CHAPTER 4-5

INVERTEBRATES: ROTIFERS

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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 loric (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.

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.

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 (Pridde & 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).
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.

**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.
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**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.

**Brachionus**

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

*Figure 13.*

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

*Figure 14.*
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.
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), Palustriola 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 adiantoides (Figure 29), Philonotis caespitosa (Figure 30).
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.
Hájková et al. (2011) demonstrated bryophyte-dwelling monogonont rotifers in springs and fens form communities that are strongly correlated with water pH 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 pH 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 (Madalinski 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.

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).

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.

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.

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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 & McDiffted 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.

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 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 cm² should be shaken vigorously in a 70 ml vial with 20 ml rainwater

Figure 37. Chara vulgaris, a potential model for bryophyte faunal communities. Photo by Mnlolf, 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 through 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.

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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).](image-url)
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.
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.

![Image](image-url)

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).
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.

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 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 bdellid 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 bdellid *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.
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."
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.

### 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).
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 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, *Ostostephanos 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 *Ostostephanos 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.](image1)

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.](image2)

**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.

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.
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.

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).
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 $0.83 \pm 0.15$ rotifers per lobule. Male and female plants had a mean ratio of $0.38 \pm 0.04$ rotifers per lobule. Sterile plants likewise tend to be younger. Since we would expect older lobules to have more rotifers due to 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.

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 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.

Figure 93. *Colura calyptrifolia*, a leafy liverwort with lobules where rotifers can live. Photo by Michael Lüth, with permission.
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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/kHhBBpqh_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 20°C, 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 *Mnioib* (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), *Drepanoclados* 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.
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 pH <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.
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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.
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).

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).
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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 observation 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 pH, especially loricate species, the low pH 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 (Bledzki & 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 *Microasterias 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.
Bielońska-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.

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).
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In Australia, Koste and Shiel (1989) identified members of the Euchlanidae, Mytilinidae, Trichotriidae, all members of Monogononta. In Sphagnum pools 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.
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 cm² 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 (Bledzki & Ellison 2003). These tubes readily filled with water. While this method may have been effective for those rotifers that swim 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.
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.

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 pH 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 pH and absent elsewhere because the pH 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 pH 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 pH.
Lecane lunaris (Figure 123) is tolerant of a broad pH 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 pH 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 pH 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 pH 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 pH 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.

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 pH 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!
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 pH being secondary (Charman & Warner 1992). As Bērziņš and Pejler (1987) indicated, pH 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.](image)

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 pitch. 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 pH 4 in culture (Błedzki & Ellison 1998). The pitcher plant water had a pH range of 3.5-6.3, dropping from the higher pH 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.](image)

**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$^2$. 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 metacommunity (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. consticta* (Figure 69), *H. gracilis*, *H. pulchra*, *Macrotrachela quadricornifera* (Figure 62-Figure 64), *Philodina acuticornis odiosa*, *P. flaveiceps* (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.
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 177. Distribution of moss-dwelling rotifers in a stretch of an Italian stream, arranged from upstream to downstream. Based on Fontaneto et al. 2005.
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.

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

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.
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.

Bielanśka-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).

**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.

**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.
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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).

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 200. *Philodina roseola*, sometimes a bryophyte dweller, 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 201. The rotifer *Lepadella* caught by the fungus *Zoophagus insidians*. Photo by Wim van Egmond, with permission.

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 Pb²⁺) 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.

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 *Macrotrotchela 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 *Pygura 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, the highest diversity among the bryophyte habitats, with the *Bdelloidea* predominating. *Habrotrocha roperi* 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.

**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.

**Acknowledgments**

Bryonetters have been wonderful in sharing their observations, making their photographs available to me, and seeking photographs from others. Robert Wallace helped me to understand the life cycle and structures of the rotifers. Paul Davison has been helpful in providing...
suggestions and offering images. Tom Thekathyil alerted me to the image of a rotifer on a *Sphagnum* cell and Des Callaghan helped me find the email address of the photographer. Tom Powers, Jean-Marie Cavanahac, and Walter Dioni helped me obtain images and permission from others. My special thanks go to Michael Plewka for his generous permission to use so many of his beautiful images from Pingfactory and his help in the identification of other images. Aydin Orstan helped me find email addresses and pointed out errors in an earlier version of the chapter. Many other photographers have also been generous with permission for the use of their images. I appreciate Claudia Ricci for her help in tracking down current names and in providing images. Caspar Chater helped me find a reference on moss repair genes. Christian Jersabek was helpful with an earlier version of this chapter and provided permission for use of his images. Diego Fontaneto taught me the difference between mucous and mucus. Willem De Smet provided an extensive review of technical information in this sub-chapter.

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