons.

Figure 15. ***Cephalodella gibba*** lateral view, a plankton and littoral species that also associates with ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 16. ***Cephalodella gibba***, a species known from bogs and from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 17. ***Cephalodella gibba*** in copulation, with the smaller male on left. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 18. ***Cephalodella rotunda***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 19. ***Cephalodella ventripes***, a species of plankton and submerged mosses. Photo by Michael Plewka <www.plingfactory.de>.

Figure 20. ***Cephalodella hoodii***, a species that occurs exclusively on submerged mosses on Svalbard. Photo by Michael Plewka <www.plingfactory.de>.

Figure 21. ***Cephalodella intuta***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 22. ***Cephalodella intuta***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 23. ***Cephalodella megalocephala***, a species that occurs exclusively on submerged mosses on Svalbard. Photo by Michael Plewka <www.plingfactory.de>.

Figure 24. ***Cephalodella sterea*** from a pond in Ontario, Canada. This species also occurs on **bog mosses**. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella forficula (Figure 26-Figure 25) is a free-swimming, tube-dwelling species (Dodson 1984) known to live among bryophytes and in bog pools (Figure 2). It is a cosmopolitan littoral species that lives mostly in small bodies of water, occasionally as part of the plankton (de Manuel Barrabin 2000). It occurs in alkaline habitats but prefers slightly "acid" water in a *p*H range around 8.2 and a temperature near 19°C. Dodson (1984) describes its tubes made of mucus in detritus-rich environments. It closes the tubes at both ends and swims back and forth in its tube, living on bacteria shed from the inner walls. Dodson considers only small rotifers <1 mm can use this feeding strategy because of surface-to-volume considerations. In high food conditions, rotifers removed from the tube immediately build another, but under starvation or low oxygen conditions they leave the tube and swim about.

Figure 25. ***Cephalodella forficula***, a species known to live among bryophytes and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 26. ***Cephalodella forficula***, a species known to live among bryophytes and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 27. ***Cephalodella forficula*** swimming. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 28. ***Cephalodella compressa*** from among ***Sphagnum.*** Photo by Jersabek *et al.* 2003, with permission.

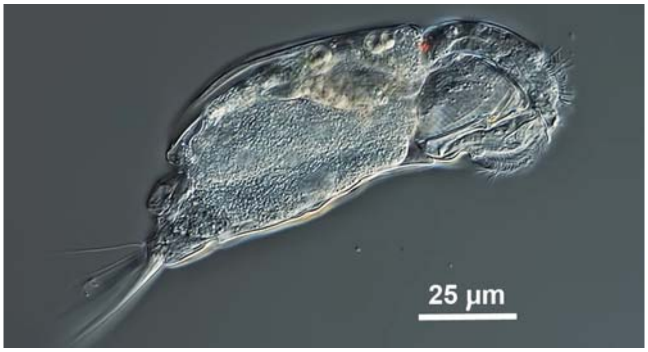

Figure 29. ***Cephalodella derbyi*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 30. ***Cephalodella elegans*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

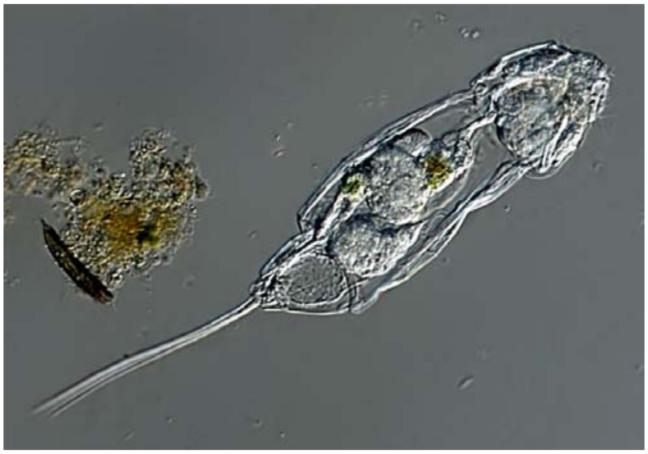

Figure 31. ***Cephalodella gigantea*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 32. ***Cephalodella licinia*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 33. ***Cephalodella lipara*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

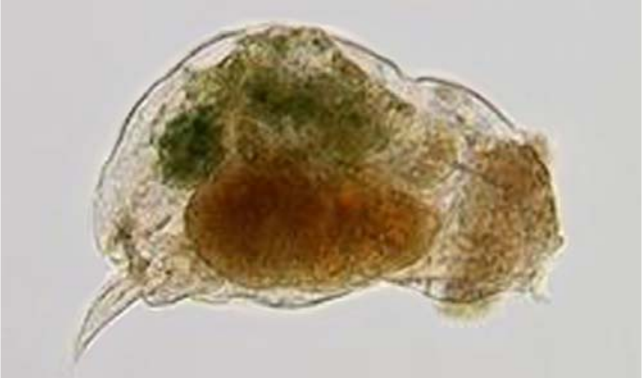

Figure 34. ***Cephalodella lipara*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 35. ***Cephalodella mira*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 36. ***Cephalodella mira*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 37. ***Cephalodella mucronata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 38. ***Cephalodella nana***, a species known from bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 39. ***Cephalodella nana***, a species known from bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 40. ***Cephalodella nelitis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

A number of ***Cephalodella*** species live in bogs, but their specific affiliation with ***Sphagnum*** (Figure 41) is not specified. These include ***Cephalodella eva*** (Figure 42-Figure 43; also with stream mosses; Horkan 1981; Jersabek *et al.* 2003), ***C. exigua*** (Figure 44) in bogs (Jersabek *et al.* 2003), ***C. hoodii*** (Figure 20; Horkan 1981), ***C. lepida*** (Figure 45; Jersabek *et al.* 2003), ***C. physalis*** (Figure 46-Figure 48; Hingley 1993; Jersabek *et al.* 2003), ***C. rostrum*** (Hingley 1993), ***C. sterea*** (Figure 24; Horkan 1981), ***C. tachyphora*** (Figure 49-Figure 50; Jersabek *et al.* 2003), and ***C. tantilla*** (Figure 51; Hingley 1993).

Figure 41. ***Sphagnum capillifolium***, member of a genus that is home for many species of rotifers. Photo by J. C. Schou, with permission.

Figure 42. ***Cephalodella eva*** from a stream in Pennsylvania, USA. This species has been collected on mosses. Photo by Jersabek *et al.* 2003, with permission.

Figure 43. ***Cephalodella eva*** from the Pocono Mountains, in Pennsylvania, USA. This species is known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 44. Side view of ***Cephalodella exigua*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 45. ***Cephalodella lepida*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

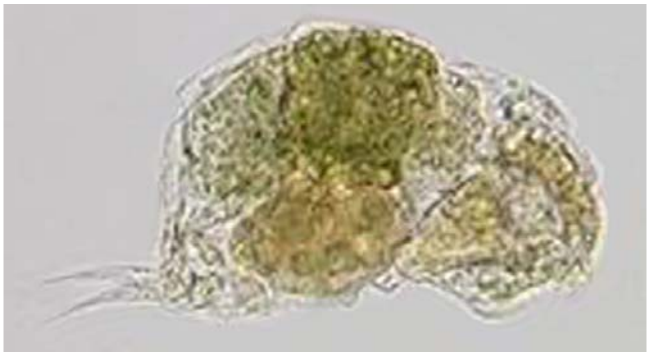

Figure 46. ***Cephalodella physalis***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 47. ***Cephalodella physalis***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 48. ***Cephalodella physalis***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 49. ***Cephalodella tachyphora*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 50. ***Cephalodella tachyphora*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 51. ***Cephalodella tantilla*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Cephalodella subsecunda (Figure 52) is known from ***Sphagnum subsecundum*** (Figure 53) (Jersabek *et al.* 2003). Some ***Cephalodella*** are known from submersed ***Sphagnum*** (Figure 41), including ***C. gracilis*** [Figure 54-Figure 55; Bielańska-Grajner *et al.* 2011; Plewka 2016; in streams Madaliński 1961), and ***C. inquilina*** (Figure 56; Jersabek *et al.* 2003). ***Cephalodella ventripes*** (Figure 19) occurs not only on ***Sphagnum*** (Hingley 1993), but as already noted, it also occurs on submerged moss and among the plankton (De Smet 1993; Plewka 2016). On Svalbard, ***Cephalodella ventripes*** var. ***angustior*** occurs mostly between submerged mosses (De Smet 1988).

Figure 52. ***Cephalodella subsecunda*** from among emergent ***Sphagnum subsecundum*** (Myers 1942). Photo by Jersabek *et al.* 2003, with permission.

Figure 53. ***Sphagnum subsecundum***, home of ***Cephalodella subsecunda*** and other rotifers. Photo by Michael Lüth, with permission.

Figure 54. ***Cephalodella gracilis***, a species from submersed ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 55. ***Cephalodella gracilis***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 56. ***Cephalodella inquilina*** from among submerged ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Other members of ***Cephalodella*** occur on submerged mosses (***Cephalodella cyclops***; Figure 57; Plewka 2016), including ***Fontinalis*** (Figure 58) (***C. dorseyi***; Figure 59; Jersabek *et al*. 2003). ***Cephalodella megalotrocha*** is also a bryophyte dweller (Horkan 1981).

Figure 57. ***Cephalodella cyclops***, a species that occurs in ponds with submerged mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 58. ***Fontinalis hypnoides*** with detritus. ***Fontinalis*** is a suitable home for ***Cephalodella dorseyi***. Photo by Janice Glime.

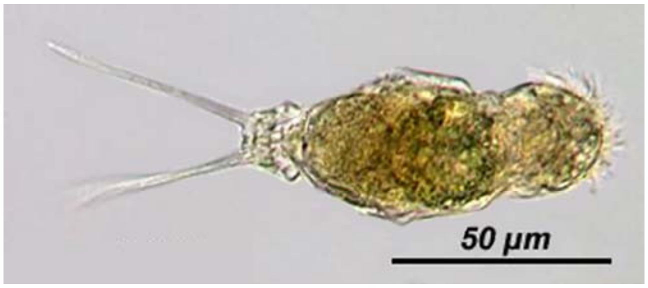

Figure 59. ***Cephalodella dorseyi*** from among ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

Drilophaga

Drilophaga judayi (Figure 60) is an ectoparasitic rotifer (but occasionally free-swimming). In the Poconos Mountains, Pennsylvania, USA, it was found only among

Sphagnum (Figure 41) (Myers 1942). In a genus of only three species, two live in association with ***Sphagnum***. The second of these is ***D. bucephalus*** (Figure 61), an ectoparasite on oligochaetes and a ***Sphagnum*** dweller (Plewka 2016).

Figure 60. ***Drilophaga judayi***, a parasitic rotifer that occurs only among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 61. ***Drilophaga bucephalus*** from ***Sphagnum.*** Photo by Michael Plewka (www.plingfactory.de), with permission.

Enteroplea

Enteroplea lacustris (Figure 62-Figure 63) occurs among ***Sphagnum*** (Figure 41) and in bog pools (Figure 2). Myers (1942) received a collection of a clump of wet ***Sphagnum*** from the Poconos Mountains, Pennsylvania, USA, and kept it in an aquarium for several months. Then a large number of ***E. lacustris*** appeared. There has been no report of it in the Poconos Mountains since.

Figure 62. ***Enteroplea lacustris***, a species that lives among ***Sphagnum*** and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 63. ***Enteroplea lacustris*** from among ***Sphagnum*** and in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Eosphora

Eosphora is a genus with only seven known species. Of these, two seem to find bryophytes suitable for habitation. ***Eosphora ehrenbergi*** (Figure 64) occurs in bog pools (Horkan 1981; Jersabek *et al*. 2003). ***Eosphora najas*** (Figure 65) is a littoral-planktonic species that eats detritus (Plewka 2016), but it is known to occur among bryophytes in streams (Madaliński 1961) and ponds (De Smet 1993).

Figure 64. ***Eosphora ehrenbergi*** male from Utah, USA, a species known from bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 65. ***Eosphora najas***, showing eyespots, a planktonic species that eats detritus. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Eothinia

Eothinia has only six species. Only one of these, ***Eothinia elongata*** (Figure 66), associates with bryophytes by living in bogs (Horkan 1981).

Figure 66. ***Eothinia elongata*** from Three Lakes, Wisconsin, USA, a species known from bogs. Photo by Jersabek *et al.* 2003, with permission.

Monommata

The bryophyte dwellers in ***Monommata*** are all associated with ***Sphagnum*** (Figure 41). Hingley (1993) reported ***Monommata actices*** (Figure 67), ***M. aeschyna***, ***M. astia*** (Figure 68), ***M. longiseta*** (Figure 69-Figure 70), ***M. maculata*** (Figure 71), and ***M. phoxa*** as ***Sphagnum*** associates. To these, Plewka (2016) added ***M. dentata*** (Figure 72) and Jersabek *et al*. (2003) added ***M. hyalina*** (Figure 73). ***Monommata aequalis*** (Figure 74; Horkan 1981) and ***M. grandis*** (Figure 75; Plewka 2016) occur in bog pools and ***Sphagnum*** ponds (Figure 2), respectively. On Svalbard, De Smet (1993) found a species of ***Monommata*** exclusively on submerged mosses.

Figure 67. ***Monommata actices***, a species that is known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 68. ***Monommata astia***, a species known to inhabit bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 69. ***Monommata longiseta***, a planktonic species that also inhabits bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 70. ***Monommata longiseta***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

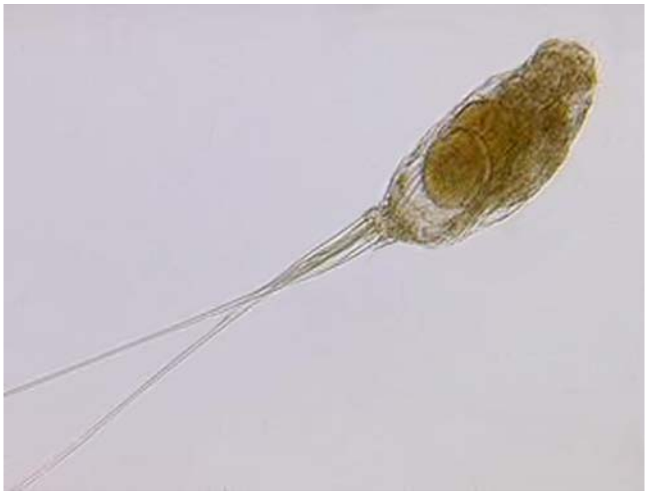

Figure 71. ***Monommata maculata***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 72. ***Monommata dentata***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 73. ***Monommata hyalina*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

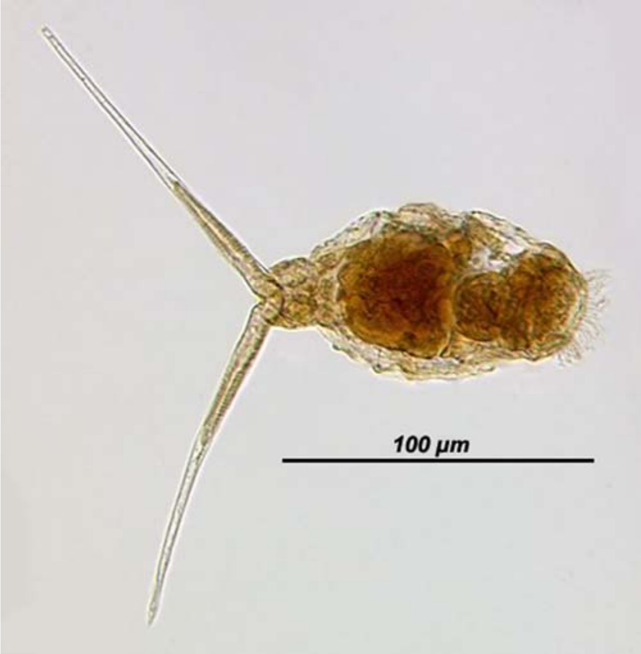

Figure 74. ***Monommata aequalis***, a bog-pool dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 75. ***Monommata grandis***, an inhabitant of ***Sphagnum*** ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Notommata

This genus likewise contributes to the rotifer fauna of ***Sphagnum*** (Figure 41). Among these ***Sphagnum*** associates one can find ***Notommata allantois*** (Figure 76; Hingley 1993; Plewka 2016), ***N. cerberus*** (Figure 77-Figure 78); Horkan 1981; Hingley 1993; Jersabek *et al.* 2003; Plewka 2016), ***N. cherada*** (Figure 79; Jersabek *et al.* 2003), ***N. contorta*** (Figure 80; Hingley 1993; Jersabek *et al.* 2003), ***N. copeus*** (Figure 81-Figure 83; Horkan 1981; Hingley 1993; Plewka 2016), ***N. cyrtopus*** (Figure 87; bog pools and other bryophytes; Horkan 1981), ***N. doneta*** (Myers 1942), ***N. falcinella*** [Figure 88; on ***Sphagnum subsecundum*** (Figure 53; Harrington & Myers 1922; Hingley 1993), ***N. fasciola*** (Figure 89; Jersabek *et al.* 2003), ***N. groenlandica*** (Figure 90-Figure 91; Hingley 1993; Plewka 2016), ***N. pachyura*** (Figure 92-Figure 94; Horkan 1981; Hingley 1993), ***N. peridia*** (Figure 95; Myers 1942), ***N. pygmaea*** (Figure 96; Myers 1942), ***N. saccigera*** (Figure 97-Figure 98; Harrington & Myers 1922; Myers 1942; Hingley 1993), and ***N. tripus*** (Figure 99-Figure 100; bog pools, others; Horkan 1981; Hingley 1993). Horkan (1981) reported ***Notommata brachyota*** from bryophytes.

Figure 76. ***Notommata allantois*** with green gut, a species that occurs in ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Notommata cerberus subsp. ***parvida***; Figure 77-Figure 78) is a cosmopolitan species known to inhabit bryophytes (de Manuel Barrabin 2000) and to live in bog pools (Horkan 1981). It is an omnivore that consumes other rotifers, desmids, diatoms, and flagellates (de Manuel Barrabin 2000). Its known *p*H is around 8.2 and temperature around 18.8°C.

Figure 77. **Notommata cerberus**, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 78. ***Notommata cerberus*** subsp. ***parvida***, a cosmopolitan species known to inhabit bryophytes and to live in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 79. ***Notommata cherada***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 80. ***Notommata contorta***, known from a ***Sphagnum*** pool. Photo by Jersabek *et al.* 2003, with permission.

Notommata copeus (Figure 81-Figure 83) is a cosmopolitan, littoral species (de Manuel Barrabin 2000) known to inhabit bryophytes. It also occasionally occurs in the plankton (de Manuel Barrabin 2000) and in bog pools (Horkan 1981). It is known from a *p*H around 7 and temperature around 6°C (de Manuel Barrabin 2000). Its food is mostly zygnematalean algae – ***Mougeotia*** (Figure 84), ***Spirogyra*** (Figure 85), and ***Zygnema*** (Figure 86), that occur in these pools.

Figure 81. ***Notommata copeus*** with mucilage & bacteria, giving it a fuzzy look. This is a species from ***Sphagnum***. Note the desmid ***Closterium*** in the upper left, a potential food item. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 82. ***Notommata copeus***, a bryophyte dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 83. ***Notommata copeus***, a species known to inhabit bryophytes and bog pools. Photo by Jersabek *et al.* 2003, with permission.

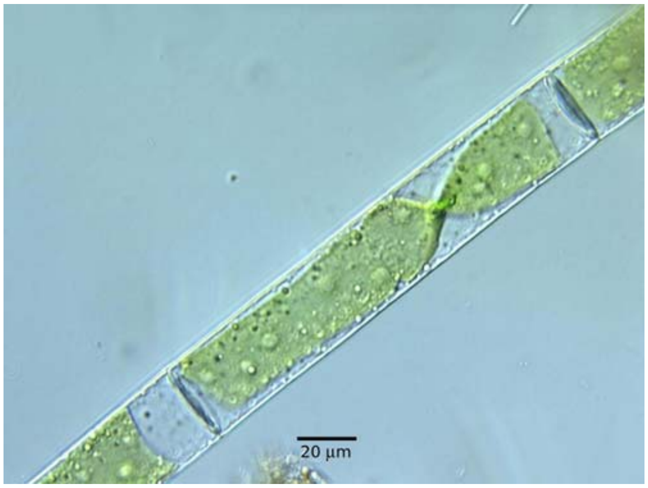

Figure 84. ***Mougeotia***, food for ***Notommata copeus***. Note the twisted chloroplast in the ***Mougeotia***. Photo by Jason Oyadomari, with permission.

Figure 85. ***Spirogyra***, food for ***Notommata copeus***. Photo from Landcare Research, Manaaki Whenua, through Creative Commons.

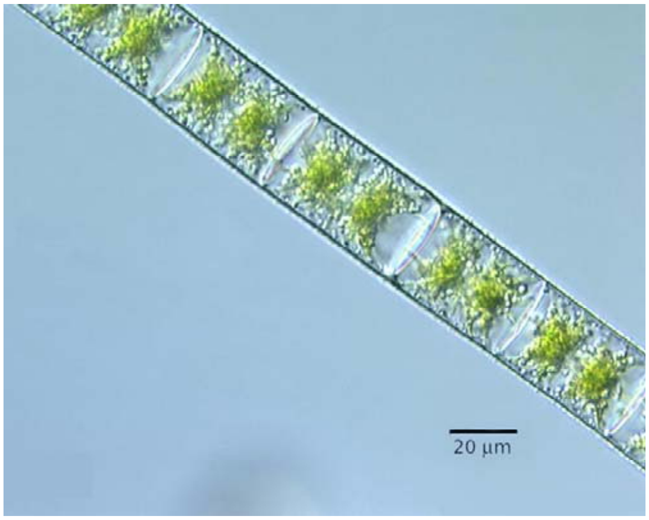

Figure 86. ***Zygnema***, food for ***Notommata copeus***. Photo by Jason Oyadomari, with permission.

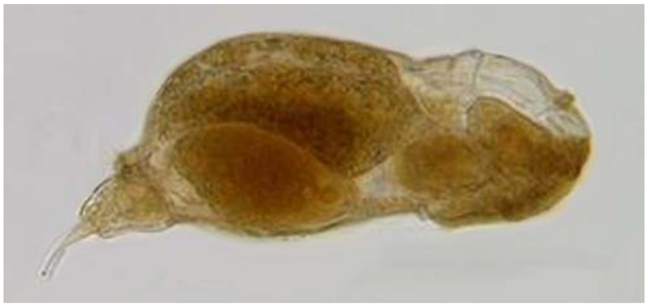

Figure 87. ***Notommata cyrtopus*** from New Jersey, USA. This species has been collected from bryophytes and is known from bog pools. Photos by Jersabek *et al.* 2003, with permission.

Figure 88. ***Notommata falcinella***, a species known from bryophytes, including ***Sphagnum subsecundum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 89. ***Notommata fasciola*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 90. ***Notommata groenlandica*** with the desmid ***Netrium***, a food item from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 91. ***Notommata groenlandica*** from a ***Sphagnum*** bog. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 92. ***Notommata pachyura*** from detritus that it can find among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 93. ***Notommata pachyura***, a species known to inhabit bryophytes and to occur in bogs. It feeds on non-colonial desmids (GLERL 2009). Photo by Jersabek *et al.* 2003, with permission.

Figure 94. ***Notommata pachyura***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 95. ***Notommata peridia***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 96. ***Notommata pygmaea***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 97. ***Notommata saccigera***, a species known to inhabit bryophytes, including ***Sphagnum*** (Myers 1942). Photo by Jersabek *et al.* 2003, with permission.

Figure 98. ***Notommata saccigera***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

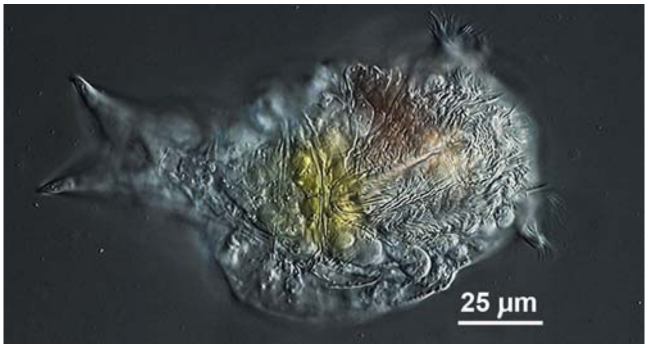

Figure 99. ***Notommata tripus*** from *Myriophyllum*. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 100. ***Notommata tripus***, a species known to inhabit bryophytes in more than one location and also occurs in bog pools. Photo by Jersabek *et al.* 2003, with permission.

On Svalbard ***Notommata glyphura*** (Figure 101) occurs on submerged mosses, but also occurs among the plankton (De Smet 1993).

Figure 101. ***Notommata glyphura***, a species of plankton and submerged mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Pleurata

Of the seven species in ***Pleurata***, three are associated with bryophytes. All of these are associated with ***Sphagnum*** (Figure 41) and include ***P. chalicodes*** (Figure 102), ***P. tithasa*** (Figure 103), and ***P. vernalis*** (Figure 104) (Jersabek *et al*. 2003). In Alaska, ***P. chalicodes*** occurs with submerged mosses in trenches of polygons (Segers *et al*. 1996).

Figure 102. ***Pleurata chalicodes*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 103. ***Pleurata tithasa*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 104. ***Pleurata vernalis*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Pleurotrocha

Although ***Pleurotrocha*** has eight species, only two of these are associated with bryophytes. ***Pleurotrocha petromyzon*** (Figure 105) occurs with the aquatic moss ***Fontinalis*** (Figure 58) (Plewka 2016). The only

Sphagnum (Figure 41) dweller seems to be ***P. robusta*** (Figure 106-Figure 107; Jersabek *et al*. 2003).

Figure 105. ***Pleurotrocha petromyzon***, a species that occurs on the aquatic moss ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 106. ***Pleurotrocha robusta*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 107. ***Pleurotrocha robusta*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Pseudoploesoma

Pseudoploesoma is a small genus with only one species, ***P. formosum*** (Figure 108-Figure 110). It occurs among ***Sphagnum*** in bog ponds (Figure 2) (Myers 1942; Jersabek *et al.* 2003).

Figure 108. ***Pseudoploesoma formosum*** from among ***Sphagnum*** in a bog pond. Photo by Jersabek *et al.* 2003, with permission.

Figure 109. ***Pseudoploesoma formosum*** from among ***Sphagnum*** in a bog pond. Photo by Jersabek *et al.* 2003, with permission.

Figure 110. ***Pseudoploesoma formosum*** from among ***Sphagnum*** in a bog pond. Photo by Jersabek *et al.* 2003, with permission.

Resticula

Three members of ***Resticula*** are associated with bryophytes and other submerged plants. ***Resticula melandocus*** (Figure 111-Figure 113) occurs in ***Sphagnum*** bogs (Figure 2) (Hingley 1993), but also is associated with the alga ***Nitella*** (Jersabek *et al*. 2003; Plewka 2016). ***Resticula nyssa*** (Figure 114-Figure 115) is a littoral species that lives on plant surfaces, including bryophytes (de Manuel Barrabin 2000), including ***Sphagnum*** (Figure 41) (Hingley 1993). On Svalbard, it occurs exclusively on submerged mosses (De Smet 1993). It prefers slightly acidic water, although the measured *p*H was 8.2. Its temperature preference is around 18.8°C (de Manuel Barrabin 2000). ***Resticula plicata*** (Figure 116) lives in ***Sphagnum*** ponds (Figure 2) (Plewka 2016).

Figure 111. ***Resticula melandocus*** from the alga ***Nitella***, but this rotifer also occurs in ***Sphagnum*** bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

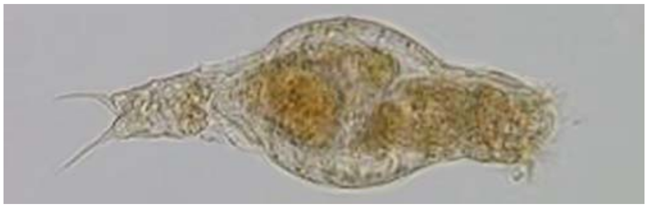

Figure 112. ***Resticula melandocus***, known from a ***Sphagnum*** bog. Photo by Jersabek *et al*. 2003, with permission.

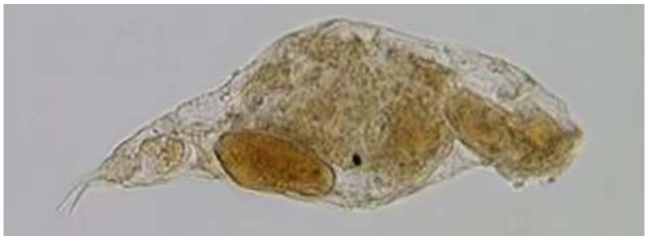

Figure 113. ***Resticula melandocus***, side view, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 114. ***Resticula nyssa***, a littoral species that lives on plant surfaces, including bryophytes. Photo by Jersabek *et al.* 2003, with permission.

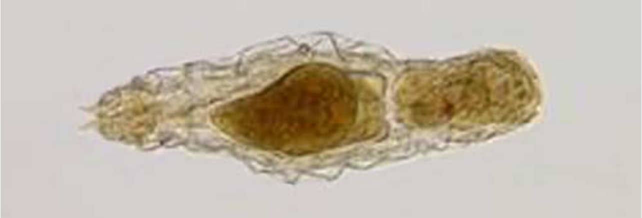

Figure 115. ***Resticula nyssa***, known from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

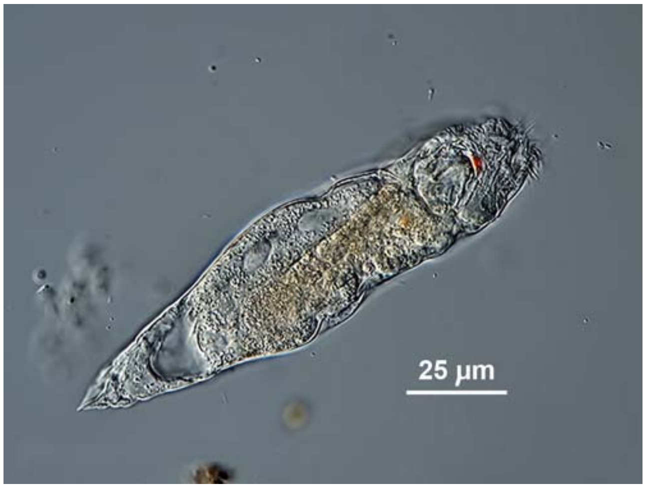

Figure 116. ***Resticula plicata***, inhabitant of ***Sphagnum*** ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Taphrocampa

Taphrocampa is a genus with only four species. Of these, two are known from ***Sphagnum*** (Figure 41): ***T. annulosa*** (Figure 117-Figure 118) and ***T. clavigera*** (Figure 119) (Hingley 1993; Jersabek *et al*. 2003).

Figure 117. ***Taphrocampa annulosa***, known from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 118. ***Taphrocampa annulosa***, lateral view, a species known from **bryophytes**. Photo by Jersabek *et al.* 2003, with permission.

Figure 119. ***Taphrocampa clavigera***, a species known from ***Sphagnum*** in more than one location. Photo by Jersabek *et al.* 2003, with permission.

Proalidae

This family lacks a hardened lorica and instead takes on a wormlike appearance. It lives in freshwater and occurs on plants, on the bottom, and among sand grains of the littoral zone as well as in damp terrestrial habitats (EOL 2012). Some are even **epizoic** on other invertebrates and some live parasitically in algae or on invertebrates.

Bryceella

This genus is **oviparous** (producing eggs that are laid and hatch later). All known species of the genus ***Bryceella*** live among ***Sphagnum*** (Figure 41). ***Bryceella tenella*** (Figure 120-Figure 121) seems to be known only from ***Sphagnum*** (Myers 1942; Hingley 1993; Jersabek *et al.* 2003; Bielańska-Grajner, *et al*. 2011). On the other hand, ***Bryceella perpusilla*** (Figure 122; Wilts *et al*. 2010) and ***B. stylata*** (Figure 123-Figure 124; Hingley 1993; Plewka 2016) both occur on ground-dwelling and epiphytic mosses as well as aquatic habitats, illustrating an ability to tolerate a wide moisture range. Segers *et al*. (1996) reports ***B. stylata*** from submerged mosses in trenches of Alaskan polygons; on Svalbard, it occurs exclusively on submerged mosses (De Smet 1993). ***Bryceella pusilla*** (Figure 125), previously known as ***Wierzejskiella vagneri***, is known from a ***Sphagnum*** bog (Plewka 2016).

Bryceella perpusilla (Figure 122) was described as a new species in 2010 from northwest Germany (Wilts *et al.* 2010). Its describers considered it to be one of the smallest rotifers (50-80 µm) and even one of the smallest metazoans known. Even its name, *perpusilla*, means very small. This small size, combined with its narrow body and dorsiventral compression, permits it to live among terrestrial mosses. The individuals glide among the mosses in a "nimble and jerky manner very fast on the moss stalks" and eat the detritus associated with the mosses. Even in the lab, they never leave the moss to swim. But they are not restricted to these terrestrial mosses. They also occur among ***Sphagnum*** (Figure 41) in Lake Gorbacz in Poland. They seem to prefer cold periods at about 10°C.

Figure 120. ***Bryceella tenella***, a ***Sphagnum*** associate. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 121. ***Bryceella tenella***, a ***Sphagnum*** associate. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 122. ***Bryceella perpusilla***, a species that lives among epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 123. ***Bryceella stylata*** (stomach stained neutral red), a species that lives in ***Sphagnum*** bogs and on epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 124. ***Bryceella stylata***, a species known from **bryophytes**. Photo by Jersabek *et al.* 2003, with permission.

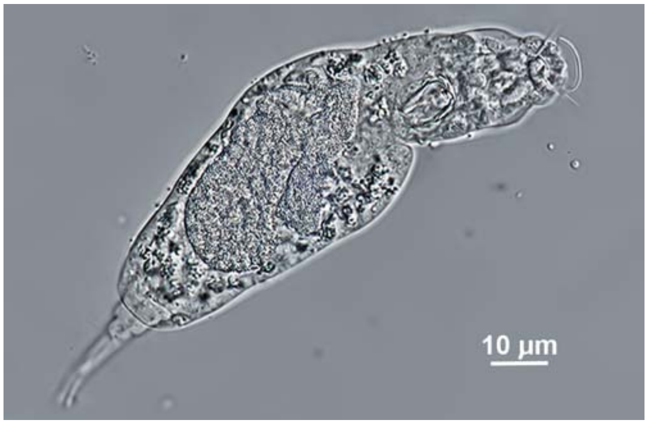

Figure 125. ***Bryceella pusilla*** from a ***Sphagnum*** bog. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Proales

Proales is a somewhat larger genus. A number of its species occur among ***Sphagnum*** (Figure 41). These include ***Proales bemata*** (Figure 126; Myers 1942), ***P. cognita*** [Figure 127-Figure 128; on ***Sphagnum cuspidatum*** (Figure 129); Jersabek *et al*. 2003], ***P. decipiens*** (Figure 130; Horkan 1981; Hingley 1993; Harrington & Myers 1922), ***P. doliaris*** (Figure 131; ***Sphagnum*** bogs; Hingley 1993; Jersabek *et al.* 2003), ***P. fallaciosa*** (Figure 132-Figure 134; Hingley 1993), ***P. latrunculus*** (current name not located; Hingley 1993), ***P. micropus*** (Hingley 1993), ***P. minima*** [Figure 135-Figure 136; on ***Sphagnum subsecundum*** (Figure 53); Hingley 1993; Plewka 2016], ***P. ornata*** (Myers 1942), ***P. palimmeka*** (Figure 137; on submerged ***Sphagnum***; Jersabek *et al*. 2003), and ***P. sordida*** (Horkan 1981).

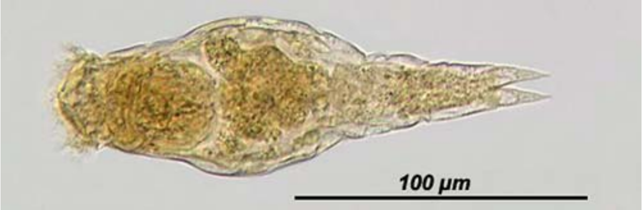

Figure 126. ***Proales bemata***, a ***Sphagnum*** dweller. Photo by Jersabek *et al.* 2003, with permission.

Figure 127. ***Proales cognita*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 128. ***Proales cognita*** from among ***Sphagnum cuspidatum***. Photo by Jersabek *et al.* 2003, with permission.

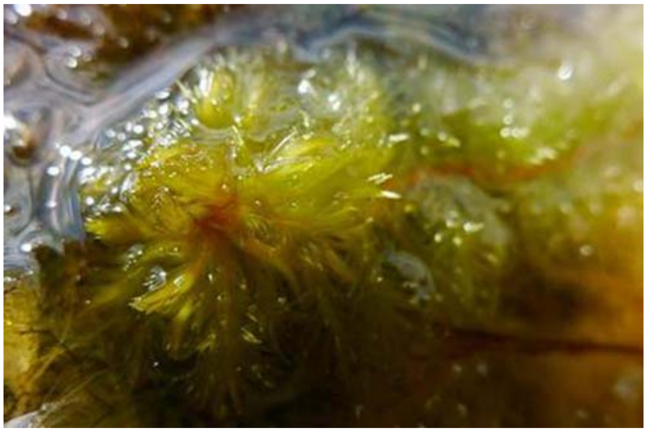

Figure 129. ***Sphagnum cuspidatum***, home of ***Cephalodella subsecunda***. Photo through Creative Commons.

Figure 130. ***Proales decipiens***, a species known to occur in bogs and to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 131. ***Proales doliaris***, a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Proales fallaciosa (Figure 132-Figure 134) is a cosmopolitan, benthic-periphytic (and planktonic) species of small water bodies (de Manuel Barrabin 2000). It is known to inhabit bryophytes, including ***Sphagnum*** (Figure 41). On Svalbard it inhabits submerged mosses (De Smet 1993). It lives in alkaline to slightly acid water with a *p*H around 8.39 and temperature around 18.8°C (de Manuel Barrabin 2000) where it feeds on bacteria, detritus, algae, and microcrustaceans (Koste & Shiel 1990).

Figure 132. ***Proales fallaciosa***, a cosmopolitan species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 133. ***Proales fallaciosa***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 134. ***Proales fallaciosa***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 135. ***Proales minima*** occurs on submersed moss, including ***Sphagnum subsecundum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 136. ***Proales minima***, a species collected from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 137. ***Proales palimmeka*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

In addition to these ***Sphagnum*** dwellers, ***Proales ardechensis*** (Figure 138) lives in a seepage area where wet mosses attach to a vertical rock face that dries up in summer (De Smet & Verolet 2009). The *p*H there is 7.35 and water temperature of 7°C. ***Proales globulifera*** (Figure 139) is part of the periphyton on ***Fontinalis*** (Figure 58) (Plewka 2016), and ***P. theodora*** (Figure 140-Figure 141) associates with bryophytes in streams and rivulets (Madaliński 1961).

Figure 138. ***Proales ardechensis***, a species that lives among wet mosses on rocks in seepage areas. Photo by Michael Verolet, with permission.

Figure 139. ***Proales globulifera***, a species periphytic on ***Fontinalis***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 140. ***Proales theodora***, a plankton species that also associates with mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 141. ***Proales theodora***, a plankton species that also occurs among mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Proales laticauda (Figure 142) is the only terrestrial member of the genus that I have found. De Smet and Verolet (2009) first described it from moss on sandstone in a firewood area. Plewka (2016) reported it from mosses where it accompanied mucilaginous green algae.

Figure 142. ***Proales laticauda***, a species that occurs on moss with mucilaginous green algae. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Proalinopsis

Proalinopsis is a genus of only seven species. Among these, three are associated with ***Sphagnum*** (Figure 41) or live in bogs. These are ***Proalinopsis caudatus*** (Figure 143-Figure 144) in bog pools (Horkan 1981; Hingley 1993; Plewka 2016), ***P. phacus*** on ***Sphagnum*** (Myers 1942), and ***P. squamipes*** (Figure 145) from a ***Sphagnum*** ditch and bogs (Hingley 1993; Jersabek *et al.* 2003). ***Proalinopsis gracilis*** (Figure 146) is known from the floating thallose liverwort ***Riccia fluitans*** (Figure 147) (Jersabek *et al.* 2003).

Figure 143. ***Proalinopsis caudatus*** from a ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 144. ***Proalinopsis caudatus***, a species known to inhabit bryophytes and to occur in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 145. ***Proalinopsis squamipes***, known from a ***Sphagnum*** ditch. Photo by Jersabek *et al.* 2003, with permission.

Figure 146. ***Proalinopsis gracilis*** from among the floating thallose liverwort ***Riccia fluitans***. Photo by Jersabek *et al.* 2003, with permission.

Figure 147. ***Riccia fluitans***, home for ***Proalinopsis gracilis.*** Photo by Christian Fischer, through Creative Commons.

Wulfertia

On Svalbard, ***Wulfertia ornata*** occurs exclusively among submerged mosses in a pool (De Smet 1993).

Scaridiidae

This is a segregate family from **Notommatidae** (Segers 1995). At least some of the species are cosmopolitan; some are pantropical. ***Scaridium*** is the only genus and has only seven species. ***Scaridium longicaudum*** (Figure 148-Figure 150) is associated with bryophytes. It is occasionally planktonic (Plewka 2016), but it can occur in bogs (Horkan 1981) and typically occurs between vegetation (De Smet, pers. comm. 14 November 2016). ***Scaridium montanum*** occurs in ***Sphagnum*** ponds.

Figure 148. ***Scaridium longicaudum*** lateral view, a periphytic species that can be found in bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 149. ***Scaridium longicaudum*** from Pocono Lake, Pennsylvania, USA. This species is known from bogs. Photos by Jersabek *et al.* 2003, with permission.

Figure 150. ***Scaridium longicaudum***, a bog species. Photos by Jersabek *et al.* 2003, with permission.

Synchaetidae

To my mind, this family has some of the most unusual-looking rotifers. It has only four genera, three of which include bryophyte associates.

Polyarthra

Polyarthra (Figure 153, Figure 157-Figure 158) reminds me of a Native American headdress. Many of the species have long blade-like flexible appendages – my association with feathers and headdresses. The members of the genus are planktonic, but a few species have been found among bryophytes. They feed by a grabbing and sucking motion.

Gilbert and Schroder (2004) suggested that the **diapause** (resting) eggs (Figure 151) that develop into amictic females in species like ***Polyarthra vulgaris*** (Figure 151-Figure 152), occasionally a moss dweller, may be an adaptation for survival in an environment that is unstable. These amictic females have a higher lipid content, reduced digestive tract, and produce a single large egg within hours of hatching, whereas the normal generation time is six days. The diapause eggs are produced by sexual reproduction of a female and small male (from small eggs; Figure 152), thus producing a **diploid egg** (one having two sets of chromosomes). Like many algae and other plants, this behavior of sexual reproduction occurs when the environment becomes unfavorable. The diapause egg is able to remain viable without hatching for extended periods of time.

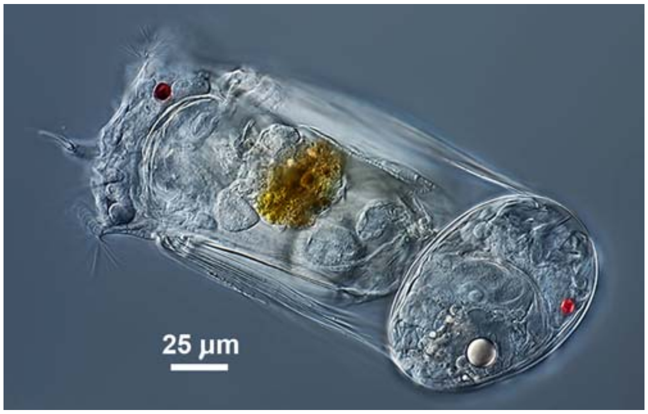

Figure 151. ***Polyarthra vulgaris*** with parthenogenetic diploid amictic egg. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 152. ***Polyarthra vulgaris*** with male eggs (smaller than female eggs). Photo by Michael Plewka (www.plingfactory.de), with permission.

Polyarthra euryptera (Figure 153) is a cosmopolitan planktonic species (de Manuel Barrabin 2000) that is known from bog pools (Horkan 1981). They occur in warm water, but are known from temperatures in the wide range of 5.9-24.9°C (de Manuel Barrabin 2000). They are seasonal, reaching a maximum population size in the summer. They generally do not occur in the hypolimnion, where they would be trapped in cold water. This species may be prey for other rotifers, including ***Asplanchna girodi*** (Figure 154) and ***Ploesoma hudsoni*** (Figure 155-Figure 156) (Guiset 1977). Their known *p*H range is 6.3-9.9.

Figure 153. ***Polyarthra euryptera***, a cosmopolitan planktonic species that is known from bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 154. ***Asplanchna girodi*** (with resting egg), a species that preys upon ***Polyarthra euryptera***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

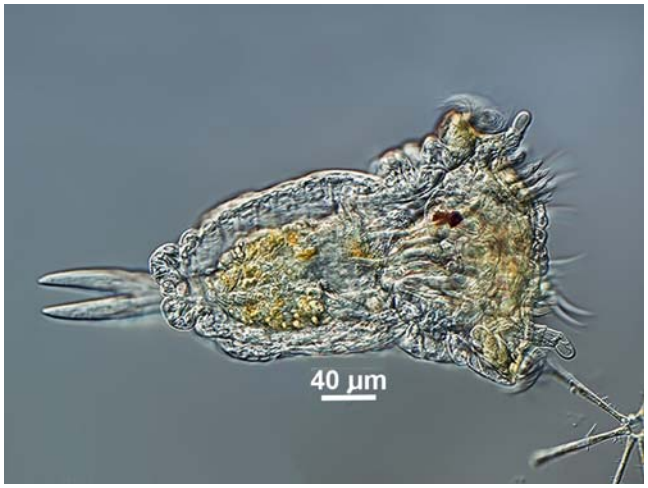

Figure 155. ***Ploesoma hudsoni*** dorsiventral view, a predator on ***Polyarthra euryptera***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 156. ***Ploesoma hudsoni*** (lateral view), a predator on ***Polyarthra euryptera***. Photo by Michael Plewka <www.plingfactory.de>, with pernission.

Polyarthra vulgaris (Figure 157-Figure 158) has likewise been found among mosses, including ***Sphagnum*** (Figure 41), in bogs (Hingley 1993), although it is a planktonic species (de Manuel Barrabin 2000). This species is cosmopolitan and present year-round. To accommodate its year-round activity, it tolerates temperatures 5.9-16-7°C. It prefers high levels of oxygen, a *p*H range of 6.6-6.9, and lives near the water surface, rarely occurring in the hypolimnion. It feeds on centric diatoms and algae in the **Cryptomonadaceae** (Pourriot 1977) and **Chrysophyceae** (Devetter 1998), as well as bacteria and one-celled **Chlorophyta** (Bogden & Gilbert 1987). Bogden and Gilbert (1987) describe the feeding as a suction that uses pharyngeal expansion. The fecundity is positively related to the amount of chlorophyll *a* present (Devetter & Sed'a 2003). They are especially important in the food web, along with other rotifers, when the hydrological conditions are unstable (Keckeis *et al.* 2003).

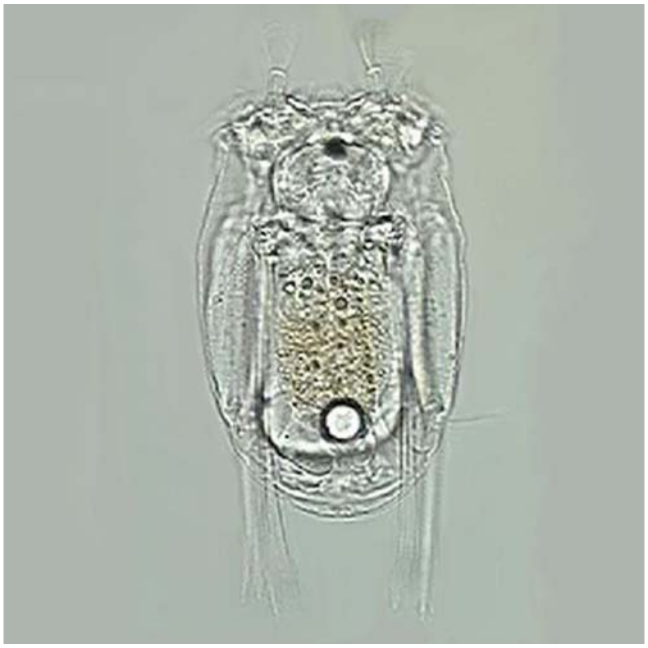

Figure 157. ***Polyarthra vulgaris*** has been found among mosses, although it is a planktonic species. Photo from Malcolm Storey, through Creative Commons.

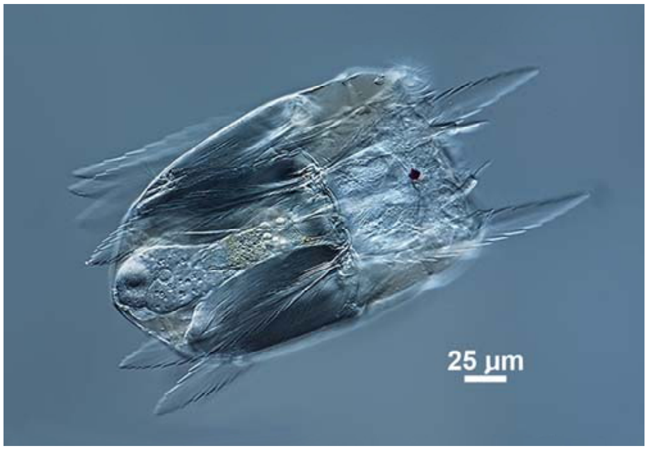

Figure 158. ***Polyarthra vulgaris***, a planktonic species that lives among ***Sphagnum*** in bogs. Photo by Michael Plewka

Synchaeta

The genus ***Synchaeta*** (Figure 159) is typically planktonic in both freshwater and marine environments, it also has members that live on bryophytes in freshwater (Hingley 1993). It also is one of the few rotifers to live in the marine environment (Brownell 1988; Wikipedia 2012), but not on bryophytes there (bryophytes do not occur in the marine environment). It prefers cold water and is absent in the warm water habitats of southeast Asia (Segers 2001).

Figure 159. ***Synchaeta***, a cold-water genus that occurs on bryophytes (Hingley 1993). Photo by Wim van Egmond, with permission.

Synchaeta pectinata (Figure 160-Figure 161) is a cosmopolitan planktonic species (de Manuel Barrabin 2000) that has been collected from bryophytes and can live in bog pools (Horkan 1981; Hingley 1993). Although it survives at temperatures of 5.9-25.5°C, it has its maximum populations at low temperatures (de Manuel Barrabin 2000). It lives in both small and large lakes at *p*H 6.3-9.3. The food is primarily algae of the **Cryptomonadaceae**, **Chrysophyceae**, and centric diatoms (Pourriot 1970). The species is often infected by the fungus *Plistophora* (*Bertramia*) *asperospora*. ***Synchaeta tremula*** (Figure 162) occurs in bogs (Horkan 1981).

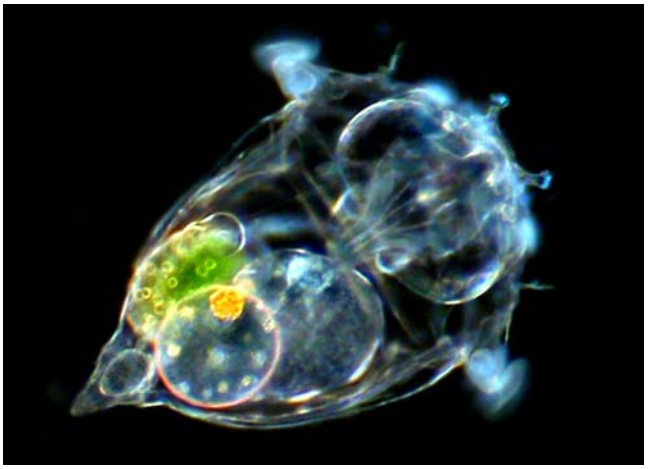

Figure 160. ***Synchaeta pectinata*** from plankton. Photo by Michael Plewka <www.plingfactory.de>), with permission.

Figure 161. ***Synchaeta pectinata***, typically a cosmopolitan planktonic species, also lives among bryophytes and can live in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 162. ***Synchaeta tremula*** from a lake in New Jersey, USA. This species also occurs in bogs. Photo by Jersabek *et al.* 2003, with permission.

Tetrasiphonidae

As nearly as I can determine, there is one genus and possibly two species in this family, although Segers (2007) only lists ***Tetrasiphon hydrocora*** (Figure 163-Figure 164); one species remains undescribed. This species is known from ***Sphagnum*** (Figure 41) and submersed mosses (Nogrady 1980; Hingley 1993; Plewka 2016).

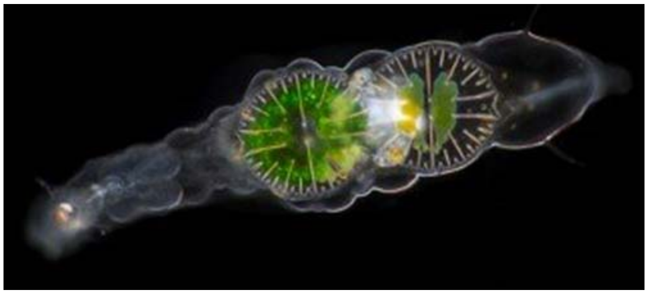

Figure 163. ***Tetrasiphon hydrocora***, a species known from ***Sphagnum***, with the desmid ***Micrasterias*** in its gut. Photo by Wim von Egmond, with permission.

Figure 164. ***Tetrasiphon hydrocora***, a species known from ***Sphagnum***. Note desmids in the gut. Photo by Jersabek *et al.* 2003, with permission.

Trichocercidae

The members of this family usually have a twisted body and strongly asymmetrical trophi. Some members are parasitic. Some live among bryophytes, including ***Sphagnum*** (Figure 41).

Elosa

Elosa has a symmetrical body, but the trophi are asymmetrical. ***Elosa worrallii*** (Figure 165) shares the genus with one other species that is sometimes considered to be conspecific with ***E. worrallii*** (Segers 2007). ***Elosa worrallii*** lives among bryophytes, including ***Sphagnum*** (Myers 1942; Hingley 1993).

Figure 165. ***Elosa worrallii*** with notch in lorica, a species known from bryophytes, including ***Sphagnum*** (Myers 1942). Photo by Michael Plewka <www.plingfactory.de>, with permission.

Trichocerca

By contrast to ***Elosa***, ***Trichocerca*** is a larger genus. ***Trichocerca bicristata*** (Figure 166-Figure 167) is planktonic, but lives in bog pools (Figure 2; Horkan 1981; Hingley 1993). ***Trichocerca brachyura*** (Figure 168) occurs in bogs in the Pocono Mountains, Pennsylvania, USA (Horkan 1981; Jersabek *et al.* 2003). ***Trichocerca cavia*** (Figure 169) is likewise a species known from ***Sphagnum*** bogs, living on submerged mosses (Hingley 1993; Plewka 2016). On Svalbard, ***T. cavia*** occurs among submerged mosses, but also occurs in the plankton (De Smet 1993). Among others known from ***Sphagnum*** bogs, Hingley (1993) included ***T. collaris*** (Figure 170), ***T. elongata*** (Figure 171), ***T. junctipes*** (***T. sejunctipes***?), ***T. longiseta*** (Figure 172-Figure 173), ***T. porcellus*** (Figure 174-Figure 175; see also Bielańska-Grajner *et al.* 2011) [also from ***Fontinalis*** (Jersabek *et al.* 2003)], ***T. rattus*** (Figure 178-Figure 179), (also Horkan 1981; Jersabek *et al.* 2003), and ***T. rosea*** (Figure 180-Figure 181; also Jersabek *et al.* 2003).

Figure 166. ***Trichocerca bicristata***, a planktonic species that lives in ***Sphagnum*** pools. Photo by Michael Plewka <www.plingfactory.de>, with permission.

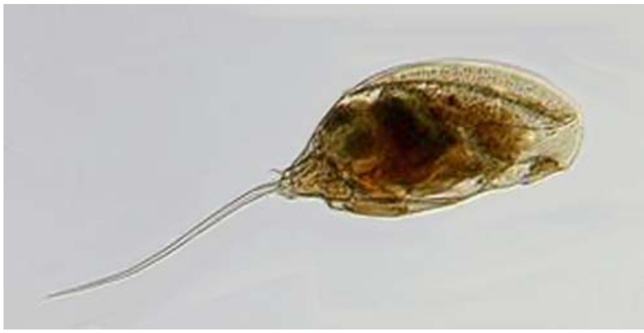

Figure 167. ***Trichocerca bicristata***, a rotifer known from bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 168. ***Trichocerca brachyura*** from the Pocono Mountains, Pennsylvania, USA. This species is known from bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 169. ***Trichocerca cavia***, a species that lives on submerged moss and in ***Sphagnum*** bogs. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 170. ***Trichocerca collaris***, known from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 171. ***Trichocerca elongata***, a species known from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 172. ***Trichocerca longiseta***, a species known from bogs. Photo by Yuuji Tsukii, with permission.

Figure 173. ***Trichocerca longiseta***, known from a bog. Photo by Jersabek *et al.* 2003, with permission.

Trichocerca major (Figure 175) and ***T. porcellus*** (Figure 174) are cosmopolitan species in small water bodies with limited nutrients (de Manuel Barrabin 2000). ***Trichocerca major*** is known from both a bog and ***Fontinalis*** (Jersabek *et al.* 2003). Both species typically occur between vegetation as periphyton (De Smet, pers. comm. 14 November 2016). ***Trichocerca porcellus*** is active in winter at temperatures around 9.5°C and occurs at a *p*H around 7.1. It lays eggs inside algal mats such as ***Aglaucoseria***, ***Fragilaria*** (Figure 176), and ***Dinobryon*** (Figure 177). It is known from bryophytes in multiple locations, including collections of the aquatic moss ***Fontinalis*** (Figure 58).

Figure 174. ***Trichocerca porcellus***, a cosmopolitan periphytic species known from the aquatic moss ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

Figure 175. ***Trichocerca major***, a species known from both a bog and ***Fontinalis***. Photo by Jersabek *et al.* 2003, with permission.

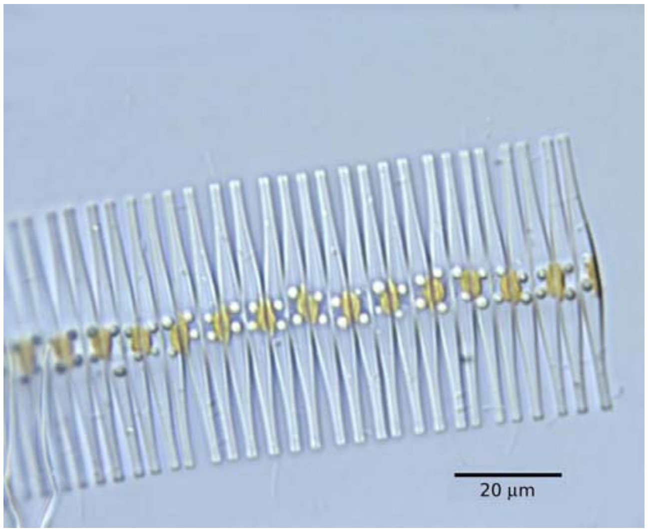

Figure 176. ***Fragilaria***, egg-laying site of ***Trichocerca porcellus***. Photo by Jason Oyadomari, with permission.

Figure 177. ***Dinobryon divergens***, in a genus that is an egg-laying site for ***Trichocerca porcellus*** and food for ***Trichocerca similis***. Photo by Frank Fox, through Creative Commons.

Figure 178. ***Trichocerca rattus*** lateral view. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 179. ***Trichocerca rattus*** f. ***carinata***, a form of a species known from ***Sphagnum*** bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 180. ***Trichocerca rosea***. This species is known from more than one bog. Photo by Jersabek *et al.* 2003, with permission.

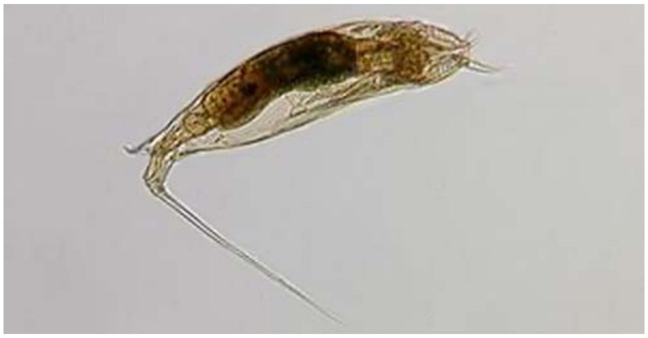

Figure 181. ***Trichocerca rosea***, a species that been found in more than one location on ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Trichocerca similis (Figure 182-Figure 183) is a planktonic rotifer, but it also is known from bryophytes and bog pools in Pennsylvania, USA (Myers 1942; Horkan 1981). It is likely to be cosmopolitan, preferring warmer waters (de Manuel Barrabin 2000). It attaches its asexual eggs to other members of the plankton (Pourriot 1970). It prefers a slightly basic *p*H of 7-9.63 and temperatures of 9.5-26.2°C (de Manuel Barrabin 2000). Food is predominantly Cryptomonadaceae and Chrysophyceae, especially *Mallomonas* (Figure 184) and *Dinobryon* (Figure 177). It is a common food item of predator rotifers such as ***Asplanchna*** (Figure 154) and *Ploesoma* (Figure 155-Figure 156) (Guiset 1977).

Figure 182. ***Trichocerca similis***, a planktonic species that also occurs with bryophytes and in bog pools. Photo by Jersabek *et al.* 2003, with permission, with permission.

Figure 183. ***Trichocerca similis***, a plankton species that lives among bryophytes and in bog pools. Photo by Michael Plewka <www.plingfactory.de>, with permission.

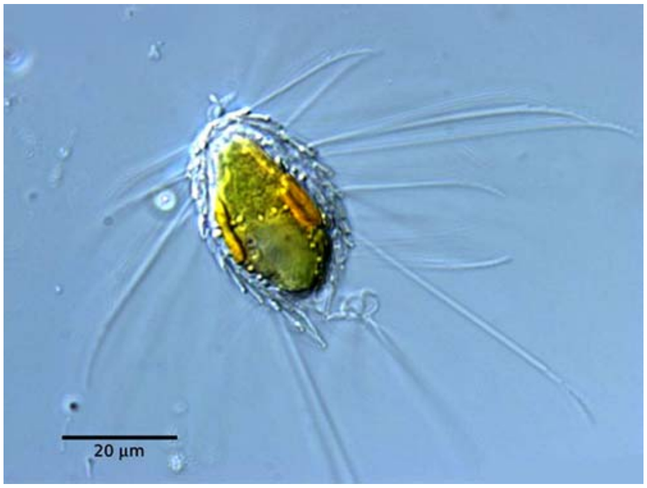

Figure 184. ***Mallomonas***, food for ***Trichocerca similis***. Photo by Jason Oyadomari, with permission.

Jersabek *et al.* (2003) added several ***Sphagnum*** (Figure 41) associates. These included ***Trichocerca edmondsoni*** (Figure 185), ***T. ornata*** (Figure 186) as a bog species and ***T. lata*** (Figure 187), ***T. parvula*** (Figure 188; these two species are easily confused), ***T. platessa*** (Figure 189), ***T. rotundata*** (Figure 190), and ***T. scipio*** (Figure 191) from among ***Sphagnum***.

Figure 185. ***Trichocerca edmondsoni*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 186. ***Trichocerca ornata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 187. ***Trichocerca lata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 188. ***Trichocerca parvula*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 189. ***Trichocerca platessa*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

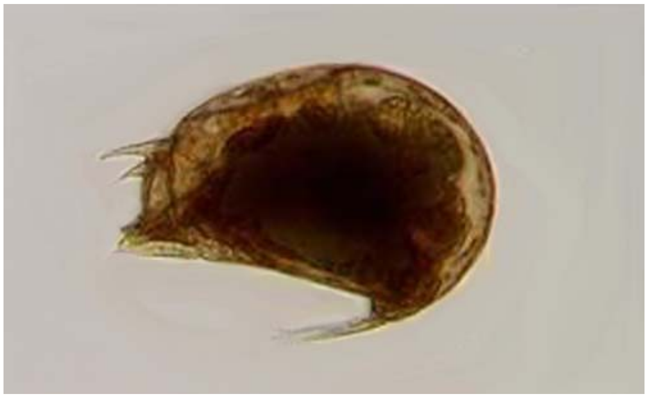

Figure 190. ***Trichocerca rotundata*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

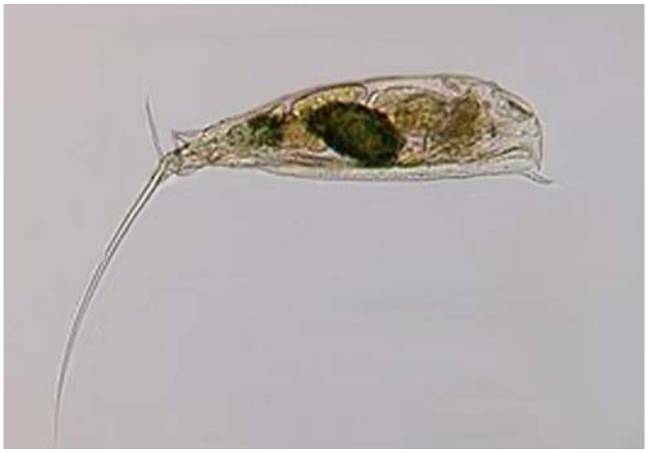

Figure 191. ***Trichocerca scipio*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Both ***Trichocerca tenuior*** (Figure 192) and ***T. tigris*** (Figure 193-Figure 195) occur in bogs (Horkan 1981; Hingley 1993), but they also both live on the thallose liverwort ***Riccia fluitans*** (Figure 147) in ponds (Jersabek *et al.* 2003). ***Trichocerca harveyensis*** (Figure 196) lives on ***Fontinalis disticha*** and seems to be the only bryophyte dweller in ***Trichocerca*** not known from ***Sphagnum*** (Figure 41) (Myers 1942; Jersabek *et al.* 2003).

Figure 192. ***Trichocerca tenuior*** from among the thallose liverwort ***Riccia fluitans***. This rotifer also occurs on bog mosses. Photo by Jersabek *et al.* 2003, with permission.

Figure 193. ***Trichocerca tigris***, a species that lives among ***Sphagnum*** and the thallose liverwort ***Riccia fluitans*** in ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 194. ***Trichocerca tigris*** from among ***Sphagnum*** in a bog and ***Riccia fluitans*** in pond. It also occurs in bog pools. Photo by Jersabek *et al.* 2003, with permission.

Figure 195. ***Trichocerca tigris***, known from ***Sphagnum*** in a bog and from the thallose liverwort ***Riccia fluitans*** in a pond. Photo by Jersabek *et al.* 2003, with permission.

Figure 196. ***Trichocerca harveyensis*** from among ***Fontinalis disticha***. Photo by Jersabek *et al.* 2003, with permission.

On Svalbard, ***T. rattus*** (Figure 178-Figure 179) occurs on submerged mosses, but also in the plankton (De Smet 1993). Horkan (1981) included ***T. similis*** (Figure 183-Figure 182) as a species of bog pools. Bielańska-Grajner *et al*. (2011) added ***T. musculus***. On Svalbard, ***T. intermedia*** (rare; Figure 197), ***T. longistyla***, ***T. obtusidens*** (Figure 198), ***T. uncinata*** (Figure 199), and ***T. weberi*** (Figure 200) occur on submerged mosses, but they also occur in the plankton (De Smet 1988, 1993).

Figure 197. ***Trichocerca intermedia***, a species of submerged mosses on Svalbard. Photo by Jersabek et al. 2003, through Creative Commons.

Figure 198. ***Trichocerca obtusidens*** Jersabek *et al*. 2003, through Creative Commons.

Figure 199. ***Trichocerca uncinata***, a species of submerged mosses and plankton on Svalbard. Photo by Jersabek *et al.* 2003, through Creative Commons.

Figure 200. ***Trichocerca weberi***, a species of submerged mosses and plankton on Svalbard. Photo by Jersabek et al. 2003, through Creative Commons.

This family is one that represents the sparse studies on rotifers living on mosses in waterfalls. It is represented by ***Trichocerca pusillus*** (Figure 201) from a waterfall in Thailand (Savatenalinton & Segers 2008), but this species is more typically a plankton species (De Smet, pers. comm. 14 November 2016).

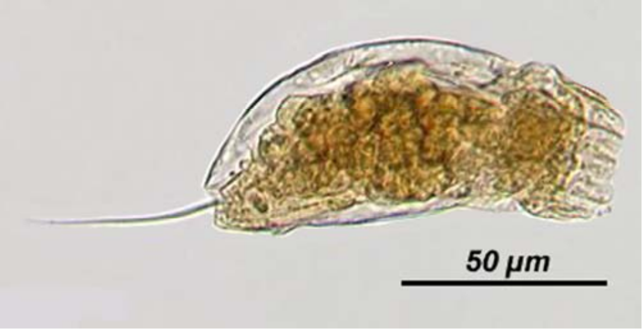

Figure 201. ***Trichocerca pusilla***, a planktonic species that can occasionally occur among wet mosses in waterfalls. Photo by Jersabek *et al.* 2003, with permission.

Trichotriidae

This family is loricate and its surface is marked with facets that have spicules or spines and are mostly granulate (Koste & Shiel 1989). The lorica extends beyond the body to the head, foot, and toes. It typically occurs both on and between aquatic plants, only occurring in the plankton when it is migrating to a new location. There are only three genera, and two of them (***Macrochaetus***, ***Trichotria***) have been collected from **bryophytes**.

Macrochaetus

Macrochaetus collinsii (Figure 203-Figure 202) inhabits bryophytes in bogs (Hingley 1993). ***Macrochaetus multispinosus*** (Figure 204) lives among ***Sphagnum*** (Figure 41; Jersabek *et al.* 2003).

Figure 202. ***Macrochaetus collinsii***, a species known to inhabit bryophytes. Photo by Jersabek *et al.* 2003, with permission.

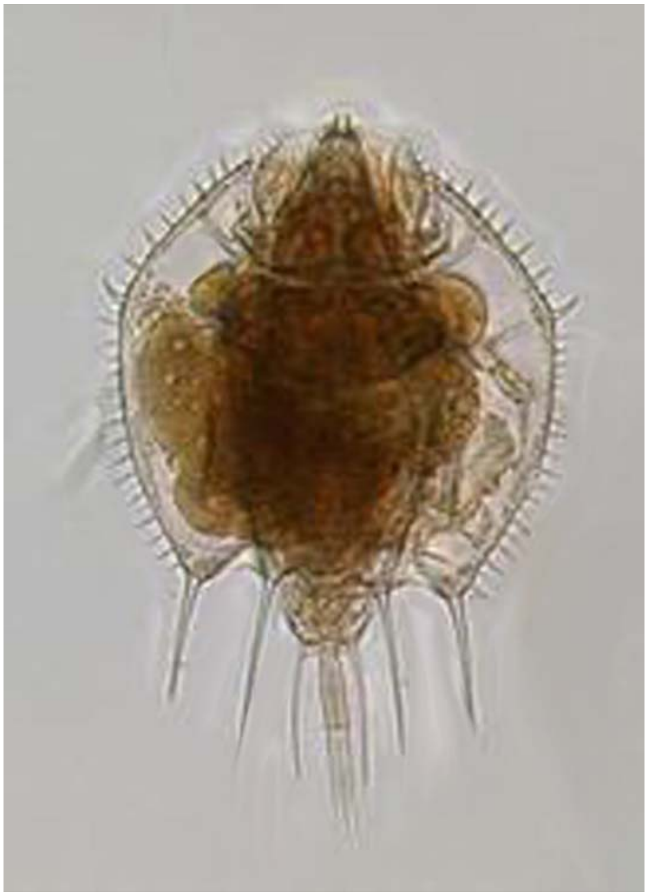

Figure 203. ***Macrochaetus collinsii***, a species known to inhabit bryophytes in bogs. Photo by Jersabek *et al.* 2003, with permission.

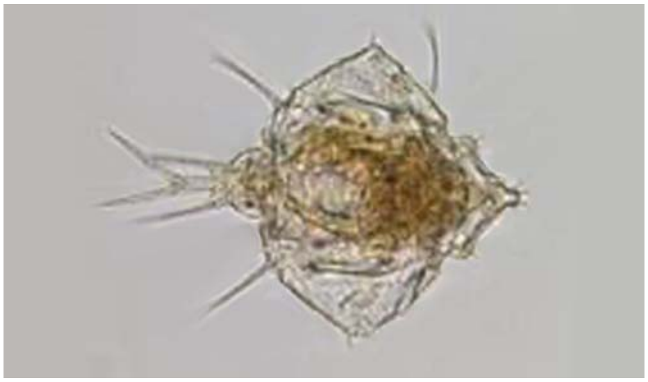

Figure 204. ***Macrochaetus multispinosus*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Trichotria

Trichotria cornuta (Figure 205), ***T. pocillum*** (Figure 206-Figure 207), ***T. tetractis*** (Figure 209-Figure 212), ***Trichotria tetractis caudata*** (Figure 210), ***T. tetractis similis*** (Figure 211), and ***T. truncata*** (Figure 213-Figure 215) all live among ***Sphagnum*** (Figure 41) in bogs (Horkan 1981; Hingley 1993; Jersabek *et al.* 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016). ***Trichotria pocillum*** is a cosmopolitan species that lives on plant substrata (de Manuel Barrabin 2000), including bryophytes, and can occur in bogs (Horkan 1981). It eats the organic detritus and algae, particularly diatoms, that accumulate among the plants (de Manuel Barrabin 2000). It is widely tolerant of mineralization but prefers a narrow *p*H range of 7.5-8.1. Its known temperatures are in the narrow range of 7.7-9.1, making it active only in winter, at least in Spanish reservoirs. ***Trichotria tetractis*** is a cosmopolitan species and has ecological relationships with ***T. pocillum*** (de Manuel Barrabin 2000). ***Trichotria tetractis*** is known from a *p*H around 8.1 and temperature around 18.8°C.

Figure 205. ***Trichotria cornuta*** from among submerged ***Sphagnum*** in a bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 206. ***Trichotria pocillum***, a plankton and detritus dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 207. ***Trichotria pocillum***, a species that lives on plant substrata (de Manuel Barrabin 2000), including bryophytes, and can occur in bogs. Photo by Jersabek *et al.* 2003, with permission.

Figure 208. ***Trichotria similis*** from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 209. ***Trichotria tetractis*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 210. ***Trichotria tetractis caudata***, a cosmopolitan species from bogs among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 211. ***Trichotria tetractis similis*** (stained) from a ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

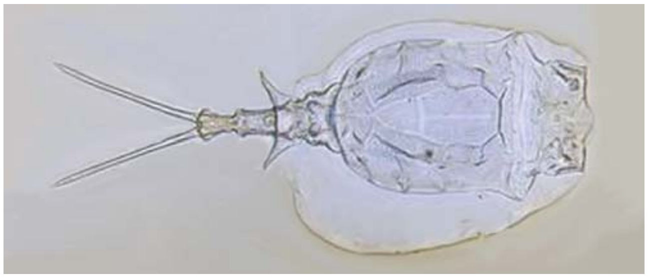

Figure 212. ***Trichotria tetractis***, a species known from ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 213. ***Trichotria truncata***, a species known from more than one ***Sphagnum*** bog. Photo by Jersabek *et al.* 2003, with permission.

Figure 214. Side view of ***Trichotria truncata***, a species known to associate with ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 215. ***Trichotria truncata***, a species known from more than one location where it is associated with bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Summary

The monogonont order **Ploimida** is continued here from the previous sub-chapter. The **Notommatidae** is a large family with a number of species collected from bryophytes. The **Proalidae** has no hardened lorica; it occurs on freshwater plants. The **Scaridiidae** is a small family with two species from bryophytes reported here. The **Synchaetidae** has mostly planktonic members, but some have been found among bryophytes. The **Tetrasiphonidae** may have only two species, and they are known from bryophytes. The **Trichocercidae** have a twisted body; two genera have species on bryophytes. The **Trichotriidae** are loricate with spicules or spines; two genera occur on bryophytes.

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Bryonetters have been wonderful in making their photographs available to me and seeking photographs from others. Tom Powers and Walter Dioni helped me obtain images and permission from others. Christian D. Jersabek very generously gave me permission to use the wealth of images from the Online Catalog of Rotifers. My special thanks go to Michael Plewka for his generous permission to use so many of his beautiful online images. Many photographers have been generous with permission for the use of their images and others have provided them online through Creative Commons and public domain sources. Aydin Orstan helped me find email addresses and pointed out errors in an earlier version of the chapter. Claudia Ricci answered my questions and helped me with current nomenclature.

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CHAPTER 4-8
INVERTEBRATES: MOLLUSCS

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CHAPTER 4-8
INVERTEBRATES: MOLLUSCS

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

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

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

Gastropoda: Snails and Slugs

Most terrestrial and freshwater snails (**Pulmonata**) have spiral shells and these may be taller than the diameter of the opening (**elongate/conical**; Figure 26) or shorter (Figure 145) (Pratt 1935). The inside body is also a spiral, but it is not the same spiral as the one of the shell. This internal spiral affects the digestive system as well. With its mouth to the ground, the snail is infamous for the positioning of the anus above the mouth on the right side of the head (Figure 2).

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

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

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

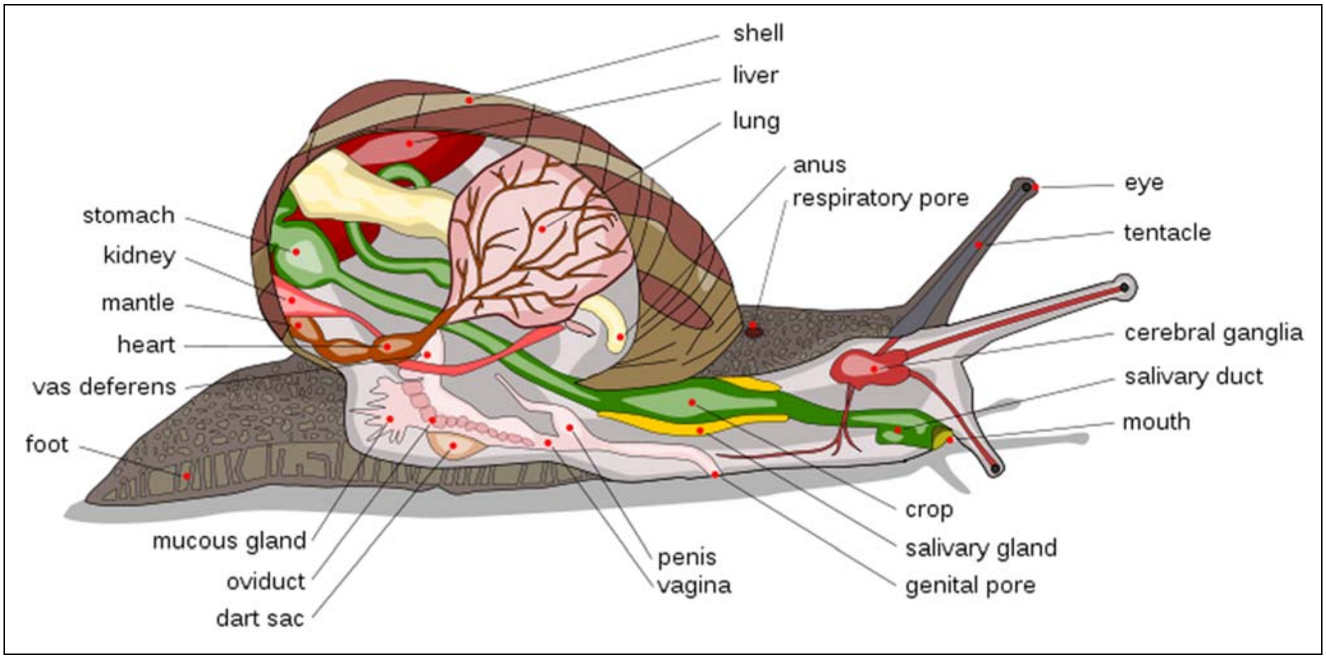

Figure 2. Snail, showing its major internal and external parts. Note the dart sac from which the love dart is ejected. Image from Wikimedia Creative Commons.

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

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

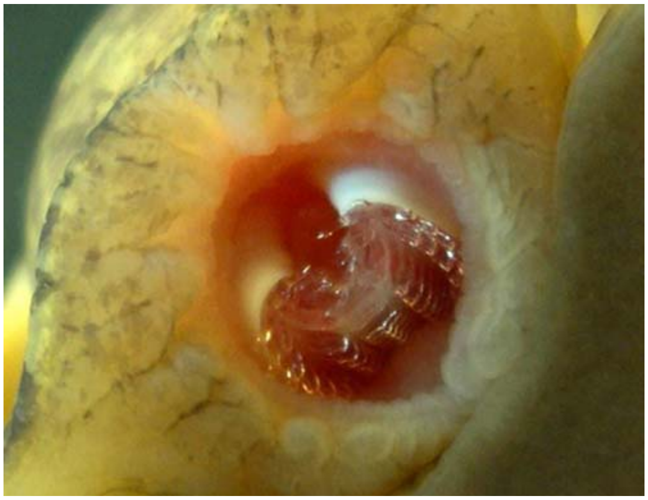

Figure 5. *Pomacea canaliculata* mouth showing **radula**. Photo by S. Ghesquiere, through Wikimedia Commons.

Reproduction

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

Some land snails are **sequential hermaphrodites**, being first male, then female (Nordsieck 2012b). Others, such as ***Arianta arbustorum*** (**Helicidae**; Figure 6), a moss-dwelling snail, have a mechanism that prevents sperm cells from fertilizing the snail's own egg cells before they reach the sperm pouch of the mate. In the aquatic **Lymneidae**, snails can reproduce using unfertilized eggs, permitting them to multiply rapidly in a new location and causing invasive species problems when they are introduced as aquarium pets.

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

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

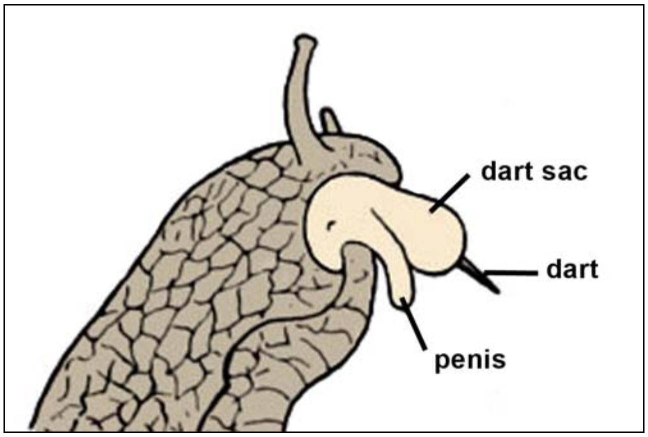

Figure 7. *Helix pomatia* head during mating. Redrawn from Johannes Meisenheimer, through Wikimedia Commons.

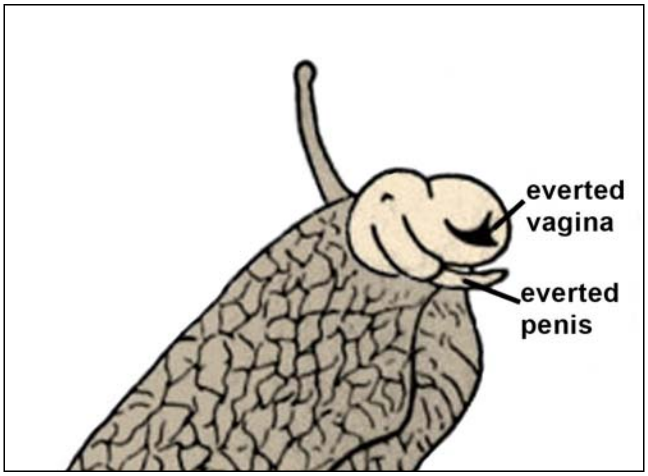

Figure 8. *Helix pomatia* head after mating, showing both male and female parts of this **simultaneous hermaphrodite**. Redrawn from Johannes Meisenheimer, through Wikimedia Commons.

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

Mating and the Love Dart

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

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

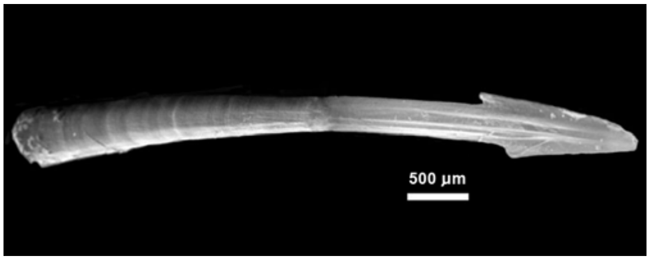

Figure 11. **Love dart** of the snail ***Monachoides vicinus***. Photo by Joris M. Koene and Hinrich Schulenburg through Wikimedia Commons.

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

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

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

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

Egg and Larval Development

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

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

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

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

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

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

Bryophyte Interactions

Glistening trails of pearly mucous (Figure 17) criss-cross mats and turfs of green, signalling the passing of snails and slugs on the low-growing bryophytes (Figure 1). In California, the white desert snail ***Eremarionta immaculata*** (Figure 18) is more common on lichens and mosses than on other plant detritus and rocks (Wiesenborn 2003). Wiesenborn suggested that the snails might find more food and moisture there. Are these molluscs simply travelling from one place to another across the moist moss surface, or do they have a more dastardly purpose (as hunters) for traversing these miniature forests?

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

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

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

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

Abundance

Snails can sometimes occur in significant numbers in moss habitats. Their need for a moist environment (Pratt 1935) would seemingly attract snails to the mosses as a moist substrate. Quantitative information on snails and slugs among bryophytes is scarce, and often only mentions that bryophytes are abundant in the habitat (*e.g.* Nekola 2002).

The study by Grime and Blythe (1969) is helpful in understanding numbers and dynamics of moss-dwelling snail populations, but we need many more studies. They found average morning populations of up to 8.5 per 100 g dry weight of moss in early September for the copse snail ***Arianta arbustorum*** (Figure 20) at Winnats Pass in Derbyshire, England. In collections totalling 82.4 g of moss, they examined snail populations in a 0.75 m^2 plot each morning on 7, 8, 9, & 12 September 1966. ***Arianta arbustorum*** numbered 0, 7, 2, and 6 on those days, respectively, with weights of 0.0, 8.5, 2.4, and 7.3 per 100 g dry mass of moss. This was surpassed only by those on

Urtica dioica (stinging nettle) reaching 14.4 and *Mercurialis perennis* (dogs mercury) reaching 16.2. Nevertheless, it takes a lot of dry moss to make 100 g.

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

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

Adaptations

Confusing the Predator

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

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

Jumping to Escape

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

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

In Canada, some of these ***Hemphillia*** (Figure 21-Figure 24) species seem safe from extinction due to sufficient abundance, but others are endangered due to increasing patchiness of suitable habitats (Leonard & Ovaska 2003). The 1994 NW Forest Plan regulates ground disturbance activities on federal lands in northern California to Washington, protecting "survey and manage" species, including several species of jumping slugs, ***Hemphillia***. ***Hemphillia dromedarius*** (dromedary snail; Figure 23-Figure 24) is officially threatened in both Canada and the United States, where it lives in the state of Washington. Legal protection of these slugs can help in the protection of mosses in these areas. However, the Bush administration was not sympathetic to this protection and it could be lost at any time with a change in administrative philosophy. Perhaps the novelty of its jumping behavior will increase public interest and sympathy and lead to its protection in yet another way.

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

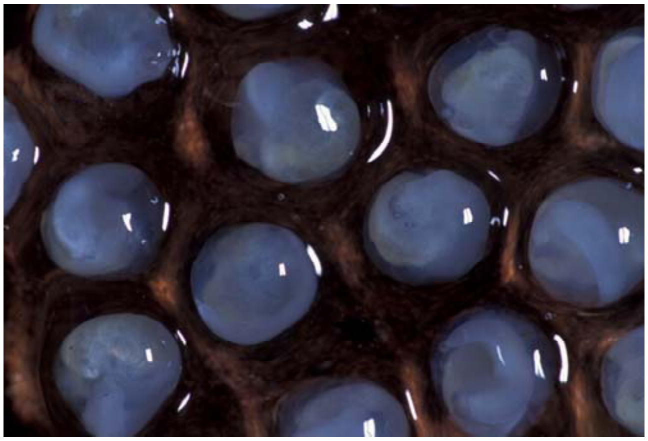

Figure 24. Eggs of ***Hemphillia dromedarius***, the dromedary jumping slug. Photo by Kristiina Ovaska, with permission.

Keeping It Small

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

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

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

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

Szlavecz (1986) determined that snail size plays an important role in their behavior, including food searching. Although one might think that larger animals need to eat more, it seems that the larger ***Monadenia hillebrandi mariposa*** (Figure 27) instead spends more time crawling and less time feeding, permitting it to travel farther. Although it prefers leaf litter, it consumes mosses as well (Figure 28). This snail lives in cool, mossy forests and sometimes hibernates among mosses, including thick moss on a bigleaf maple branch (Sandelin 2012).

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

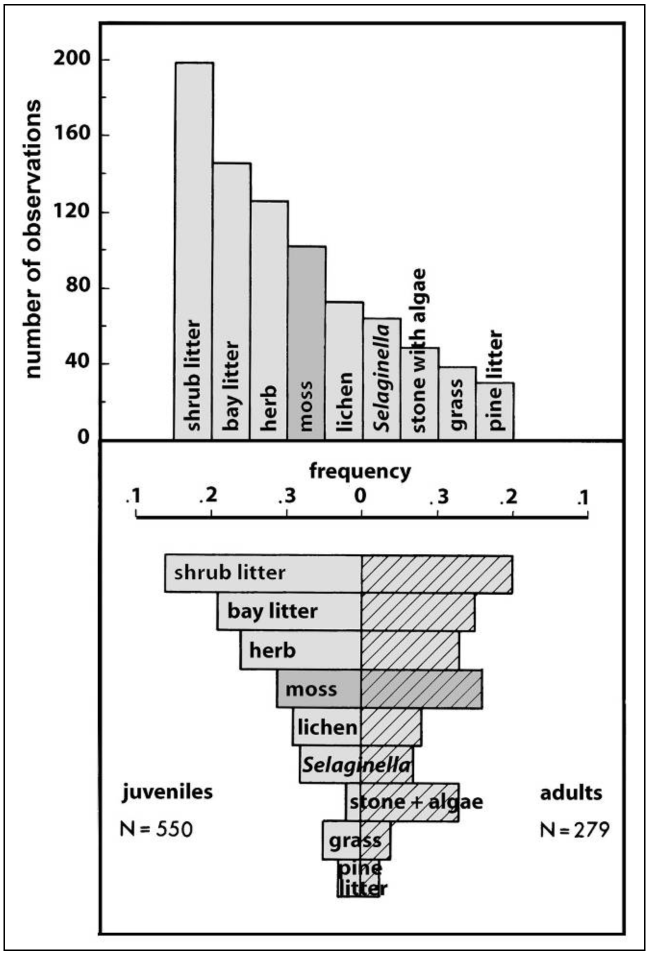

Figure 28. Laboratory selection of foods by the snail ***Monadenia hillebrandi mariposa***. **Upper**: all data combined. **Lower:** juveniles vs adults. Redrawn from Szlavecz 1986.

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

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

Conical Shape

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

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

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

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

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

Avoiding Desiccation

Bryophytes remain moist long after their epiphytic and rock substrata, and even those on dry soil can become moist, collecting fog or light rainfall that never reaches the soil. Hence, they can become a refuge for snails and slugs seeking moisture. Such is often the case for the banana slug, ***Ariolimax columbianus*** (Figure 15), in the Pacific lowlands, USA. This slug leaves its moist cover on a moss-covered fallen log to forage at night, then returns to the moss (Sandelin 2012). Taking advantage of the moisture at night, this slug can travel nearly 0.5 km in search of more suitable conditions.

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

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

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

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

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

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

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

No Shell – Slugs

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

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

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

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

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

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

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

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

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

In Search of Food

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

Guy Brassard reported to me that Stéphane Leclerc has taken a picture of a slug in Quebec, Canada, eating a ***Buxbaumia aphylla*** (Figure 43-Figure 44) capsule! Michael Lüth (Bryonet 23 September 2017) observed and photographed a slug grazing on the capsule of ***Buxbaumia viridis*** (Figure 45). Dave Kofranek reports tasting it – it tastes like cucumbers (Bryonet 24 September 2017).

Figure 43. ***Buxbaumia aphylla*** that are immature and have not been eaten. Photo by Štěpán Koval, with permission.

Figure 44. ***Buxbaumia aphylla*** that may have been damaged by a herbivore. Photo by Janice Glime.

Figure 45. ***Buxbaumia viridis*** with slug eating capsule. Photo by Michael Lüth, with permission.

Low Palatability?

Often it appears that the palatability index for bryophytes is low (Jennings & Barkham 1975). Furthermore, snails and slugs seem to be less interested in grazing things with awns than those without. Robin Stevenson (pers. comm. January 2008) has seen ***Bryum argenteum*** (Figure 46-Figure 47) that is completely grazed over, but never observed such grazing on an awned ***Grimmia*** species (Figure 42). Could it just be that there is no nutrition in an awn, or do they have trouble gliding across the furry tips of leaves?

Figure 46. ***Bryum argenteum***, a moss with no awns and a food source for snails and slugs. Photo by Michael Lüth, with permission.

Figure 47. ***Bryum argenteum*** showing lack of awns. Photo from UBC website, with permission from Shona Ellis.

But awns, even in ***Grimmia pulvinata*** (Figure 48), may not deter all snails (Figure 48). Szlavecz (1986) was able to identify the awned ***Grimmia trichophylla*** (Figure 49) in the feces of the California snail, ***Monadenia hillebrandi mariposa*** (Figure 27) and also demonstrated that the spine tips of the tracheophyte *Selaginella hansenii* (Hansen's spikemoss; Figure 50) did not deter feeding or crawling. Perhaps it depends on the density of the hair tips, since ***Grimmia trichophylla*** (Figure 49) and *S. hansenii* (Figure 50) have much less dense hairs than ***G. pulvinata*** (Figure 48), and on the particular species and size of snail or slug. On the other hand, it appears that the slugs are able to graze the lower margins of a clump, apparently resting on the substrate without the need to traverse the awns (Figure 48).

Figure 48. ***Grimmia pulvinata*** exhibiting grazing that girdles the base of the clump in a pattern typical of snail or slug grazing, but also known for isopods. Photo by Robin Stevenson, with permission.

Michael Lüth has observed snails grazing on ***Orthotrichum*** (Figure 51) and Terry McIntosh has seen slugs grazing on other bryophytes, with both observers indicating that the damage to the moss was similar to that shown for ***Grimmia pulvinata*** in Figure 48 (Bryonet 12 January 2008). On the other hand, Frank Greven (Bryonet 13 January 2008) has seen this pattern as a result of grazing by isopods (wood lice). Robin Stevenson (pers. comm. 14 January 2008) agrees that isopods might be deterred by the awns, causing them to eat in such a pattern. But in this case, after climbing up a bridge coping, the snail or whatever might have found that this moss provided the best choice available.

Figure 49. ***Grimmia trichophylla*** in Bretagne (Brittany), France, showing somewhat less imposing awns than those of ***Grimmia pulvinata***. Photo by Michael Lüth, with permission.

Figure 50. ***Selaginella hansenii***, a spine-tipped tracheophyte eaten by the snail ***Monadenia hillebrandi mariposa***. Photo by J. E. (Jed) and Bonnie McClellan © California Academy of Sciences, with permission.

Figure 51. ***Orthotrichum urnigerum***, member of a genus known to be grazed by snails. Photo by Michael Lüth, with permission

Low Nutritional Quality?

That rasping tongue is not always enough to accomplish the task of obtaining nutrients from mosses. Oyesiku and Ogunkolade (2006) experimented with snails and the moss ***Bryoerythrophyllum campylocarpum***. In laboratory experiments, snails (***Limicolaria aurora***; Figure 52) gained the most weight when fed ***Bryoerythrophyllum campylocarpum*** paste. Snails that had only unground moss actually lost weight. Those in the field experiment (restricted to ***B. campylocarpum***) either lost weight or remained the same. Fecal matter of field snails had fragments of moss that had lost chlorophyll from their cells as well as that of abundant algae and **Cyanobacteria**. Presence of snails on the moss was seasonal from April until October, when moisture and lower temperature of the moss may have provided favorable habitat. This experiment suggests that in this case the snail was unable to penetrate the cells of the moss, making it an unlikely food source in nature. Rather, the researchers suggest that snails most likely use moss as a moist and cool habitat.

Figure 52. Shell of ***Limicolaria aurora***. Photo by David G. Robinson, USDA APHIS PPQ at Bugwood.org, through public domain.

Food for Some

Clearly for some slugs and snails there are bryophytes that do indeed seem palatable. Ochi (1960) reported that the thallose liverwort ***Conocephalum conicum*** (Figure 53) served as food for a slug. Merrifield (2000) found evidence of heavy grazing on epiphytic bryophytes, particularly the moss ***Syntrichia laevipila*** (Figure 54), of Oregon white oaks (*Quercus garryana*) in the Willamette Valley, Oregon, USA, and considered that either springtails or slugs were likely responsible. She considered that the abundance of gemmae on ***S. laevipila*** may be a response to this grazing.

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

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

Algae growing on mosses, especially in the aquatic habitat, could be a prominent source of food for gastropods. In the Negev Desert, adult desert snails (***Sphincterochila zonata***) fed exclusively on algae on the soil surface, creating an algal turnover of 142 kg hectare^{-1}, despite being active for only 8-27 days in winter during the rainy period (Shachak & Steinberger 1980). Other Negev Desert snails feed on the mosses themselves. ***Sphincterochila boissieri*** (Figure 55) feeds on shrubs there, but its feces indicate that it also feeds on the moss ***Tortula atrovirens*** (=***Desmatodon convolutus***; Figure 56) (Yom-Tov & Galun 1971). This is a snail that has color morphs of brown and white, but they apparently don't affect its temperature (Yom-Tov 1971; Slottow *et al*. 1993). However, their rodent predators choose more brown than white snails, enough to be significantly different (Slottow *et al*. 1993).

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

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

Szlavecz (1986) examined feeding preferences in 31 individuals of the snail ***Monadenia hillebrandi mariposa*** (Figure 27). Collections of field feces indicated that they consumed the mosses ***Rhytidiadelphus*** sp. (Figure 57) and ***Grimmia trichophylla*** (Figure 58) in nature, among other things. In the lab, they preferred shrub and bay litter over mosses, but preferred mosses and lichens over grasses and pine litter. More green moss than brown occurred in the feces, whereas brown material was more common from consumed tracheophytes (Figure 59).

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

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

Grime and Blythe (1969) found bryophytes in the feces of four species of snails out of the six examined from Winnats Pass, Derbyshire, England, on 13 October. But then, tracheophyte foods often become less nutritious as the plants prepare for winter. Studies by Chatfield (1973), Williamson & Cameron (1976), and Richter (1976) indicate that at least juvenile snails might do best on a mixed diet. But for ***Cepaea nemoralis*** (Figure 60-Figure 61), it appears that even though mosses are part of their habitat, they are seldom part of the diet (Williamson & Cameron 1976).

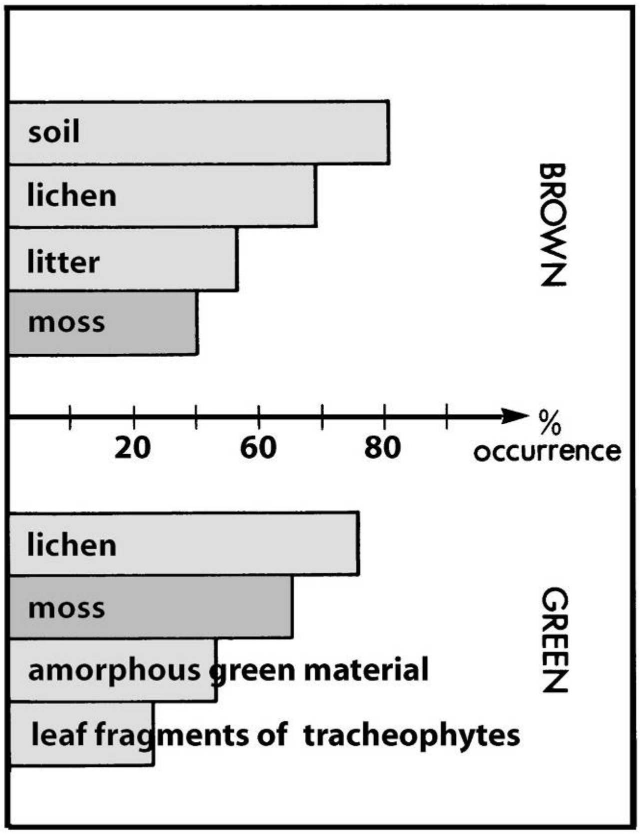

Figure 59. Comparison of green and brown portions of plant material eaten by the **snail *Monadenia hillebrandi mariposa***. Modified from Szlavecz 1986.

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

In the tropical montane rainforest of Brazil, those small, flattened snails in the **Charopidae** (Figure 62) eat bryophytes (Maciel-Silva & dos Santos 2011). Both ***Canalohypopterygium tamariscinum*** (syn. = ***Hypopterygium tamarisci***; Figure 63) and ***Lopidium concinnum*** (Figure 64) had evidence of leaf herbivory, mostly in the beginning of the rainy season (September to December). A species of snail in the **Charopidae** and a moth larva in the **Geometridae** were the culprits. Using an index of damage (ID) in 2007, 2008, Maciel-Silva and dos Santos found that ***C. tamariscinum*** had higher damage (68%, 35%) than ***L. concinnum*** (38%, 23%) in these two years (Figure 65). These rates were lower than those for tracheophytes. They found no correlation with phenols, proteins, or the ratio between them (Figure 65).

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

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

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

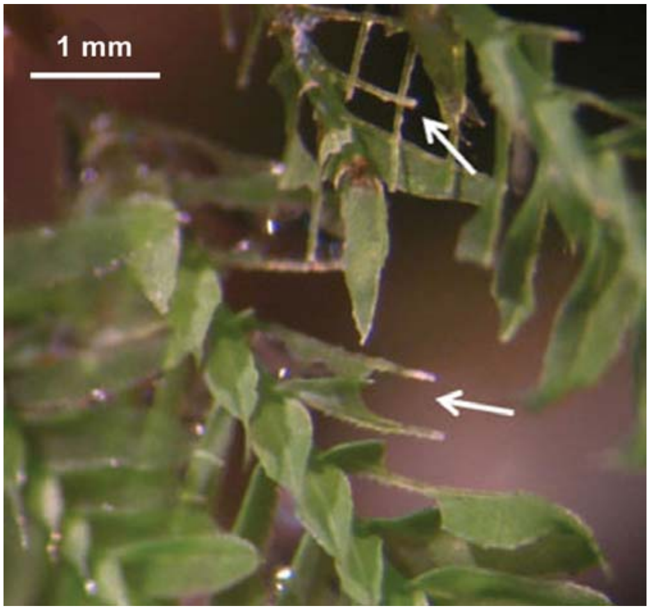

Figure 64. Evidence of **Charopidae** herbivory on ***Lopidium concinnum*** from an Atlantic Forest, Brazil. Photo by Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

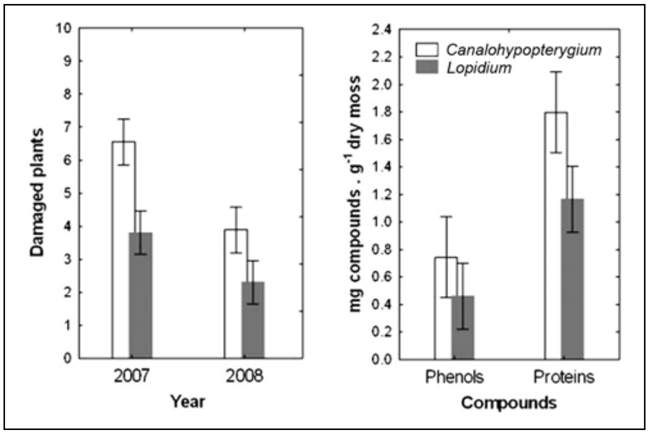

Figure 65. **Charopidae** and **Geometridae** damage to mosses in 10 colonies of plants. Image from Adaises Maciel-Silva and Nivea Dias dos Santos.

An Avoidance of Gametophores?

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

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

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

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

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

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

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

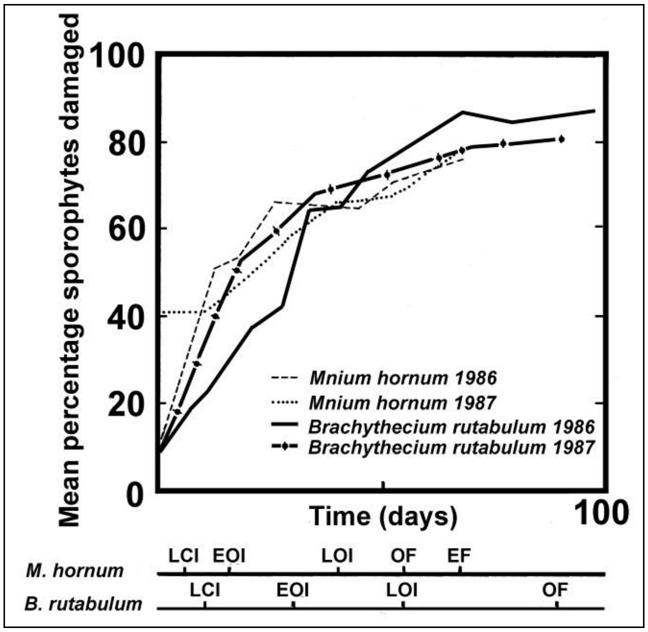

Figure 72. Relative damage by slugs (***Arion*** spp.) of sporophyte stages of two species of bryophytes. n=300-500 at day 0. **LCI** = late calyptra stage; **EOI** = early operculum intact; **LOI** = late operculum intact; **OF =** operculum fallen; **EF** = empty and fresh. Redrawn from Davidson *et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

The slugs consumed only trivial amounts of ***Brachythecium rutabulum*** shoots (Figure 66; Davidson 1989). ***Mnium hornum*** (Figure 77) was also ignored, but after 5-7 days of starvation ***Arion rufus*** (10-15cm long; Figure 73) and ***A. subfuscus*** (5-7 cm long; Figure 75) ate significant quantities of shoots of this species. The garden slug ***Arion hortensis*** (Figure 74) still ignored the moss even after 7 days of starvation.

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

Figure 74. ***Arion hortensis*** *s.s.* at Bridge House, Swavesey, UK. Photo by Brian Eversham, with permission.

Figure 75. ***Arion subfuscus***, a slug known to consume ***Mnium hornum***. Photo by Gary Bernon, USDA APHIS at Bugwood.org, through public domain.

Presence of moss cells of ***Brachythecium rutabulum*** (Figure 76) and ***Mnium hornum*** (Figure 77-Figure 78) in the feces of previously starved ***Arion*** suggest that the leafy mosses are not digested well (Davidson *et al*. 1990). On the other hand, all three species of slugs named above readily consumed ***Funaria hygrometrica*** (0.4-6.5 mg wet weight per slug; Figure 69) in overnight feeding trials. The importance of mosses as food may rest with the organisms living on the mosses – fungi, bacteria, protozoa, rotifers, *etc*., making indigestibility of the mosses inconsequential.

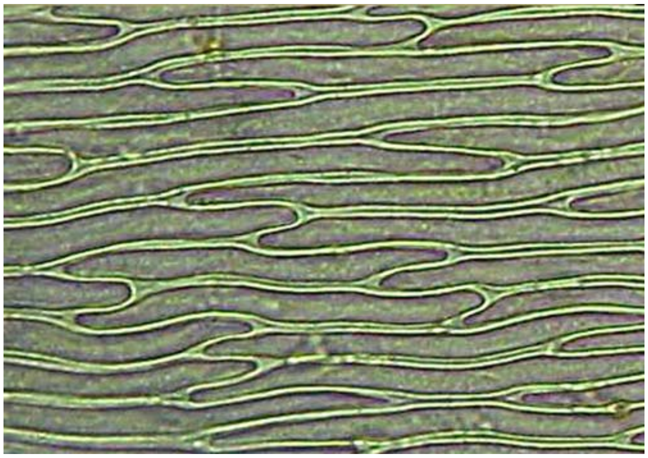

Figure 76. ***Brachythecium rutabulum*** cells as they might be seen in feces. Photo by Tom Thekathyil, with permission.

Figure 77. ***Mnium hornum*** shoots – a species that was ignored in experiments until the slugs were starved. Photo by Janice Glime.

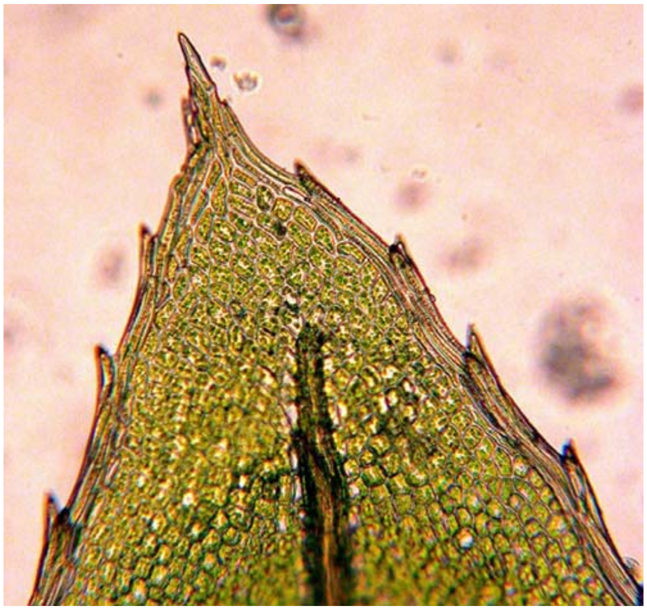

Figure 78. ***Mnium hornum*** leaf tip cells, what one might see in feces. Photo by Bob Klips, with permission.

It is perhaps not surprising that snails eat the capsules of ***Splachnum*** (Figure 79). This genus has odors that attract flies, so they may serve as attractants to gastropods as well.

Figure 79. Snail on setae of ***Splachnum*** capsules in Alaska, eating capsules. Photo courtesy of Blanka Shaw.

Indirect evidence suggests that slugs and snails graze capsules of ***Buxbaumia viridis*** (Gordon Rothero, Birds feeding on moss capsules, Bryonet-l, 10 April 2003; Figure 80). Stark (1860) relayed a story of the ill fate of collected specimens of ***Buxbaumia aphylla*** (bug-on-a-stick moss; Figure 81) on their journey from Scotland to England. A slug had inadvertently been included in the package and it managed to destroy their prized specimens. On the other hand, ***B. aphylla*** can fool you. After repeated observations with my graduate student, Chang-Liang Liao, we have discovered in the field that what appeared to me to be grazing on capsules of ***Buxbaumia aphylla*** is really only the splitting of the capsule top as it dries (Figure 81), and that this occurs on nearly every capsule.

Figure 80. ***Buxbaumia viridis*** capsules. Note that the leafy part belongs to another species of moss. Photo by Adolf Ceska, with permission.

Figure 81. ***Buxbaumia aphylla*** showing exposed green spores in the capsule that has split open. Photo by Janice Glime.

Slugs also eat hornworts (**Anthocerotophyta**; Figure 82). Bisang (1996) reported that they especially eat the green sporophytes.

Figure 82. ***Phaeoceros carolinianus***, a hornwort with mostly green sporophytes, a food source for slugs. Photo by Michael Lüth, with permission.

Deterrents to Herbivory

Longton (pers. comm. 1996) has speculated that phenolic compounds that protect the leafy gametophytes deter herbivory, especially on perennials. This could account for greater herbivory on the annual ***Funaria hygrometrica*** (Figure 83) than on perennial ***Brachythecium rutabulum*** (Figure 66) or ***Mnium hornum*** (Figure 77). The phenolic compounds in the latter two species were released only after severe hydrolysis, leading Davidson *et al*. (1990) to suspect that the phenolic acids might be tightly bound to cellulose in the cell wall. The greater palatability of the ***F. hygrometrica*** supports the general theory that perennials invest more resources in defense against herbivory than do annuals such as ***F. hygrometrica***.

Figure 83. Young sporophytes of ***Funaria hygrometrica*** before spores form. Photo by Michael Lüth, with permission.

Given the choice of capsules or vegetative material, both ***Arion rufus*** (Figure 3, Figure 70, Figure 73) and ***A. subfuscus*** (Figure 84) preferred immature capsules (see Figure 85 with a slug on immature capsules of ***Leucolepis acanthoneuron***) of all three mosses, with ***Mnium hornum*** (Figure 77) being top choice (Davidson 1989). Setae were generally ignored, but ***A. subfuscus*** did occasionally eat ***M. hornum*** and ***Brachythecium rutabulum*** (Figure 66) setae. All three slugs also ate protonemata in the laboratory, and for ***B. rutabulum*** and ***Funaria hygrometrica*** (Figure 83) the protonemata were eaten just as much by ***A. rufus*** and ***A. subfuscus*** as were immature capsules. In fact, dry weight consumption exceeded that of immature capsules. Young shoots were also eaten, but less readily.

Figure 84. ***Arion subfuscus***, a slug that prefers immature capsules. Photo by Sanja 565658, through Creative Commons.

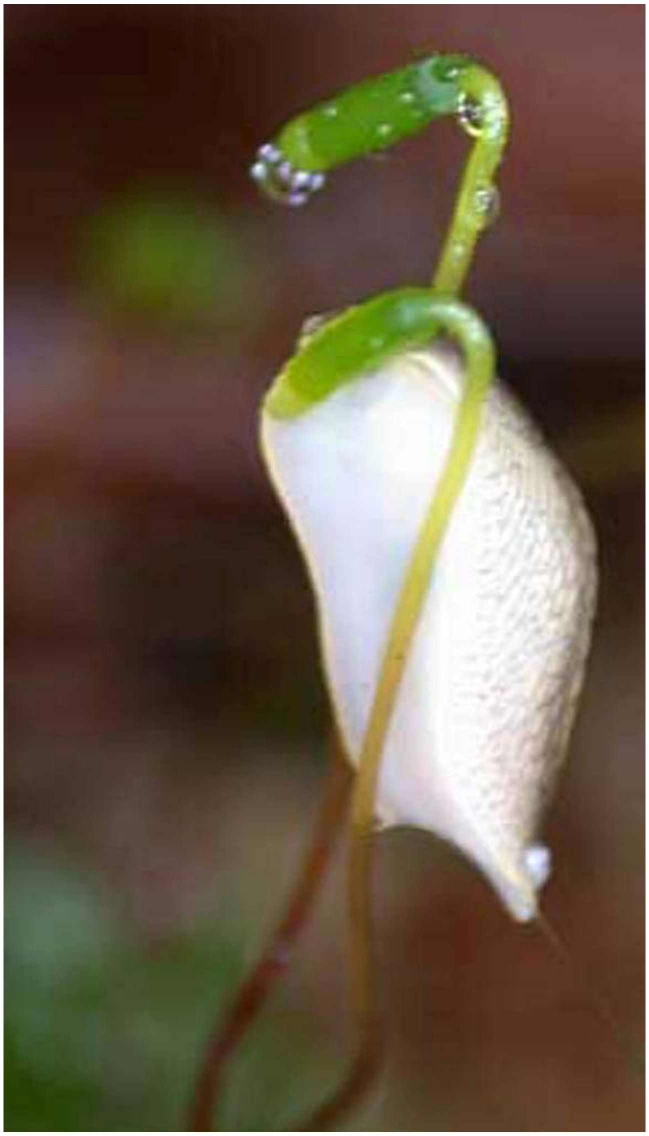

Figure 85. Slug browsing on immature capsule of the moss ***Leucolepis acanthoneuron***. Photo from UBC website, with permission.

Davidson and Longton (1987) suggested that ***Arion hortensis*** (Figure 74) was restricted by the physical structure of the capsule to consuming developing spores from broken capsules in ***Polytrichum commune*** (Figure 86); no spores were eaten from unbroken capsules. When approaching ***Mnium hornum*** (Figure 77), the slugs would withdraw their tentacles, then retreat, suggesting some sort of chemical deterrent; they behaved similarly in the presence of extracts from the capsule. It is likely that hydroxycinnamic and phenolic acids in this species and in ***Brachythecium rutabulum*** (Figure 66) provided this chemical protection against herbivory (Davidson *et al*. 1989). Stems of both species were apparently protected by ferulic and possibly m- and p-coumaric acids bound in the cell walls of the shoots (Davidson *et al*. 1989), explaining the preference of the slugs for capsules. On the other hand, when moss extracts were placed on communion wafers, the slugs ate them more readily, suggesting that chemistry alone was not the likely deterrent (Anonymous 1987; Davidson *et al*. 1990). Rather, some physical feature of the mosses, perhaps the cell wall, deterred these slugs.

Figure 86. ***Polytrichum commune*** capsules showing the persistent hairy calyptra and waxy capsule that is only eaten by snails when the capsule is broken. Photo by Michael Lüth, with permission.

Digestibility

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

Caution must be used in conducting laboratory experiments with food choices. Jennings and Barkham (1975) found that bryophytes all gave low palatability scores when six species of slugs, including the three in the Davidson (1989) study, had a choice of foods. The wider range of choices in the field may permit them to avoid the less palatable bryophytes.

Role in Bryophyte Competition with Lichens

Rosso and McCune (2003) found that molluscs on shrubs in the Pacific Northwest, USA, exhibited significant herbivore activity on the lichens. Bryophytes, on the other hand, had little change in cover between stems in exclusions and those available for herbivory. It appears that the mollusc herbivory on lichens (Boch *et al.* 2011) may benefit the bryophytes by contributing to the successful competition of the bryophytes over the lichens in the understory of these forests.

Palatable Gametophytes

Des Callaghan (Bryonet 10 June 2011) reports slugs feasting on the gametophytes of ***Hookeria lucens*** (Figure 87) near a stream. In only six days they completely removed all the plants by dining on them, leaving behind only a stump and a slime trail (Figure 88). This was a research station, so Callaghan needed to find a way to discourage the slugs. Suggestions from Bryonetters included sprinkling ground glass around the study area (Michael Richardson, Bryonet 10 June 2011); putting out cups of beer to attract and drown the slugs or putting curry powder or other hot substance around the mosses (Janice Glime, Bryonet 10 June 2011); copper rings that are effective in gardens and could be made with a coil of wire (David Bell, Bryonet 10 June 2011).

Figure 87. ***Hookeria lucens*** in healthy condition. Photo by Des Callaghan, with permission.

Figure 88. Temperature/humidity data logger with ***Hookeria lucens*** eaten by slugs. Photo by Des Callaghan, with permission.

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

Aquatic Grazing

Grazing by gastropods (slugs and snails) can be so severe as to define distribution of a bryophyte species. Lohammar (1954) found that in northern Europe ***Fissidens fontanus*** (Figure 89) was absent in lakes where ***Fontinalis antipyretica*** (Figure 90) was also absent. Gerson (1982) suggested that scarcity of ***Fissidens*** in some places is due to snail grazing. In the presence of ***Fontinalis***, this smaller moss lives among the ***Fontinalis*** fronds where it is presumably protected from snail grazing by the inedible forest of ***Fontinalis*** surrounding it and the density of the ***Fontinalis*** stems.

Figure 89. ***Fissidens fontanus***, a moss that seems to be vulnerable to snail grazing except where it is protected by ***Fontinalis*** species. Photo by Michael Lüth, modified by Janice Glime, with permission.

Figure 90. ***Fontinalis antipyretica***, a moss that apparently protects the smaller ***Fissidens*** from grazing by snails. Photo by Bernd Haynold, through Wikimedia Commons.

It may be that in the aquatic habitat the snail effect on some bryophytes is much greater than in the terrestrial habitat. But it is not necessarily all bad. Steinman (1994) opined that snail grazing could account for the apparent unresponsiveness of epiphytes following phosphorus enrichment in a woodland stream in Tennessee, USA, where bryophytes were prominent. And some bryophytes seem prepared to fight back. The thallose liverwort ***Ricciocarpos natans*** (Figure 91) exhibits molluscicidal properties that are active against the snail carrier of **schistosomiasis** (Wurzel *et al.* 1990).

Figure 91. ***Ricciocarpos natans***, a species with molluscicidal properties, floating on the water surface. Photo by Janice Glime.

Bryophyte Antifeedants

Based on the foregoing discussion, it appears that at least some bryophytes are able to discourage browsing by slugs (Frahm & Kirchhoff 2002). Alcohol extracts of the moss ***Neckera crispa*** (Figure 92) and leafy liverwort ***Porella obtusata*** (Figure 93) have antifeedant activity against the slug ***Arion lusitanicus*** (Figure 94). Extracts of 0.5% dry weight of the moss had low activity, whereas those from the liverwort exhibited moderate activity at only 0.05%. At 0.25% the antifeedant activity of ***Porella obtusata*** was complete. It is likely that this activity is not specific for slugs and may discourage insects, bacteria, and fungi as well.

Figure 92. ***Neckera crispa***, a moss that has antifeedant activity against the slug ***Arion lusitanicus***. Photo by Michael Lüth, with permission.

On the other hand, ***Arion lusitanicus*** (Figure 94), also known as the murder slug, easily eats the thallose liverwort ***Marchantia polymorpha*** (Figure 95) (Nils Cronberg, Bryonet 7 April 2016). Cronberg has observed this species feeding on ***Marchantia*** and has noticed that as the slug had invaded the wetland, ***Marchantia polymorpha*** had disappeared in parallel with the invasion.

Figure 93. ***Porella obtusata***. Photo by Jan-Peter Frahm, with permission.

Figure 94. ***Arion lusitanicus***, a slug that traverses mosses, but finds ***Neckera crispa*** and ***Porella obtusata*** unpalatable. Photo by Mogens Engelund, through Wikipedia Commons.

Figure 95. ***Marchantia polymorpha*** showing a nibbled thallus on the upper left, about 1/3 down and 1/3 over from the corner. It also has a tear that is not likely the result of herbivory. Photo by James K. Lindsey, with permission.

Dispersal Agents

It appears that slugs are not all bad in the bryophyte world and may instead be a necessary vector for some propaguliferous taxa (Stolzenburg 1995). Slugs and snails (Figure 96) leave a trail of mucous as they go, and as you well know if you have handled these molluscs, this secretion can be sticky. It is therefore no surprise that these animals have dispersal abilities.

Figure 96. Snails such as this one traversing epiphytic mosses in Japan may be effective dispersal agents. Photo by Janice Glime.

Slugs are able to disperse the brood branches of ***Dicranum flagellare*** (Figure 97) (Kimmerer & Young 1995). These tiny branches become entrapped in the secretions and are deposited in the ensuing slime trail. Kimmerer and Young found that these can be transported at least 23 cm from the colony, although the mean distance in their study was only 3.7 cm.

Figure 97. ***Dicranum flagellare*** showing the tight flagellate branches that can be dispersed by **slugs**. Photo by Janice Glime.

And it appears that the secretion increases the ability of the propagule to adhere to its substrate without affecting the germination rate. In fact, experiments by Davidson (1989) suggest that passage of spores through the slug's digestive system may enhance germination success. All plates containing mature spores from slug (***Arion*** spp.; Figure 94) fecal pellets produced shoots, whereas only 80% of the plates with uneaten mature ***Mnium hornum*** (Figure 67-Figure 68) spores and 70% of those with uneaten ***Brachythecium rutabulum*** (Figure 98) spores produced shoots.

Figure 98. ***Brachythecium rutabulum***, for which the spores germinate better if they have passed through the gut of a slug (***Arion***). Photo by Michael Lüth, with permission.

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

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

Although we know that bryophyte spores reach the mollusc gut, experiments are needed to see if spores expelled in feces are able to colonize successfully. Davidson (1989) found that ***Brachythecium rutabulum*** (Figure 98) and ***Mnium hornum*** (Figure 77) spores eaten by ***Arion*** species actually germinated better than controls.

Manfred Türke sent me images of mosses in the feces of the slug ***Arion vulgaris*** (Figure 99). I was amazed at the size of the fragment of moss in the feces (Figure 100-Figure 101). This is a potential means for dispersal, but the various species of bryophytes must be tested for viability. Digestive enzymes and extreme *p*H could damage the moss cells. On the other hand, the pathogenic fungi ***Phytophora*** spp. (Figure 102) survive as both oospores and filaments and are viable after passing through the digestive system of this slug species (Telfer *et al.* 2015). This was demonstrated by culturing the feces on agar.

Figure 99. ***Arion vulgaris***, a slug that eats mosses, potentially dispersing them. Photo by Dilian Georgiev through Creative Commons.

Figure 100. ***Arion vulgaris*** feces with bryophytes and other material in it. Photo courtesy of Manfred Türke.

Figure 101. ***Arion vulgaris*** bryophyte from slug feces. Photo courtesy of Manfred Türke.

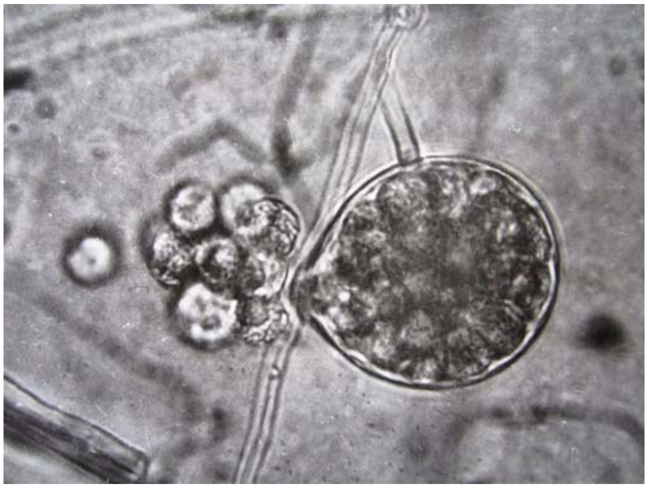

Figure 102. ***Phytophthora parasitica*** zoosporangia, a genus that survives passage through the gut of ***Arion vulgaris***. Photo by Tashkoskip, through Creative Commons.

To provide additional information on the potential dispersal ability of slug feces, Boch *et al.* (2013) fed capsules of four bryophyte species [***Bryum pallescens*** (Figure 103), ***Funaria hygrometrica*** (Figure 69), ***Leptobryum pyriforme*** (Figure 104), ***Pellia endiviifolia*** (Figure 105)] to three slug species [***Arion vulgaris*** (Figure 99), ***A. rufus***; Figure 3, Figure 70, Figure 73), ***Limax cinereoniger*** (Figure 106)]. Among the 117 bryophyte samples, 51.3 % of the spore cultures had germination following gut passage.

Figure 103. ***Bryum pallescens*** with capsules. Spores of this species pass through the guts of several slugs and retain their viability. Photo by David T. Holyoak, with permission.

Figure 104. ***Leptobryum pyriforme*** with capsules. Spores are able to pass through the guts of at least some slugs and remain viable. Photo by Michael Lüth, with permission.

Figure 105. ***Pellia endiviifolia*** with sporophytes. The spores of this species are able to pass through the gut of several slug species and remain viable. Photo by Janice Glime.

Figure 106. ***Limax cinereoniger*** on a mat of moss. Photo by Michal Maňas through Creative Commons.

Boch *et al.* (2013) found that germination rates did not differ among the bryophyte species, but the species of slug had strong effects. Among these three slugs, ***Limax cinereoniger*** (Figure 106) ate the lowest percentage of the bryophytes provided, and even correcting for that, they had the lowest percentage of feces samples (12.9%) producing protonemata. On the other hand, 76% of those of ***Arion vulgaris*** (Figure 99) and 74% of those of ***Arion rufus*** (Figure 3, Figure 70, Figure 73) produced protonemata (Figure 107).

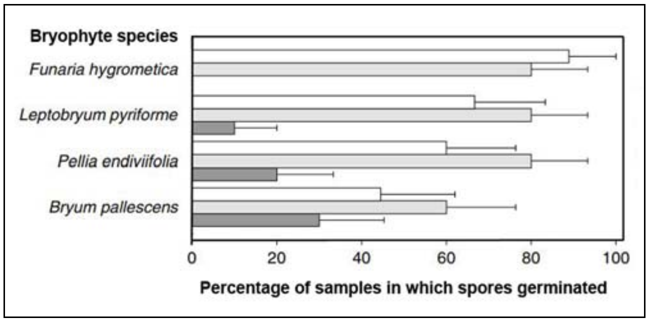

Figure 107. Comparison of spore germination from bryophytes cultured from the feces of three species of slugs. White bars = ***Arion rufus***; light grey bar = ***Arion vulgaris***, dark grey bar = ***Limax cinereoniger***. Redrawn from Boch *et al.* (2013).

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

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

Nevertheless, documentation of the effect of the slugs on the bryophyte community is meager. Boch and coworkers (2015) designed a factorial common garden experiment to determine some of the effects of slugs on the bryophyte vegetation. They collected sporophytes of 11 native and 1 invasive bryophyte species [***Barbula convoluta*** (Figure 108), ***Brachythecium rutabulum*** (Figure 98), ***Brachythecium velutinum*** (Figure 109), ***Bryum*** sp. (Figure 103), ***Campylopus introflexus*** (Figure 110), ***Ceratodon purpureus*** (Figure 111), ***Funaria hygrometrica*** (Figure 69), ***Leptobryum pyriforme*** (Figure 112), ***Marchantia polymorpha*** (Figure 95), ***Phascum cuspidatum*** (Figure 113), ***Plagiomnium affine*** agg. (Figure 114), ***Pohlia*** sp. (Figure 115)], representing 8 families. They used three enclosure treatments: slugs previously fed with bryophyte sporophytes, slugs that had not been fed sporophytes, no slugs. The researchers demonstrated that bryophyte **cover** increased in 21 days from 1.4% to 3.9% in plots where slugs had been fed, an increase that was 2.8 times higher than in the other two treatments. After eight months, the **species richness** was 2.6X higher (5.8 vs 2.2) than in the other treatments. The researchers concluded that the slugs contributed to increasing bryophyte cover and diversity by reducing the dominance of tracheophytes. The early increase in cover in the enclosures with slugs fed sporophytes suggests that they also accomplish dispersal.

Figure 108. ***Barbula convoluta*** with capsules. Photo by Kristian Peters, with permission.

Figure 109. ***Brachythecium velutinum*** with unopened capsules. Photo by Michael Lüth, with permission.

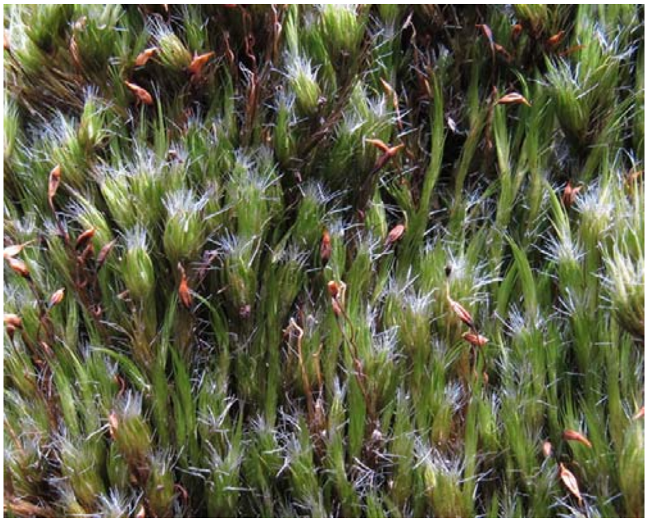

Figure 110. ***Campylopus introflexus*** with capsules. Photo by Michael Lüth, with permission.

Figure 111. ***Ceratodon purpureus*** with young capsules, showing the normal proliferation. Photo by Michael Lüth, with permission.

Figure 112. ***Leptobryum pyriforme*** with numerous immature capsules. Photo by Michael Lüth, with permission.

Figure 113. ***Phascum cuspidatum*** with unopened capsules. Photo by Michael Lüth, with permission.

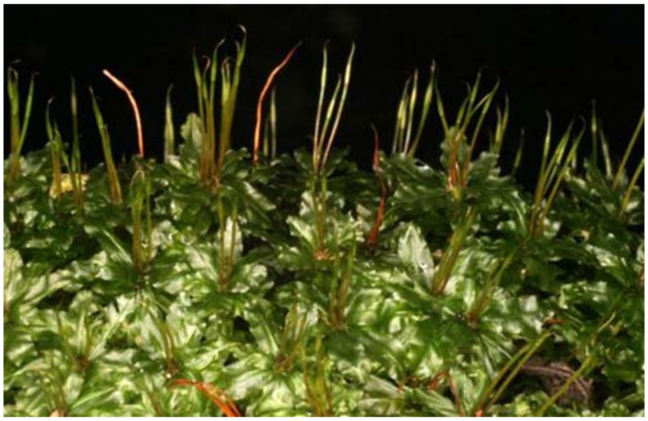

Figure 114. ***Plagiomnium affine*** with developing capsules. Photo by Jan-Peter Frahm, with permission.

Figure 115. ***Pohlia nutans*** with immature capsules. Photo by Michael Lüth, with permission.

When the question of bryophyte dispersal by slugs arose on Bryonet, Scott Redhead (Bryonet 26 August 2016) suggested that this might even occur in the **Splachnaceae**. To that suggestion, Michael Lüth posted an image of ***Tetraplodon mnioides*** (Figure 116) showing one uneaten capsule and one that had been removed by an animal, possibly a slug, documenting his own observations of capsule herbivory. Christian Schröck (Bryonet 26 August 2016) likewise observed grazed capsules in ***Voitia*** and ***Tetraplodon***. However, we need observations of feeding to determine the identity of the herbivores.

Figure 116. ***Tetraplodon mnioides*** with one capsule eaten by an unidentified herbivore. Photo by Michael Lüth, with permission.

Lüth (2010) suggested that the pre-dispersal stage of the capsules on **Splachnaceae** are likely to attract herbivores that differ from the flies that spread the spores. At this earlier stage, the capsules have a different odor from that during the dispersal stage. This odor lasts for only a short time and is therefore often missed by field biologists. On Bryonet (26 August 2016), Lüth explained that ***Splachnum ampullaceum*** smells like *Vaccinium oxycoccos* and occurs in the same habitats, often blending with these cranberries. And ***Tetraplodon mnioides*** (Figure 116) smells like ***Vaccinium myrtillus***. Although not all evolutionary successes are linked to adaptation, it makes one wonder if these early odors are adaptive to facilitate a longer dispersal and subsequent deposition in dung, although one might assume that would require a larger mammal, not a slug.

Figure 117. ***Splachnum ampullaceum*** sporophytes with a cranberry of similar color to the right. Photo by Michael Lüth, with permission.

I think most people would consider dispersal by snails and slugs to be distance-limited. But perhaps, with the help of birds, this is not so limited. Kawakami *et al.* (2003)

demonstrated that the Japanese White-eyes (***Zosterops japonicus***; Figure 118) and the Brown-eared Bulbuls (***Hypsipetes amaurotis***; Figure 119) are birds that eat snails. In fact, five species of snails are able to remain in their shells and appear in the feces. If these snails had eaten moss spores, those spores might be transported a considerable distance, yet be viable in the gut of the snail. It is probably a rare event. Lots of questions remain in this relationship, but the scenario brings up interesting hypotheses.

Figure 118. ***Zosterops japonicus***, a bird that passes intact snails through the gut. Photo by Dick Daniels, through Creative Commons.

Figure 119. ***Hypsipetes amaurotis***, a bird that passes intact snails through the gut. Photo by Nubobo, through Creative Commons.

Malone (1965) discovered another possibility, exemplified by the Killdeer (***Charadrius vociferus***; Figure 120). Malone found two species of freshwater snails attached to the feet of the Killdeer. These were able to remain attached and viable long enough to effect dispersal. The snail ***Galba obrussa*** was able to survive 14 hours on Killdeer feet out of water. But the likelihood that an aquatic snail is carrying bryophyte spores is small due the rarity of capsules. Nevertheless, if a wetland snail has similar behavior, it has a better chance of having consumed spores from wetland mosses.

Figure 120. ***Charadrius vociferus***, a species that disperses snails on its feet. Photo by Andrew C, through Creative Commons.

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

Bryophytes as Home

Because of their small movement space, bryophytes can serve as safe sites for smaller snails. Birds can be significant consumers of snails, particularly during migration (Shachak & Steinberger 1980), and bryophytes can make the snails less conspicuous, if not hiding them completely. In terrestrial habitats, arachnids such as spiders and daddy-long-legs (**Opiliones**) are also predators on snails (Nyffeler & Symondson 2001). While some spiders can probably navigate the spaces within the moss mat, it seems unlikely that most mature daddy-long-legs could manage without getting caught. In addition to the arachnids, carabid beetles prey on terrestrial gastropods (Symondson 2004). Some of these beetles use a pump mechanism to extract the gastropod remains from its shell.

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

In a study of bryophyte inhabitants in the Bükk Mountains of Hungary, Varga (2008) found the tiny gastropods ***Punctum pygmaeum*** (Figure 121) and ***Pupilla muscorum*** (Figure 150) among the terrestrial mosses ***Plagiobryum zieri*** (Figure 122), ***Hypnum cupressiforme*** (Figure 123), and ***Tortella tortuosa*** (Figure 124). Standen (1898) found ***Punctum pygmaeum*** from moss shakings. From my own observations, it appears that snails and slugs are common on and even in bryophyte clumps, but finding documentation on the use of bryophytes by these small species evades even the aggressive Google search.

Figure 121. The tiny ***Punctum pygmaeum*** on ***Ena montanum***, both on a moss. Photo by Stefan Haller, with permission.

Figure 122. ***Plagiobryum zieri***, a moss that supports the gastropods ***Punctum pygmaeum*** and ***Pupilla muscorum***. Photo by Michael Lüth, with permission.

Figure 123. Slug on ***Hypnum***. Photo by Janice Glime.

Figure 124. ***Tortella tortuosa*** in Europe. Photo by Michael Lüth, with permission.

The European snails ***Azeca goodalli*** (Figure 125), ***Euconulus fulvus*** (Figure 126), ***Columella edentula*** (Figure 127), ***Discus*** (subgen ***Goniodiscus***) ***rotundatus*** (Figure 128), ***Lauria cylindracea*** (Figure 129-Figure 130, ***Vertigo pusilla*** (Figure 131), and ***Vitrina pellucida*** (Figure 132) live among mosses, among other substrata (Cloudsley-Thompson & Sankey 1961). ***Carychium tridentatum*** (Figure 133), ***Discus rotundatus***, ***Cepaea hortensis*** (Figure 134), ***Oxychilus navarricus*** (formerly *O. helveticus*; Figure 135), and several rare species of ***Aegopinella*** (formerly in *Retinella*) [***A. pura*** (Figure 136), ***A. nitidula*** (Figure 137-Figure 138)] are known under mossy brick rubble (Verdcourt 1954). ***Clausilia bidentata*** (10-11 mm; Figure 139) is also rare, but can be found under moss. Standen (1898) reported on ***Clausilia rugosa*** (Figure 140) swarming on mossy walls in the UK and feeding on mosses and lichens. Standen (1898) found the snail ***Acme lineata*** on a patch of the thallose liverwort ***Marchantia*** sp. (Figure 95).

Figure 125. ***Azeca goodalli*** shell. Photo by Francisco Welter Schultes, through Creative Commons.

Figure 126. ***Euconulus fulvus***. Photo by Brian Eversham, with permission.

Figure 127. ***Columella edentula***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 128. ***Discus rotundatus*** on moss. Photo by Christophe Quintin, through Creative Commons.

Figure 129. ***Lauria cylindracea*** on bark. Photo by Christophe Quintin, through Creative Commons.

Figure 130. ***Lauria cylindracea***, whose small size can be seen in comparison to this seed. Photo by Christophe Quintin, through Creative Commons.

Figure 131. ***Vertigo pusilla*** on bark. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 132. ***Vetrina pellucida*** on bark. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 133. ***Carychium tridentatum*** on moss-covered branch. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 134. ***Cepaea hortensis*** venturing into one of the **Pottiaceae** mosses. Photo by Stefan Haller, with permission.

Figure 135. ***Oxychilus navarricus*** on the moss ***Rhytidiadelphus squarrosus***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 136. ***Aegopinella pura*** on leaf litter. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 137. ***Aegopinella nitidula*** on moss. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 138. ***Aegopinella nitidula*** showing shell coils. Photo by Brian Eversham, with permission.

Figure 139. ***Clausilia bidentata*** on moss. Photo by Christophe Quintin, through Creative Commons.

Figure 140. ***Clausilia rugosa*** on bark, a species that eats mosses and lichens. Photo by O. Gargominy, through Creative Commons.

Eucobresia diaphana (Figure 141) lives in humid, cool places on mountains and in forests of Europe, where it is likely to encounter mosses, as seen in Figure 141 (Welter Schultes 2012b), but other than this picture, I can't verify what use it might make of them.

Figure 141. ***Eucobresia diaphana*** on a species of the moss ***Tortula***. Photo by Stefan Haller, with permission.

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

Not surprisingly, new species still lurk amid the bryophytes. Efford (1998) found a new species of the carnivorous New Zealand endemic genus ***Rhytida*** (Figure 142), and reported observations by others of ***R. patula*** and ***R. meesoni perampla*** crawling on mosses and tree trunks at night. These and other New Zealand snails often fall prey to introduced predators. ***Wainuia urnula*** (Figure 143), another night-active snail on mosses, tree trunks, and rocks, was readily eaten by possums, rats, and hedgehogs in captivity. Efford (2000) found that 82% of the 315 ***W. urnula*** snails examined had an unusual food in the feces and gut – terrestrial amphipods. Its relative, ***W. edwardi*** (Figure 144), did not consume amphipods, and no other gastropod is known to consume them. The adaptation for consuming amphipods appeared to be largely behavioral, although there were some differences in the teeth.

Figure 142. ***Rhytida otagoensis***, member of a carnivorous genus that has some moss-dwellers. Image by James Atkinson, with permission.

Figure 143. ***Wainuia urnula***, a tiny night-active New Zealand endemic snail that traverses mosses, as shown here. Photo by Andrew Spurgeon, with permission.

Figure 144. ***Wainuia edwardi***, member of a genus that lives among mosses. Photo by James W. Atkinson, with permission.

Epiphytic

Wiesenborn (2003) observed snails in the Riverside Mountains of California and found that the active snails preferred epiphytic mosses (Figure 145) and lichens compared to plant detritus and four sizes of rocks as habitat. They suggested that the epiphytes could provide these snails with food or moisture. Tree bark soon becomes a desert after the rain dries up, but mosses remain moist much longer, permitting the snails to be active longer and to search there for food where other small invertebrates likewise take refuge from desiccation.

Figure 145. ***Monachoides incarnatus*** on bark where it often encounters bryophytes. Photo by Stefan Haller, with permission.

Tropical islands, especially Hawaii, are particularly vulnerable to invasive species. With all the visitor traffic and import/export business, hitchhikers easily reach the islands. Snails are among these, and may be one of the causes of the apparent extinction of the bird called Po'ouli (***Melamprosops phaeosoma***; Figure 146) (Mountainspring *et al.* 1990). This native Hawaiian bird is especially adapted to feeding on land snails and insects on branches and under mosses, lichens, and bark. Its toes are large and are used for prying up moss and bark to acquire tree snails. The bill is stout, withstanding the force needed for manipulating the snails. Its demise is due largely to increased activity and habitat modification by feral pigs, avian disease, and possible gene pool impoverishment due to low numbers. But it also suffers competition for food by the introduced garlic snail (***Oxychilus alliarius***; Figure 147), a native of northwestern Europe (Welter Schultes 2012a) that emits a garlic odor when it is disturbed. This species is likewise a moss-dweller of mountain slope forests. It feeds on living and dead plant tissue, but it also consumes small snails and the eggs of other snails and slugs (Oxychilus 2011).

Figure 146. Po'ouli (***Melamprosops phaeosoma***) on a mossy branch. Note the sturdy beak used to pry loose bark or crush snails found under bryophytes. Photo through Wikimedia Commons.

Figure 147. ***Oxychilus alliarius*** on moss on bark. Photo © Roy Anderson <habitas.org.uk>, with permission.

The slug ***Prophysaon vanattae*** (scarletback taildropper; Figure 148) is one of those slugs that seems to find a safe site under mosses on trees on Vancouver Island, Canada (Kristiina Ovaska, pers. comm. 30 June 2009). But it also hangs on epiphytic moss mats in the moist deciduous forest there and may even lay eggs there (Figure 149).

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

Figure 148. ***Prophysaon vanattae***, the scarletback taildropper, can be found hiding under mosses. Photo by Kristiina Ovaska, with permission.

Figure 149. ***Prophysaon vanattae*** with eggs on a moss. Photo by Kristiina Ovaska, with permission.

Calcareous Areas

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

Pupilla muscorum (Figure 150) is named for its occurrence among mosses in Great Britain, although it also occurs under stones and in leaf litter (Ehrmann 1956). This tiny (3-4 mm high shell) moss snail often prefers calciferous ground, but others describe it as indifferent to limestone content (Nordsieck 2012a). These snails are **ovoviviparous**. The eggs can survive over winter inside the female's body and are laid in the favorable conditions of spring. At that point, it is not the eggs that must survive because the juveniles usually hatch during oviposition. ***Pupilla triplicata*** (Figure 151) is likewise a moss dweller in Hungary and elsewhere (Deli *et al.* 2002).

Figure 150. ***Pupilla muscorum***. Photo by Malcolm Storey, through Creative Commons.

Figure 151. ***Pupilla triplicata***, a European moss dweller. Photo by O. Gargominy, through Creative Commons.

Another tiny conical snail (2-3 mm) of calcareous areas is ***Acicula fusca*** (Figure 152) in moss on chalk cliffs at Ballycastle, and on chalk underlying basalt at Black Head, Antrim, UK (Anderson 1996). And ***Pomatias elegans*** (Figure 153) occurs on mosses in limestone areas in the Burren, County Clare, UK (Platts *et al*. 2003).

Figure 152. ***Acicula fusca***, a tiny snail that lives among mosses on chalk cliffs. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 153. ***Pomatias elegans*** at Cheddar, Somerset, UK. Photo by Roger S. Key, with permission.

Trochulus (formerly ***Trichia***) ***plebeia*** (Figure 154) occurs in wet mossy areas by springs in limestone areas (Gilbert *et al*. 2005). ***Trochulus villosus*** (Figure 155) lives in the German Alps and requires high moisture (Welter Schultes 2010), making bryophytes useful for maintaining that moisture. This strange genus of snails has hairs on its shell that help to hold it against wet surfaces (Gilbert *et al*. 2005). I don't have any indication that these hairs offer any particular help for living among bryophytes, but if they have any tactile properties, they could help keep it from getting stuck between branches by warning that the passage was getting too narrow.

Figure 154. ***Trochulus plebeia***, a hairy snail, at Sugley Wood, UK. Photo by Brian Eversham, with permission.

Figure 155. ***Trochulus villosus*** on mosses in Germany. Photo by Stefan Haller, with permission.

The European family **Clausiliidae**, known as door snails, derive their name from the "sliding door" that covers the opening of the shell (Wikipedia 2012a). This calcareous door is known as a **clausilium**, hence the family name. It permits the snail to retreat into its shell and seal it off against predators. ***Cochlodina laminata*** (Figure 156), the plaited door snail, lives "between mosses" as well as leaf litter, but may also be found climbing trees in deciduous forests and montane pine forests (Welter Schultes 2012b). ***Clausilia dubia*** (Figure 157) is a calciphilic inhabitant of humid, shady rocks and old walls, but also lives on tree trunks "full of moss." Michael Proctor (pers. comm. 23 April 2016) informed me that this species is very common on Carboniferous limestone in Yorkshire Dales, UK, in the bryophyte and lichen habitats. ***Macrogastra ventricosa*** (Figure 158), the ventricose door snail, lives in places with plentiful mosses on the forest floor or on tree trunks, mostly in the mountains (Welter Schultes 2012b). ***Macrogastra attenuata*** (Figure 159) lives between moss-covered rocks as well as on stones, rocks, and leaf litter in montane forests.

Figure 156. ***Cochlodina laminata*** on bark where it appears to be grazing mosses. Photo by Andrew Dunn, through Creative Commons.

Figure 157. ***Clausilia dubia*** with moss. Photo by O. Gargominy, through Creative Commons.

Figure 158. ***Macrogastra ventricosa*** on moss. Photo by J. C. Schou, Biopix, through Creative Commons.

Figure 159. ***Macrogastra attenuata***, a species of moss-covered rocks in montane forests of Europe. Photo by Niels Sloth, with permission.

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

Bogs and Mires

True bogs are acid, poor fens are acid, intermediate fens have intermediate *p*H levels, and rich fens are basic. For a snail, that *p*H range is an important consideration in choice of habitat because of the need for calcium in forming a shell. Because of this relationship, most malacologists have considered ***Sphagnum*** (Figure 160) peatlands, heathlands, and pine forests as unsuitable habitats for snails and consequently have poor snail biodiversity (Karlin 1961; Kerney & Cameron 1979; Horsák & Hájek 2003).

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

But some snails actually thrive in the low *p*H of bogs and other acid habitats. One such snail is ***Vertigo malleata*** (Figure 161), an extreme **calcifuge**. The degree to which snails have been overlooked in these habitats is exemplified by finding this new species in 60 sites out of 100 acid sites investigated from Maine to Florida, USA (Coles & Nekola 2007). In the bogs it was found primarily in leaf litter on top of the ***Sphagnum*** (Figure 160). Nekola (Jeff Nekola, pers. comm. 16 April 2012) informed me that ***Vertigo malleata*** was virtually absent in the ***Sphagnum*** itself, occurring only where there was leaf litter on top of the ***Sphagnum***. It would be interesting to watch its behavior if it is placed amid the ***Sphagnum***. Is it avoiding ***Sphagnum***, or seeking food only found among the litter? In more northern locations, ***V. cristata*** (Figure 162) or ***V. perryi*** may be present in bogs, but again, they only occur in the leaf litter, not among the ***Sphagnum*** (Jeff Nekola, pers comm. 16 April 2012). ***Vertigo cristata*** is likewise common in pine and spruce forests, heaths, and ***Sphagnum*** peatlands (Nekola & Coles 2010).

Figure 160. ***Sphagnum*** blanket bog, a habitat that does not provide enough calcium for snails. Photo from Creative Commons.

Figure 161. ***Vertigo malleata*** from Lewis Ocean Bay, South Carolina, USA. This snail lives in ***Sphagnum*** peatlands, but avoids the ***Sphagnum***, living in patches of leaf litter on top of it. Photo by Jeff Nekola, with permission.

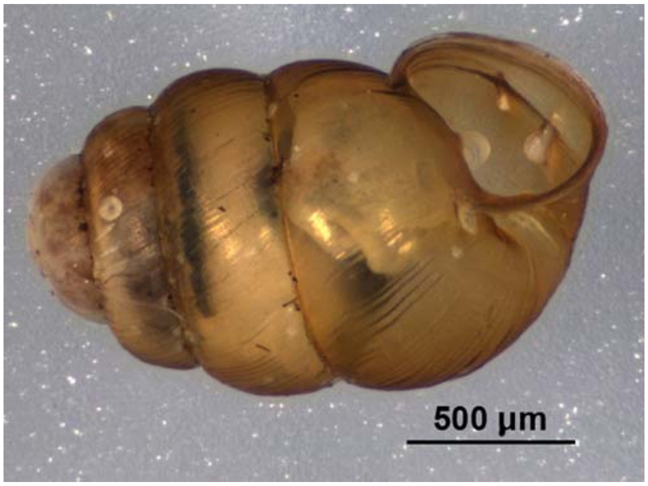

Figure 162. ***Vertigo cristata***, a species that lives on leaf litter, but not ***Sphagnum***, in bogs. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

It appears that other snails that live in bogs and poor fens likewise typically avoid the ***Sphagnum*** (Figure 160). Like ***Vertigo malleata*** (Figure 161), ***Gastrocopta tappaniana*** occurs in decomposing leaf litter of fens, pocosins, and ***Sphagnum*** bogs (Nekola & Coles 2010). Even ***Vertigo perryi***, a resident on the sides of ***Sphagnum*** hummocks, occurs on sedge leaf litter there. And ***Vertigo ventricosa*** (Figure 163) occurs in well-decomposed graminoid and broadleaf plant litter in the ***Sphagnum*** peatlands and poor fens.

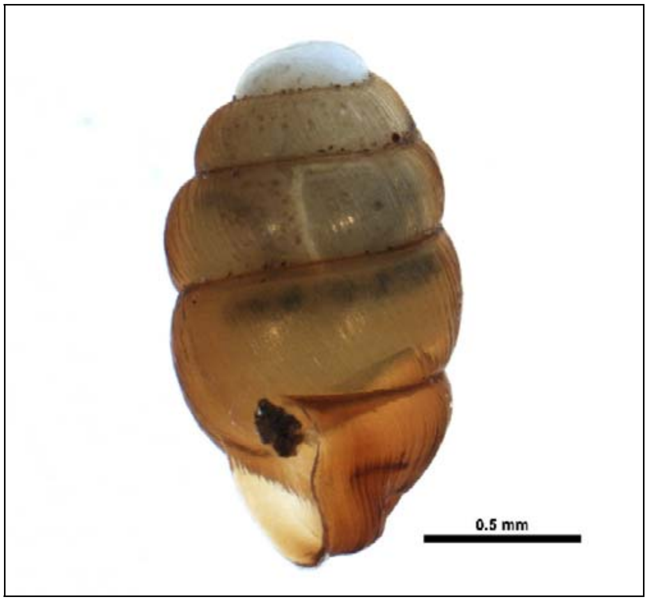

Figure 163. ***Vertigo ventricosa***, a species of litter in peatlands. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Slugs have much less need for that important element – calcium (Ca). In boggy habitats, these gastropods would seem to have little choice but to travel across bryophytes (Stanisic 1996). ***Deroceras laeve*** (Figure 164) is among the slugs that traverse the complicated topography of bogs and mires. But their specific relationships to the bryophytes seems unknown. On the other hand, another member of the genus, **Deroceras reticulatum** (Figure 165), is a ubiquitous slug, but Anderson (2010) points out that raised and blanket peat or exposed ground above 300 m are the only habitats where it is not likely to be found. Hence, it appears that physiological differences are important in separating these slugs.

Figure 164. **Deroceras laeve** (marsh slug) at Flitwick Moor, Bedfordshire, UK. Photo by Brian Eversham, with permission.

Figure 165. **Deroceras reticulatum** on a bed of mosses (not **Sphagnum**). Photo © Roy Anderson <habitas.org.uk>, with permission.

Aquatic

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

Frost (1942) found a strong difference in gastropod inhabitants among bryophytes between an acid and an alkaline stream in her River Liffey survey in Ireland. In the limestone stream, she found 17 snails among the bryophytes, but she found none in the acid stream. Moss inhabitants in the limestone stream included ***Ancylus fluviatilis*** (Figure 166) and a species of ***Planorbis*** (Figure 167). She pointed out that these molluscs were only occasionally found among the mosses.

Figure 166. ***Ancylus fluviatilis*** showing its close adherence to the substrate. Photo by Mauro Mariani, through Wikimedia Commons.

Figure 167. ***Planorbarius corneus***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Invasive species such as the carnivorous ***Euglandina rosea*** (Figure 168), a native of tropical North America, can have severe effects on native snail species elsewhere (Kinzie 1992). In Hawaii, this species has endangered the aquatic **endemic** (Hawaii only) lymnaeid snails due to its seek and capture behavior. The few surviving individuals are primarily restricted to streamside seeps or damp mosses and liverworts covering rocks near waterfalls.

Figure 168. ***Euglandina rosea***, an invasive carnivore. Photo through Wikimedia Commons.

Plant Protectors

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

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

Mussels (Bivalve Molluscs)

Mussels are not common bryophyte inhabitants, but can occasionally occur there in aquatic environs. Frost (1942) found ***Sphaerium corneum*** (Figure 169) and four species of ***Pisidium*** (Figure 170) among the mosses in the limestone stream in her River Liffey, UK, survey, but their typical niches were elsewhere in the stream.

Some bivalve molluscs and other organisms can actually turn the relationship around and provide a home for the bryophytes. Yes, some of these animals actually have mosses growing on them. Neumann and Vidrine (1978) found ***Fissidens fontanus*** (Figure 89) and ***Leptodictyum riparium*** (Figure 171) growing on freshwater mussel shells.

Figure 169. ***Sphaerium corneum*** on an aquatic plant. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 170. ***Pisidium amnicum***. Photo © Roy Anderson <habitas.org.uk>, with permission.

Figure 171. ***Leptodictyum riparium***, a moss known to grow on freshwater mussels**.** Photo by Michael Lüth, with permission.

ECHINODERMATA

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

Summary

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

The white desert snail, ***Eremarionta immaculata***, is common on bryophytes and seems to prefer them as a habitat. The copse snail, ***Arianta arbustorum*** is a night-active inhabitant. More quantitative studies have shown that some slugs and snails prefer bryophytes. More active snails might be found at night, whereas tiny snails might take refuge in the bryophytes during the day.

Adaptations include "jumping" (***Hemphillia***), small size, conical snail, hibernation/estimation, and no shell (slugs). Snails might use them as a safe site to escape spiders, daddy-long-legs, and beetles, whereas other predators may lurk among the bryophytes. In streams, bryophytes may protect them from fish, ducks, shore birds, and amphibians.

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

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

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

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

Gastropods can be common among epiphytes, avoid acid habitats, and abound in limestone habitats.

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

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

Acknowledgments

Bryonetters have been wonderful in making their photographs available to me and seeking photographs from others. Paul Davison has been helpful in providing suggestions and offering images. And a long time ago Allen Neumann sent me a specimen of a clam shell with *Fissidens fontanus* growing on it. Numerous photographers and malacologists have been helpful in providing images and information. Michael Lüth's photographs are a valued contribution. I thank all those photographers who have made their images available through the public domain.

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