

CHAPTER 4-5

INVERTEBRATES: ROTIFERS

TABLE OF CONTENTS

Rotifera – Rotifers.....	4-5-2
Reproduction.....	4-5-2
Bdelloidea	4-5-4
Monogononta	4-5-5
Bryophytes as Habitat	4-5-6
Habitat Characteristics	4-5-6
Abundance	4-5-9
Sampling	4-5-10
Extraction Techniques	4-5-11
Adaptations	4-5-11
Particle Feeders	4-5-14
Spines.....	4-5-14
Small Size	4-5-14
Mobility vs Attachment?.....	4-5-15
Protection	4-5-15
Dormant States.....	4-5-17
Physiological Adaptations.....	4-5-17
Anhydrobiosis.....	4-5-17
Changes During Anhydrobiosis	4-5-17
Longevity during Anhydrobiosis.....	4-5-19
Age Differences	4-5-20
Size Differences – Aquatic vs Terrestrial.....	4-5-20
Reproductive Effects.....	4-5-20
Temperature Protection	4-5-20
Recovery Rate.....	4-5-20
The Bryophyte Connection	4-5-20
Other Protections during Anhydrobiosis	4-5-21
Surviving Fungi	4-5-21
Food	4-5-21
Role in the Food Web	4-5-24
Specific Habitats	4-5-25
Lobule Dwellers.....	4-5-25
Retort Cells	4-5-28
Roofs.....	4-5-28
Arctic and High Arctic.....	4-5-30
Antarctic.....	4-5-31
Nunataks	4-5-34
Bog and Fen Habitats.....	4-5-35
Species Richness	4-5-36
Abiotic Factors	4-5-40
Acidity	4-5-40
Surface Configuration	4-5-41
Pitcher Plants	4-5-43
Aquatic Bryophytes.....	4-5-43
Streams.....	4-5-43
Waterfalls	4-5-46
Krakatau.....	4-5-47
Seasons	4-5-48
Danger amidst the Bryophytes	4-5-48
Ozone Hole and Pollution Dangers?	4-5-50
Summary	4-5-51
Acknowledgments	4-5-51
Literature Cited	4-5-52

CHAPTER 4-5

INVERTEBRATES: ROTIFERS

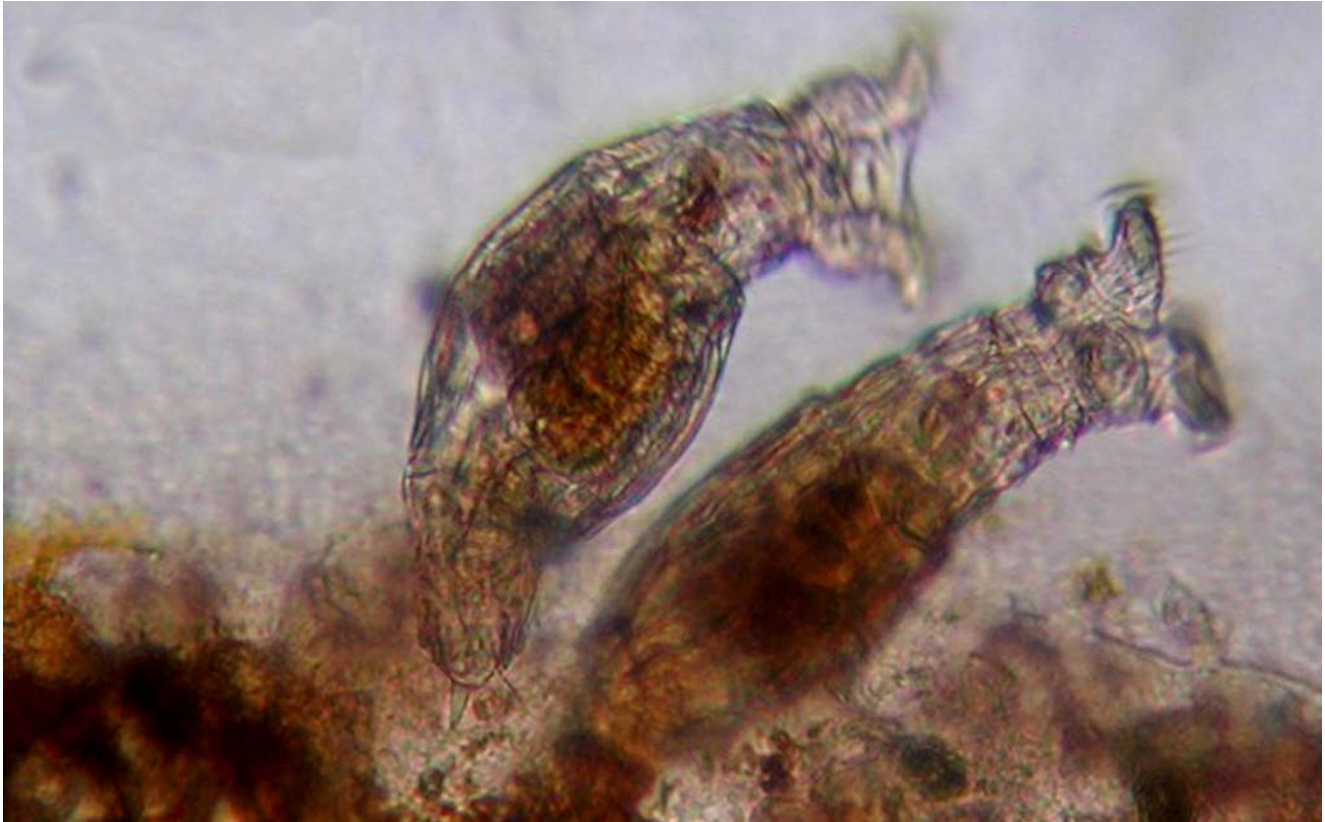


Figure 1. Two **bdelloid rotifers** that commonly inhabit bryophytes. Photo by Paul Davison, with permission.

Rotifera – Rotifers

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

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

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

Not much bigger than some protozoa (mostly 0.1-0.5 mm long, but up to 2 mm), they form a phylum of their own, the **Rotifera**, with at least 2000 species (Howey

1999). They are multicellular and even possess a primitive brain, at least in females (Hingley 1993).



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

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



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

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



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

It is likely that many species of rotifers remain to be described. The most likely habitat for these discoveries is

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

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

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

Reproduction

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

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



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

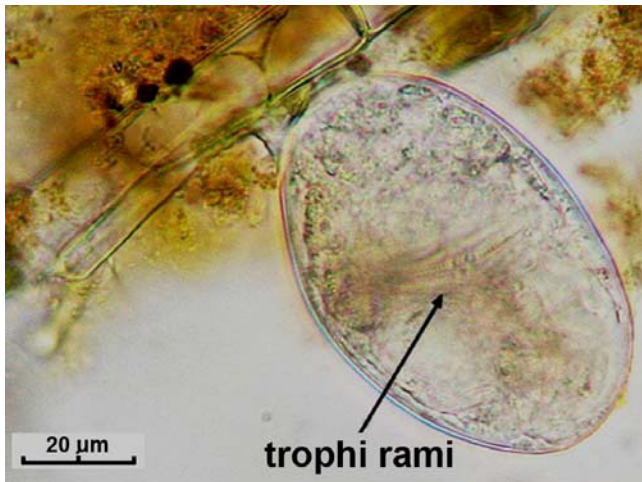


Figure 6. Egg of rotifer on an algal filament. Photo by Michel Verolet, with permission.



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

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



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



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

Bdelloidea

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

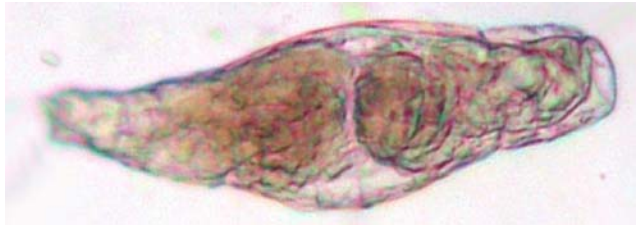


Figure 10. **Bdelloid rotifer** taken from bryophytes. Photo courtesy of Dan Spitale.

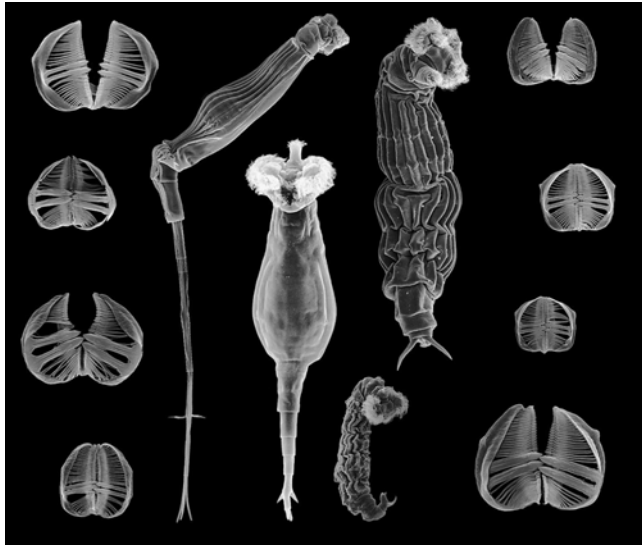


Figure 11. Examples of **bdelloid rotifers** and **trophi**, the hardened part of the **mastax**. Photos by Diego Fontaneto, through Creative Commons

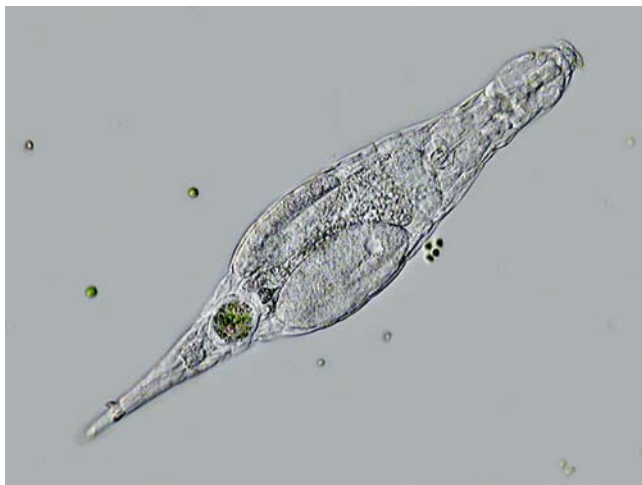


Figure 12. **Adineta vaga**, a moss dweller that is 0.2-0.3 mm when extended. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Monogononta

The **Monogononta** is the second major class of rotifers, and by far the largest (ca 1500 species) (Wikipedia 2012a). Among these are members that have both sexual and asexual reproduction. The short-lived, uncommon males, however, serve only for reproduction and thus are much smaller than females. Some males are so reduced that they have little more than a bladder and a penis! One such monogonont is the mostly planktonic genus

Brachionus (Wikipedia 2011; Figure 2, Figure 7, Figure 13-Figure 14). In this genus, with some members occurring among bryophytes, increases in population density can induce sexual reproduction. The sexually produced eggs can become resting eggs that survive unfavorable conditions (Plewka 2014). It appears that at least in **Brachionus calyciflorus** (Figure 13) only one allele is needed to turn off sexual reproduction and force all reproduction to be parthenogenetic. **Brachionus urceolaris** (Figure 14) sometimes lives among bryophytes (Figure 7; Hingley 1993), but it is primarily a cosmopolitan planktonic species like the other **Brachionus** species (EOL 2016). It is mostly parthenogenetic, but it occasionally produces males.



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



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

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



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

Bryophytes as Habitat

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

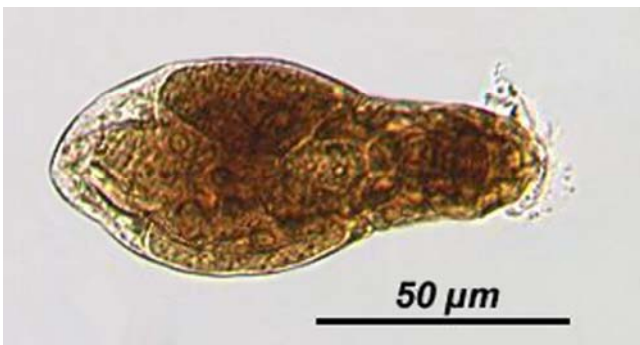


Figure 16. *Elosa worrallii*, a *Sphagnum* dweller. Photo by Jersabek *et al.* 2003 from Rotifer World Catalog, through Creative Commons.

Rotifers occur with bryophytes in both aquatic and terrestrial habitats, with bryophytes often providing a water space in the latter. Duggan (2001) points out that the **periphytic** (living on plant surfaces) species of rotifers have received little attention compared to the **planktonic**

(drifting in open water) species. Bryophytes are among these **macrophytic** (referring to plants that are visible without a microscope) substrates that support the periphyton, but Duggan did not include them in his study, considering bryophytes to be a separate habitat. **Periphytic** rotifers seem to have preferences among macrophyte species based on differences in physical structure or complexity, food concentration or composition, chemical factors, macrophyte age, and differences in protection from predation they provide (Duggan 2001). The same factors are likely to control bryophyte choices as well.

Terrestrial and wetland rotifers crawl through the spaces among leaves and branches of bryophytes, living in the water film surrounding the plant (Hingley 1993). In her website on rotifers, Jean-Marie Cavanilhac (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; Duggan *et al.* 2001). Likewise, bryophyte species composition explains most of the variation in monogonont rotifers in springs and fens

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



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



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



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



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



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



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



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



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



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



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



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



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



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

Hájková *et al.* (2011) demonstrated bryophyte-dwelling monogonont rotifers in springs and fens form communities that are strongly correlated with water 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 (Madaliński 1961). Other factors that contribute to substrate choice include temperature, oxygen content, trophic levels, chemistry, food availability, and predators (Pejler & Bērziņš 1989).

Abundance

An average of 700 rotifers can exist per gram on the soil-dwelling mosses *Ceratodon purpureus* (Figure 31) and *Polytrichum juniperinum* (Figure 32), rock-dwelling moss *Schistidium apocarpum* (Figure 33), and bog/fen

species of *Sphagnum* (Gerson 1982). Consider that a rough estimate for a handful of moss is about 10 grams.



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



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



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

Aquatic rotifers can occupy a significant portion of the meiofauna (minute organisms living in soil and aquatic sediments) of aquatic mosses such as *Fontinalis antipyretica* (Figure 34) (Vlčková *et al.* 2002). Out of 20 taxa, *Bdelloidea* formed the dominant group with about 76% of the total meiofauna numbers. Linhart (2000) found that clumps of *Fontinalis antipyretica* was inhabited by 151 times the densities of meiofaunal invertebrates

compared to adjacent mineral substrate. During winter in two streams in the Czech Republic, Linhart found 182,672-390,057 individuals per 100 mL of *F. antipyretica*. That's about a handful of moss. Rotifers (**Bdelloidea**) were the dominant organisms, occupying up to 74% of the meiofauna. The rotifers seemed to be reduced by high amounts of organic matter, whereas **Chironomidae** (Figure 35) benefitted. These differences account for the dominance of rotifers (**Bdelloidea**) in Mlýnský náhon (76% of the community), whereas in Bystřice, the dominant group was **Chironomidae** (34%) (Vlčková *et al.* 2002).



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



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

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

Aquatic mosses can contribute significantly to biodiversity by providing a 3-d habitat. Linhart *et al.* (2002a) and Vlčková *et al.* (2002) found that rock rip-rap

overgrown by aquatic mosses (*Fontinalis antipyretica*; Figure 34) in a side channel of the Morava River, Czech Republic, contributed both habitat and food source for the meiofauna. Both the habitat and the food source were realized through the fine particulate matter trapped by the mosses. In this habitat, **Bdelloid** rotifers dominated as 76% of the organisms among 18 meiofaunal taxonomic groups.

Sampling

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

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



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

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

May (1986) suggests that sampling sediments can be done in one day and the dormant individuals or resting eggs

cultured to permit identification. But this method is not only time-consuming, it may not enable one to see those individuals hiding among the bryophytes, especially in pockets, folds, and cells.

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

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

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

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



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

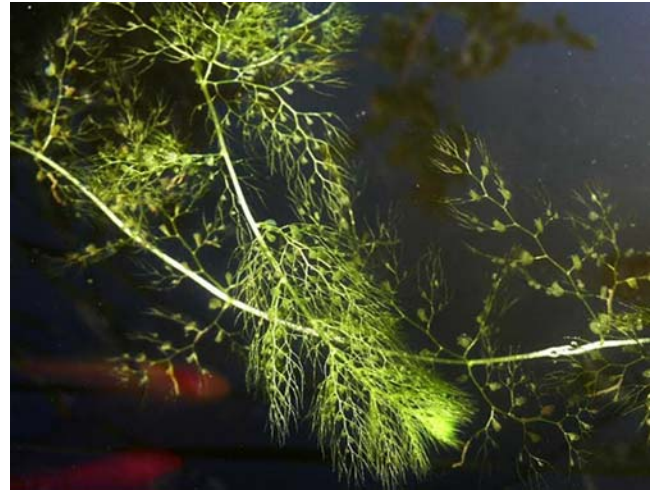


Figure 38. *Utricularia vulgaris*, a potential structural model for bryophyte rotifer communities. Photo by Erastos Kampouropoulos, through Creative Commons.

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

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

Extraction Techniques

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

But some rotifers are too small for this technique and are likely to be missed. Peters *et al.* (1993) suggest a different method that appears to be a somewhat reliable quantitative technique. They tested it on 74 samples of mixed *Brachythecium rutabulum* (Figure 39) and *Ceratodon purpureus* (Figure 31), both terrestrial mosses. Their criteria for establishing a method were that it should not kill the organisms because some must be alive to be identified, it must be equally effective for all species, it must be quantifiable, and it should be economical in both equipment cost and time. Bryophyte samples 1 cm^2 should be shaken vigorously in a 70 ml vial with 20 ml rainwater

for 15 seconds. If the sample is dry, it should soak for 24 hours in rainwater first. After shaking, put the sample and water in a Petri dish with a grid. Then put the moss back in the vial. Rotifers can be counted with a dissecting microscope at 40-50X. This should be repeated nine more times with material from the same sample, using a new Petri dish each time. From each of these samples, take 50 rotifers at random and make a separate slide for each. These can be stored for weeks in a moist chamber. This method needs more testing to check for attached species, species bias, and reliability of quantitative measures.



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

Sakuma *et al.* (2002) tested two methods (covering method; picking-up method) of obtaining epiphytic rotifers from lake vegetation (Figure 40). Their "covering method"

involved shaking a vegetation sample in a 2-L jar of filtered lake water (40 μ m 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 μ m filter and fixed with sugar formalin (see Haney & Hall 1973).

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

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

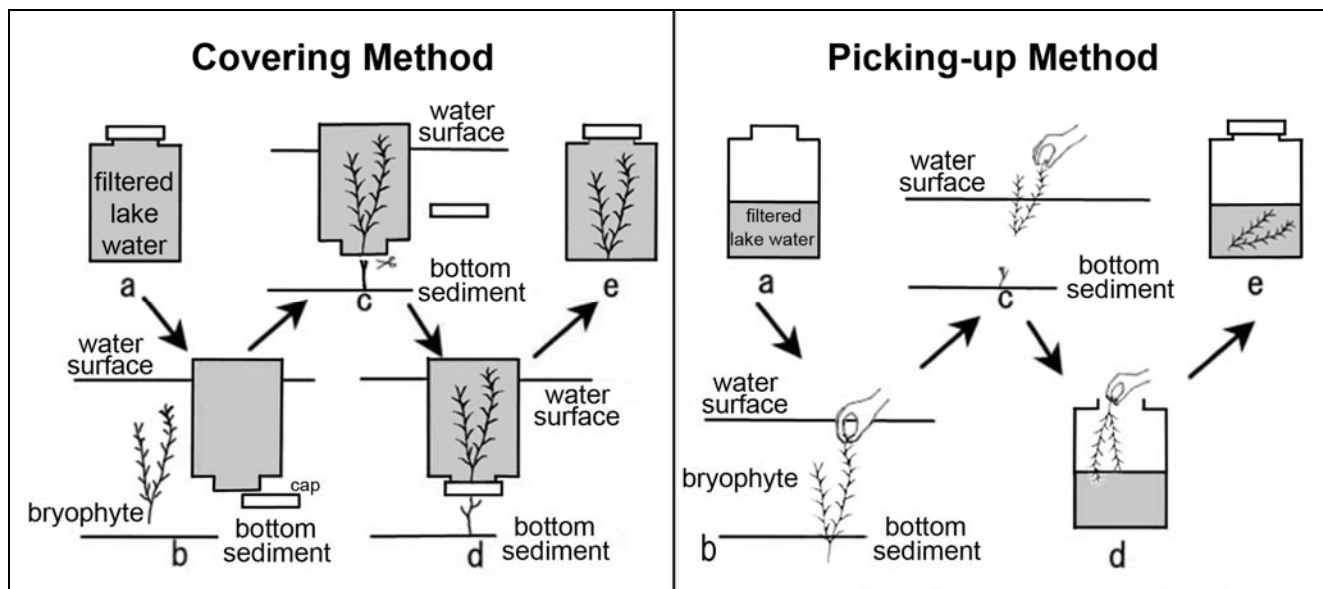


Figure 40. Methodology for the "covering method" and "picking-up method." Modified from Sakuma *et al.* (2002).

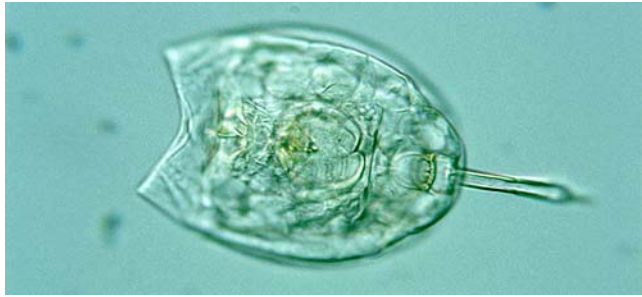


Figure 41. *Lecane crenata*, a genus that is underestimated in the "picking-up method." Photo by Yuuji Tsukii, with permission.



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



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

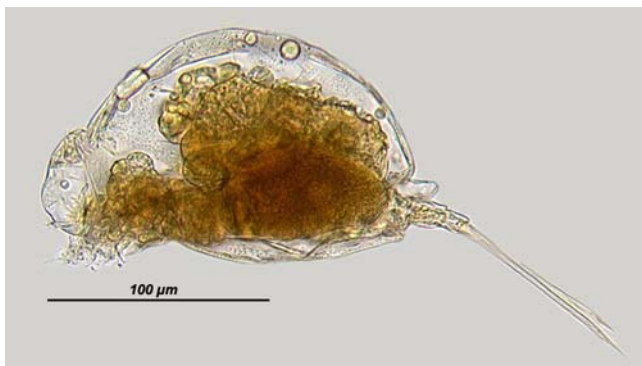


Figure 44. *Mytilina acanthophora* ssp. *trigona*, a genus that seems to be adequately represented by the "picking-up" method. Photo by Jersabek *et al.* 2003, with permission.



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

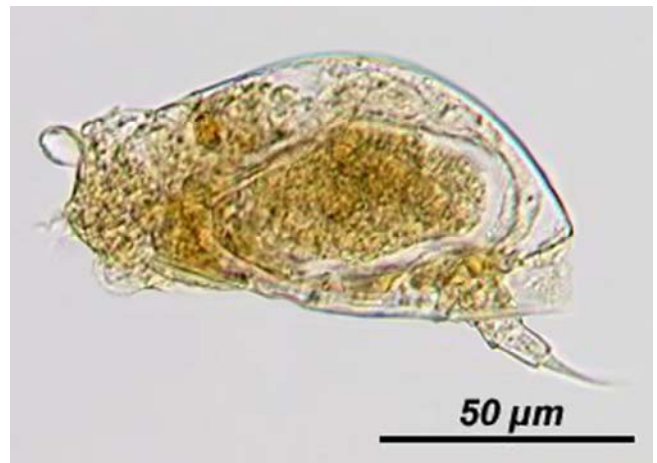


Figure 46. *Colurella uncinata*, a genus that seems to be adequately represented by the "picking-up" method. Photo by Jersabek *et al.* 2003, through Creative Commons.

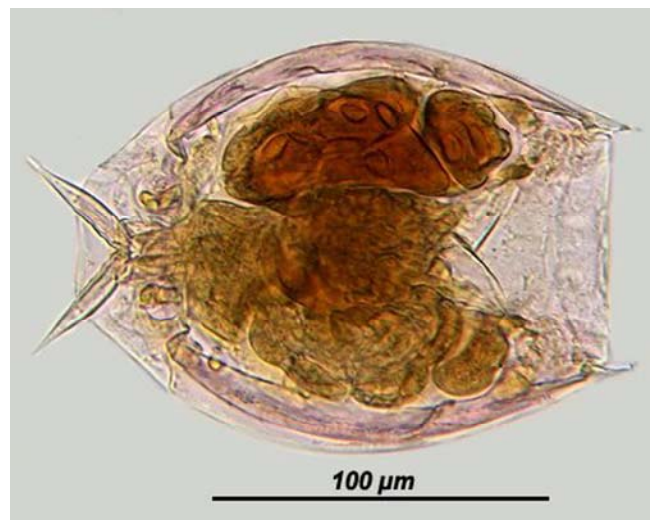


Figure 47. *Lecane depressa* subsp. *brachydactyla*. *Lecane* is a genus that remains mostly with the substrate when plants are shaken in water. Photo by Jersabek *et al.* 2003, with permission.



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



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

Adaptations

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

Particle Feeders

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

Spines

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



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

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

Small Size

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

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

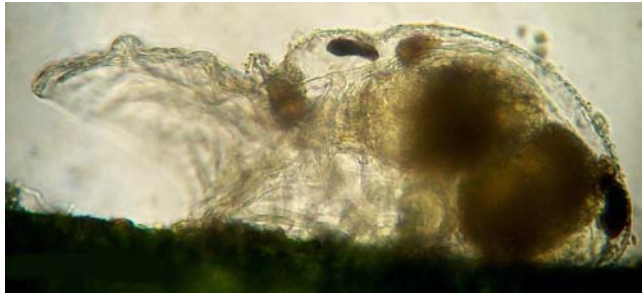


Figure 51. *Cupelopagis vorax*, a rotifer that finds a moss leaf too small for its feeding needs. Photo by Jean-Marie Cavanilhac at Micscape, with permission.

Mobility vs Attachment?

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



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

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

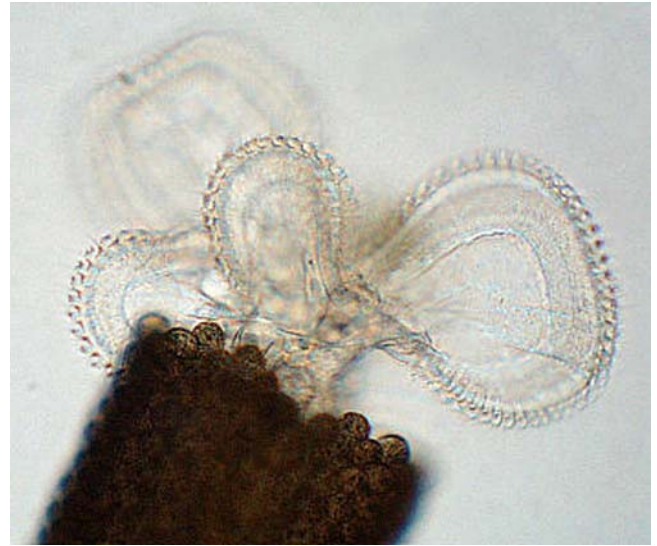


Figure 53. Wheels of cilia (**corona**) on *Floscularia* sp. Photo by Martin Mach, with permission.

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

Protection

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

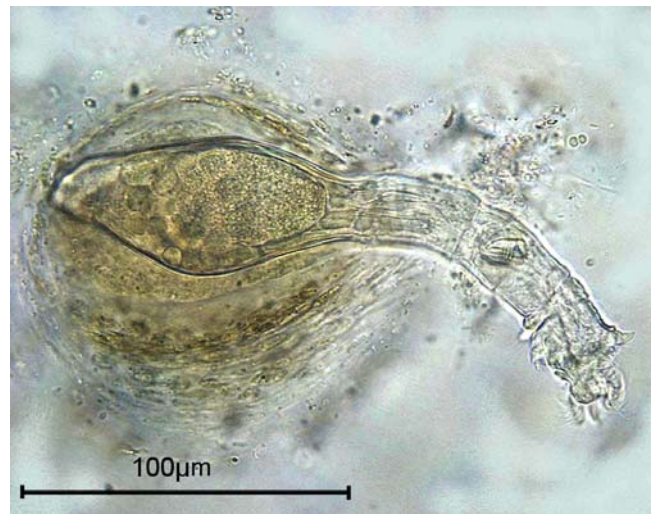


Figure 54. *Habrotrocha* sp. surrounded with mucus it has secreted, presumably providing it with protection against desiccation. Photo by Michel Verolet, with permission.

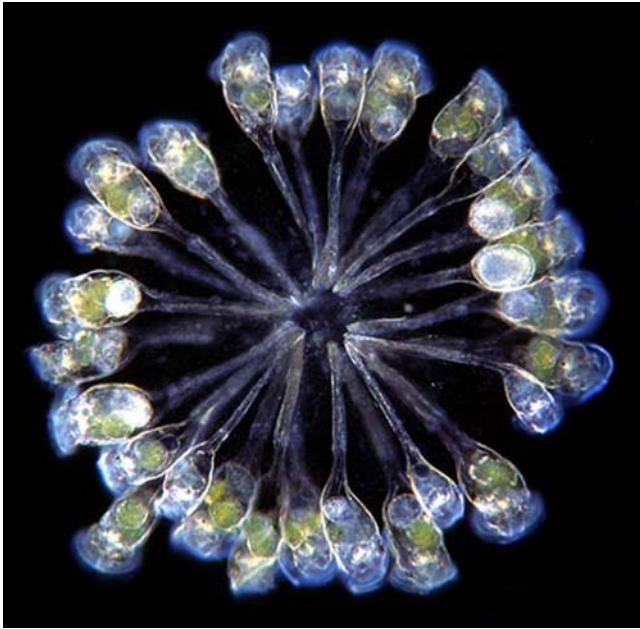


Figure 55. Colonial species of *Conochilus*, a genus that uses mucus as protection. Photo by Wim van Egmond, with permission.



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



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

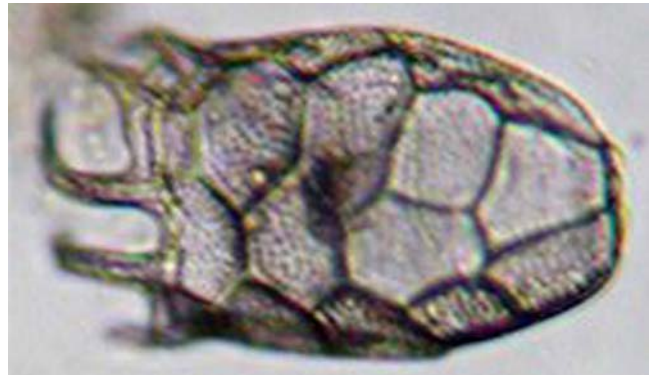


Figure 58. Armor of the rotifer *Keratella* sp. Photo by Paul Davison, with permission.

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



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

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

Dormant States

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

Physiological Adaptations

Anhydrobiosis

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

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

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

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



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

Changes During Anhydrobiosis

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

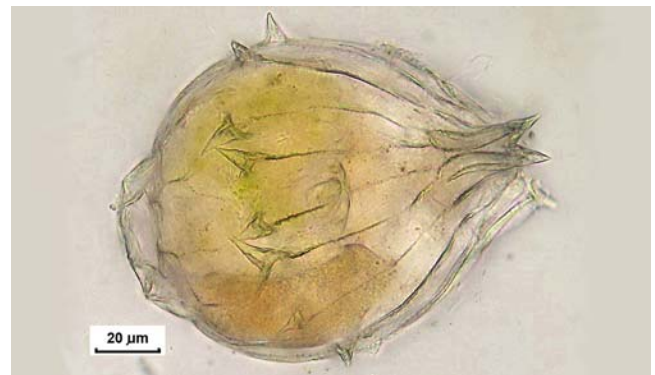


Figure 61. Tun of a rotifer, *Pleuretra brycei*, a moss dweller. Photo by Michel Verolet, with permission.

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

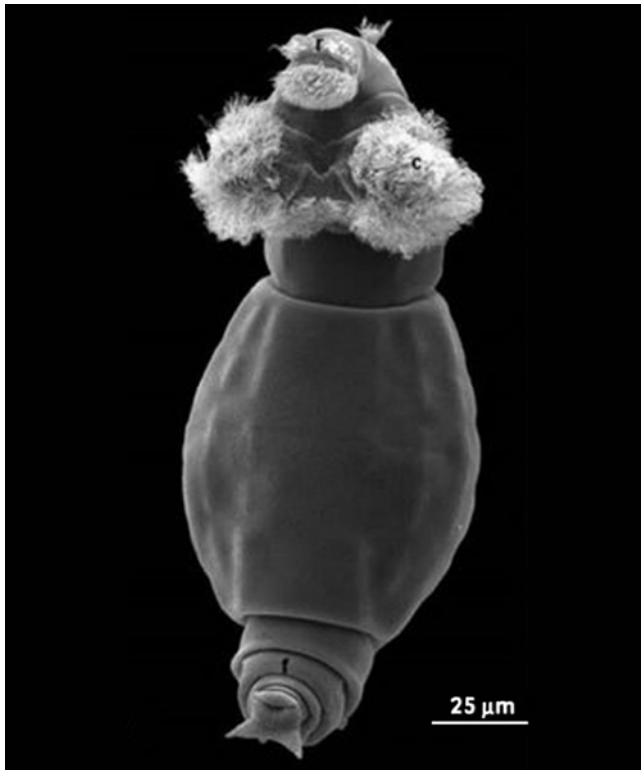


Figure 62. *Macrotrachela quadricornifera*. Photo by Diego Fontaneto and Giulio Melone, with permission.

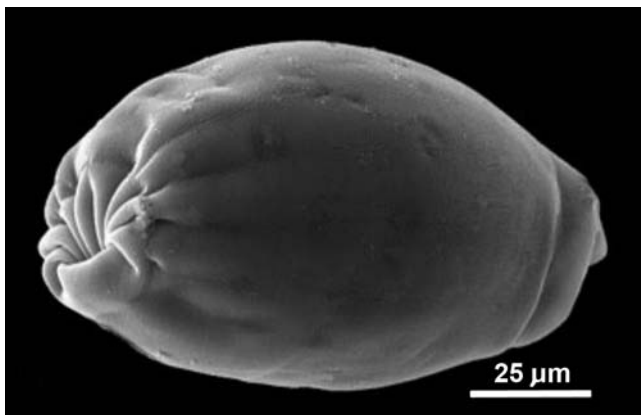


Figure 63. *Macrotrachela quadricornifera* contracting as it dries. Photo by Claudia Ricci, with permission.

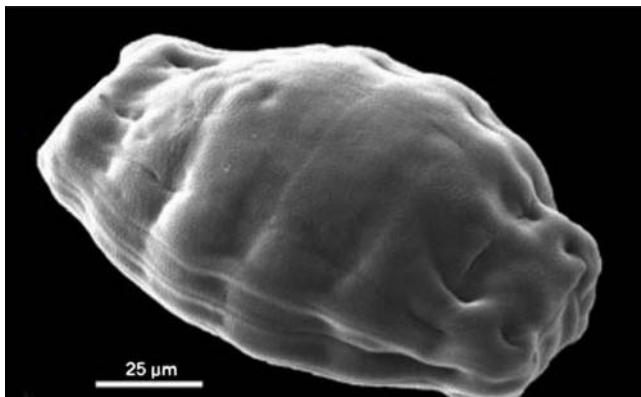


Figure 64. *Macrotrachela quadricornifera* tun. Photo by Diego Fontaneto & Giulio Melone, with permission.

Macrotrachela quadricornifera (Figure 62-Figure 64) 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* (Figure 62-Figure 64).

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

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



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

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

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



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

Longevity during Anhydrobiosis

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

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

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



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



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

Age Differences

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

Size Differences – Aquatic vs Terrestrial

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

Reproductive Effects

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

Furthermore, the aquatic (non-moss) strains of *Macrotrachela quadricornifera* (Figure 62-Figure 64) invested maximum resources in reproduction (**r strategists**), consequently reducing their survival, whereas the moss-dwelling strains were long-lived and invested fewer resources in their reproduction (**K strategists**) (Ricci 1991). Ricci points out that the moss habitat experiences a much greater temperature fluctuation in a shorter period of time than would occur in the aquatic non-moss habitats. Ricci suggests that the terrestrial moss habitat has much more important limiting factors – availability of food and moisture, whereas a wide temperature range with sudden changes must be tolerated.

Temperature Protection

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

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

Recovery Rate

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

The Bryophyte Connection

The data for *Macrotrachela quadricornifera* (Figure 62) and other species raise the question of how these animals survive on bryophytes. To partially answer this question, Ricci *et al.* (1987) collected mosses from a spring-fed pond in Italy. Hence, it is likely that the humidity remained higher than that of the laboratory. Furthermore, the mosses themselves provide capillary spaces that can lock in water for a longer period of time than that of the surroundings. Unlike the rotifers that depend on eggs for reproduction, bdelloid rotifers in this study had a much lower hatching rate (19%) compared to 40-100% (Pourriot & Snell 1983) reported for those species that depend on resting eggs to colonize new environments. *Macrotrachela quadricornifera* (Figure 62-Figure 64) is a parthenogenetic rotifer, requiring no partner to reproduce. Therefore, its life on a moss leaf is not dependent on finding a partner in what can be an isolated habitat. The ability of the moss leaf to disperse in the wind provides a means for the rotifer likewise to disperse.

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

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

Other Protections during Anhydrobiosis

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



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

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



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

Surviving Fungi

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

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

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

Food

Rotifers obtain their food by rotating **cilia** in the **corona** (Figure 71) that directs the food into the mouth. This enables them to eat small particles of organic matter, bacteria, algae, protozoa, and even other rotifers (Wikipedia 2012b). [These same cilia can be used for

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



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

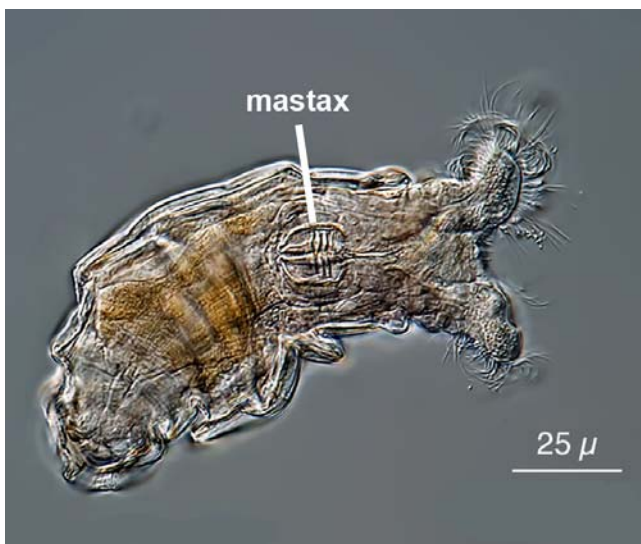


Figure 72. *Dissotrocha scutellata* showing **mastax**. This species has been collected on the moss *Andreaea rupestris* growing on a rock in the open. Photo by Michael Plewka <www.plingfactory.de>, with permission.



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



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

Food choices differ with habitat, even within the same species. The bdelloid rotifer *Macrotrachela quadricornifera* (Figure 62-Figure 64) is a filter feeder whose food preference and survivorship both differ among the habitat strains (Ricci 1991). Moss dwellers were unable to survive on yeast (*Saccharomyces cerevisiae*) alone, whereas the two aquatic strains survived and grew. One of the moss-dwelling strains was unable to eat the one-celled green alga *Chlorella pyrenoidosa* (see Figure 75). The other moss strain did best on the bacterium *Escherichia coli*, which resulted in poor growth of all the other strains. It appears that the habitat may influence the types of enzymes available for digestion of food. We cannot, however, say if this is an environmental response during development or a genetic one that has persisted through a number of moss-dwelling generations.

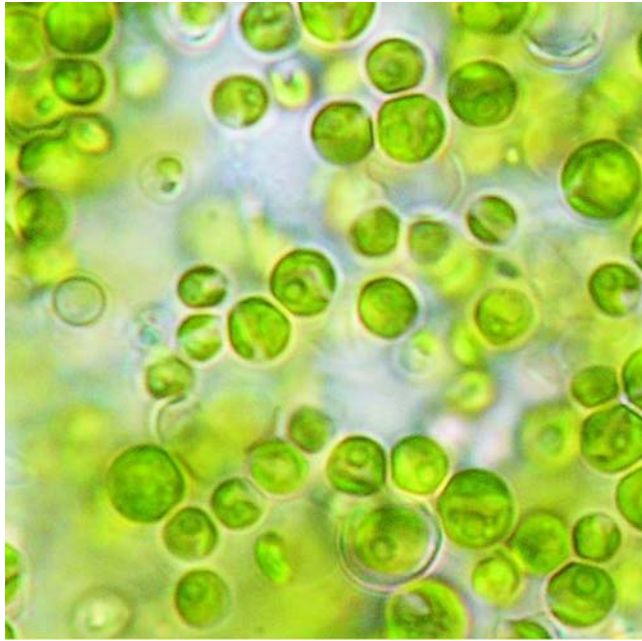


Figure 75. *Chlorella vulgaris*; *C. pyrenoidosa* a rejected food for moss-dwelling *Macrotrachela quadricornifera*. Photo by Sarah Duff, through Creative Commons.

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



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

A few rotifers actually bite their food. For example, among the moss dwellers, this method is used by *Lindia torulosa* (Figure 77-Figure 78) and *Notommata*

groenlandica (Figure 79), but there are many others as well (Plewka 2016).



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



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



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

Role in the Food Web

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

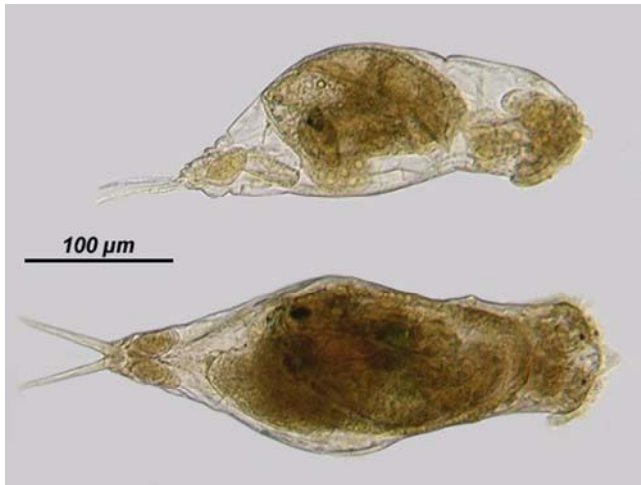


Figure 80. *Dicranophorus robustus*, a bryophyte dweller that eats smaller rotifers on bryophytes. Photo from Jersabek *et al.* 2003, through Creative Commons.



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

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



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



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

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

Specific Habitats

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

Lobule Dwellers

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

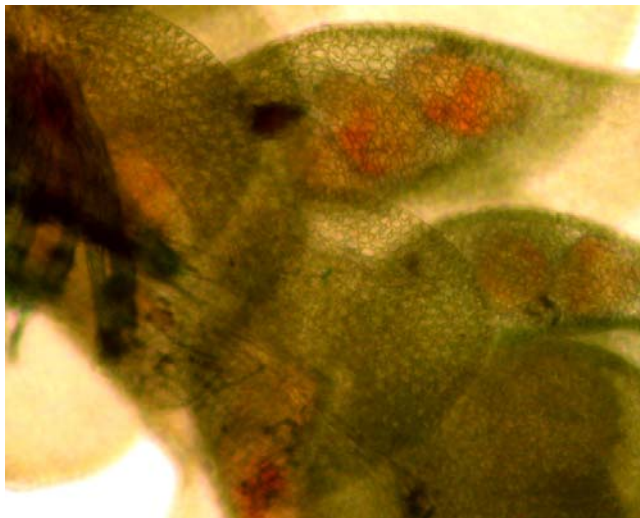


Figure 84. *Acrolejeunea emergens* with several orange invertebrates in the lobules. These appear to be resting stages of rotifers. Photo courtesy of Claudine Ah-Peng.



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

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



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

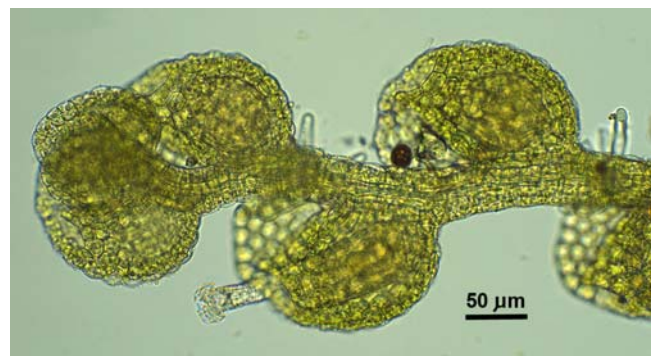


Figure 87. *Microlejeunea ulicina* with a rotifer emergent from a lobule. Scale is 50 μm . Photo courtesy of Blanka Shaw.

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

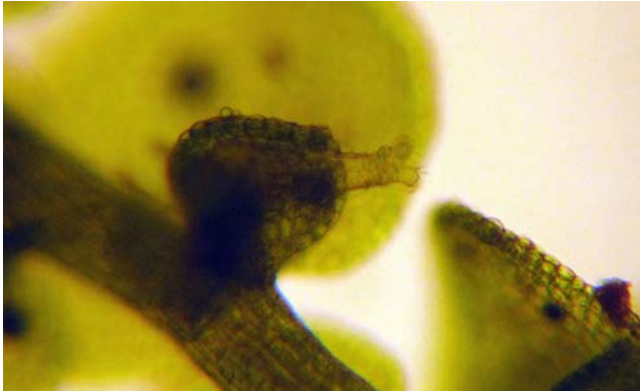


Figure 88. *Frullania eboracensis* with a rotifer in its lobule. Photo by Robert Klips, with permission.

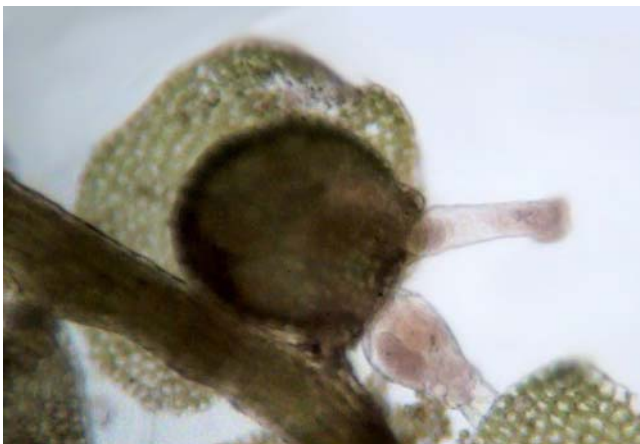


Figure 89. Bdelloid rotifers in lobules of *Frullania eboracensis*. Photo courtesy of Mark Pokorski.



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



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

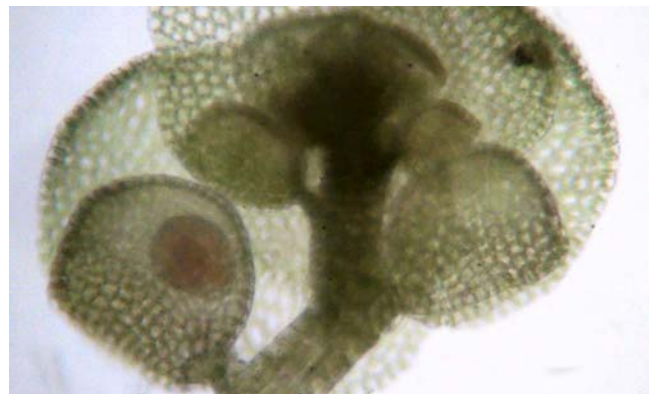


Figure 92. Lobules of *Frullania eboracensis* with dormant rotifers. These dormant stages could be resting eggs or cysts. Photo courtesy of Mark Pokorski.

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



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

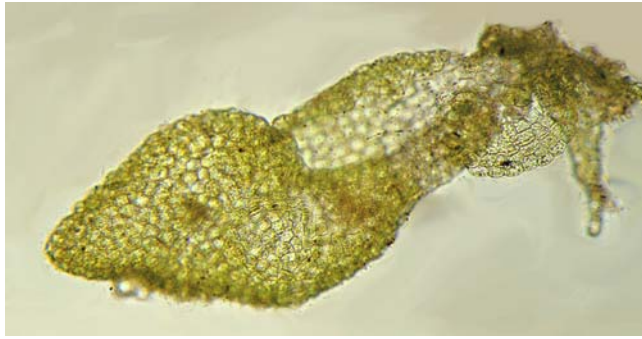


Figure 94. *Colura* leaf with lobule where rotifers often live. Photo courtesy of Jan-Peter Frahm.



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



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



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

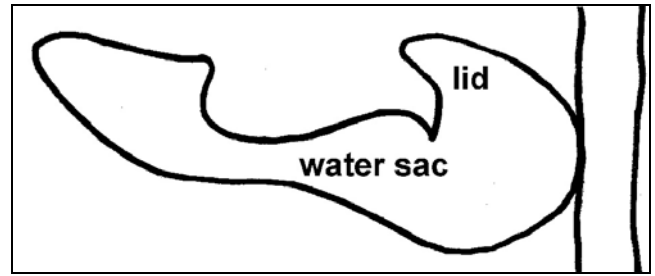


Figure 98. Lobule of *Pleurozia purpurea* showing the trap and lid. Redrawn from Hess *et al.* 2005.



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

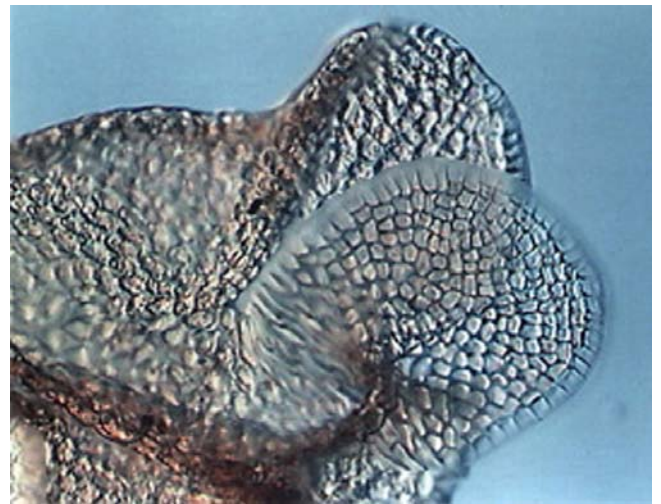


Figure 100. Lobule of *Pleurozia purpurea* showing lid. Photo courtesy of Sebastian Hess.

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

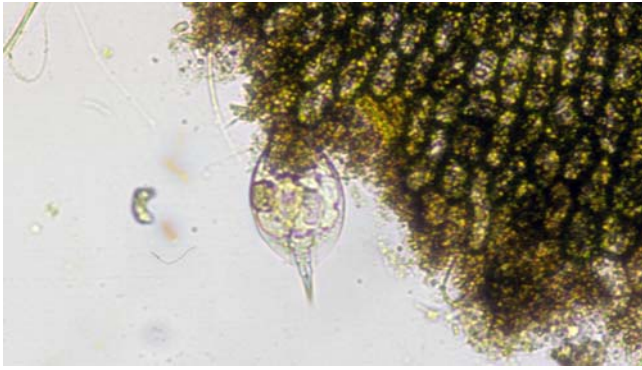


Figure 101. This *Lepadella* species, with its "wheels" hidden and its toes showing, is feeding on detrital material associated with the liverwort *Jungermannia cordifolia*. Photo courtesy of Javier Martínez Abaigar.

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



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



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

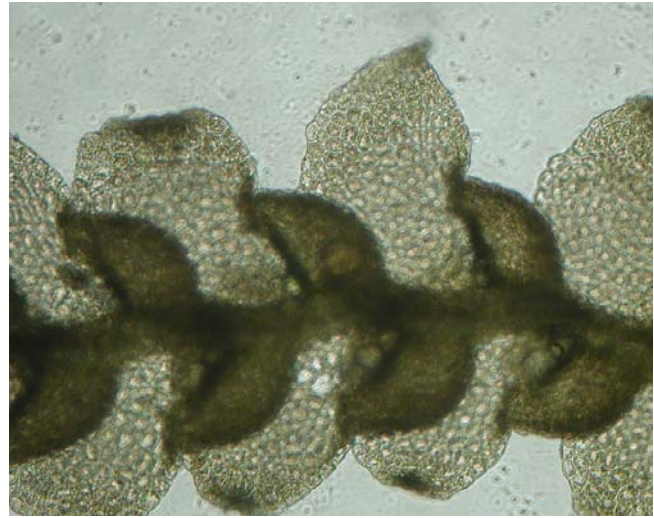


Figure 104. *Harpalejeunea molleri* with lobules that are home for rotifers. Photo by Jan-Peter Frahm, with permission.

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.

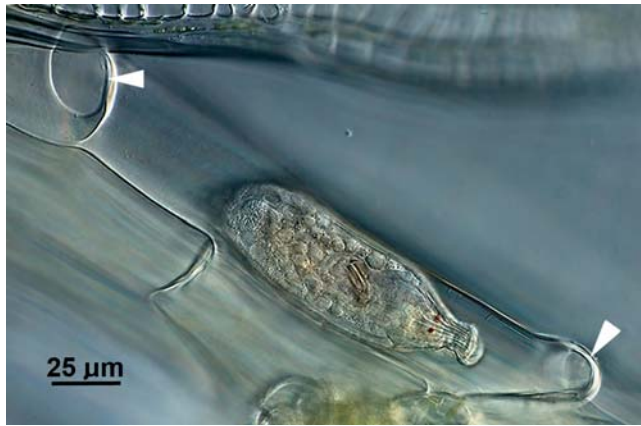


Figure 106. *Habrotrocha roeperi* in retort cell. Arrows indicate protruding pores. Photo by Michael Plewka <www.plingfactory.de>, with permission.



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



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

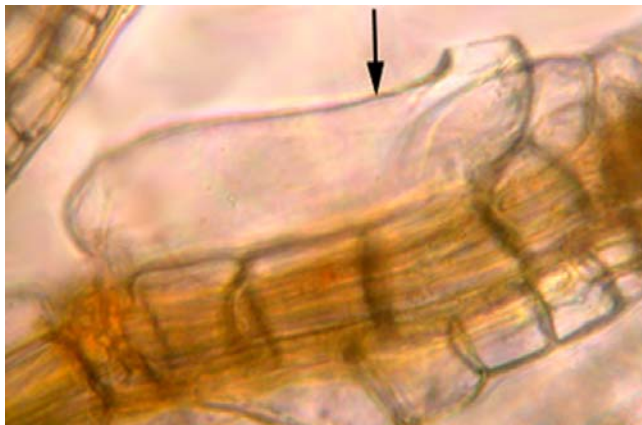


Figure 108. Retort cell of *Sphagnum*, lacking spiral thickenings. Picture with permission from Wilf Schofield, University of British Columbia botany web site.

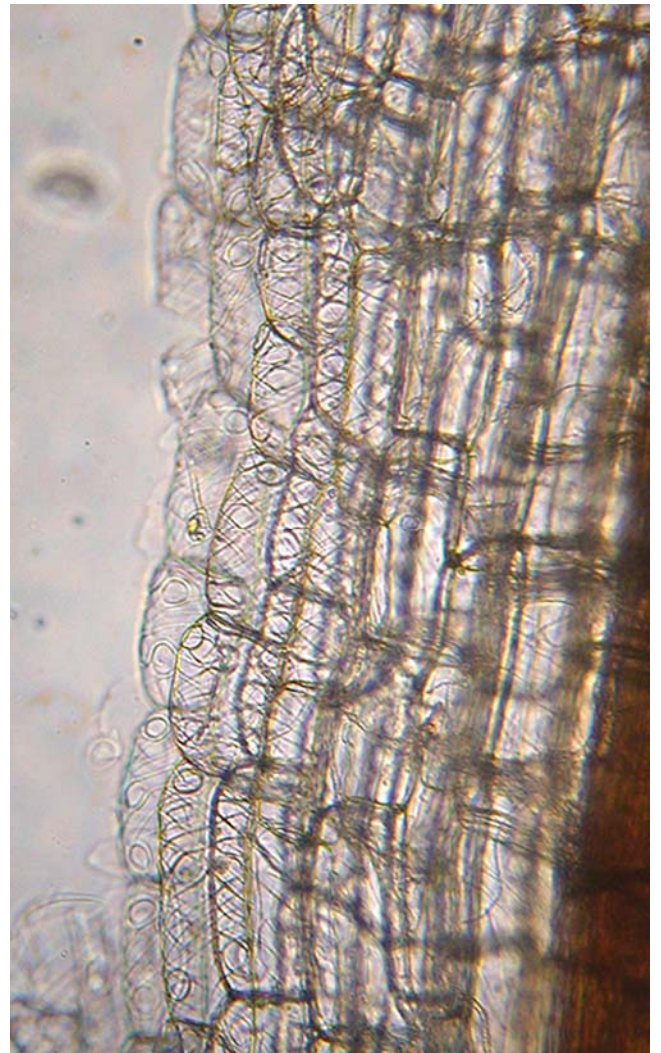


Figure 110. *Sphagnum papillosum* outer stem cells in longitudinal view showing fibrils and pores that are flat against the cell surface. Rotifers do not inhabit these. Photo from UBC Botany website, with permission from Shona Ellis.



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.

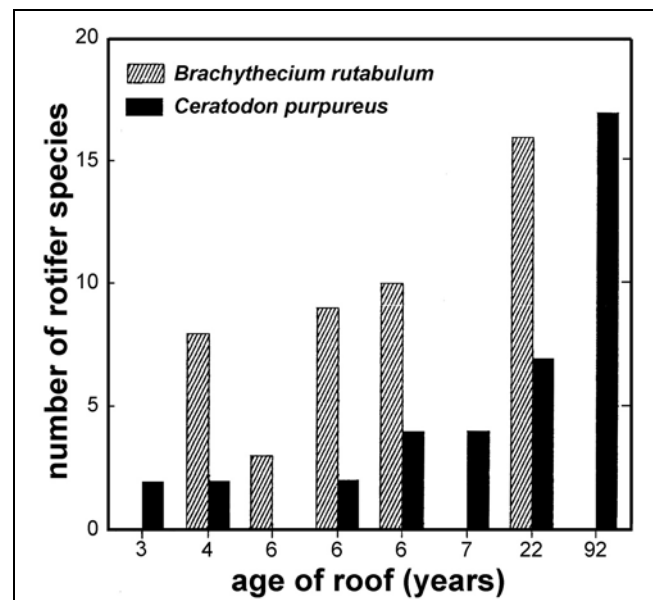


Figure 114. Succession of rotifer species that increase in number with age of roof. Redrawn from Hirschfelder *et al.* 1993.

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 *Mniobia* (Figure 67) among mosses. Most of the bdelloids he located were contracted and could not be identified. In addition, he found the monogononts *Lindia torulosa* (Figure 115), *Colurella adriatica* (Figure 3), and *C. colurus*.



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

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

The Antarctic mosses sport an active community of invertebrates that move among the stems and branches. Priddle and Dartnall (1978) showed experimentally that wind caused mixing in summer, resulting in the transport of larval rotifers from shallow portions of the lake. Priddle

and Dartnall found six rotifer species along the stems of aquatic mosses [*Warnstorfia sarmentosa* (Figure 116), *Drepanocladus* sp. (probably *Sanionia uncinata*; Figure 117)]. Two of these rotifers were bdelloids and four were sessile monogonont species. These rotifers preferred the middle stem zones of mosses where the highest growths of epiphytic algae and other epiphytic organisms occurred. Of these, four species chose leaf axils, whereas the other two settled on the bare underside of the leaf.



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



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

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

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



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



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



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



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

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.



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

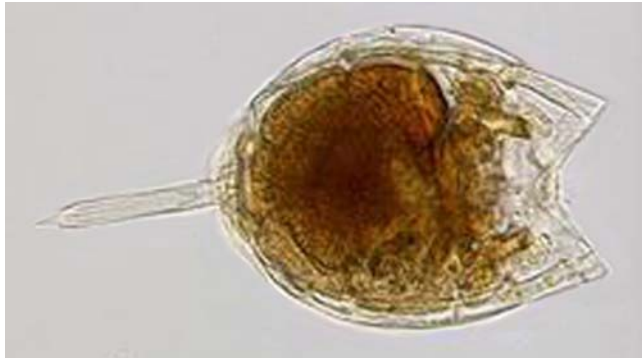


Figure 123. *Lecane lunaris*, a bryophyte dweller in the Antarctic. Photo from Jersabek *et al.* 2003, with permission.

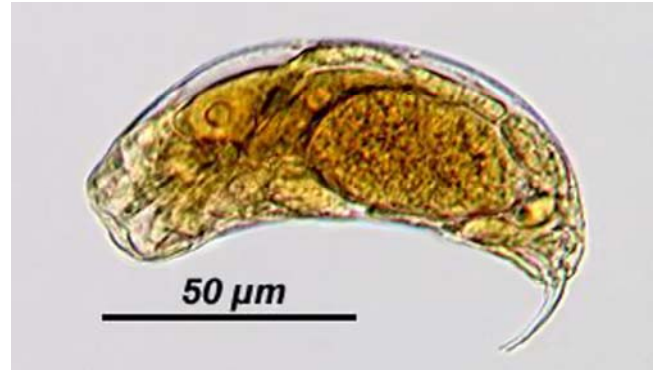


Figure 127. *Trichocerca brachyura*, an Antarctic moss dweller. Photo by Jersabek *et al.* 2003, with permission.

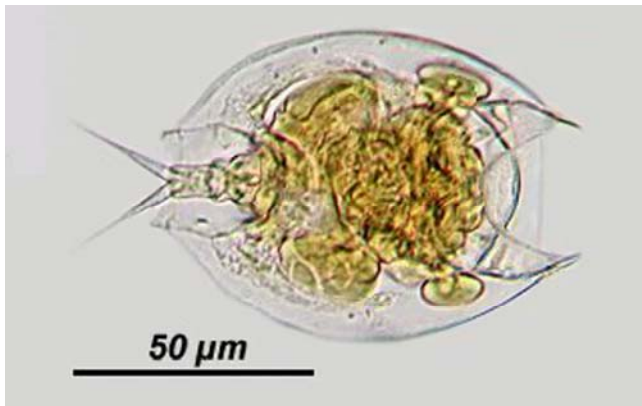


Figure 124. *Lepadella patella*, an Antarctic moss dweller. Photo by Jersabek *et al.* 2003, with permission.



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

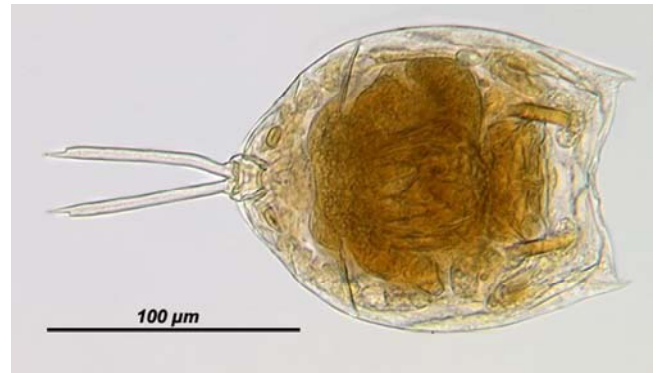


Figure 128. *Lecane curvicornis*, member of a genus that has several species living on mosses in the Antarctic. Photo by Jersabek *et al.* 2003, with permission.

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



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



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

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

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



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

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

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

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

Nunataks

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



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

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

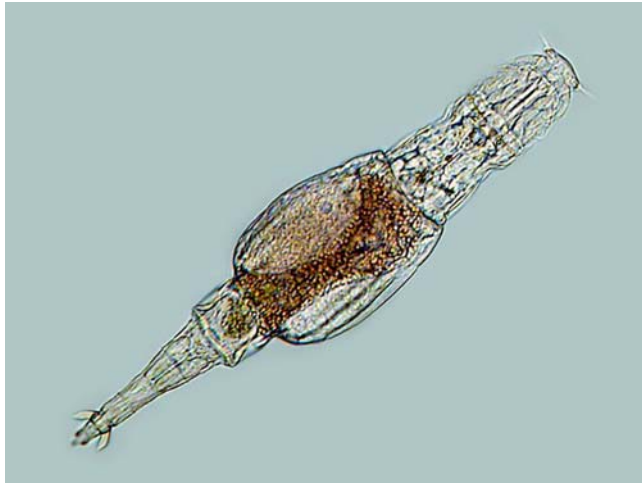


Figure 133. *Adineta steineri*, an epiphytic moss dweller that also lives in Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission.

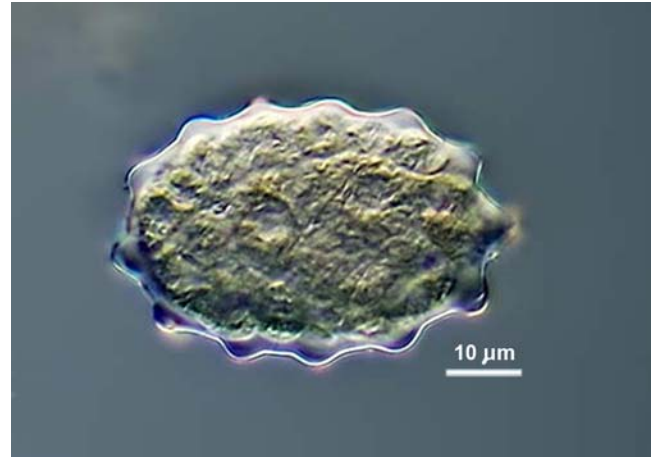


Figure 136. Egg, probably from *Philodina plena*, a species that occurs in Antarctic moss carpets. Photo by Michael Plewka <www.plingfactory.de>, with permission

Bog and Fen Habitats

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

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

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

Nevertheless, an important deterrent for many rotifers is that *Sphagnum* acidifies its surroundings (Clymo 1963, 1964; Williams *et al.* 1998) and may account for a higher species diversity in rich fens than in *Sphagnum* peatlands. Since many rotifer species are intolerant of a low 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



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



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

the rotifers that process the detritus (Błędzki & Ellison 1998, 2002).

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

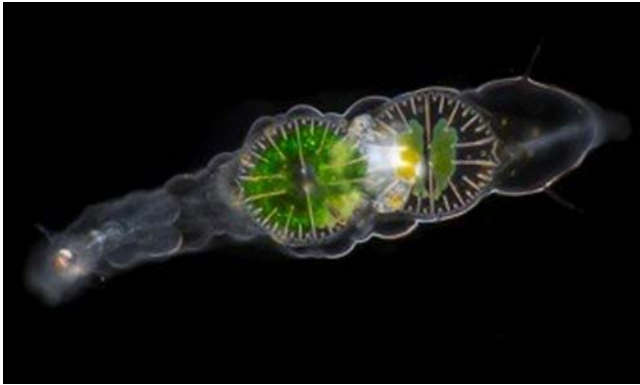


Figure 137. *Tetrasiphon hydrocora* with the desmid *Micrasterias rotata* in its gut. Photo by Wim von Egmond, with permission.

Species Richness

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

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



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

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



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



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

Bielańska-Grajner *et al.* (2011) selected *Habrotrocha angusticollis* (Figure 4), *Dicranophorus capucinus* (Figure 141), *Keratella serrulata* (Figure 142), and *Lepadella elliptica* for further analysis and found that abiotic factors were important determinants of distribution. Nevertheless, the researchers found that the highest density of rotifers occurred in a raised bog dominated by *Sphagnum angustifolium* (Figure 157), but this might suggest that a number of rotifer species may prefer the same abiotic conditions as this moss. Francez and Dévaux (1985) similarly found the highest proportion of characteristic rotifer species in a low moor where *Sphagnum angustifolium* was dominant.



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



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

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



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



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



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

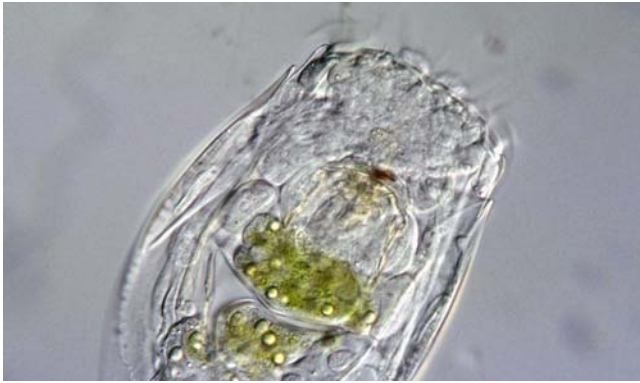


Figure 146. *Euchlanis*, a genus having species of peatland rotifers. Photo by Yuuji Tsukii, with permission.



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



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



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

In Australia, Koste and Shiel (1989) identified members of the *Euchlanidae*, *Mytilinidae*, *Trichotriidae*, all members of *Monogononta*. In *Sphagnum* pools

(Figure 150) they found *Diplois daviesiae* and *Euchlanis meneta* (Figure 151) in acid water and on submerged *Sphagnum* (Figure 150). *Trichotria truncata* (Figure 152), an acidophile, occurred among *Sphagnum*.

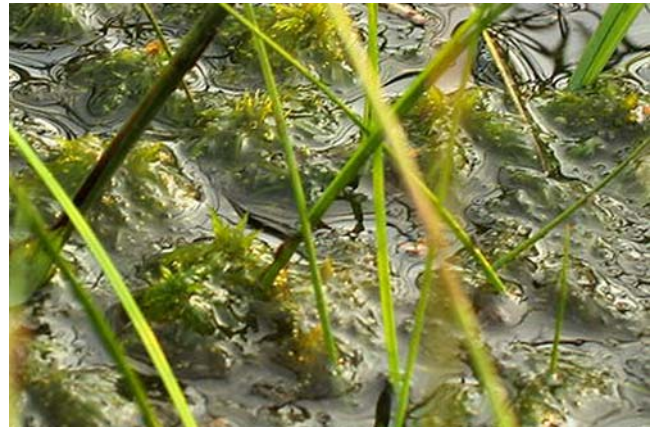


Figure 150. Submersed *Sphagnum cuspidatum*, potential home for the rotifers *Diplois daviesiae*, *Euchlanis meneta*, and *Trichotria truncata*. Photo by Andrew Spink, with permission.



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

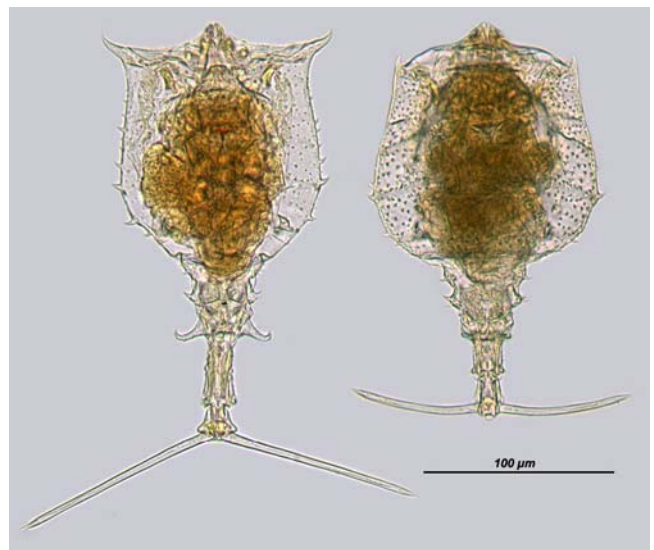


Figure 152. *Trichotria truncata*, a *Sphagnum*-dwelling acidophile. Photo by Jersabek *et al.* 2003, with permission.

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

Most Canadian peatland studies concentrated on the plants and vertebrates. Warner and Asada (2006) were among the first to include invertebrates in an extensive survey. In a **poor fen** (similar to a bog in bryophyte species composition) in Newfoundland, Canada, Bateman and Davis (2007) found 25 **bdelloid** and 39 **monogonont** rotifers. Among these, 27 were new records for Canada and 13 new for North America. They found an average of 354 rotifers per 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 (Błedzki & Ellison 2003). These tubes readily filled with water. While this method may have been effective for those rotifers that swam in the pore water, their methodology most likely missed attached species that rarely enter open water, such as *Collotheca* (Figure 48) and *Lecane* (Sakuma *et al.* 2002).

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

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



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

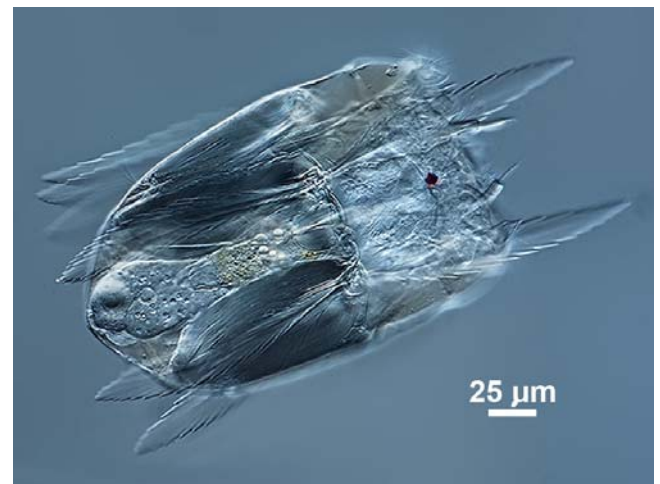


Figure 154. *Polyarthra vulgaris*, a common bog species in association with *Sphagnum*. Photo by Michael Plewka <www.plingfactory.de>, with permission.



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



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

Abiotic Factors

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

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



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

Acidity

The acidity of the water may play a role in distribution, but it is difficult to determine if it is a direct or indirect effect. Bērziņš and Pejler (1987) found that **oligotrophic** (low nutrient) species occur at a *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*.



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



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



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

Lecane lunaris (Figure 123) is tolerant of a broad 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.

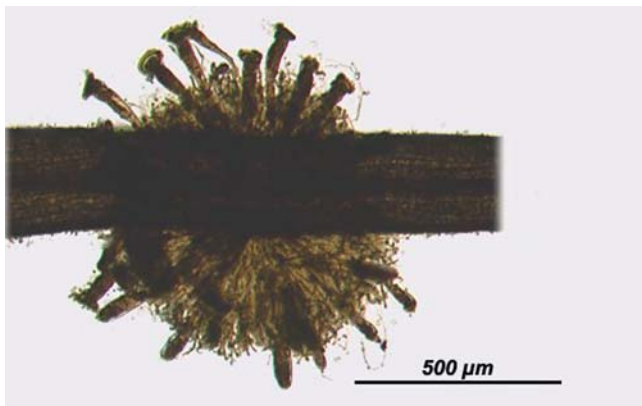


Figure 161. *Ptygura mucicola*, a species that lives in colonies of *Gloeotrichia* amid *Sphagnum*. Photo by Jersabek *et al.* 2003, with permission.



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

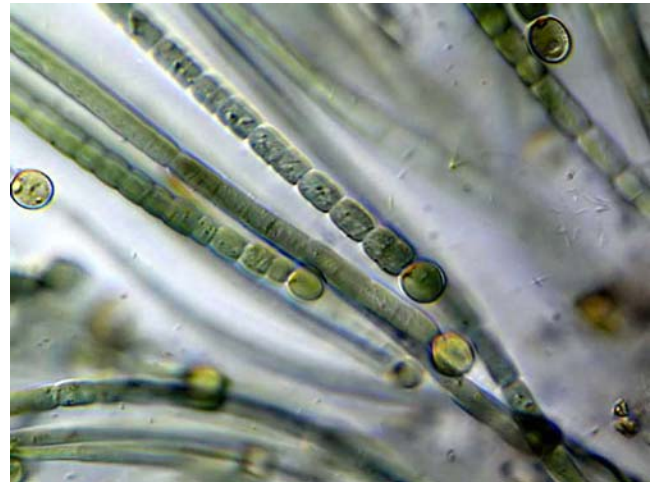


Figure 163. *Gloeotrichia* sp. with heterocysts, home for *Ptygura mucicola socialis* in peatlands. Photo from <www.diatom.org>, through Creative Commons.

Surface Configuration

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

Sphagnum (Figure 25-Figure 27, Figure 109-Figure 112, Figure 150) leaf morphology seems to play a role in the location of the rotifers. The rotifer *Collotheca gracilipes* lived on the concave side of a submerged moss leaf along with the green algae *Bulbochaete* (Figure 164) and *Oedogonium* (Figure 165) (Edmondson 1940). And *Collotheca cucullata* occurred on the concave side of a *Sphagnum* leaf (Figure 166) in a different peatland at 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!



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

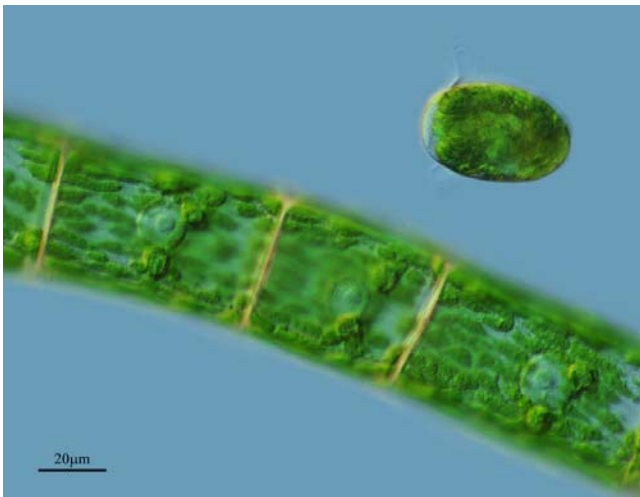


Figure 165. *Oedogonium*, a green alga that shares the *Sphagnum* leaf with the rotifer *Collotheca gracilipes*. Photo from Proyecto Agua, through Creative Commons.

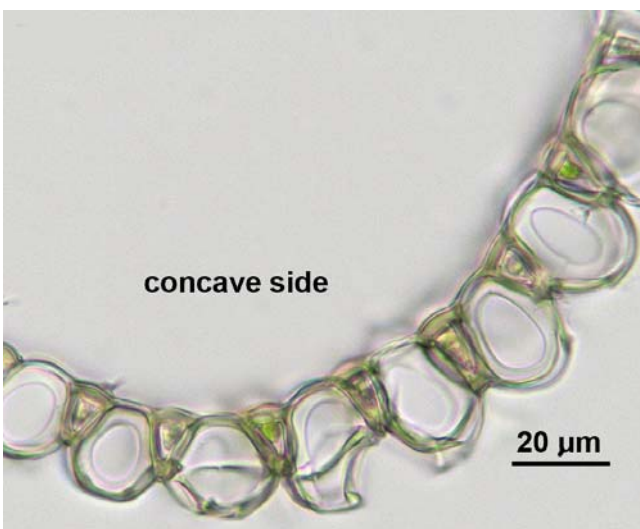


Figure 166. *Sphagnum subnitens* leaf cross section showing concave side where some species of *Collotheca* live. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



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



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

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

Like the **Protozoa (Rhizopoda)**, rotifers have both horizontal and vertical distribution patterns among the *Sphagnum* (Figure 25-Figure 27, Figure 109-Figure 112) (Meisterfeld 1977) and this may account for some variation in the distribution patterns of animals that prey upon them. But this vertical zonation also reflects the food available to the microfauna (Strüder-Kypke 1999). Differences in light and nutrients result in a denser colonization in the upper part where photosynthetic cryptomonads can provide food and mobile ciliate protozoa can take advantage of these food sources. Lower in the mat, but within the upper 30 cm, sessile ciliates and heterotrophic flagellates predominate. Moisture seems to be the dominant

determiner of species assemblages, with 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.

Rotifers in the pitcher plant leaves are important in the cycling of nitrogen and phosphorus (Błedzki & Ellison 1998, 2002). By eating the detritus, they convert these two nutrients into forms usable by the pitcher plants. In their study of Massachusetts, USA, pitcher plants (*Sarracenia purpurea*; Figure 169), Błedzki and Ellison (1998) found that *Habrotrocha rosa* (Figure 65) could provide a pitcher plant leaf with 8.8-43 mg of N and 18.2-88 mg of P in a single growing season, far exceeding that supplied by insects and rainfall. The rotifers accomplish this by having populations of ca. 400 individuals per leaf pitcher. These rotifers can excrete $\sim 5.2 \mu\text{g NO}_3\text{-N}$, $\sim 3.91 \mu\text{g NH}_4\text{-N}$, and $\sim 18.4 \mu\text{g PO}_4\text{-P}$ 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.

Aquatic Bryophytes

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

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

Streams

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



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



Figure 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 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 175. *Philodina vorax*, a species that lives on epiphytic mosses, *Sphagnum*, and streambank mosses. 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.

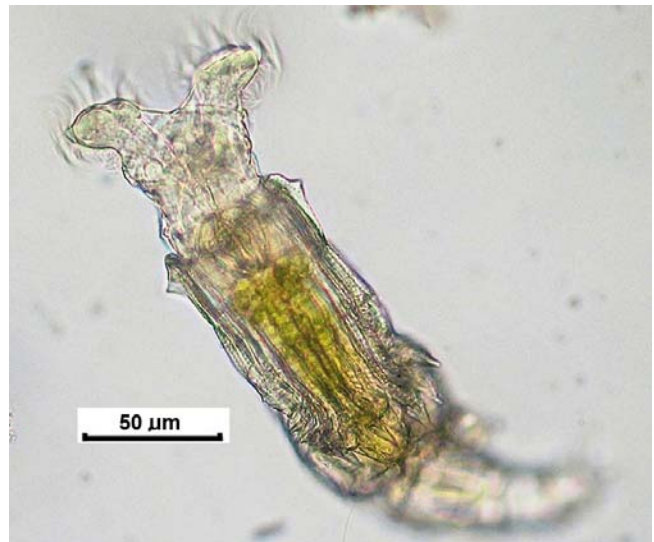


Figure 176. *Pleuretra cf brycei*, a species that lives among *Brachythecium*. Photo by Michel Verolet, with permission

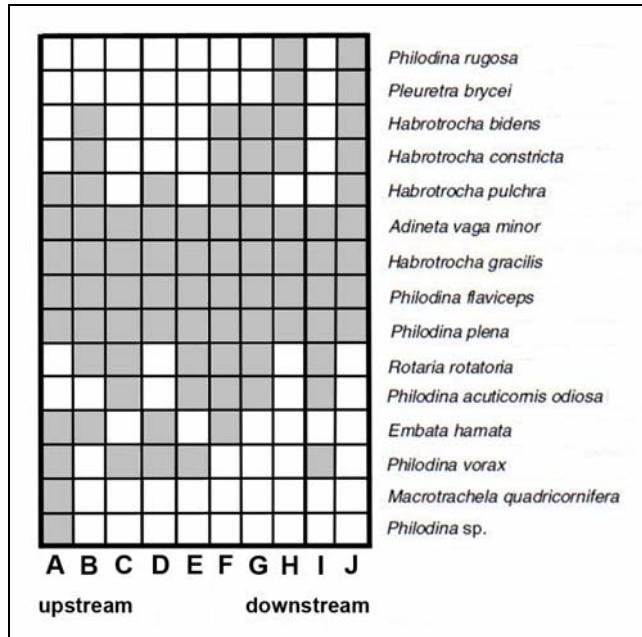


Figure 177. Distribution of moss-dwelling rotifers in a stretch of an Italian stream, arranged from upstream to downstream. Based on Fontaneto *et al.* 2005.

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

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

Linhart *et al.* (2002b) considered the stream bryophyte-rotifer association to result from the exposure of the stream bryophytes to water current (Wulforst 1994). Historically, the bryophytes have been considered to be refuge sites from flow (Madaliński 1961; Elliot 1967; Gurtz & Wallace 1984; Suren 1992) due to the reduction of flow within the moss mat (Gregg & Rose 1982; Madsen & Warncke 1983; Sand-Jensen & Mebus 1996). But for

small invertebrates, this argument is questionable because the flow rates at the surface layer of gravel or bedrock sediments are similar to those within the moss mats (Williams & Hynes 1974; Gregg & Rose 1982; Angradi & Hood 1998). On the other hand, the **Monogononta** do seem to be affected by the flow within the mats of *Fontinalis antipyretica* (Figure 34). Could it be ease of food capture rather than protection from flow that determines where they are able to live? Or refuge from predators?

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

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

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

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



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

Waterfalls

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

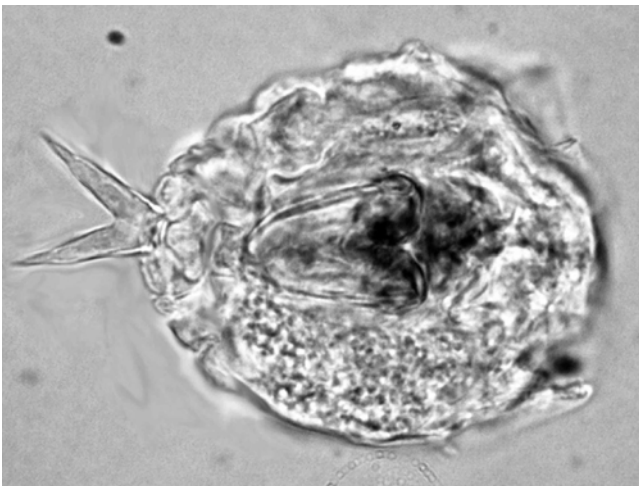


Figure 179. *Lecane martensi*, a species that was discovered among mosses in a waterfall. Photo by Savatenalinton & Segers 2008, through Creative Commons.



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



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



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

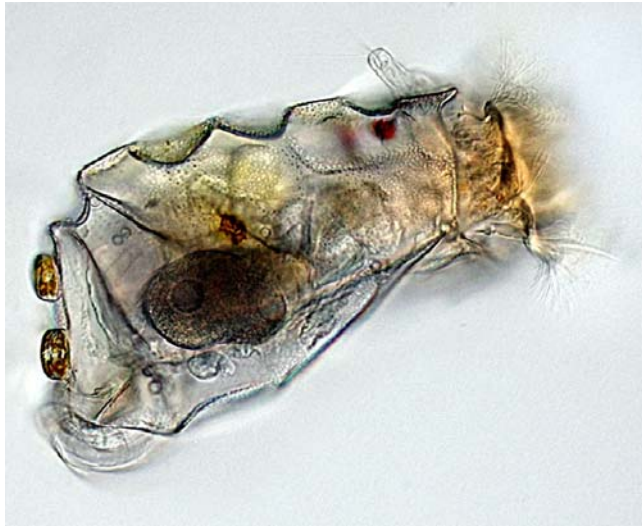


Figure 183. *Brachionus angularis* lateral view showing its armored lorica. This is a planktonic species that can occur in waterfalls. Photo by Michael Plewka <www.plingfactory.de>, with permission.



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



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

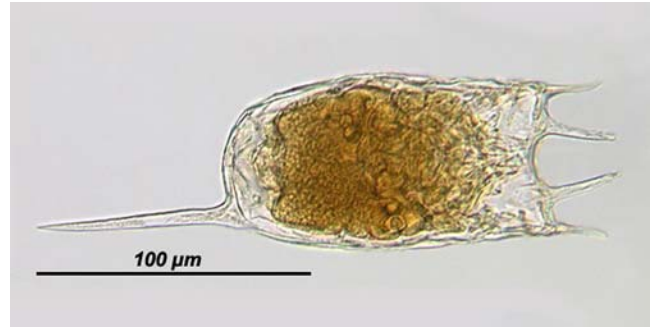


Figure 186. *Keratella tropica*, a planktonic species that can occur among mosses in waterfalls. Photo by Jersabek *et al.* 2003, with permission.



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

Krakatau

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

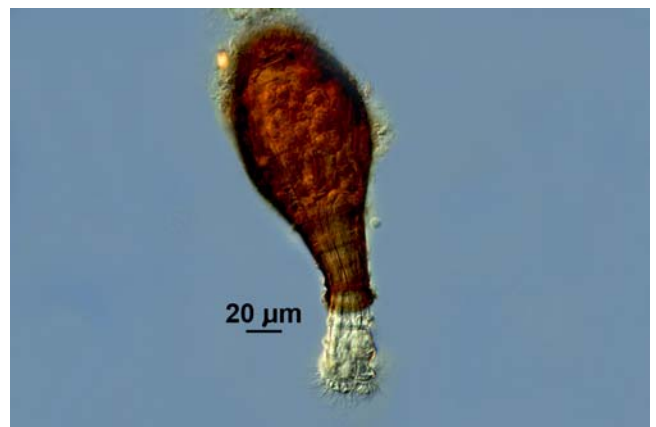


Figure 188. *Habrotrocha angusticollis*, a moss dweller. Photo by Proyecto Agua, through Creative Commons.



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



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

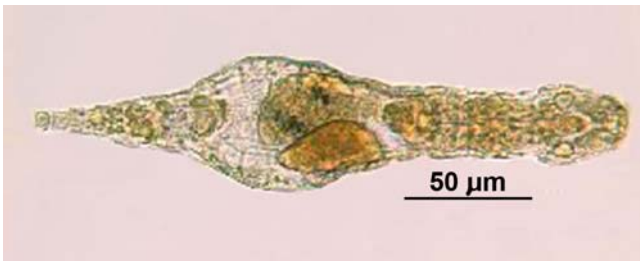


Figure 191. *Adineta gracilis*, a moss resident on Krakatau. Photo by Jersabek *et al*. 2003, with permission.

Seasons

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

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

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

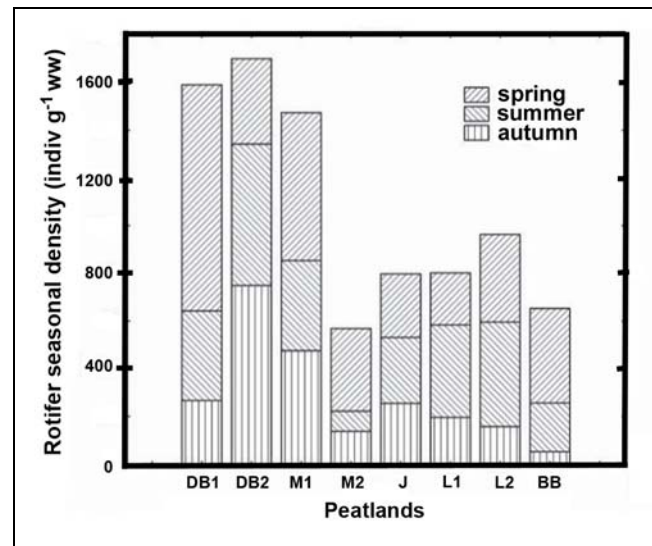


Figure 192. Seasonal changes in moss-dwelling rotifers from eight peatlands in eastern Poland. DB1, DB2, & M1 = raised bogs; M1 & J = poor fens; L1 & L2 = intermediate fen; BB = rich fen. Modified from Bielańska-Grajner *et al.* 2011.

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

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

Danger amidst the Bryophytes

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

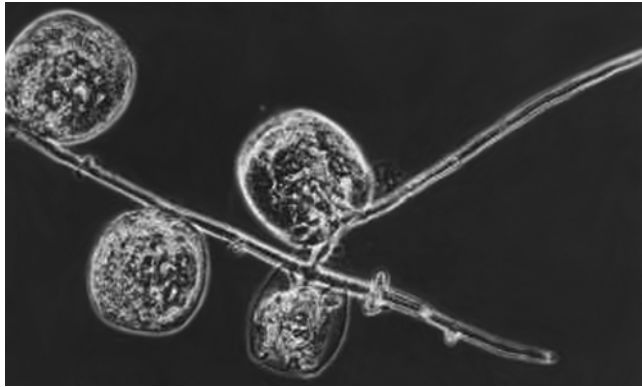


Figure 193. *Lecophagus longispora* infecting four rotifers. Photo by George Barron, with permission.

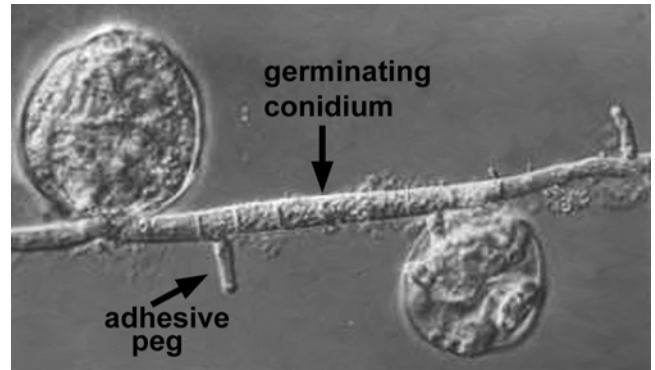


Figure 196. *Lecophagus muscicola* that has captured two rotifers and two adhesive pegs. Photo by George Barron, with permission.

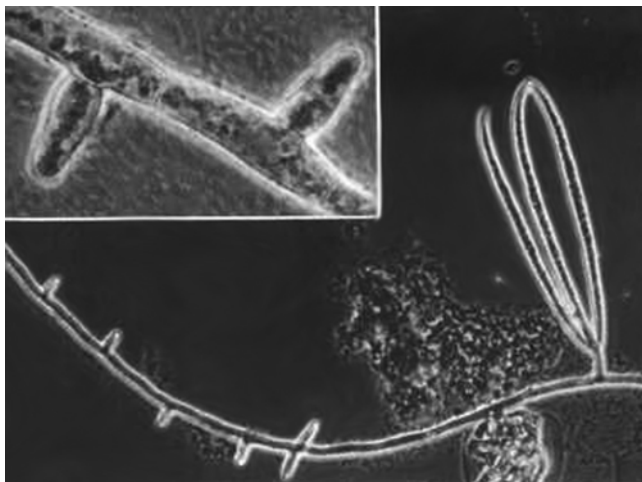


Figure 194. *Lecophagus longispora*, fungus that traps **tardigrades** and **rotifers** and may be a threat in mosses. Lower image is hypha of fungus with cluster of conidia and adhesive pegs. Inset shows adhesive pegs. Photos by George Barron, with permission.

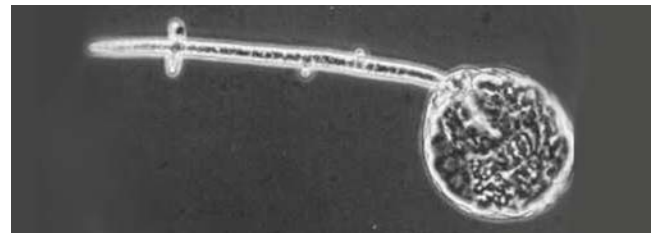


Figure 197. *Lecophagus longispora* infecting a rotifer; hypha shows adhering pegs. Such infections are also known for tardigrades. Photo by George Barron, with permission.



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

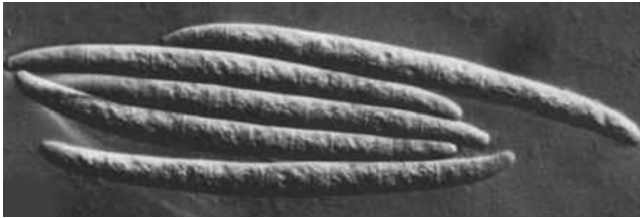


Figure 199. Conidia (X600) of *Lecophagus muscicola*. Photo by George Barron, with permission.

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 loricated rotifers (Prowse 1954).

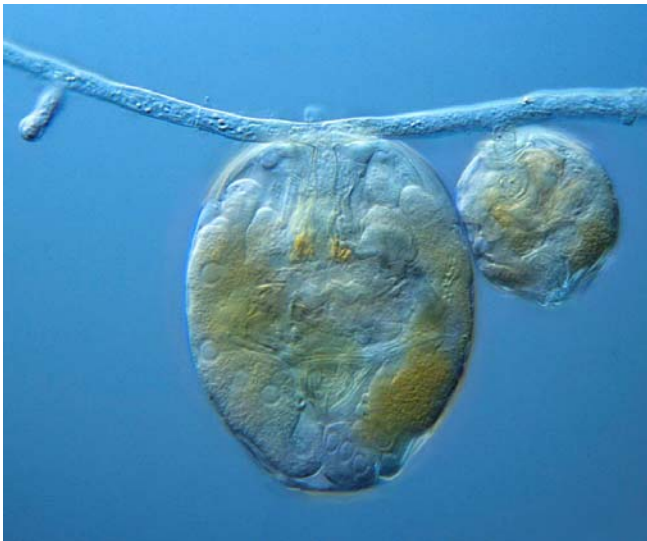


Figure 200. *Philodina roseola*, sometimes a bryophyte dweller, caught by the fungus *Zoophagus insidians*. Photo by Wim van Egmond, with permission.

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

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

due to its reproductive differences. These conidiospores are sometimes referred to as gemmae.

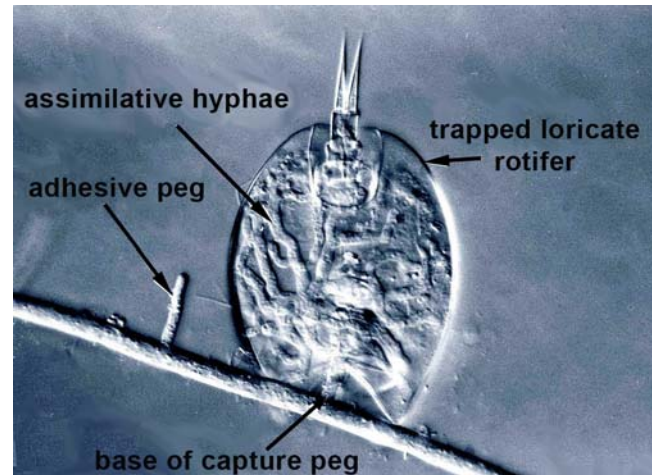


Figure 201. The rotifer *Lepadella* caught by the fungus *Zoophagus insidians*. Photo by Wim van Egmond, with permission.

Ozone Hole and Pollution Dangers?

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



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

Responses of functional groups to air pollution is often ignored in favor of simpler studies on single species. Nguyen-Viet *et al.* (2007) examined the effects of

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



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

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

Summary

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

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

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

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

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

Acknowledgments

Bryonettors 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 Cavanilah, 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 Plingfactory 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.

Literature Cited

- Alpert, P. 2000. The discovery, scope, and puzzle of desiccation tolerance in plants. *Plant Ecol.* 151: 5-17.
- Angradi, T. and Hood, R. 1998. An application of the plaster dissolution method for quantifying water velocity in the shallow hyporheic zone of an Appalachian stream system. *Freshwat. Biol.* 39: 301-315.
- Badcock, R. M. 1949. Studies in stream life in tributaries of the Welsh Dee. *J. Anim. Ecol.* 18: 193-208.
- Baqai, Aisha, Guruswamy, Vivek, Liu, Janie, and Rizki, Gizem. 2000. Introduction to the Rotifera. Rotifers: The "wheel animalcules." Accessed 21 September 2016 at <<http://www.ucmp.berkeley.edu/phyla/rotifera/rotifera.html>>
- Barnhisel, D. R. 1991. The caudal appendage of the cladoceran *Bythotrephes cederstroemi* as defense against young fish. *J. Plankton Res.* 13: 529-537.
- Barron, George. 2012. War of the Microworlds. Accessed 123 May 2012 at <<http://www.uoguelph.ca/~gbarron/2008/lollipop.htm>>.
- Bartos, E. 1949. Additions to knowledge of moss-dwelling fauna of Switzerland. *Hydrobiologia* 2: 285-295.
- Bateman, L. E. and Davis, C. C. 1980. The Rotifera of hummock-hollow formations in a poor (mesotrophic) fen in Newfoundland, Canada. *Internat. Rev. Gesamt. Hydrobiol.* 65: 127-153.
- Bateman, L. E. and Davis, C. C. 2007. The Rotifera of hummock-hollow formations in a poor (mesotrophic) fen in Newfoundland. *Internat. Rev. gesamt. Hydrobiol. Hydrogr.* 65: 127-153.
- Becquerel, P. 1950. La suspension de la vie au-dessous de 1/20 K absolu par démagnétisation adiabatique de l'alun de fer dans le vide le plus élevé. *Compt. Rend. Acad. Sci.* 231: 261-263.
- Beauchamp, P. de. 1913. Rotifères. Deuxième Expédition Antarctique Française (1908-1910) commandée par le Dr. Jean Charcot. Sciences naturelles: Documents scientifiques. Masson et Cie, Paris. 105-116.
- Bērziņš, B. and Pejler, B. 1987. Rotifer occurrence in relation to pH. *Hydrobiologia* 147: 107-116.
- Bielańska-Grajner, I., Cudak, A., and Mieczan, T. 2011. Epiphytic rotifer abundance and diversity in moss patches in bogs and fens in the Polesie National Park (Eastern Poland). *Internat. Rev. Hydrobiol.* 96: 29-38.
- Błędzki, L. A. and Ellison, A. M. 1998. Population growth and production of *Habrotrocha rosa* Donner (Rotifera: Bdelloidea) and its contribution to the nutrient supply of its host, the northern pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae). *Hydrobiologia* 385: 193-200.
- Błędzki, L. A. and Ellison, A. M. 2002. Nutrients regeneration by rotifers in New England (U.S.A.) bogs. *Verh. Internat. Ver. Limnol.* 28: 1328-1331.
- Błędzki, L. A. and Ellison, A. M. 2003. Diversity of rotifers from northeastern U.S.A. bogs with new species records for North America and New England. *Hydrobiologia* 497: 53-62.
- Broca, P. 1860. Réviviscence des animaux sesséchés. *C. R. Soc. Biol. Paris* 3, pp. 1-139.
- Bryce, D. L. 1929. On three cases of encystment among rotifers. *J. R. Microsc. Soc.* 49: 217-221.
- Burger, A. 1948. Studies on moss dwelling bdelloids (Rotifera) of eastern Massachusetts. *Trans. Amer. Microsc. Soc.* 67: 111-142.
- Caprioli, M. and Ricci, C. 2001. Recipes for successful anhydrobiosis in bdelloid rotifers. *Hydrobiologia* 446/447: 13-17.
- Cavanilah, J.-M. 2004. The fascinating world of rotifers. based on March 2004 edition of Micscape Magazine. Accessed 25 January 2012 at <<http://www.microscopy-uk.org.uk/mag/artmar04/jmcrotif.html>>.
- Cavanilah, J.-M. 2016. Microscopy-UK. Accessed 30 September 2016 at <<http://www.microscopy-uk.org.uk/>>.
- Charman, D. J. and Warner, B. G. 1992. Relationship between testate amoebae (Protozoa: Rhizopoda) and microenvironmental parameters on a forested peatland in north-eastern Ontario. *Can. J. Zool.* 70: 2474-2482.
- Clément, P., Amsellem, J., Cornillac, A.-M., and Ricci, C. 1980. An ultrastructural approach to feeding behaviour in *Philodina roseola* and *Brachionus calyciflorus* (rotifers) III. Cilia and muscles. *Conclusions. Hydrobiologia* 73: 137-141.
- Clymo, R. S. 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. *Ann. Bot. N. S.* 27: 309-324.
- Clymo, R. S. 1964. The origin of acidity in *Sphagnum* bogs. *Bryologist* 67: 427-431.
- Danchin, E. G. J., Flot, J.-F., Perfus-Barbeoch, L., and Doninck, K. Van. 2011. Genomic perspectives on the long-term absence of sexual reproduction in animals. In: Pontarotti, P. (ed.). *Evolutionary Biology – Concepts, Biodiversity, Macroevolution and genome Evolution*. Springer, Berlin, Heidelberg, pp. 223-242.
- Dartnall, H. J. G. 1980. Freshwater biology at Rothera Point, Adelaide Island: I. General description of the pools and the fauna. *Brit. Antarct. Surv. Bull.* 50: 51-54.
- Dartnall, H. J. G. 1995. Rotifers, and other aquatic invertebrates, from the Larsemann Hills, Antarctica. *Papers Proc. Royal Soc. Tasmania* 129: 17-23.
- Dartnall, H. J. G. 1997. Three new species of *Enicetruncus* (Rotifera) from Antarctica. *Quekett J. Microsc.* 38: 15-20.
- Dartnall, H. J. G. 2000. A Limnological Reconnaissance of the Vestfold Hills. Vol. 141., ANARE Reports Australian Antarctic Division, Department of the Environment and Heritage, Kingston, UK, pp. 1-55.

- Dartnall, H. J. G. 2005a. New species of *Keratella* (Rotifera, Monogononta Brachionidae) from South Georgia and the Falkland Islands. *Quekett J. Microsc.* 40: 41-46.
- Dartnall, H. J. G. 2005b. Freshwater invertebrates of subAntarctic South Georgia. *J. Nat. Hist.* 39: 3321-3342.
- Dartnall, H. J. G. and Hollowday, E. D. 1985. Antarctic rotifers. *Brit. Antarct. Surv. Sci. Repts.* 100: 1-46.
- Denekamp, N. Y., Reinhardt, R., Kube, M., and Lubzens, E. 2010. Late Embryogenesis Abundant (LEA) proteins in nondesiccated, encysted, and diapausing embryos of rotifers. *Biol. Repro.* 82: 714-724.
- Deneke, R. 2000. Review of rotifers and crustaceans in highly acidic environments of pH values ≤ 3 . *Hydrobiologia* 433: 167-172.
- Dick, M. W. 1990. The systematic position of *Zoopagus insidians*. *Mycol. Res.* 94: 347-354.
- Donner, J. 1980. Einige neue Forschungen über bdelloide Rotatorien, besonders in Böden. *Rev. d'E'col. Biol. Sol* 17: 125-143.
- Donner, P. J. 1964. Die Rotatorien-Synusien submerser Makrophyten der Donau bei Wien und mehrerer Alpenbäche. *Arch. Hydrobiol./Suppl.* 27: 227-324.
- Donner, P. J. 1972. Die Rädertierbestände submerser Moose und weiterer Merotope im Bereich der Stauräume der Donau an der deutsch-österreichischen Landesgrenze. *Arch. Hydrobiol. (Suppl.)* 44: 49-114.
- Drazina, T., Spoljar, M., Primc-Habdija, B., and Habdija, I. 2011. Small scale patterns of meiofauna in bryophytes. In: 7th Symposium for European Freshwater Sciences, July 2011.
- Duggan, I. C. 2001. The ecology of periphytic rotifers. *Hydrobiologia* 446/447: 139-148.
- Duggan, I. C., Green, J. D., Thompson, K., and Shiel, R. J. 1998. Rotifers in relation to littoral ecotone structure in Lake Rotomanuka, North Island, New Zealand. In: *Rotifera VIII: A Comparative Approach*. Springer Netherlands, pp. 179-197.
- Duggan, I. C., Green, J. D., Thompson, K., and Shiel, R. J. 2001. The influence of macrophytes on the spatial distribution of littoral rotifers. *Freshwat. Biol.* 46: 777-786.
- Dumont, H. J., Velde, I. Van de, and Dumont, S. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19: 75-97.
- Edmondson, W. T. 1940. The sessile Rotatoria of Wisconsin. *Trans. Amer. Microsc. Soc.* 59: 433-459.
- Edmondson, W. T. 1949. A formula key to the rotatorian genus *Ptygura*. *Trans. Amer. Microsc. Soc.* 68: 127-135.
- Egmond, Wim. van. 2003. Micro Gastronomy. Accessed 13 May 2012 at <<http://www.microscopy-uk.org.uk/mag/indexmag.html?http://www.microscopy-uk.org.uk/mag/artsep03/menu.html>>.
- Elliot, J. M. 1967. Invertebrate drift in a Dartmoor stream. *Arch. Hydrobiol.* 63: 202-237.
- EOL. 2016. *Brachionus urceolarus*. Accessed 9 August 2016 at <<http://eol.org/pages/1062529/overview>>.
- Epp, R. W. and Lewis, W. M. 1984. Cost and speed of locomotion for rotifers. *Oecologia* 61: 289-292.
- Fish, D. and Hall, D. W. 1978. Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher plant *Sarracenia purpurea*. *Amer. Midl. Nat.* 99: 172-183.
- Fontaneto, D. and Ricci, C. 2004. Rotifera: Bdelloidea. In: Yule, C. M. and Yong, H. S. (eds.). *Freshwater Invertebrates of the Malaysian Region*. Academy of Sciences Malaysia, Kuala Lumpur, Malaysia, pp. 121-126.
- Fontaneto, D. and Ricci, C. 2006. Spatial gradients in species diversity of microscopic animals: The case of bdelloid rotifers at high altitude. *J. Biogeogr.* 33: 1305-1313.
- Fontaneto, D. and Smet, W. H. De. 2015. Rotifera, Chapter 4. In: Schmidt-Rhaesa, A. (ed.). *Handbook of Zoology: Gastrotricha, Cycloneuralia and Gnathifera*, Vol. 3, De Gruyter, Berlin, pp. 217-300.
- Fontaneto, D., Melone, G., and Ricci, C. 2005. Connectivity and nestedness of the meta-community structure of moss dwelling bdelloid rotifers along a stream. *Hydrobiologia* 542: 131-136.
- Fontaneto, D., Boschetti, C., and Ricci, C. 2008. Cryptic diversification in ancient asexuals: Evidence from the bdelloid rotifer *Philodina flaviceps*. *J. Evol. Biol.* 21: 580-587.
- Fontaneto, D., Iakovenko, N., Eyres, I., Kaya, M., Wyman, M., and Barraclough, T. G. 2011. Cryptic diversity in the genus *Adineta* Hudson & Gosse, 1886 (Rotifera: Bdelloidea: Adinetidae): A DNA taxonomy approach. *Hydrobiologia* 662: 27-33.
- Fontaneto, D., Iakovenko, N., and Smet, W. H. De. 2015. Diversity gradients of rotifer species richness in Antarctica. *Hydrobiologia* 761: 235-248.
- Fox, Richard. 2001. Invertebrate Anatomy OnLine. Bdelloidea[®]. Moss rotifers. Accessed on 26 July 2009 at <<http://webs.lander.edu/rsfox/invertebrates/bdelloidea.html>>.
- Francez, A.-J. 1981. Rotifères de quelques tourbières d'Auvergne. *Ann. Stat. Biol. Besse-en-Chandesse* 15: 276-287.
- Francez, A. J. and Dévaux, J. 1985. Répartition des rotifères dans deux lacs-tourbières du Massif Central (France). [Distribution of rotifers in two peat bogs in the Massif Central (France).]. *Hydrobiologia* 128: 265-276.
- Fussmann, G. F., Ellner, S. P., Shertzer, K. W., and Hairston, N. G. Jr. 2000. Crossing the Hopf bifurcation in a live predator-prey system. *Science* 290: 1358-1360.
- Gerson, U. 1982. Bryophytes and invertebrates. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman & Hall, New York. pp. 291-332.
- Giard, A. 1894. L'anhydrobiose ou ralentissement des phénomènes vitaux. *C. R. Soc. Biol. Paris* 46, pp. 497-500.
- Gilbert, D. and Mitchell, E. A. D. 2006. Microbial diversity in *Sphagnum* peatlands. In: Martini, I. P., Cortizas, A. M., and Chesworth, W. *Peatlands: Evolution and Records of Environmental and Climate Changes*. Elsevier, Oxford, UK, pp. 287-318.
- Gilbert, J. J. 1974. Dormancy in rotifers. *Trans. Amer. Microscop. Soc.* 93: 490-513.
- Gladyshev, E. and Meselson, M. 2008. Extreme resistance of bdelloid rotifers to ionizing radiation. *Proc. Natl. Acad. Sci.* 105: 5139-5144.
- Goddard, K. A. and McDiffett, W. F. 1983. Rotifer distribution, abundance, and community structure in four habitats of a freshwater marsh. *J. Freshwat. Ecol.* 2: 199-211.
- Green, J. 2003. Associations of planktonic and periphytic rotifers in a tropical swamp, the Okavango Delta, Southern Africa. *Hydrobiologia* 490: 197-209.
- Gregg, W. W. and Rose, F. L. 1982. The effects of aquatic macrophytes on the stream microenvironment. *Aquat. Bot.* 14: 309-324.
- Guidetti R., and Jönsson, K.I. 2002. Long-term anhydrobiotic survival in semi-terrestrial micrometazoans. *J. Zool.* 257: 181-187.

- Gurtz, M. E. and Wallace, J. B. 1984. Substrate-mediated response of stream invertebrates to disturbance. *Ecology* 65: 1556-1569.
- Hájková, P., Bojková, J., Fránková, M., Opravilová, V., Hájek, M., Kintrová, K., and Horsák, M. 2011. Disentangling the effects of water chemistry and substratum structure on moss-dwelling unicellular and multicellular micro-organisms in spring-fens. *J. Limnol.* 70(Suppl. 1): 54-64.
- Hale, Alan. 2012. *Sphagnum angustifolium*. British Mosses and Liverworts. A Field Guide. Accessed 27 November 2012 at <<http://www.bbsfieldguide.org.uk/content/sphagnum-angustifolium>>.
- Halsey, L. A., Vitt, D. H., and Gignac, L. D. 2000. *Sphagnum*-dominated peatlands in North America since the last glacial maximum: Their occurrence and extent. *Bryologist* 103: 334-352.
- Hand, S. C., Menze, M. A., Toner, M., Boswell, L., and Moore, D. 2011. LEA proteins during water stress: Not just for plants anymore. *Ann. Rev. Physiol.* 73: 115-134.
- Haney, J. F. and Hall, D. J. 1973. Sugar-coated *Daphnia*: A preservation technique for Cladocera. *Limnol. Oceanogr.* 18: 331-333.
- Hansson, L.-A., Dartnall, H. J. G., Ellis-Evans, J. C., MacAlister, H., and Tranvik, L. J. 1996. Variation in physical, chemical and biological components in the subAntarctic lakes of South Georgia. *Ecography* 19: 393-403.
- Heinis, F. 1928. Die Moosfauna des Krakatau. *Treubia* 10: 231-244.
- Hess, S., Frahm, J.-P., and Theisen, I. 2005. Evidence of zoophagy in a second liverwort species, *Pleurozia purpurea*. *Bryologist* 108: 212-218.
- Hingley, M. 1993. Microscopic Life in *Sphagnum*. Illustrated by Hayward, P. and Herrett, D. *Naturalists' Handbook* 20. [i-iv]. Richmond Publishing Co. Ltd., Slough, England, 64 pp., 58 fig. 8 pl. (unpaginated).
- Hingley, M. 1999. Microscopic life in *Sphagnum*, with an exploration of some associated epiphytes and endophytes. *Quekett J. Microsc.* 38: 275-284.
- Hirschfelder, A., Koste, W., and Zucchi, H. 1993. Bdelloid rotifers in aerophytic mosses: Influence of habitat structure and habitat age on species composition. In: Gilbert, J. J., Lubzens, E., and Miracle, M. R. (eds.). 6. International Rotifer Symposium, Banyoles, Spain, 3-8 Jun 1991. Rotifer Symposium VI. *Hydrobiologia* 255/256: 343-344.
- Howey, Richard L. 1999. Welcome to the Wonderfully Weird World of Rotifers. *Micscape Magazine*. Accessed 10 May 2012 at <<http://www.microscopy-uk.org.uk/mag/indexmag.html?http://www.microscopy-uk.org.uk/mag/artnov99/rotih.html>>.
- Jacobs, M. H. 1909. The effects of desiccation on the rotifer *Philodina roseola*. *J. Exper. Zool.* 4: 207-263.
- Janiec, K. 1993. The freshwater micro- and meiofauna of Admiralty Bay, King George Island, South Shetland Islands. *Proceedings of the National Institute of Polar Research, Symposium of Polar Biology* 6: 133-138.
- Janiec, K. 1996a. The comparison of freshwater invertebrates of Spitsbergen (Arctic) and King George Island (Antarctic). *Polish Polar Res.* 17: 173-202.
- Janiec, K. 1996b. Short distance wind transport of microfauna in maritime Antarctic (King George Island, South Shetland Islands). *Polish Polar Res.* 17: 203-211.
- Janiec, K. and Salwicka, K. 1996. Monogonont composition in different freshwater habitats on Spitsbergen (Arctic) and King George Island (Antarctica). *Proceedings of the International Symposium on Environmental Research in the Arctic*, 19-21 July 1995, Tokyo, Japan. *Mem. Natl. Inst. Polar Res. Spec. Issue* 51: 91-98.
- Jennings, P. G. 1976. The Tardigrada of Signy Island, South Orkney Islands, with a note on the Rotifera. *Brit. Antarct. Surv. Bull.* 44: 1-25.
- Jersabek, C. D., Segers, H., and Morris, P. J. 2003. An illustrated online catalog of the Rotifera in the Academy of Natural Sciences of Philadelphia (version 1.0: 2003-April-8). [WWW database]. Accessed 23 February 2012 at <<http://rotifer.acnatsci.org/rotifer.php>>.
- Kamisugi, Y., Whitaker, J. W., and Cuming, A. C. 2016. The transcriptional response to DNA-double-strand breaks in *Physcomitrella patens*. *PLoS ONE* 11(8): e0161204. doi:10.1371/journal.pone.0161204.
- Kaya, M., Herniou, E. A., Barraclough, T. G., and Fontaneto, D. 2009. Inconsistent estimates of diversity between traditional and DNA taxonomy in bdelloid rotifers. *Organisms Divers. Evol.* 9(1): 3-12.
- Kaya, M., Smet, W. H. De, and Fontaneto, D. 2010. Survey of moss-dwelling bdelloid rotifers from middle Arctic Spitsbergen (Svalbard). *Polar Biol.* 33: 833-842.
- Koste, W. and Shiel, R. J. 1989. Rotifera from Australian Inland Waters. III. Euchlanidae, Mytilinidae and Trichotriidae (Rotifera: Monogononta). *Trans. Royal Soc. S. Austral.* 113: 85-114.
- Kuczyńska-Kippen, N. 2008. Spatial distribution of zooplankton communities between the *Sphagnum* mat and open water in a dystrophic lake. *Polish J. Ecol.* 56: 57-64.
- Kuczyńska-Kippen, N. M. and Nagengast, B. 2006. The influence of the spatial structure of hydromacrophytes and differentiating habitat on the structure of rotifer and cladoceran communities. *Hydrobiologia* 559: 203-212.
- Kukhta, A. E., Semenov, S. M., and Tonoyan, G. A. 1990. Analysis of the seasonal population dynamics of moss-inhabiting rotifers and their sensitivity to medium acidification changes using a statistical model. *Biol. Zhurn. Armenii* 43(5): 387-393.
- Likens, G. E. and Gilbert, J. J. 1970. Notes on quantitative sampling of natural populations of planktonic rotifers. *Limnol. Oceanogr.* 15: 816-820.
- Linhart, J. 2002. Bdelloidea/Monogononta abundance ratio: A possible measure of the relation of stream rotifers to flow velocity? *Biologica* 39-40: 101-110.
- Linhart, J., Fiurásková, M., and Vlčková, S. 2000. Meiofauna inhabiting an aquatic moss *Fontinalis antipyretica*: Preliminary results. In: Rulík, M. (ed.). *Proceedings of the XII Limnological Conference: Limnologie na prelomu tisíciletí*, Kouty nad Desnou, Czech Republic, pp. 190-193.
- Linhart, J., Fiurásková, M., and Uvíra, V. 2002a. Moss- and mineral substrata-dwelling meiobenthos in two different low-order streams. *Arch. Hydrobiol.* 154: 543-560.
- Linhart, J., Vlčková, S., and Uvíra, V. 2002b. Moss-dwelling meiobenthos and flow velocity in low-order streams. *Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium* (2001-2002). *Biologica* 39-40: 111-122.
- Madaliński, K. 1961. Moss dwelling rotifers of Tatra streams. *Polskie Arch. Hydrobiol.* 9: 243-263.
- Madsen, T. V. and Warncke, E. 1983. Velocities of currents around and within submerged aquatic vegetation. *Arch. Hydrobiol.* 97: 389-394.
- Marotta, R., Leasi, F., Uggetti, A., Ricci, C., and Melone, G. 2010. Dry and survive: Morphological changes during anhydrobiosis in a bdelloid rotifer. *J. Struc. Biol.* 171: 11-17.

- May, L. 1986. Rotifer sampling - a complete species list from one visit? *Hydrobiologia* 134: 117-120.
- May, L. 1989. Epizoidic and parasitic rotifers. *Hydrobiologia* 186/187: 59-67.
- Meisterfeld, R. 1977. Die horizontale und vertikale Verteilung der Testaceen (Rhizopoda, Testacea) in *Sphagnum*. *Arch. Hydrobiol.* 79: 319-356.
- Merrifield, K. and Ingham, R. E. 1998. Nematodes and other aquatic invertebrates in *Eurhynchium oreganum* (Sull.) Jaeg., from Mary's Peak, Oregon Coast Range. *Bryologist* 101: 505-511.
- Meyer, C., Gilbert, D., Gaudry, A., Franchi, M., Nguyen-Viet, H., Fabure, J., and Bernard, N. 2010. Relationship of atmospheric pollution characterized by gas (NO₂) and particles (PM10) to microbial communities living in bryophytes at three differently polluted sites (rural, urban, and industrial). *Microb. Ecol.* 59: 324-334.
- Murray, J. 1913. Australasian Rotifera. *J. Royal Microsc. Soc.* 33: 455-461, pl.19
- Newsham, K. K., Rolf, J., Pearce, D. A., and Strachan, R. J. 2004. Differing preferences of Antarctic soil nematodes for microbial prey. *Eur. J. Soil Biol.* 40: 1-8.
- Nguyen-Viet, H., Gilbert, D., Mitchell, E. A. D., Badot, P.-M., and Bernard, N. 2007. Effects of experimental lead pollution on the microbial communities associated with *Sphagnum fallax* (Bryophyta). *Microbial Ecol.* 54: 232-241.
- Nogrady, T. 1980. Canadian rotifers II. Parc Mont Tremblant, Quebec. *Hydrobiologia* 71: 35-46.
- Örstan, A. 1998. Factors affecting long-term survival of dry bdelloid rotifers: A preliminary study. *Hydrobiologia* 387/388: 327-331.
- Overgaard-Nielsen, C. 1967. Studies on the soil microfauna. 1. The moss-inhabiting nematodes and rotifers. *Naturv. Skr. Laerde Selsk. Skr.* 1: 1-98.
- Pejler, B. 1995. Relation to habitat in rotifers. *Hydrobiologia* 313/314: 267-278.
- Pejler, B. and Bērziņš, B. 1989. On choice of substrate and habitat in brachionid rotifers. *Hydrobiologia* 186/187: 137-144.
- Pejler, B. and Bērziņš, B. 1993a. On choice of substrate and habitat in bdelloid rotifers. *Hydrobiologia* 255/256: 333-338.
- Pejler, B. and Bērziņš, B. 1993b. On the ecology of mire rotifers. *Limnologia* 23: 295-300.
- Pejler, B. and Bērziņš, B. 1994. On the ecology of *Lecane* (Rotifera). *Hydrobiologia* 273: 77-80.
- Pennak, R. W. 1953. Fresh-water Invertebrates of the United States. Ronald Press Co., N. Y., 769 pp.
- Pennak, R. W. 1962. Quantitative zooplankton sampling in littoral areas. *Limnol. Oceanogr.* 7: 487-489.
- Pennak, R. W. 1966. Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. *Trans. Amer. Microsc. Soc.* 85: 329-349.
- Peters, U., Koste, W., and Westheide, W. 1993. A quantitative method to extract moss-dwelling rotifers. *Hydrobiologia* 255/256: 339-341.
- Petz, W. 1997. Ecology of the active soil microfauna (Protozoa, Metazoa) of Wilkes Land, East Antarctica. *Polar Biol.* 18: 33-44.
- Plewka, Michael. 2013. *Habrotrocha pusilla* var. *textris*. Plingfactory. Accessed 9 August 2016 at <<http://plingfactory.de/Science/Atlas/KennkartenTiere/Rotifers/01RotEng/source/Habrotrocha%20pusilla%20textris.html>>
- Plewka, Michael. 2014. Rotifer Resting Eggs. Plingfactory. Accessed 9 August 2016 at <<http://www.plingfactory.de/Science/Atlas/KennkartenTiere/Rotifers/01RotEng/source/Resting%20eggs.html>>.
- Plewka, Michael. 2016. Rotifers: Species List Alphabetical. Accessed 14 August 2016 at <<http://www.plingfactory.de/Science/Atlas/Artenlisten/RotiferEArtList1.html>>
- Pontin, R. M. and Shiel, R. J. 1995. Periphytic rotifer communities of an Australian seasonal floodplain pool. *Hydrobiologia* 313/314: 63-67.
- Pourriot, R. 1979. Rotifères Du Sol. *Rev. Ecol. Biol. Sol* 16: 279-312.
- Pourriot, R. and Snell, T. W. 1983. Resting eggs in rotifers. *Hydrobiologia* 104: 213-224.
- Powell, M. J., Heyburn, T., and Toadvine, S. 1990. *Zoophagus insidians* has reproductive and cellular morphology of a zygomycete. *Mycologia* 82: 460-470.
- Priddle, J. and Dartnall, H. J. G. 1978. The biology of an Antarctic aquatic moss community. *Freshwat. Biol.* 8: 469-480.
- Prowse, G. A. 1954. *Sommerstorffia spinosa* and *Zoophagus insidians* predacious on rotifers, and *Rozellopsis inflata* the endoparasite of *Zoophagus*. *Trans. Brit. Mycol. Soc.* 37: 134-150.
- Puterbaugh, M. N., Skinner, J. J., and Miller, J. M. 2004. A nonrandom pattern of rotifers occupying lobules of the hepatic, *Frullania eboraensis*. *Bryologist* 107: 524-530.
- Rahm, P. G. 1923. Biologische und physiologische Beiträge zur Kenntnis der Moosfauna. *Z. Allg. Physiol.* 20: 1-34.
- Rahm, P. G. 1926. Die trockenstarre (Anabiose) der moostierwelt. *Biol. CentBl.* 46: 452-477.
- Rahm, P. G. 1937. A new ordo of tardigrades from the hot springs of Japan (Furu-yu section, Unzen). *Annot. Zool. Japan* 16: 345-352.
- Ramazotti, G. 1958. Note sulle biocenosi dei muschi. *Mem. Ist. Ital. Idrobiol. Dott Marco Marchi* 10: 153-206.
- Ricci, C. 1983. Life histories of some species of Rotifera Bdelloidea. *Hydrobiologia* 104: 175-180.
- Ricci, C. 1987. Ecology of bdelloids: How to be successful. *Hydrobiologia* 147: 117-127.
- Ricci, C. 1991. Comparison of five strains of a parthenogenetic species, *Macrotrachela quadricornifera* (Rotifera, Bdelloidea). 1. Life history traits. *Hydrobiologia* 211: 147-155.
- Ricci, C. 1998. Anhydrobiotic capabilities of bdelloid rotifers. *Hydrobiologia* 387/388: 321-326.
- Ricci, C. 2001. Dormancy patterns in rotifers. *Hydrobiologia* 446/447: 1-11.
- Ricci, C. and Melone, G. 1984. *Macrotrachela quadricornifera* (Rotifera, Bdelloidea); a SEM study on active and cryptobiotic animals. *Zool. Scripta* 13(3): 195-200.
- Ricci, C., Vaghi, L., and Manzini, M. L. 1987. Desiccation of rotifers (*Macrotrachela quadricornifera*). *Ecology* 68: 1488-1494.
- Ricci, C., Pagani, M., and Bolzern, A. M. 1989. Temporal analysis of clonal structure in a moss bdelloid population. *Hydrobiologia* 186: 145-152.
- Ricci, C., Melone, G., Santo, N., and Caprioli, M. 2003a. Morphological response of a bdelloid rotifer to desiccation. *J. Morph.* 257: 246-253.
- Ricci, C., Shiel, R., Fontaneto, D., and Melone, G. 2003b. Bdelloid rotifers recorded from Australia with description of *Philodinavus aussiensis* n. sp. *Zool. Anz.* 242: 241-248.

- Ricci, C., Caprioli, M., and Santo, N. 2004. Feeding and anhydrobiosis in bdelloid rotifers: A preparatory study for an experiment aboard the International Space Station. *Invert. Biol.* 123: 283-288.
- Ricci, C., Caprioli, M., Fontaneto, D., and Melone, G. 2008. Volume and morphology changes of a bdelloid rotifer species (*Macrotrachela quadricornifera*) during anhydrobiosis. *J. Morphol.* 269: 233-239.
- Rydin, H. and Jeglum, J. K. 2013. *The Biology of Peatlands*. Oxford University Press, Oxford, 381 pp.
- Sakuma, M., Hanazato, T., Nakazato, R., and Haga, H. 2002. Methods for quantitative sampling of epiphytic microinvertebrates in lake vegetation. *Limnology* 3: 115-119.
- Sand-Jensen, K. and Mebus, J. R. 1996. Fine-scale patterns of water velocity within macrophyte patches in streams. *Oikos* 76: 169-180.
- Savatenalinton, S. and Segers, H. 2008. Rotifers of waterfall mosses from Phu Hin Rong Kla National Park, Thailand, with the description of *Lecane martensi*, new species (Rotifera: Monogononta: Lecanidae). *Raffles Bull. Zool.* 56: 245-249.
- Sayre, R. M. and Brunson, L. K. 1971. Microfauna of moss habitats. *Amer. Biol. Teacher* Feb. 1971: 100-102, 105.
- Schmid-Araya, J. M. 1995. Disturbance and population dynamics of rotifers in bed sediments. *Hydrobiologia* 313-314: 279-290.
- Schramm, U. and Becker, W. 1987. Anhydrobiosis of the bdelloid rotifer *Habrotrocha rosa* (Aschelminthes). *Z. Mikrosk.-Anat. Forsch* 101: 1:17.
- Schwarz, A. M., Green, J. D., Green, T. G. A., and Seppelt, R. D. 1993. Invertebrates associated with moss communities at Canada Glacier, southern Victoria Land, Antarctica. *Polar Biol.* 13: 157-162.
- Searles, P. S., Flint, S. D., Díaz, S. B., Rousseaux, M. C., Ballaré, C. L., and Caldwell, M. M. 1999. Solar ultraviolet-B radiation influence on *Sphagnum* bog and *Carex* fen ecosystems: First field season findings in Tierra del Fuego, Argentina. *Global Change Biol.* 5: 225-234.
- Segers, H. 1996. The biogeography of littoral *Lecane* Rotifera. *Hydrobiologia* 323: 169-197.
- Segers, H. 2001. Zoogeography of the Southeast Asian Rotifera. *Hydrobiologia* 446-447: 233-246.
- Segers, H. 2007. Annotated checklist of the rotifers (Phylum Rotifera) with notes on nomenclature, taxonomy and distribution. *Zootaxa* 1564: 1-104.
- Shiel, R. J. and Green, D. J. 1996. Rotifera recorded from New Zealand, 1859-1995, with comments on zoogeography. *N. Z. J. Zool.* 23: 2, 191-207.
- Sládeček, V. 1983. Rotifers as indicators of water quality. *Hydrobiologia* 100: 169-201.
- Smet, W. H. De. 1988. Rotifers from Bjørnøya (Svalbard), with the description of *Cephalodella evabroedi* n. sp. and *Synchaeta lakowitziana arctica* n. subsp. *Fauna Norv. Ser. A*, 9: 1-18.
- Smet, W. H. De. 2001. Freshwater Rotifera from plankton of the Kerguelen Islands (SubAntarctica). *Hydrobiologia* 446/447: 261-272.
- Smet, W. H. De and Beyens, L. 1995. Rotifers from the Canadian High Arctic (Devon Island, Northwest Territories). *Hydrobiologia* 313/314: 29-34.
- Sohlenius, B. and Boström, S. 1996. Distribution patterns of microfauna (nematodes, rotifers and tardigrades) on nunataks in Dronning Maud Land, East Antarctica. *Polar Biol.* 16: 191-200.
- Sohlenius, B. and Boström, S. 2005. The geographic distribution of metazoan microfauna on East Antarctic nunataks. *Polar Biol.* 28: 439-448.
- Sohlenius, B. and Boström, S. 2006. Patch-dynamics and population structure of nematodes and tardigrades on Antarctic nunataks. *Eur. J. Soil Biol.* 42: 321-325.
- Steiner, W. A. 1994a. The influence of air pollution on moss-dwelling animals. 2. Aquatic fauna with emphasis on Nematoda and Tardigrada. *Rev. Suisse Zool.* 101: 699-724.
- Steiner, W. A. 1994b. The influence of air pollution on moss-dwelling animals. 4. Seasonal and long-term fluctuations of rotifer, nematode and tardigrade populations. *Rev. Suisse Zool.* 101: 1017-1031.
- Steiner, W. A. 1995a. Influence of air pollution on moss-dwelling animals. 3. Terrestrial fauna, with emphasis on Oribatida and Collembola. *Acarologia (Paris)* 36(2): 149-173.
- Steiner, W. A. 1995b. The influence of air pollution on moss-dwelling animals. 5. Fumigation experiments with SO₂ and exposure experiments. *Rev. Suisse Zool.* 102(1): 13-40.
- Strüder-Kypke, M. C. 1999. Periphyton and sphagnicolous protists of dystrophic bog lakes (Brandenburg, Germany). I. Annual cycles, distribution and comparison to other lakes. *Limnologica* 29: 393-406.
- Suatoni, E., Vicario, S., Rice, S., Snell, T., and Caccone, A. 2006. An analysis of species boundaries and biogeographic patterns in a cryptic species complex: The rotifer *Brachionus plicatilis*. *Molec. Phylog. Evol.* 41: 86-98.
- Sudzuki, M. 1964. On the microfauna of the Antarctic region. 1. Moss-water community at Langhovde. In *JARE 1956-1962 Scientific Reports, Series E*, 19: 41, 11 pl.
- Sudzuki, M. 1979. On the microfauna of the Antarctic region. III. Microbiota of the terrestrial interstices. *Proceedings of the Symposium on Terrestrial Ecosystem in the Syowa Station area. Memoirs of National Institute of Polar Research, Special Issue* 11: 104-125, pl. 1-10.
- Suren, A. M. 1992. Meiofaunal communities associated with bryophytes and gravels in shaded and unshaded alpine streams in New Zealand. *N. Z. J. Marine Freshwat. Res.* 26: 115-125.
- Tunnacliffe, A. and Lapinski, J. 2003. Resurrecting Van Leeuwenhoek's rotifers: A reappraisal of the role of disaccharides in anhydrobiosis. *Philosoph. Trans. Royal Soc. London B Biol. Sci.* 358: 1755-1771.
- Tunnacliffe, A., Lapinski, J., and McGee, B. 2005. A putative LEA protein, but no trehalose, is present in anhydrobiotic bdelloid rotifers. In *Rotifera* x(pp. 315-321). Springer Netherlands.
- Turner, P. N. and Silva, C. Da. 1992. Littoral rotifers from the state of Mato Grosso, Brazil. *Studies on Neotropical Fauna and Environment* 27: 227-241.
- Vlčková, S., Linhart, J., and Uvíra, V. 2002. Permanent and temporary meiofauna of an aquatic moss *Fontinalis antipyretica* Hedw. *Acta Univers. Palack. Olom. Biol.* 39-40: 131-140.
- Waggoner, B. M. and Poinar, G. O. Jr. 1993. Fossil habrotrichid rotifers in Dominican amber. *Experientia* 49: 354-357.
- Wallace, R. L. and Snell, T. W. 1991. Rotifers. Chapt. 8. In: Thorp, J. H. and Covich, A. P. (eds.). *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, New York, pp. 187-248.
- Wallace, R. L., Snell, T. W., Ricci, C., and Nogrady, T. 2006. *Rotifera. Vol. 1. Biology, Ecology and Systematics. Guides to the Identification of the Microinvertebrates of the*

- Continental Waters of the World, Kenobi, Ghent/Backhuys, Leiden, 299 pp.
- Warner, B. G. and Asada, T. 2006. Biological diversity of peatlands in Canada. *Aquat. Sci* 68: 240-253.
- Warner, B. G. and Chmielewski, J. G. 1992. Testate amoebae (Protozoa) as indicators of drainage in a forested mire, Northern Ontario, Canada. *Arch. Protistenk.* 141(3): 179-183.
- Whisler, H. C. and Travland, L. B. 1974. The rotifer trap of *Zoophagus*. *Arch. Microbiol.* 101: 95-107.
- Wikipedia. 2011. *Brachionus*. Updated 11 September 2011. Accessed 26 January 2012 at <<http://en.wikipedia.org/wiki/Brachionus>>.
- Wikipedia. 2012a. Rotifer. Updated 19 January 2012. Accessed 24 & 26 January 2012 at <<http://en.wikipedia.org/wiki/Rotifer>>.
- Wikipedia. 2012b. Rotifer. Updated 7 May 2012. Accessed 10 May 2012 at <<http://en.wikipedia.org/wiki/Rotifer>>.
- Wikipedia. 2016. Rotifers. Last updated 16 September 2016. Accessed 22 September 2016 at <en.wikipedia.org/wiki/Rotifer#Reproduction_and_life_cycle>.
- Williams, C. J., Yavitt, J. B., Wieder, R. K., and Cleavitt, N. L. 1998. Cupric oxide oxidation products of northern peat and peat-forming plants. *Can. J. Bot.* 76: 51-62.
- Williams, D. D. and Hynes, H. B. N. 1974. The occurrence of benthos deep in the substratum of a stream. *Freshwat. Biol.* 4: 233-256.
- Wilson, C. G. 2011. Desiccation-tolerance in bdelloid rotifers facilitates spatiotemporal escape from multiple species of parasitic fungi. *Biol. J. Linn. Soc.* 104: 564-574.
- Wilts, E. F., Martinez Arbizu, P., and Ahlrichs, W. H. 2010. Description of *Bryceella perpusilla* n. sp. (Monogononta: Proalidae), a new rotifer species from terrestrial mosses, with notes on the ground plan of *Bryceella remane*, 1929. *Internat. Rev. Hydrobiol.* 95: 471-481.
- Wulforst, J. 1994. Selected faunal elements of the hyporheos and in submerged moss clumps (bryorheal) along an acidification gradient in two brooks in Harz Mountains, West Germany. *Verh. Internat. Verein. Limnol.* 25: 1575-1584.

