CHAPTER 4-6

INVERTEBRATES: ROTIFER TAXA – BDELLOIDEA

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

Taxa on Bryophytes

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

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

correlate with habitat and closest relatives seem to occur in "normal" habitats.

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

CLASS BDELLOIDEA

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

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

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

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

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

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

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

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

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

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

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

Adinetidae

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

Adineta

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

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

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

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

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

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

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

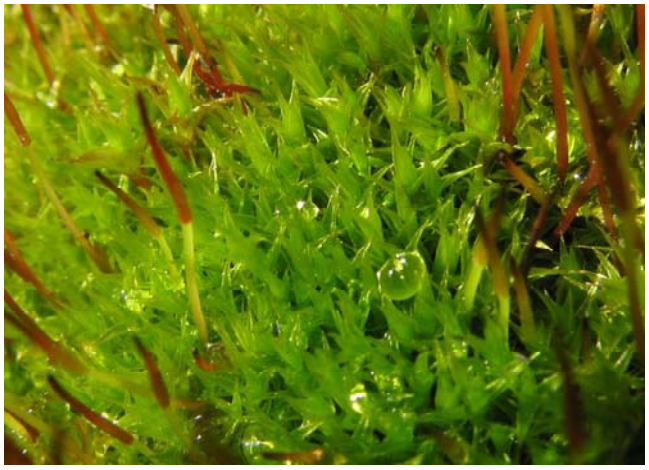

Figure 8. ***Ceratodon purpureus***, home for ***Adineta vaga*** *var*. ***rhomboidea***. Photo by Jiří Kameníček, with permission.

Other species occur on bryophytes in various habitats. In most cases, the habitat is simply listed as moss, or some other non-bryophyte habitat and moss. These include ***Adineta cuneata*** (Figure 9) on moss (Plewka 2016), ***A. steineri*** (Figure 10) on epiphytic mosses (Hirschfelder *et al*. 1993; Plewka 2016), and ***A. tuberculosa*** (Figure 11) on moss (Horkan 1981; Plewka 2016).

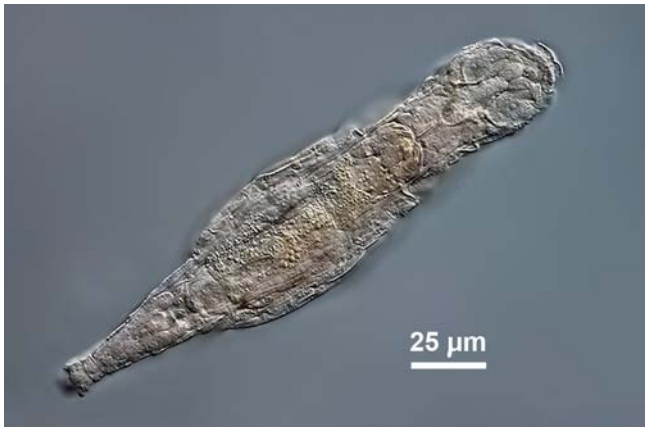

Figure 9. ***Adineta cuneata*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

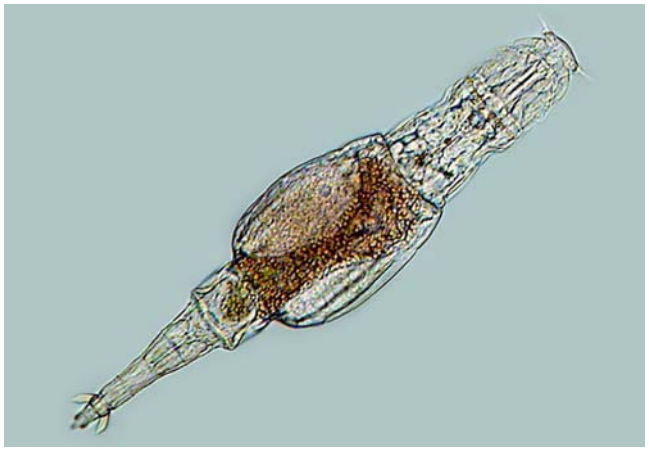

Figure 10. ***Adineta steineri***, a species that lives on epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 11. ***Adineta tuberculosa***, a moss inhabitant. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bradyscela

In addition to the ***Adineta*** species, ***Bradyscela clauda*** (Figure 12) occurs on the terrestrial moss ***Brachythecium rutabulum*** (Figure 13) (Madaliński 1961; Plewka 2016).

Figure 12. ***Bradyscela clauda*** with retracted cilia, from ***Brachythecium rutabulum.*** Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 13. ***Brachythecium rutabulum***, home for ***Bradyscela clauda*** in Europe. Photo by Michael Lüth, with permission.

Habrotrochidae

The **Habrotrochidae** is a family with three genera, all of which occur among mosses.

Habrotrocha

Habrotrocha species are common inhabitants among ***Sphagnum*** (Figure 6) (Bateman 1987; Peterson *et al*. 1997; Błedzki & Ellison 1998) as well as other mosses. ***Habrotrocha*** is able to survive decreasing moisture with the protection of a mucous matrix (Kutikova 2003). This is particularly helpful when mosses are drying. The members of ***Habrotrocha*** accumulate various small adhering particles, thus further providing them a shelter to protect them while they are dry.

Habrotrocha ampulla (Figure 14), ***H. angusticollis*** (Figure 15-Figure 16), ***H. collaris*** (Figure 37-Figure 38), ***H. constricta*** (Figure 28-Figure 29), and ***H. lata*** (Figure 17-Figure 18) live among or on ***Sphagnum*** in ***Sphagnum*** ponds (Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016).

Figure 14. ***Habrotrocha ampulla*** from among ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

Figure 15. ***Habrotrocha angusticollis***, a bryophyte dweller. Photo by Yuuji Tsukii, with permission.

Figure 16. ***Habrotrocha angusticollis*** from ***Sphagnum*** ponds. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 17. ***Habrotrocha lata***, a species collected from **bryophytes** in more than one location. Photo through Proyecto Agua, with permission.

Figure 18. ***Habrotrocha lata*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Some species of ***Habrotrocha*** use the protection of ***Sphagnum*** **retort** cells (Figure 19-Figure 21) for their homes (Plewka 2016). These are special cells that have a pore in a flask-like neck at the end of the stem epidermal

cell. The rotifers that live there extend outward from the pore to feed. This is particularly true for ***Habrotrocha reclusa*** (Figure 22), known from ***Sphagnum subsecundum*** (Figure 7) (Myers 1942) and ***H. roeperi*** (Figure 23; Bielańska-Grajner *et al*. 2011; Plewka 2016).

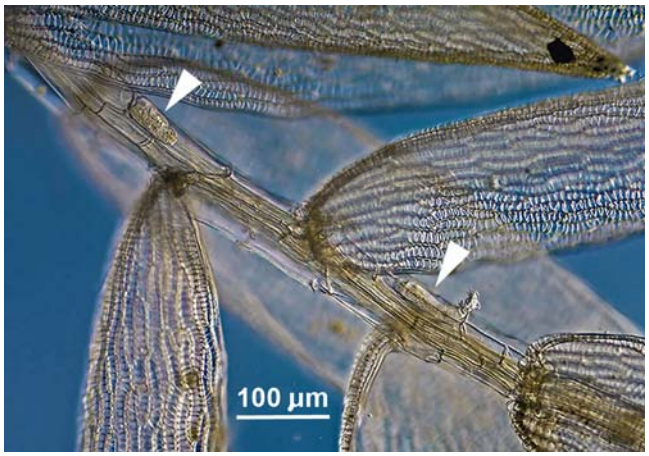

Figure 19. ***Sphagnum*** showing retort cells with ***Habrotrocha roeperi*** (arrows), a retort cell dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

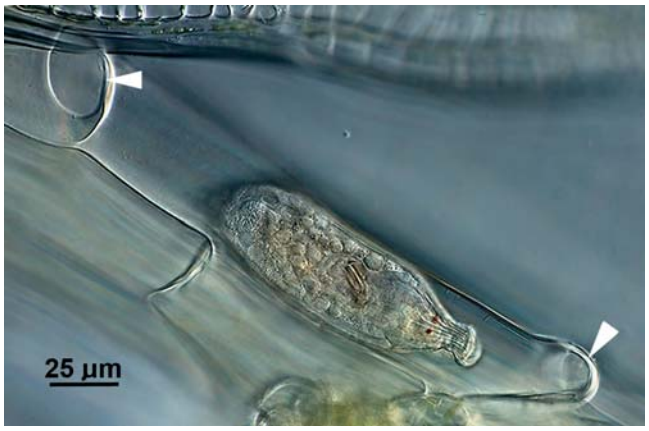

Figure 20. ***Habrotrocha roeperi*** in a retort cell. Arrows indicate the pores. Photo by Michael Plewka <www.plingfactory.de>, with permission.

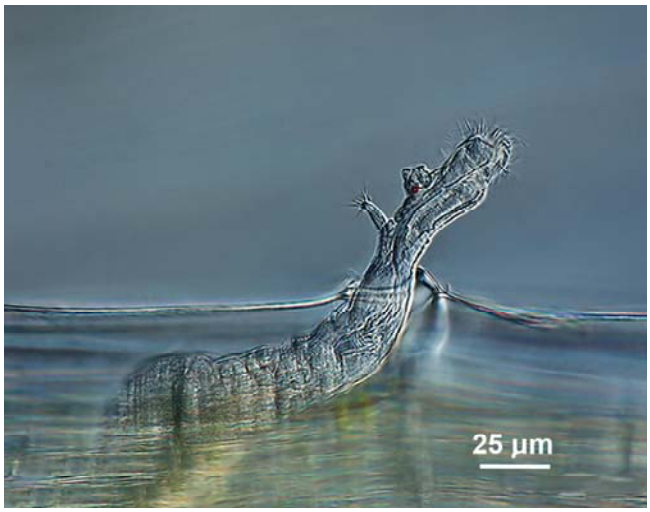

Figure 21. ***Habrotrocha roeperi*** extending out of a retort cell, a position in which it can attempt to trap food. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 22. ***Habrotrocha cf. reclusa***, a retort cell dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 23. ***Habrotrocha roeperi***, a retort cell dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Bog habitats for ***Habrotrocha*** (Figure 24), in particular ***H. rosa*** (Figure 25), include pitcher plants (***Sarracenia purpurea***, Figure 26), where the rotifers are a major food source for co-habiting members of the **Culicidae** (mosquitoes) (Bateman 1987), causing the mosquito population numbers to rise (Błedzki & Ellison 1998). The pitcher plants are common plants among the ***Sphagnum*** (Figure 6) in bogs and provide a pool of water in their leaves. The rotifers are an important source of N and P in the bog/fen-dwelling pitcher plants.

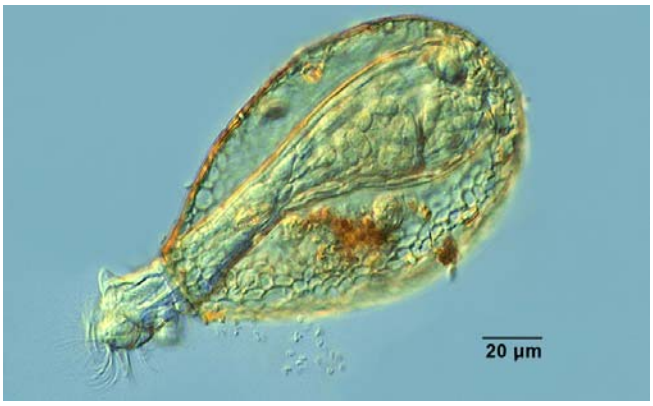

Figure 24. ***Habrotrocha***, a genus with many species that occur on **bryophytes**. Photo by Proyecto Agua Water Project through Creative Commons, with permission.

Figure 25. ***Habrotrocha rosa***, a species that lives in pitcher plants. Photo by Rkitko at Wikipedia Commons.

Figure 26. ***Sarracenia purpurea***, a bog plant that provides a watery home for ***Habrotrocha rosa***. Photo by Pouzin Oliver, through Creative Commons.

There are many species in ***Habrotrocha*** that live among bryophytes. These include ***H. bidens*** (Figure 27) on mosses on the ground (Hingley 1993; Plewka 2016), ***H. constricta*** (Figure 28-Figure 29) on ***Sphagnum***, water mosses, and **epiphytic** bryophytes (those growing on trees) (Myers 1942; Horkan 1981; Hingley 1993; Plewka 2016), ***H. novemdens*** (Figure 30) on mosses (Plewka 2016), ***Habrotrocha pavida*** on the mosses ***Ceratodon purpureus*** (Figure 8) and ***Bryum argenteum*** (Figure 31) (Yakovenko 2000), ***H. pusilla*** (Figure 32) in mucilage on moss (Horkan 1981; Plewka 2016), and ***H. quinquedens*** (Figure 33) on both wet and dry mosses (Plewka 2016). Some species also occur in the lobules of the leafy liverwort ***Frullania*** (Figure 34-Figure 35; Michel Verolet).

Figure 27. ***Habrotrocha bidens*** from moss on ground. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 28. ***Habrotrocha constricta***, a species that lives on both water moss and epiphytic moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 29. ***Habrotrocha constricta***, a species known from bryophytes. Photo by Jersabek *et al.* 2003, with permission.

Figure 30. ***Habrotrocha novemdens*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 31. ***Bryum argenteum***, home of ***Habrotrocha pavida***. Photo by Manju Nair, through Creative Commons.

Figure 32. ***Habrotrocha pusilla***, a species that lives in mucilage on moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Hirschfelder *et al*. (1993) examined the rotifers among epiphytic bryophytes and added ***Habrotrocha flava***, ***H. fusca***, and ***H. insignis***.

Figure 33. ***Habrotrocha quinquedens***, a species that lives on both wet and dry mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

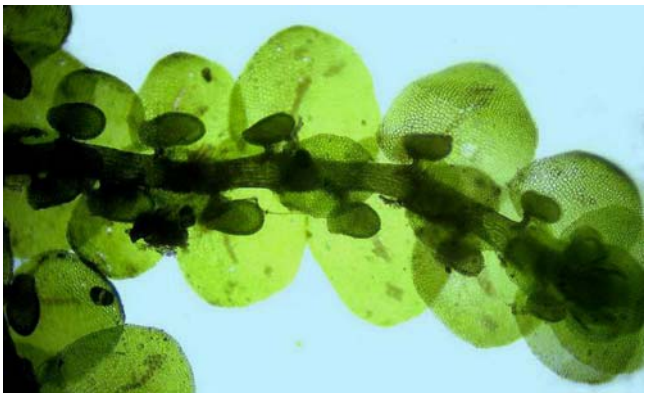

Figure 34. ***Habrotrocha*** on ***Frullania***, peeking out of the hood-shaped lobules. Photo by Michel Verolet, with permission.

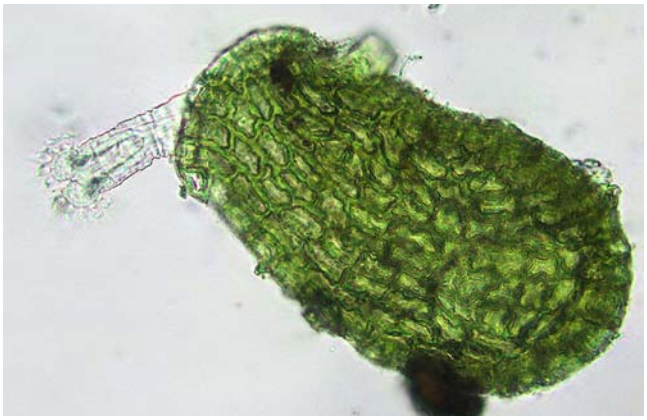

Figure 35. ***Habrotrocha*** in ***Frullania*** lobule. Photo by Michel Verolet, with permission.

A number of additional species are known from bryophytes, but with no additional details. Madaliński (1961) reported ***H. microcephala*** and ***H. tridens*** (see also Bielańska-Grajner *et al*. 2011) from the environs of Tatra streams. Horkan (1981) reported ***Habrotrocha aspera*** (Figure 36; see also Plewka 2016); see also Hingley 1993 for bog mosses), and ***H. pulchra***. Hingley (1993) added ***H. longula***, and ***H. minuta***; Peters *et al*. (1993) added ***H. eremita***. It appears that 1993 was a good year for bryophyte rotifer studies.

Figure 36. ***Habrotrocha aspera***, a moss inhabitant. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 37. ***Habrotrocha collaris***, a species known from bryophytes, including ***Sphagnum***. Photo by Jersabek *et al.* 2003, with permission.

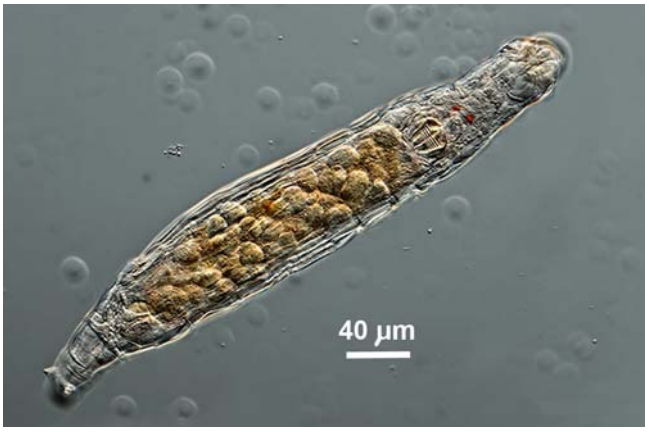

Figure 38. ***Habrotrocha collaris*** with two red eyespots, a bryophyte dweller, including ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Otostephanos

The genus ***Otostephanos*** has species on ***Sphagnum*** (Figure 6), but others occur on terrestrial mosses. ***Otostephanos auriculatus*** (Figure 39-Figure 40) occurs on ***Sphagnum*** and ***O. jolantae*** (Figure 41) occurs in ***Sphagnum*** ponds (Plewka 2016). ***Otostephanos monteti*** (Figure 42) lives on the emergent moss ***Drepanocladus aduncus*** (Figure 43) (Yakovenko 2000). ***Otostephanos cuspidilabris*** is known from "soggy" plants of the moss ***Atrichum*** sp. (Figure 44-Figure 45) (Yakovenko 2000). ***Otostephanos macrantennus*** is a bryophyte dweller (Ricci 1998). Two species live among dry mosses, ***O. regalis*** (Figure 46) on roof mosses (Hirschfelder *et al.* 1993; Plewka 2016) and ***O. torquatus*** (Figure 47) on mosses on concrete (Peters *et al.* 1993; Plewka 2016).

Figure 39. ***Otostephanos auriculatus*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 40. ***Otostephanos auriculatus***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

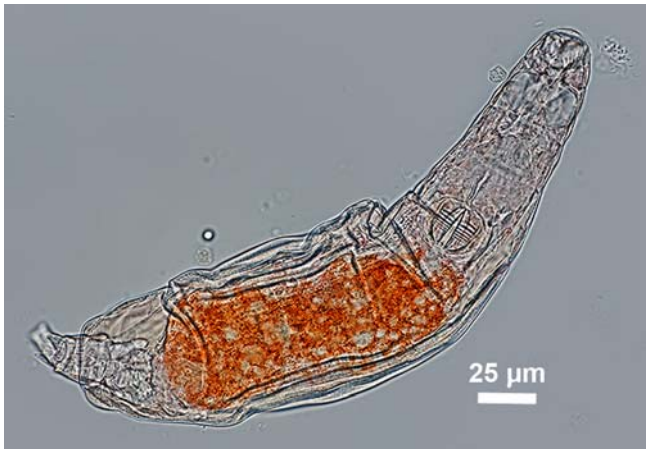

Figure 41. ***Otostephanos jolantae*** from ***Sphagnum*** pond. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 42. ***Otostephanos monteti***, a species that lives on the emergent moss ***Drepanocladus aduncus***. Photo by Michael Plewka <www.plingfactory.de>., with permission.

Figure 43. ***Drepanocladus aduncus***, home for ***Otostephanos monteti***. Photo by Bob Klips, with permission.

Figure 44. ***Atrichum angustatum*** streamside habitat and home of ***Otostephanos cuspidilabris***. Photo by Bob Klips, with permission.

Figure 45. ***Atrichum angustatum***, home of ***Otostephanos cuspidilabris***. Photo by Bob Klips, with permission.

Figure 46. ***Otostephanos*** *cf.* ***regalis*** from dry moss on roof. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 47. ***Otostephanos torquatus*** from dry moss on concrete. Michael Plewka <www.plingfactory.de>, with permission.

Scepanotrocha

Some members of a second genus seem also to find the retort cells of ***Sphagnum*** to be a suitable home. ***Scepanotrocha rubra*** (Figure 48-Figure 49) lives in these cells, extending out of them to feed (Figure 48) (Myers 1942; Plewka 2012).

Figure 48. ***Scepanotrocha rubra*** in a retort cell of a ***Sphagnum*** stem. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 49. ***Scepanotrocha rubra***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

In addition to the retort dwellers, ***Scepanotrocha corniculata*** (Figure 50) lives on mosses, ***S. semitecta*** (Figure 51) is a ***Sphagnum*** (Figure 6) dweller, and ***S. simplex*** (Figure 52) lives on epiphytic mosses as well as ***Sphagnum***, once again demonstrating the seemingly wide range of microhabitats used by a single rotifer species (Plewka 2016).

Figure 50. ***Scepanotrocha cf. corniculata*** from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 51. ***Scepanotrocha semitecta*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 52. ***Scepanotrocha simplex***, a species that lives on both epiphytic mosses and ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Philodinavidae

Only two species from this family seem to be moss dwellers. ***Philodinavus paradoxus*** (Figure 53) lives in

lakes, rivers, and streams (Madaliński 1961; Ricci & Melone 1998; Plewka 2016) and is preyed upon by flatworms, larger moss-dwelling rotifers, and nematodes (Schmid-Araya & Schmid 1995). It is tiny (200 µm long) and creeps with leech-like movements, being unable to swim (Ricci & Melone 1998). Instead, its strong foot anchors it to its substrate, a feature of importance in streams and rivers. Its corona is poorly developed and it obtains its food by browsing, facilitated by the ciliated buccal field and trophi protruding throughout the mouth. Its disjunct distribution in Europe and New Zealand may indicate a lack of collecting and lack of experts on this group.

Figure 54. ***Henoceros falcatus***, a stream moss dweller. Photo by Michel Verolet, with permission.

Figure 53. ***Philodinavus paradoxus***, a species from stream mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Within its short lifetime of only 20 days, ***Philodinavus paradoxus*** can produce 6-7 eggs (Ricci & Melone 1998). These seem to have about the same resistance to desiccation damage as adults, with only 10% of each surviving 7 days of desiccation, a desiccation intolerance that is typical of aquatic rotifer taxa.

Henoceros falcatus is commonly found in the same mosses in running waters with ***Philodinavus paradoxus*** (Diego Fontaneto, pers. comm. 2 November 2016). Ricci and Melone (1998) reported this species from mosses. They noted that ***H. falcatus*** was first found in mosses submerged in streams in South Africa (Milne 1916). Later ***H. falcatus*** was found in similar habitats in Europe, South America, Asia, and Hawaii (Schmid-Araya 1995; Turner 1996). The two species co-occur in Austria (Schmid-Araya 1995) and in Valle Argentina, Italy. It seems to be common for these two species to co-occur, suggesting similar ecological requirements. In fact, rather than being rare (Schmid-Araya 1995; Ricci & Melone 1998), Fontaneto *et al*. (2007) consider them to be fairly common in their specialized habitat of stream mosses.

Philodinidae

The philodinids use their cilia or foot and rostrum (Figure 55) to facilitate swimming (Hickernell 1917). At high temperatures these rotifers engage in active swimming, but in cold water they creep like a leech with the cilia retracted. During feeding, they attach themselves by the foot and use the cilia to direct food to the pharynx. When drying occurs, the animal forms a ball and dries up. The ball is formed by retracting both the head and the foot into the trunk of the rotifer and losing all the water, pulling the organs together and eliminating spaces. When they get water again, they resume their normal shape in ten minutes or less.

Ceratotrocha and *Didymodactylos*

This family has many bryophyte-dwelling species. ***Ceratotrocha cornigera*** is the only member of its genus documented from bryophytes, including bogs (Horkan 1981; Hingley 1993). ***Didymodactylos carnosus*** (Figure 55) likewise is known from mosses (Ricci & Melone 2000; Plewka 2016).

Figure 55. ***Didymodactylos carnosus***, common in moss. Note the two rings of cilia. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Dissotrocha

Dissotrocha has several known bryophyte-dwelling species. ***Dissotrocha aculeata*** (Figure 56), ***D. macrostyla*** (Figure 57), and ***D. spinosa*** occur on or among ***Sphagnum*** (Figure 6) (Horkan 1981; Hingley 1993; Bielańska-Grajner

et al. 2011; Plewka 2016). ***Dissotrocha scutellata*** (Figure 58-Figure 59) is known from the moss ***Andreaea rupestris*** (Figure 60-Figure 61), a rock dweller that dries out frequently (Plewka 2016).

Figure 56. ***Dissotrocha aculeata***, a species known from ***Sphagnum*** and **other mosses**. Photo by Jersabek *et al.* 2003, with permission.

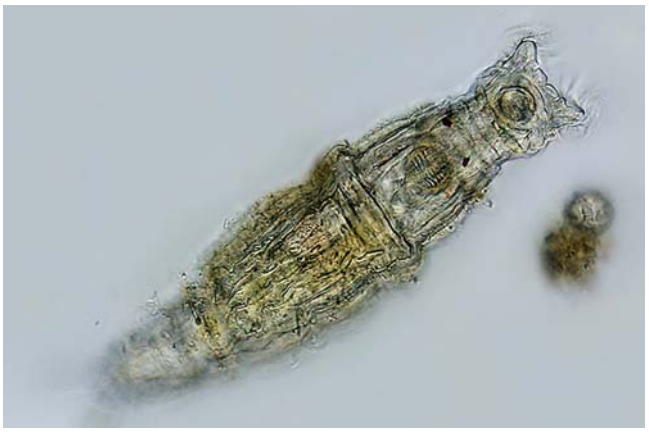

Figure 57. ***Dissotrocha macrostyla*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 58. ***Dissotrocha scutellata***, a dweller on ***Andreaea rupestris***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 59. ***Dissotrocha scutellata***, a species that lives on the exposed rock-dwelling moss ***Andreaea rupestris***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 60. ***Andreaea rupestris***, home for ***Dissotrocha scutellata***. Photo by Michael Lüth, with permission.

Figure 61. ***Andreaea rupestris***, home for ***Dissotrocha scutellata***. Photo by Michael Lüth, with permission.

Macrotrachela

A number of species of the large genus ***Macrotrachela*** occur on mosses. Some of these are from ***Sphagnum*** (Figure 6), including ***Macrotrachela concinna*** (Myers 1942; Hingley 1993), ***M. crucicornis*** (Myers 1942), ***M. decora*** (Figure 62) (Plewka 2016), and ***M. papillosa*** (Figure 63) (Horkan 1981; Hingley 1993).

Figure 62. ***Macrotrachela cf. decora*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 63. ***Macrotrachela papillosa***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Other species occur in contrasting habitats of both ***Sphagnum*** (Figure 6) and mosses growing on trees. These include ***M. multispinosa*** (Figure 64-Figure 65; Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003), ***M. nana*** in stream environs (Figure 67; Madaliński 1961; Bielańska-Grajner *et al*. 2011; Plewka 2016), ***M. plicata*** (Figure 66; Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016), and ***M. quadricornifera*** (Figure 68; Myers 1942; Horkan 1981; Hingley 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016).

Figure 64. ***Macrotrachela multispinosa brevispinosa***, a species that occurs on submerged mosses and mosses on limestone and trees. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 65. ***Macrotrachela multispinosa*** from among epiphytic mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 66. ***Macrotrachela plicata*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 67. ***Macrotrachela nana*** from ***Sphagnum***, tree moss, and other mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 68. ***Macrotrachela quadricornifera***, a species from ***Sphagnum*** and epiphytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Others are known only as epiphytes, including ***M. aculeata*** (Figure 69; Plewka 2016), ***M. magna*** (Figure 70; Plewka 2016), and ***M. tuberilabris*** (Figure 71; Plewka 2016).

Figure 69. ***Macrotrachela aculeata*** from mosses on trees. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 70. ***Macrotrachela magna*** from epiphytic moss, showing its extended position. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 71. ***Macrotrachela tuberilabris*** from moss on tree. Michael Plewka <www.plingfactory.de>, with permission.

Additional members of the genus occurred on various mossy substrates, including ***Macrotrachela ehrenbergii*** (Figure 72) on ***Sphagnum*** (Figure 6), mosses on walls, and epiphytes (Peters *et al.* 1993; Jersabek *et al.* 2003; Plewka 2016), ***M. habita*** (Figure 74) on ***Sphagnum***, moss on trees, rocks, and ground (Myers 1942; Horkan 1981; Hirschfelder *et al*. 1993; Jersabek *et al.* 2003; Plewka 2016), ***M. insolita*** (Figure 75) on mosses submerged in pond (Hirschfelder *et al*. 1993; Plewka 2016) and in peatlands (Bielańska-Grajner *et al*. 2011), ***M. musculosa*** (Figure 76) on ***Sphagnum***, ground mosses, and epiphytic mosses (Myers 1942; Hirschfelder *et al*. 1993; Plewka 2016), ***M. punctata*** (Figure 77-Figure 78) on dry mosses on rocks (Hirschfelder *et al.* 1993; Plewka 2016); ***M. zickendrahti*** (Figure 79) on ***Sphagnum*** and other mosses (Jersabek *et al.* 2003; Plewka 2016). For ***M. muricata***, I have found little information except it occurs on mosses (Horkan 1981).

Figure 72. ***Macrotrachela ehrenbergii***, a species that lives among mosses on walls and trees as well as on ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 75. ***Macrotrachela insolita***, s species that lives in ponds with submerged moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

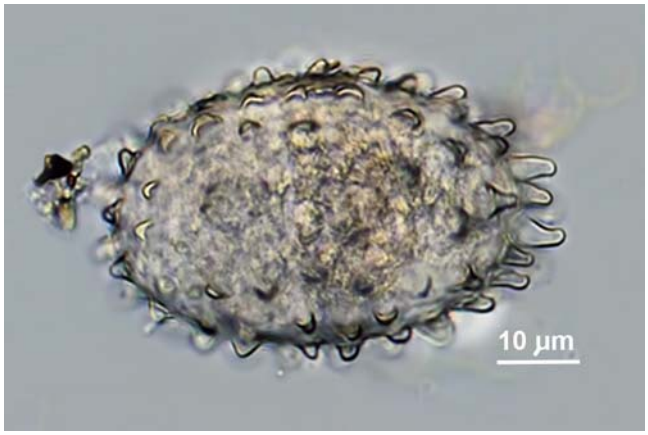

Figure 73. ***Macrotrachela ehrenbergii*** egg. The projections may help to preserve it during drought. Photo by Michael Plewka <www.plingfactory.de>, with permission.

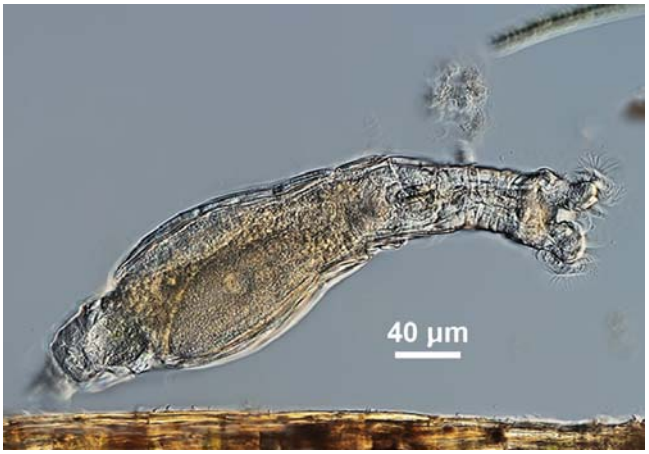

Figure 76. ***Macrotrachela musculosa***, a species from mosses on ground and trees. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 74. ***Macrotrachela habita***, a species from moss on trees, rocks, and ground. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 77. ***Macrotrachela punctata***, a species from dry moss on rocks. Here it is contracted with cilia out. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 78. ***Macrotrachela punctata***, a species of dry moss on rocks. Here it is extended with cilia contracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 79. ***Macrotrachela zickendrahti***, a species from moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

The absence of records for moss dwellers may be common. For example, Ricci (1980) found ***Macrotrachela plicatula*** (Figure 80) among mosses in Uganda. This was the first time it had been found since its 1911 description as a new species.

Figure 80. ***Macrotrachela plicatula*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Mniobia

Mniobia likewise has its ***Sphagnum*** (Figure 6) dwellers, including those found by Hingley (1993): ***M. incrassata*** (Figure 81-Figure 82), ***M. magna*** (Figure 84), ***M. obtusicornis*** (Figure 85), ***M. symbiotica*** (see also Hudson 1889; Horkan 1981). Among these, ***M. incrassata*** is known from other mosses as well (Plewka 2016). ***Mniobia scarlatina*** (Figure 83; Jersabek *et al*. 2003) and ***M. tetraodon*** (Myers 1942; Horkan 1981) occur on epiphytic mosses. ***Mniobia symbiotica*** also occurs in the lobules of the leafy liverwort ***Frullania eboracensis*** (Figure 86-Figure 88), an epiphyte in eastern USA (Biechele 2014).

Figure 81. ***Mniobia incrassata*** from moss, showing exterior of lorica. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 82. ***Mniobia incrassata*** from moss, showing rotifer inside lorica. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 83. ***Mniobia scarlatina*** from among epiphytic mosses. Photo by Jersabek *et al*. 2003, with permission.

Figure 84. ***Mniobia magna***, a moss inhabitant, including epiphytes, with its body shortened and cilia out. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 85. ***Mniobia cf. obtusicornis***, a ***Sphagnum*** dweller. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 86. ***Frullania eboracensis*** on bark – home for ***Mniobia symbiotica***. Photo by Janice Glime

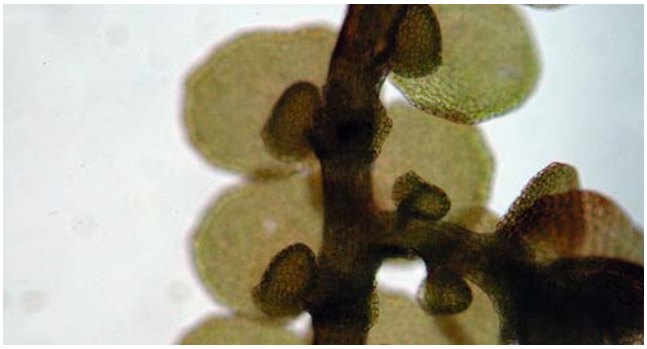

Figure 87. ***Frullania eboracensis*** showing lobules that serve as home for ***Mniobia symbiotica***. Photo by Bob Klips, with permission.

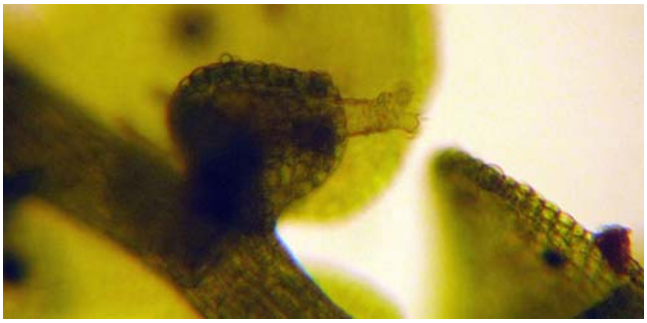

Figure 88. ***Frullania eboracensis*** from Ohio, USA, with a rotifer in a lobule – possibly ***Mniobia symbiotica***. Photo by Bob Klips, with permission.

Mniobia orta (Peters *et al*. 1993) and ***M. russeola*** (Horkan 1981; Hirschfelder *et al*. 1993) are also bryophyte dwellers.

Pleuretra

The genus ***Pleuretra*** seems to prefer habitats that dry out. ***Pleuretra humerosa*** (Figure 89-Figure 90) occurs on dry mosses on granite (Plewka 2016). ***Pleuretra lineata*** (Figure 91-Figure 93) occurs on the mosses ***Andreaea rupestris*** (Figure 60-Figure 61) and ***Grimmia pulvinata*** (Figure 94) (Hirschfelder *et al*. 1993; Plewka 2016), both species of exposed rocks. ***Pleuretra brycei*** (Figure 95-Figure 96) is also a bryophyte dweller, but among ***Sphagnum*** (Figure 6-Figure 7) and demonstrates the spines that help to protect it among the bryophytes (Madaliński 1961).

Figure 89. ***Pleuretra humerosa***, a species of dry mosses on granite. It is shown here in its extended position that is used during its inchworm movement. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 90. ***Pleuretra humerosa***, a species of dry moss on granite, shown here in its contracted shape with cilia out. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 91. ***Pleuretra lineata***, a species that lives on ***Andreaea rupestris*** and ***Grimmia pulvinata***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 92. ***Pleuretra lineata***, a species that lives on the mosses ***Andreaea rupestris*** and ***Grimmia pulvinata***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

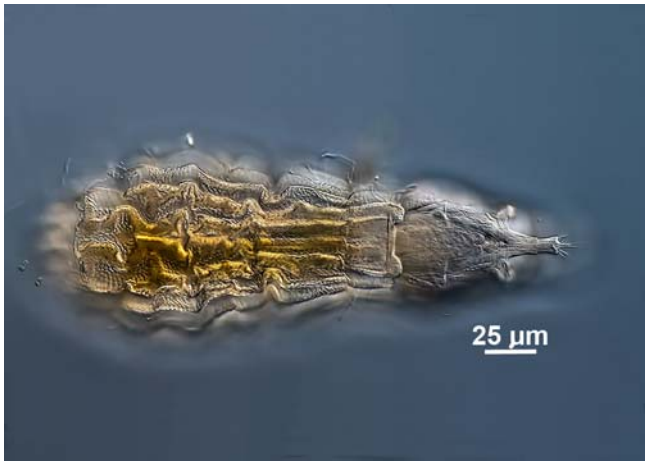

Figure 93. ***Pleuretra lineata***, inhabitant of ***Andreaea rupestris*** and ***Grimmia pulvinata***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 94. ***Grimmia pulvinata***, home of ***Pleuretra lineata***. Photo by Michael Lüth, with permission.

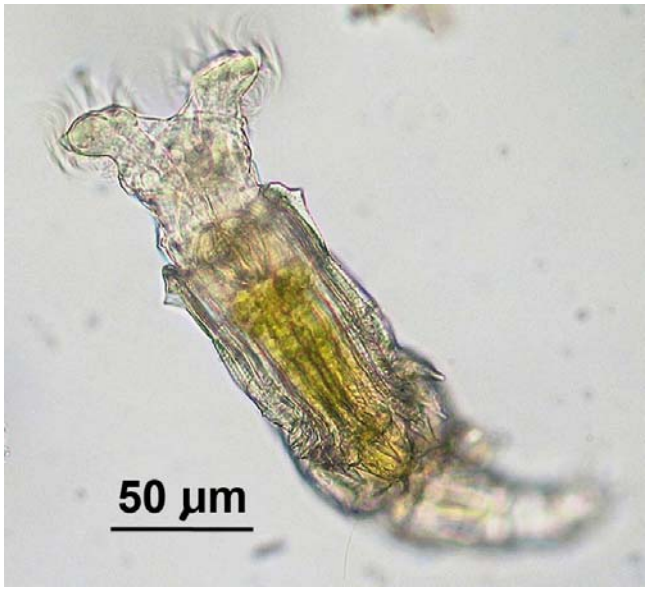

Figure 95. ***Pleuretra cf brycei***, a bryophyte dweller. Photo by Michel Verolet, with permission.

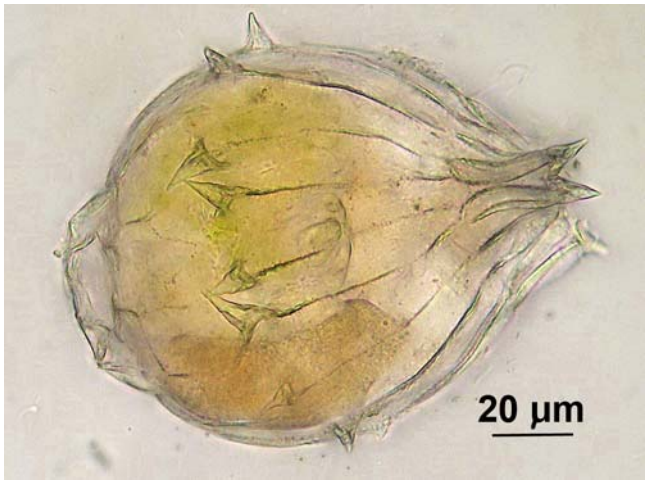

Figure 96. ***Pleuretra*** *cf* ***brycei*** tun, demonstrating the spines that help to protect it. Photo by Michel Verolet, with permission.

Philodina

Philodina acuticornis (Figure 97), ***P. nemoralis*** (Figure 98), and ***P. brevipes*** live on ***Sphagnum*** (Figure 6) (Hingley 1993). ***Philodina citrina*** (Figure 99-Figure 100), ***P. plena*** (Figure 101), ***P. proterva***, and ***P. vorax*** (Figure 102) all occur on ***Sphagnum*** (Figure 6) (Hirschfelder *et al*. 1993; Jersabek *et al*. 2003; Bielańska-Grajner *et al*. 2011; Plewka 2016). But ***P. plena*** also occurs on epiphytes (Myers 1942) and ***P. citrina*** and ***P. vorax*** live on epiphytic mosses and mosses on rock or concrete. ***Philodina nemoralis*** (Figure 103; Plewka 2016) and ***P. rugosa*** (Figure 105; Horkan 1981; Hingley 1993; Fontaneto *et al*. 2007; Plewka 2016) live in contrasting submersed and dry habitats, including on epiphytic mosses. Other rotifers on epiphytic mosses include ***Philodina childi*** (Figure 104; Horkan 1981; Hingley 1993; Plewka 2016). Other members of the genus that are associated with bryophytes include ***P. erythrophthalma***, ***P. flaviceps*** (Figure 106), and ***P. roseola*** (Figure 107-Figure 111) (Horkan 1981; Hirschfelder *et al*. 1993; Madaliński 1961; Plewka 2016).

Figure 97. ***Philodina acuticornis***, a species that likes green algae among ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 98. ***Philodina nemoralis***, a species of submersed, dry, and epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 99. ***Philodina citrina*** from ***Sphagnum*** bogs and mosses on stones. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 100. ***Philodina citrina***, a species known from ***Sphagnum*** bogs and epiphytic mosses. Photo by Jersabek *et al.* 2003.

Figure 101. ***Philodina plena*** occurs on ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 102. ***Philodina vorax***, a species that occurs on ***Sphagnum***, epiphytic mosses, and mosses on concrete. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 103. ***Philodina nemoralis***, a species that occurs on submersed, dry, and epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 104. ***Philodina childi*** occurs on epiphytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 105. ***Philodina rugosa***, a species that lives on epiphytic mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 106. ***Philodina flaviceps***, a species that occurs on moss. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 107. ***Philodina roseola***, a species that can be found on bryophytes. Photo by Michael Plewka <www.plingfactory.de>, with permission.

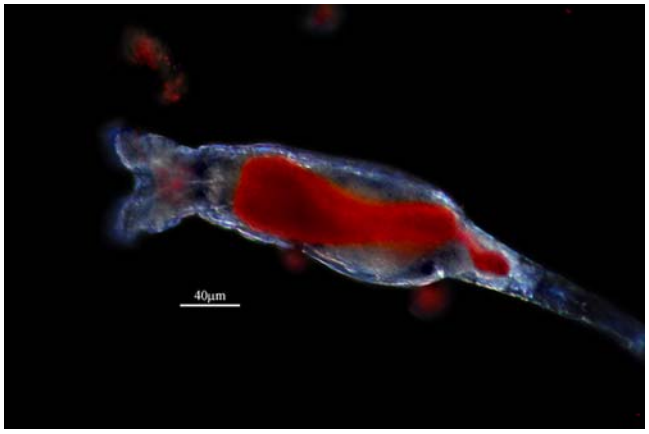

Figure 108. ***Philodina roseola***, a species that can be found on bryophytes. Photo from Proyecto Agua, with permission.

Figure 109. ***Philodina roseola*** with eggs, a species known to inhabit **bryophytes**. Photo by Jersabek *et al*. 2003, with permission.

Rotaria

Rotaria (Figure 110) is a genus that moves like a leech, permitting it to move among bryophytes. The genus ***Rotaria*** is able to move among mosses and other substrata by creeping with its head and foot (van Egmond 1999). The foot is sticky, enabling it to attach to a surface while it feeds (Dickson & Mercer 1966; Schmid-Araya 1998). The anterior cilia (Figure 111) make a current that directs the food toward the pharynx for ingestion.

Figure 110. ***Rotaria***, fully extended as it would be for its leech-like movement. This is a genus with several bryophyte-dwelling species that can move about the bryophytes in this manner. Photo by Wim van Egmond, with permission.

Figure 111. ***Rotaria***, showing the two wheels that direct the food into the gullet. Photo by Yuuji Tsukii, with permission.

Several species of ***Rotaria*** live in association with ***Sphagnum*** (Figure 6). These include ***R. citrina*** (Figure 112-Figure 113), ***R. haptica***, ***R. macroceros*** (Figure 114), ***R. macrura*** (Figure 115-Figure 116; see also Horkan 1981; Bielańska-Grajner *et al*. 2011), ***R. magnacalcarata***, ***R. neptunia*** (Figure 117-Figure 118), ***R. neptunoida*** (Figure 119), ***R. quadrioculata***, ***R. socialis*** (Figure 120), ***R. spicata***, and ***R. tardigrada*** (Figure 121; see also Bielańska-Grajner *et al*. 2011) (Hingley 1993; Plewka 2016). In addition to the ***Sphagnum*** dwellers, ***R. rotatoria*** (Figure 122) and ***R. macrura*** live on mosses (Madaliński 1961; Horkan 1981; Plewka 2016) as well as living in peatlands (Bielańska-Grajner *et al*. 2011). ***Rotaria sordida*** (Figure 123) is unusual in living not only on mosses on limestone, but also in living on the thallose liverwort ***Marchantia polymorpha*** (Figure 124; Horkan 1981; Hirschfelder *et al*. 1993; Plewka 2016) and in peatlands (Bielańska-Grajner *et al*. 2011).

Figure 112. ***Rotaria citrina*** from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 113. ***Rotaria citrina*** with 2 daughters (see the two mastax), from ***Sphagnum***. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 114. ***Rotaria macroceros***, known from **bog pools**. Note the long antenna in the middle of the head. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 115. ***Rotaria macrura***, a ***Sphagnum*** associate. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 116. ***Rotaria macrura*** from among ***Sphagnum*** and other mosses, showing fully extended foot. Photo by Jersabek *et al*. 2003, with permission.

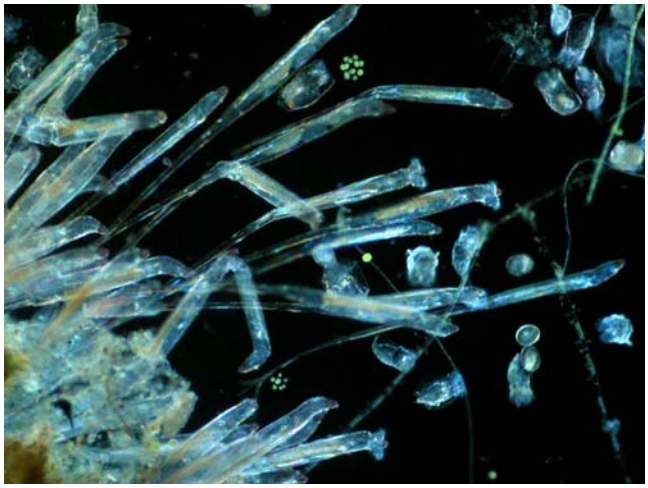

Figure 117. ***Rotaria neptunia*** colony. Photo by Michael Plewka <www.plingfactory.de>, with pernission.

Figure 118. ***Rotaria neptunia*** anterior. Photo by Michael Plewka <www.plingfactory.de>, with pernission.

Figure 119. ***Rotaria neptunoida***, a ***Sphagnum*** dweller, extended while creeping. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 120. ***Rotaria socialis***, an inhabitant of ***Sphagnum*** and other mosses. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 121. ***Rotaria tardigrada*** creeping, with its corona retracted. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 122. ***Rotaria rotatoria***, a species known from bryophytes in more than one location. Photo by Jersabek *et al.* 2003, with permission.

Figure 123. ***Rotaria sordida sordida***, a species that lives on the thallose liverwort ***Marchantia polymorpha*** and moss on limestone. Photo by Michael Plewka <www.plingfactory.de>, with permission.

Figure 124. ***Marchantia polymorpha***, home for ***Rotifera sordida***. Photo by David T. Holyoak, with permission.

Desiccation Tolerance

Ricci (1998) compared the desiccation survival percentage of rotifers in the **Philodinidae** from water vs those from terrestrial mosses. The rotifers from terrestrial mosses survived seven days of desiccation better than did those from the water (Figure 125). The 2-day-old rotifers (juveniles) had poor resistance to desiccation. ***Rotaria rotatoria***, *R. neptunia*, and ***Otostephanos macrantennus***, all from bodies of water that do not dry out, did not recover from desiccation at any life stage. On the other hand, ***Philodina acuticornis*** and ***R. neptunoida*** likewise live in permanent bodies of water (including among mosses) and do withstand desiccation. Ricci also summarized indications of desiccation tolerance of **Bdelloidea** reported in the literature and from her own studies (Table 1).

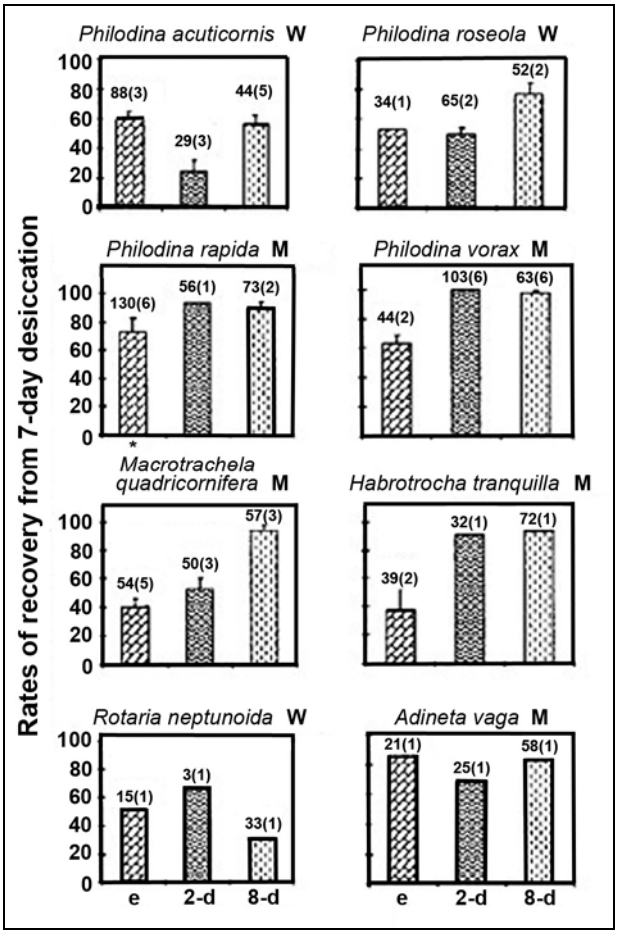

Figure 125. Recovery rates of rotifers collected from terrestrial mosses (**M**) and from water bodies (**W**). Life stages are **e** = newly laid eggs or embryos; **2-d** = 2-day-old juveniles; **8-d** = 8-day-old adults. Numbers above bars = sample size; (number) = number of replicates. Bars represent mean recovery rates among replicates; vertical lines = standard error. *Percentage viability adjusted to control. Redrawn from Ricci (1998).

Table 1. Genera of **Bdelloidea** that inhabit mosses compared to those from water, among genera for which desiccation tolerance is known. Adapted from Ricci (1998). Habitats are based on Donner (1965).

Adinetidae			
Adineta	moss, water	+	Dobers 1915; Örstan 1995
Bradyscela	moss	(+)	Donner 1976
Habrotrochidae			
Habrotrocha	mainly moss & soil	+	Schramm & Becker 1987
Otostephanos	moss, *Sphagnum*	(+)	Murray 1911
Scepanotrocha	moss, soil	(+)	Donner 1976
Philodinavidae			
Abrochtha	water	+	Ricci 1998
Henoceros	water	+	Ricci 1998
Philodinavus	water	+	Ricci 1998
Philodinidae			
Didymodactylos	moss	(+)	Donner 1976
Macrotrachela	moss, water	+	Dobers 1915; Ricci *et al.*1987
Mniobia	moss, soil	+	Dobers 1915
Pleuretra	moss	(+)	Murray 1911
Philodina	moss, water	+	Jacobs 1909; Ricci 1998
Rotaria	mainly water, soil	+	Ricci 1998

Summary

The rotifers in **Bdelloidea** are the most frequently represented rotifers on bryophytes.The bryophyte dwellers are usually not also planktonic and typically attach to the bryophytes by their toes. They move like an inchworm or use their cilia. They obtain their food from the microscopic organisms and detritus among the mosses. Only females exist and the eggs can typically survive desiccation. Mucus helps these rotifers to survive desiccating conditions.

Bryophyte-dwelling **Bdelloidea** include four families known from bryophytes: **Adinetidae**, **Habrotrochidae**, **Philodinavidae**, **Philodinidae**. The **Adinetidae** are known from bogs and other bryophytes. The **Habrotrochidae** have a number of species from bogs and from other bryophytes. Many of the species live in such small niches as ***Sphagnum*** retort cells and liverwort lobules. The **Philodinavidae** has two moss dwelling species that often occur together in streams. The **Philodinidae** creep in cold water and live attached on plants; a number of species occur on bryophytes. The **Philodinidae** terrestrial moss dwellers tested have greater desiccation tolerance than do the aquatic species. Adults are more desiccation tolerant than juveniles.

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