

CHAPTER 5-3

TARDIGRADE HABITATS

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CHAPTER 5-3

TARDIGRADE HABITATS



Figure 1. *Echiniscus* sp., member of a genus that is common on bryophytes. Photo by Martin Mach, with permission.

Bryophyte Habitats

Tardigrades exist in both aquatic and terrestrial habitats worldwide, and in both cases can be found with bryophytes (Figure 1) (and lichens and leaf litter) (Utsugi *et al.* 1997). The tropics seem unfavorable (Mathews 1938), perhaps for the same reasons that temperate stream bryophytes are uncommon in lowland tropical waters – they are warm and wet at the same time, encouraging bacterial and fungal growth.

Most of the more than 900 known tardigrade species are **limnoterrestrial** (Garey *et al.* 2008). That is, they live in a thin surface film of water, most commonly on bryophytes, lichens, algae, and other plants. They can only remain active while this film of water exists. Of the 910 species reviewed by Garey *et al.* (2008), only 62 species, in 13 genera, are truly aquatic and unknown from limnoterrestrial habitats. Nevertheless, many of the limnoterrestrial species can at least occasionally be found in freshwater. In these terrestrial habitats, pH of the substrate, oxygen tension, moisture content of the bryophyte, thickness of the bryophyte mat or cushion, and altitude (and its attendant conditions) all contribute to the habitat distribution.

I have taken the liberty of changing the word "moss," used in many tardigrade studies, to "bryophyte." I have

learned from one of my kind tardigrade reviewers that people who study tardigrades often do not understand leafy liverworts and lump them into mosses. Hence, unless I could determine that the researcher definitely had in mind only mosses (and not also liverworts), I used the term bryophytes. I also learned that many ecologists include mosses in the category of "soil"! Others include them in "litter." While this lumping can be a useful concept for some aspects of functional ecology, one needs to be aware of it when searching for bryological literature or interpreting soil literature.

Tardigrades are especially common on tree bark bryophytes (**epiphytes**), presumably due to having similar tolerances to drying (Crum 1976). They are known from all seven continents and up to 6600 m altitude in the Himalayas (Ehrenberg 1859 in Fontoura *et al.* 2009). Collins and Bateman (2001) examined factors affecting tardigrade distribution in Newfoundland and learned that in this case altitude and type of bedrock were important in determining tardigrade distribution. Moisture and rate of drying further defined their distribution. And in some cases, competitive exclusion or interspecific competition seemed to be determining factors for community composition.

Specificity

Species assemblages seem to be similar throughout the world. Is this due to lack of taxonomic understanding or to widespread dispersal? In the following sections we will examine what we know about factors affecting tardigrade communities under different circumstances.

It appears that many tardigrades have little preference for bryophytes versus lichens (Meyer & Hinton 2007). But even those cryptogams, supporting their wet-dry requirements, are usually not unique habitats for the tardigrades, with the same species of bryophytes and lichens also present in soil, leaf litter, and additional habitats. Several studies have attempted to show any species preferences for bryophytes, but typically with no success (Kathman & Cross 1991; Miller & Heatwole 1995; Meyer & Hinton 2007). Further evidence of non-specificity is in their distribution. Meyer and Hinton (2007) report that the Nearctic realm shares 82 species of tardigrade with the Neotropical realm. Everything is everywhere! On the other hand, 30% of the Nearctic species are known from only one site. One of the problems in describing the tardigrade habitat is that substrate records are inconsistent or absent for many collections.

But some studies have indicated that lichens and mosses may be preferred over other substrata. Working in China, Beasley *et al.* (2006) found 18 species of tardigrades from three provinces, primarily in lichens and bryophytes.

One of the most common tardigrades among bryophytes is *Milnesium tardigradum* (Figure 21) and the less common *Macrobiotus hibiscus*. Hinton and Meyer (2008) reported these among liverworts (*Jungermannia* sp.; Figure 2) in a suburban lawn in central Georgia (USA).



Figure 2. *Jungermannia atrovirens*, member of a genus where tardigrades have been found in a lawn in Georgia, USA. Photo by Michael Lüth, with permission.

Liverworts are rarely mentioned in tardigrade studies. However, Hinton and Meyer (2007) reported *Echiniscus virginicus* and *Milnesium tardigradum* from liverworts. In their study, they collected handfuls of mosses, liverworts, and lichens from 54 parishes in Louisiana, USA. They found 51 species in the region: 19 in Texas, 16 in Louisiana, 10 in Mississippi, 33 in Alabama, 3 in Georgia, and 15 in Florida. Of these 51 cryptogam dwellers, 20 are widely distributed in the region and 18 are

apparently cosmopolitan. Hinton and Meyer suggested that *Biserovus bindae*, *Echiniscus cavagnaroi*, *Echiniscus kofordi*, *Hexapodibius christenberryae*, *Minibiotus fallax*, and *Parhexapodibius pilatoii*, along with a new variant of *Macrobiotus* cf. *hufelandi*, may represent a distinctive southeastern USA regional fauna living among cryptogams. On the other hand, *Echiniscus cavagnaroi* and *Echiniscus kofordi* are known only in the Neotropical Region and in the Galapagos Islands, but *Minibiotus fallax* was described in Australia. These three species are frequently encountered in mosses and lichens.

Habitat Differences

Several tardigrade researchers have considered five types of bryophyte habitats (Mihelčić 1954/55, 1963; Ramazzotti 1962; Hofmann 1987):

- bryophytes that are submerged
- bryophytes that are permanently moist
- bryophytes growing in shady places and rarely dry
- bryophytes that dry out frequently and receive direct sunlight regularly
- bryophytes that are extremely exposed and often dry for a longer period.

Ito (1999) was able to identify six groupings of tardigrades, based on habitat preference, in his altitudinal study on Mt. Fuji, Japan. Kaczmarek *et al.* (2011) likewise found altitudinal relationships in Costa Rica. They furthermore found a higher diversity among mosses than among lichens or liverworts, although they admitted to a possible bias due to unequal sampling. Tardigrades from these substrates were most common from 2000 to 2400 m asl and above 3200 m asl.

Tardigrades do not have much control over their dispersal, typically depending on dispersal of the substrate. This may help to explain the observations on two morphotypes of the moss *Grimmia*. In this case, the tardigrade distribution was very patchy. There were no differences in distribution patterns on the two *Grimmia* morphotypes, despite their representation of different moisture conditions (Bettis 2008). Bettis suggested that the greater rainfall during the winter of observation might account for the lack of difference. But tardigrades are well known for their great tolerance of extremes, so their greatest limitation may be dispersal.

Acid or Alkaline?

Bartels (2005) reported greater diversity in limestone habitats than elsewhere. It appears that acid can be an uncomfortable or lethal milieu. *Hypsibius dujardini* (Figure 13) had reduced activity after only five minutes at pH 3 and died at pH 2.8. Even at pH 4.0, it had reduced activity after 30 hours.

But in Giessen, Germany, Hofmann (1987) found a somewhat different relationship. The four most abundant species [*Macrobiotus hufelandi* (Figure 7), *Ramazzottius* (formerly in *Hypsibius*) *oberhaeuseri* (Figure 3), *Milnesium tardigradum* (Figure 21), and *Echiniscus testudo* (Figure 4)] had similar preferences for alkaline substrata, but the remaining species, as a group, had a preference for the acidic habitats, thus presenting greater tardigrade species diversity among the acid substrata and the mosses that inhabited them.



Figure 3. *Ramazzottius oberhaeuseri*, a bryophyte dweller that cannot tolerate constant moisture. Photo by Martin Mach, with permission.

Hingley (1993) found only two genera in her acid peatland studies: *Diphyscon* (*D. scoticum*) (Figure 29) and *Macrobiotus* (Figure 6). To that Pilato (2009) added *Bindius triquetrus* from *Sphagnum* (Figure 5) in Sicily. Distribution is patchy (Romano *et al.* 2001), requiring greater sampling effort. One must wonder, is the paucity of reports of aquatic tardigrades on bryophytes a realistic representation of a meager aquatic fauna, or are there simply too few studies that have looked for them?

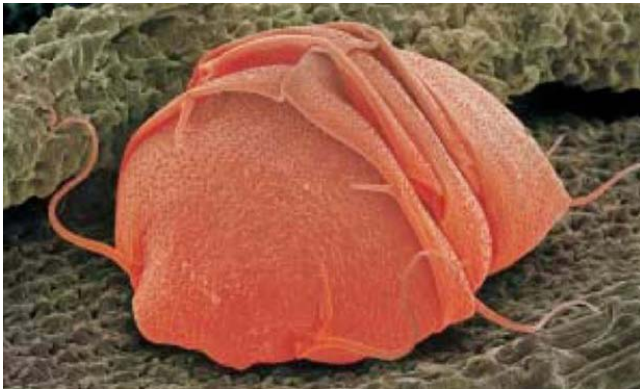


Figure 4. *Echiniscus testudo* tun on a bryophyte leaf. Photo by Power & Syred, through Creative Commons.



Figure 5. *Sphagnum fuscum*, a species that forms hummocks where a tardigrade could find moisture but usually avoid being flooded. Photo by Michael Lüth, with permission.

Altitude

Many researchers have shown a relationship between altitude and the distribution of tardigrades (Rodríguez-Roda 1951; Nelson 1973, 1975; Ramazzotti & Maucci 1983; Dastyh 1985, 1987, 1988; Beasley 1988), suggesting that species richness increases with altitude. Bertolani and Rebecchi (1996) found that some species were typical of high altitudes or latitudes. Some researchers have even classified the tardigrades based on

altitudinal groupings (lowland, upland, montane, etc.) (Ramazzotti & Maucci 1983; Dastyh 1987, 1988). Collins and Bateman (2001) found that in Newfoundland, Canada, the lowland class could be further divided into locations up to 100 m and those above (101-200 m).

Table 1 compares the altitudinal abundance of 45 species of tardigrades associated with bryophytes on mountains in British Columbia, Canada (~48-60°N), with those of **riparian** epiphytes (inhabiting trees on banks of natural water courses) in Alabama, USA (~33°N). Although the latitudes are quite different, six species are common to both, but six species differ. The three most abundant Alabama species were common to both, but the very common *Macrobiotus hufelandi* (Figure 7) was absent in the Alabama collections. These data suggest that there may be more than just chance determining the species and abundance differences.

But not all altitudinal studies have supported these conclusions (*e.g.* Kathman & Cross 1991). It is interesting that Meininger and Spatt (1988) found that altitude was not influential in determining distribution and abundance of moss-dwelling tardigrades in Alaska, USA. Likewise, Guil *et al.* (2009) found that the altitudinal differences could be explained by differences in soil, climate, vegetation structure, and litter type. Nevertheless, Ramazzotti and Maucci (1983) considered certain species to occur only above 500 m. This may simply be a lack of sufficient collecting – they claimed that *Macrobiotus harmsworthi* (Figure 6) was one of these "montane" species, but Dastyh (1985) later reported it from locations between 0 and 1100 m altitude on Spitsbergen Island, Norway. Furthermore, Dastyh (1980, 1988), showed a large correlation between Tardigrada species and altitude in the Tatra Mountains in Poland. Certainly latitude must be considered in making comparisons of altitude. And local moisture regimes are likely to play a major role in altitudinal relationships.

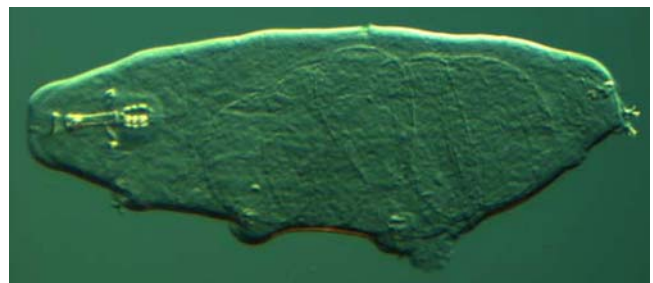


Figure 6. *Macrobiotus harmsworthi*, a common tardigrade on bryophytes and elsewhere. Photo by Paul J. Bartel, with permissions.

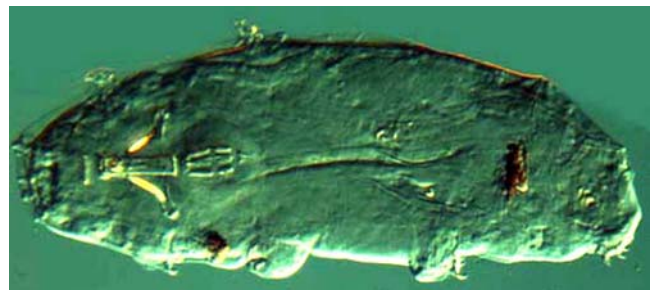


Figure 7. *Macrobiotus hufelandi*, one of the most abundant tardigrades on bryophytes. Photo by Paul J. Bartels, with permission.

Table 1. Altitudinal distribution of numbers of tardigrades in eleven bryophyte samples each, from six altitudes on five mountains on Vancouver Island, British Columbia, Canada, from Kathman & Cross 1991, and from 108 riparian epiphytic bryophyte samples representing 6 sites at Choccolocco Creek, Alabama, USA, from Romano *et al.* 2001. Those highlighted in grey occur in both sites.

	Altitude (m)						riparian
	150	450	750	1050	1350	>1525	
<i>Astatumen trinacriae</i>							3
<i>Bertolanius</i> [=Amphibolus] <i>weglarskae</i>	0	0	0	0	0	2	
<i>Calohypsibius ornatus</i>	0	3	10	4	2	3	
<i>Diphascon</i> [=Hypsibius] <i>scoticum</i>	22	18	11	13	30	16	
<i>Diphascon belgicae</i>	1	0	0	6	2	1	
<i>Diphascon iltisi</i>	0	1	0	0	0	0	
<i>Diphascon modestum</i>	12	0	1	4	0	0	
<i>Diphascon nodulosum</i>	14	4	1	16	17	26	
<i>Diphascon pingue</i> sl	70	318	45	7	40	27	
<i>Diphascon prorsirostre</i>	4	38	16	3	8	5	
<i>Diphascon recameri</i>	49	47	2	3	13	1	
<i>Echiniscus</i> cf. <i>arctomys</i>							28
<i>Echiniscus horningi</i>	2	1	1	3	3	5	
<i>Echiniscus mauccii</i>	6	3	0	3	1	7	16
<i>Echiniscus quadrispinosus</i>	0	0	2	14	4	1	
<i>Echiniscus</i> sp. n.							24
<i>Echiniscus wendti</i>	2	3	3	0	38	3	
<i>Hypechiniscus gladiator</i>	0	0	0	0	0	0	
<i>Hypsibius convergens</i>	199	203	188	78	54	26	
<i>Hypsibius dujardini</i>							1
<i>Insuetifurca arrowsmithi</i>	0	0	40	0	1	0	
<i>Isohypsibius lunulatus</i>	6	9	0	0	0	0	
<i>Isohypsibius sattleri</i>	96	49	28	4	8	0	
<i>Isohypsibius woodsae</i>	0	0	0	2	0	0	
<i>Itaquascon pawlowskii</i>	1	0	0	2	0	1	
<i>Macrobiotus crenulatus</i>	1	0	0	0	0	0	
<i>Macrobiotus echinogenitus</i> (Figure 8)	0	0	10	79	48	0	737
<i>Macrobiotus harmsworthi</i>	177	459	284	44	8	10	
<i>Macrobiotus hufelandi</i>	3039	1710	2061	1116	1586	662	
<i>Macrobiotus islandicus</i>							1
<i>Macrobiotus lazzaroi</i>	10	0	0	0	0	0	
<i>Macrobiotus</i> sp. A	1	0	0	0	0	0	
<i>Mesocrista spitzbergensis</i>	5	1	0	2	2	0	
<i>Milnesium tardigradum</i>	21	24	2	0	2	4	87
<i>Minibiotus</i> cf. <i>intermedius</i>							27
<i>Minibiotus intermedius</i>	2	1	12	3	0	0	
<i>Murrayon hibernicus</i>	0	0	0	14	1	0	
<i>Paramacrobiotus</i> [=Macrobiotus] <i>areolatus</i>	31	16	0	0	0	0	476
<i>Paramacrobiotus</i> [=Macrobiotus] <i>richtersi</i>	0	0	0	0	0	1	4
<i>Platicrista cheleusis</i>	8	1	2	13	10	13	
<i>Pseudechiniscus goedeni</i>	0	5	0	0	0	2	
<i>Pseudechiniscus juanita</i>	0	0	3	0	0	0	44
<i>Ramazottius baumanni</i>	18	44	8	7	5	3	
<i>Ramazottius oberhaeuseri</i>	11	2	0	1	1	0	
<i>Testechiniscus laterculus</i>	0	0	0	0	39	0	
SUM OF INDIVIDUALS	3808	2960	2730	1421	1923	819	1448
NUMBER OF SPECIES	27	23	21	24	24	22	12



Figure 8. *Macrobiotus echinogenitus*, a tardigrade living on riparian bryophytes at Choccolocco Creek Alabama, USA. Photo by Paul J. Bartels, with permission.

Using PCA analysis, Kathman and Cross (1991) also reported no relationship between altitude and abundance on Vancouver Island, British Columbia, on the western coast of Canada (Table 1 suggests a decreasing trend in number of individuals might be present). Collins and Bateman (2001) later reported that altitude was one of the major determining factors in tardigrade distribution in Newfoundland, eastern coast of Canada. Rodriguez-Roda (1951 in Kathman & Cross 1991) found that altitude had a distinct effect on the abundance of tardigrades in Spain, with numbers increasing with altitude and reaching a maximum between 1000 and 2000 m. Dastych (1980) likewise found that tardigrades in the Tatra Mountains of Poland increased with altitude, again with the maximum numbers between 1000 and 2000 m. In one of his later studies, Dastych (1985) reported a seemingly opposite effect, demonstrating that the number of species and individuals decreased with increasing altitude in West Spitsbergen, Norway. The differences between studies may be a matter of scale and the fact that only some species are affected by altitude within the study range, but moisture regimes are likely to differ as well.

Nelson (1973, 1975) found that only seven of the 21 bryophyte-dwelling species on Roan Mountain, Tennessee, USA, were affected by altitude. Bertrand (1975) found three altitudinal groups in the Aigoual Mountains of France. Beasley (1988) divided the tardigrades from 1052-3567 m in New Mexico, USA, into altitudinal ranges. Ito (1999) examined tardigrades at 17 stations on Mt. Fuji, Japan, finding little distributional pattern related to altitude (950-2380 m). Rather, the distribution related to habitat.

Collins and Bateman (2001) found that tardigrades of Newfoundland, Canada, were affected by both altitude (Table 2) and type of bedrock, but that moisture content and rate of desiccation of the mosses and lichens where they live also contributed to their distributional pattern.

Table 2. Decline in number of species with increasing altitude in Newfoundland. From Collins and Bateman 2001.

Altitude	Total number of species found at each altitude	Mean number of tardigrade species at each site
0->100 m	28	2.75
101->200 m	15	1.75
200+ m	8	1.88

Differences in techniques, lack of or differences in statistical analyses to support purported differences, and misidentification could contribute to the apparent differences in relationships among these studies, but moisture regimes most likely play a major role. In some cases, competitive exclusion appears to play a role (Collins & Bateman 2001). Nevertheless, it is likely that the effect of altitude, if it exists, depends in part on both latitude and scale.

Polar Bryophytes

Because of their relative abundance, and the predominance of mosses and lichens in the Antarctic flora,

we have learned some interesting aspects of their faunal ecology and physiology there.

As early as 1976, 23 species of tardigrades were known from Antarctica (Jennings 1976). That's not bad for that early date in a place with limited vegetation, harsh climate, and limited opportunity for collecting, not to mention the distance to be travelled for colonization. Most of these tardigrade species have worldwide distribution (Venkataraman 1998). In the short Antarctic summers, the tardigrades multiply quickly, using parthenogenesis.

Unlike most habitats elsewhere, the tardigrades in the Antarctic moss turf do exhibit a vertical zonation pattern. Schwarz *et al.* (1993) found that protozoa, rotifers, nematodes, and tardigrades dominated the moss-dominated flushes at Canada Glacier, southern Victoria Land, Antarctica. Mites were of less importance. These invertebrates occurred in the range of 5 to 10.83 mm depth in the moss clumps. Post melt samples had a greater percentage of all groups of organisms in the upper 5 mm of mosses compared to those at that depth range in the pre-melt samples, suggesting either migration or rapid reproduction once melting occurred.

Venkataraman (1998), in clumps of *Bryum argenteum* (Figure 9) from continental Antarctica, found that the tardigrades only live down to 15 cm depth in the 30 cm deep turfs. If they prefer to eat rotifers, they can only find those down to 10 cm. Their slow movement could limit the distance they can reasonably move downward and still return for food in a timely manner. Ramazzotti (1972) estimated that tardigrades could travel an average of 17.7 cm h⁻¹, seemingly enough speed to travel another 10 cm, but perhaps not in the cold and not during the daytime feeding period when downward movement would be most beneficial to avoid drying.

Temperature may play a role in the zonation of these Antarctic bryophytes. Bryophyte temperatures in the Antarctic can differ considerably from those of the air and may provide a warm refuge for activity even on cold days. Bryophytes exhibit a sharp temperature zonation on sunny days when there is no snow cover (Jennings 1979). The surface is subject to evaporative cooling in the polar winds while the moss layer immediately below that interface is quiet and often dark in color, absorbing the heat like a black body, as seen by the temperatures shown in Figure 10. Hence, in summer the moss turf has temperatures much higher than that of the air and at the beginning and end of the summer season the temperatures fluctuate around freezing for a considerable time, even if the mosses are snow-covered.

Sohlenius and Boström (2006) described tardigrade communities from moss cushions on four ice-free mountains (nunataks) in Antarctica. Tardigrades occurred in 32% of the 91 samples of mosses. No invertebrates at all occurred in 8% of the samples. They considered stochastic processes (random events) accounted for the uneven colonization of the moss cushions, most likely as a result of random dispersal. They suggested that nematodes seem to offer competition, whereas the rotifers seem to provide a food choice.



Figure 9. *Bryum* sp. cushions in Antarctica, demonstrating the deep turfs that can house tardigrades. Photo courtesy of Catherine Beard.

Tardigrades manage to survive the extreme cold of the long Antarctic winter as a **tun** (see Chapter 4-6). But other physiological adaptations are needed to combat the extremes of temperature that can be experienced in a single Antarctic day (see for example Figure 10).

Both *Bertolanius nebulosus* and *Richtersius coronifer* (Figure 11) endure ice formation as they proceed through the onset of freezing temperatures (Westh & Kristensen 1992). Both are able to supercool to -6 or -7°C before they succumb to freezing. These two tardigrades are common in Polar areas, as well as elsewhere. *Richtersius coronifer* (Figure 11) spends its Arctic winters in drought-resistant mosses as a frozen or dry individual. *Bertolanius nebulosus* has adopted a somewhat different strategy, spending its cold period in moist mosses and algae as a frozen cyst, or occasionally as an egg or adult.

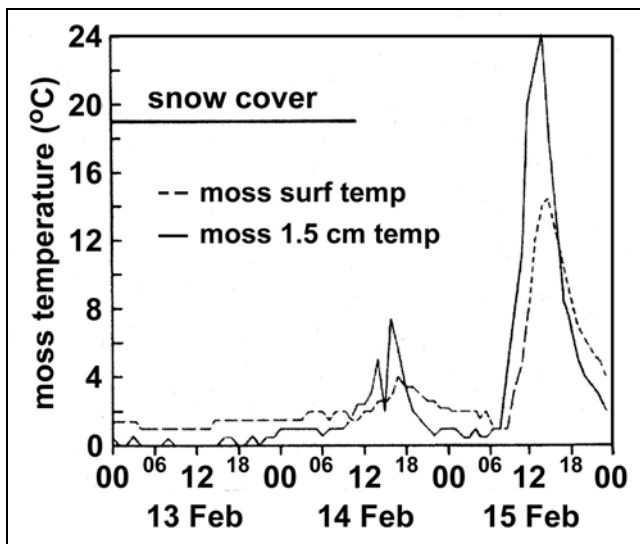


Figure 10. Comparison of moss surface temperature with that of 1.5 cm depth in moss cover on Signy Island in the Antarctic on three days in February, 1973. Redrawn from Jennings 1979.



Figure 11. *Richtersius coronifer*, a tardigrade that survives Arctic winters on mosses in a frozen state. Photo by Martin Mach, with permission.

It appears that adapted tardigrades can survive extreme conditions for a long time. Newsham *et al.* (2006) experimented in a way that might be considered cruelty to animals (but not unlike Mother Nature herself). They partially dried a bit of the leafy liverwort *Cephaloziella varians* from Rothera Point on the Wright Peninsula, Adelaide Island, western Antarctic Peninsula, then stored it frozen at -80°C for six years and two months. They then rapidly thawed the liverwort at 10°C . You guessed it! Tardigrades survived, along with nematodes and a bdelloid rotifer. Only two individuals [*Diphascion* sp. (see Figure 12), *Hypsibius* cf. *dujardini* (Figure 13)] out of fifteen tardigrades (13%) made it, but that is still remarkable! The eleven individuals of *Macrobiotus furciger* (Figure 14) and one of *Echiniscus* sp. did not. Nematodes fared a bit better, with 31% survival out of 159 individuals.

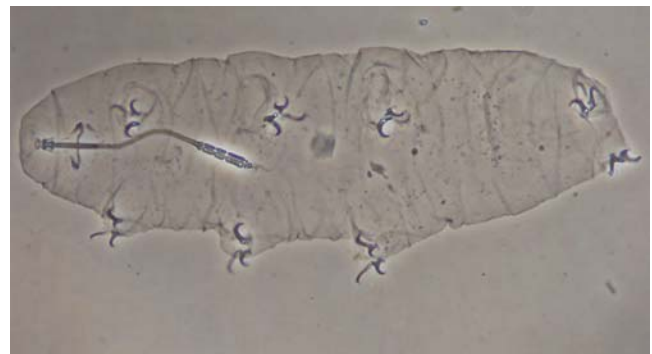


Figure 12. *Diphascion scoticum*, a moss-dwelling representative of a genus in which one member survived storage at -80°C for six years! Photo by Łukasz Kaczmarek, with permission.

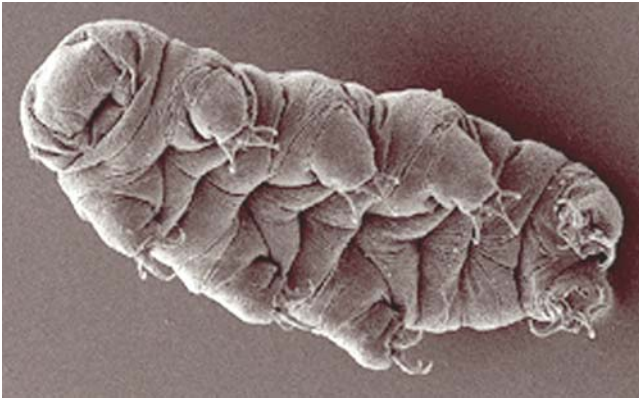


Figure 13. *Hypsibius dujardini*, a species that survived -80°C for six years. Photo by Rpgch, through Wikimedia Commons.

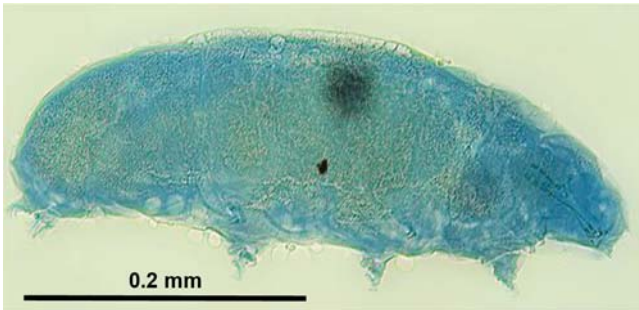


Figure 14. *Macrobiotus furciger*. Photo by Smithsonian Institution, through EOL Creative Commons.

Sømme and Terje Meier (1995) examined *Echiniscus jenningsi* (Figure 15), *Macrobiotus furciger* (Figure 14), and *Diphascion chilense* from Mühlig-Hofmannfjella, Dronning Maud Land, Antarctica to ask similar winter survival questions. They compared both hydrated and dehydrated individuals. After 600 days at -22°C , both hydrated and dehydrated tardigrades had high survival rates. After 3040 days, the dry individuals still had a high rate of survival. However, at -80°C hydrated *Echiniscus jenningsi* (Figure 15) did not fare as well as the others, decreasing in survivorship as time increased from 7 to 150 days. At -180°C , all hydrated individuals of these three species rapidly died, but all dehydrated species had good survivorship after 14 days at -180°C .

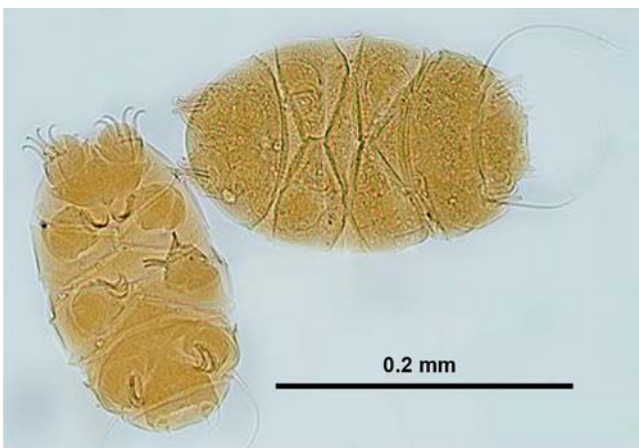


Figure 15. *Echiniscus jenningsi*. Photo by Smithsonian Institution, through EOL Creative Commons.

It is incredible that some Antarctic tardigrades can survive temperatures as low as -80°C in a **hydrated** state (Sømme & Meier 1995; Sømme, 1996)! The ability to survive short periods in a hydrated condition just below a freezing temperature is important to survival in bryophyte clumps that regularly warm in the day and freeze at night. Ice crystals on the bryophytes would most likely help to dehydrate the tardigrades as temperatures plummeted to well below freezing, facilitating their survival during the long and very cold winters. Furthermore, the ability to survive low temperatures for years would permit tardigrades to survive dispersal across the ice or remain viable within it until a suitable habitat or conditions are reached.

But how do the rapidly changing temperatures of the environment affect the ability of the tardigrade to move about on the bryophyte to seek food? The **beneficial acclimation hypothesis** (BAH) predicts that animals will have their best performance at the temperature to which they are acclimated. Li and Wang (2005) tested this hypothesis with the moss-dwelling species *Macrobiotus hufelandi* (Figure 7, Figure 19), collected from the Qinling Mountains in central China. They acclimated the water bears to 2 and 22°C for two weeks. Using walking speed and percentage of time moving, they compared performance at the acclimation temperature with that at the alternate temperature. They found that both walking speed and percentage of time moving was significantly faster when the tardigrades were kept at their acclimation temperature than when they were placed at the higher or lower experimental temperature.

But in the Antarctic, we have seen that such extreme temperature fluctuations within a single day are not unusual. Could this be a threat to the water bears, who must find food, often adhering bacteria and algae, on the moss? And others eat nematodes and other moving targets. One factor to consider is that in the experiments of Li and Wang, only 1.5 minutes acclimation were provided at the new temperature before measurements began, lasting another 3-5 minutes. This seems unrealistic as a representation of nature. The next question to ask is how fast can the tardigrades acclimate to a new temperature?

Danger may lurk among the Antarctic bryophytes. Gray *et al.* (1982) isolated eighteen taxa of predaceous fungi from among Antarctic mosses and soil samples. Among these eight different trapping mechanisms were present. The fungus *Monacrosporium ellipsosporum* seemed to be associated primarily with calcicolous mosses. Although these are nematode-trapping fungi, they may also catch the occasional tardigrade. More importantly, it indicates that the moss habitat is suitable for parasitic fungi that might attack other invertebrate groups such as tardigrades.

Miller *et al.* (1996) actually looked at the role of bryophytes vs other cryptogamic substrata in harboring tardigrades on the Windmill Islands in East Antarctica. *Pseudechiniscus suillus* (Figure 16), *Macrobiotus* sp. (see Figure 7, Figure 19), *Hypsibius antarcticus*, *Ramajendas frigidus*, *Diphascion chilense*, and *Diphascion pingue* (Figure 17) occurred among mosses and lichens. Three of these had positive associations with each other and with bryophytes: *Pseudechiniscus suillus*, *Hypsibius*

antarcticus, and *Diphascon chilense*. These three species had a strong negative association with algae and lichens.



Figure 16. *Pseudechiniscus suillus* group, an Antarctic bryophyte dweller that avoids lichens. Photo by P. J. Bartels, with permission.



Figure 17. *Diphascon pingue*, a moss and lichen dweller in Swedish forests and in the Antarctic. Photo by Michael Collins, with permission.

Forest Bryophytes

Forests have a much more tempered climate than the Antarctic. Trees reduce the rate of water loss and shade the bryophytes and their fauna from the heat of the bright sun.

Jönsson (2003) examined bryophytes in Swedish forests and found sixteen species of tardigrades, five of which were previously undescribed for that region [*Murrayon dianae* (Figure 36), *Isohypsibius sattleri*, *Platicrista angustata* (Figure 18), *Diphascon belgicae*, *D. pingue* (Figure 17)]. Jönsson found that the pine forest had the most species compared to clearcut areas, but that abundance differed little from that of clearcut areas. Of the sixteen species of tardigrades recorded, the cosmopolitan *Macrobiotus hufelandi* (Figure 19) was by far the most abundant. The weft growth form seemed to harbor more tardigrades than did other bryophyte growth forms.



Figure 18. *Platicrista angustata*. Photo by Michael Collins, with permission.



Figure 19. *Macrobiotus hufelandi*. Photo by Martin Mach, with permission.

Schuster and Greven (2007) conducted a 54-month study of the tardigrade fauna of the moss *Rhytidiadelphus squarrosus* in the Black Forest of Germany. They found 24 species, dominated by *Macrobiotus hufelandi* (56%), *M. richtersi* (18%), and *Diphascon pingue* (12%). Diversity tended to be higher in winter, but the three dominant species generally declined in winter and increased from spring until fall. Rainfall, humidity, and temperature seemed to play a major role in changes in seasonal abundance.

Epiphytes

Whereas forest floor bryophyte dwellers are protected by snow in winter, bryophytes on trees (**epiphytes**) are often above the winter snow level. In summer they have intermittent wet and dry periods and in winter they often have exposures to extreme temperatures, lacking the protective cover of snow. In the Cincinnati, Ohio, USA area, bark-inhabiting bryophytes provide homes to numerous tardigrades, with the greatest species richness in environs of high humidity and clean air (Meininger *et al.* 1985). Hence, cities afford a less hospitable environment due to the lower humidity and decreased air quality.

Despite their seemingly unfriendly habitat, epiphytic bryophytes are particularly suitable as a tardigrade habitat. Indeed, this habitat seems to house the most species. The frequency of wetting and drying of these bryophytes seems to be most suitable to the tardigrade life cycle. Richness seems to run about 4-16 species. Hooie and Davison (2001; Hooie Tardigrade diversity) found the following tardigrades associated with the epiphytic moss *Ulota crispa* (Figure 20) on four tree species (*Acer saccharum*, *Acer rubrum*, *Betula lenta*, *Tilia americana*) in the Great Smoky Mountains National Park, USA:

Echiniscus cf. *oihonnae*

Echiniscus virginicus

Hypechiniscus gladiator

Macrobiotus hufelandi (Figure 19)

Milnesium tardigradum (Figure 21)

Minibiotus cf. *pustulatus*

Paramacrobiotus tonollii (Figure 23)

Pseudechiniscus (Figure 22)



Figure 20. *Ulota crispa*, an epiphytic moss that houses a number of tardigrade species. Photo by Michael Lüth, with permission.

In a study of riparian tardigrades, Romano *et al.* (2001) reported on the tardigrades on epiphytic bryophytes in Alabama, USA. Using 108 samples, they extracted 1588 tardigrades from three tree species on six sampling dates. Like Riggan (1962) for forest bryophytes, Romano *et al.* (2001) found that *Macrobiotus* species (Figure 6-Figure 8) were the most abundant (1358 of the 1588 tardigrades, 86%). They found no differences among tree species, bryophyte species, or seasons, but there were site differences, possibly suggesting dispersal limitations. Although relative humidity and temperature did not seem to influence abundance, precipitation did. Interestingly, as precipitation increased, the number of tardigrades decreased. Beasley (1981) found that higher humidity resulted in lower tardigrade abundance in the Caribbean National Rain Forest at Luquillo, Puerto Rico. This further supports the hypothesis that periods of anhydrobiosis are required in the life of a tardigrade and that lack of them shorten the length of life. However, if only active periods are considered, there may be little difference.



Figure 21. *Milnesium tardigradum*. A cosmopolitan bryophyte inhabitant. Photo by Martin Mach, with permission.



Figure 22. *Pseudechiniscus juanita*. Photo by Paul J. Bartels, with permission.

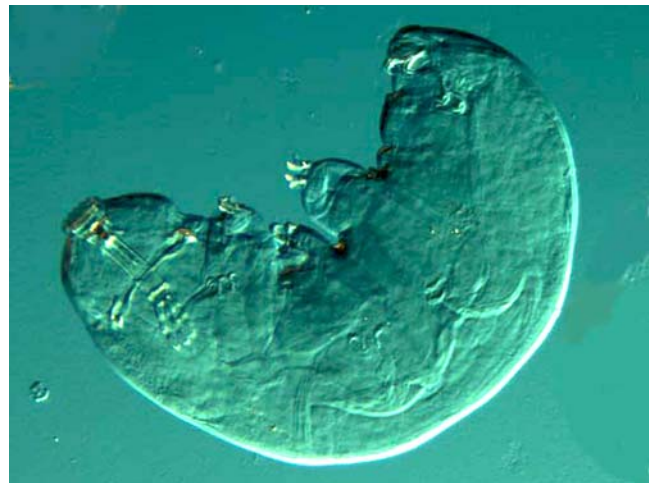


Figure 23. *Paramacrobiotus tonollii*, a tardigrade known from *Ulota crispa* in the Smoky Mountains. Photo by Martin Mach, with permission.

Briones *et al.* (1997) suggested that during periods of high precipitation the film of water surrounding the bryophytes may become anoxic, killing the tardigrades. This could especially be a problem in the riparian zone, where the bryophytes, and hence the tardigrades, were under water during several collection periods. Diversity of tardigrades was somewhat low in the Alabama, USA,

riparian sites (Table 1), with only twelve species overall (Romano *et al.* 2001). Mosses included *Anomodon* (Figure 24), *Leucodon* (Figure 25), and *Schwetschkeopsis* (Figure 26), all epiphytes.



Figure 24. *Anomodon rugelii*, an epiphytic moss. Photo by Michael Lüth, with permission.



Figure 25. *Leucodon sciuroides*, an epiphytic moss that compresses and curls its branches upward when it dries. Photo by Michael Lüth, with permission.



Figure 26. *Schwetschkeopsis fabronia*, an epiphyte from Asia and North America, and home for tardigrades. Photo by Misha Ignatov, with permission.

As in the Alabama study, Jerez Jaimes (2002) found a low diversity of only seven species on the moss *Calymperes palisotii* (Figure 27) on six species of trees on the campus of the University of Puerto Rico at Mayagüez. The highest species richness was on *Mangifera indica* (mango) and *Swietenia macrophylla* (mahogany).

When collections came from trees and shrubs from all 67 counties in Florida, only 20 species of tardigrades were found (Meyer 2006, 2008). Meyer also found no specificity for a particular bryophyte (47 species included) or ecological region, but there was specificity for bryophytes as opposed to foliose lichens.

There seemed to be an avoidance of one moss species, *Aulacomnium heterostichum* (Figure 28), with no tardigrades occurring on it (Meyer 2008). Bartels and Nelson (2006), working in the Great Smoky Mountains National Park, USA, increased the number of known species in the park from three to 42 from multiple substrates, a further testimony to how little known these organisms are. Bartels and Nelson found that more tardigrades occurred in bryophytes at breast height on a tree than at the tree bases, perhaps again relating to longer or more frequent dry periods.

Diphascon [= *Hypsibius*] *scoticum* (Figure 29), a very common tardigrade, inhabits mosses on logs (Cushman, pers. comm. 1970). It would be interesting to compare the log-dwelling tardigrade taxa with those living on epiphytic bryophytes of the same species. Presumably, the log habitat would have longer moist periods. Based on the findings discussed above of Bartels and Nelson (2006) and Romano *et al.* (2001), one might expect more on the epiphytes, where alternating wet and dry periods might fit better with the apparent dormancy requirements of the tardigrades.



Figure 27. *Calymperes palisotii*, a moss that had the lowest tardigrade diversity on the University of Puerto Rico campus, Mayagüez. Photo by Claudio Delgadillo Moya, with permission.



Figure 28. *Aulacomnium heterostichum*, a moss that seems to be avoided by tardigrades. Photo by Janice Glime.



Figure 29. *Diphyscon scoticum*, a very common tardigrade, one that has been found among mosses on logs. Photo by Paul J. Bartels, with permission.

Aquatic

Few truly aquatic tardigrades seem to exist. Garey *et al.* (2008) reported that of the more than 900 species of tardigrades they reviewed, most live in the water film on the surface of bryophytes, lichens, algae, and other photosynthetic organisms. Of their 910 species of tardigrades, only 62 (in 13 genera) were truly aquatic. In New Zealand, tardigrades represented only 2.4% of the fauna among the bryophytes of an unshaded stream in the alpine zone on South Island (Suren 1991a). In a more extensive study there, they represented only 1.2% of the invertebrates collected among mosses in 103 streams in one study (Suren 1993). Similar small numbers were present among the moss *Fontinalis antipyretica* (Figure 34) in the Czech Republic, where one stream had 1541 per mL of moss (0.6% of the fauna in the moss) and another stream had only 545 per mL (0.1%) (Vlčková *et al.* 2001/2002). In the Colorado Rocky Mountains, Elgmork and Sæther (1970) found most of the tardigrades *Dactylobiotus* cf *macronyx* (formerly *Macrobotus macronyx*) associated with algae, but they also reported them from *Fontinalis* beds (Figure 34) and other submerged mosses.

In streams, flow velocity may cause tardigrades to seek refuge among mosses. Suren (1992) reported high densities of tardigrades (*Dactylobiotus* [= *Macrobotus*] *dispar*; Figure 30-Figure 31) associated with mosses in alpine streams of New Zealand. In an earlier study Suren (1991b) found that the colonization of this species on artificial mosses was at a reduced density compared to that on mosses [*Fissidens rigidulus* (Figure 32), *Cratoneurosis relaxa*, *Bryum blandum* (Figure 33)].

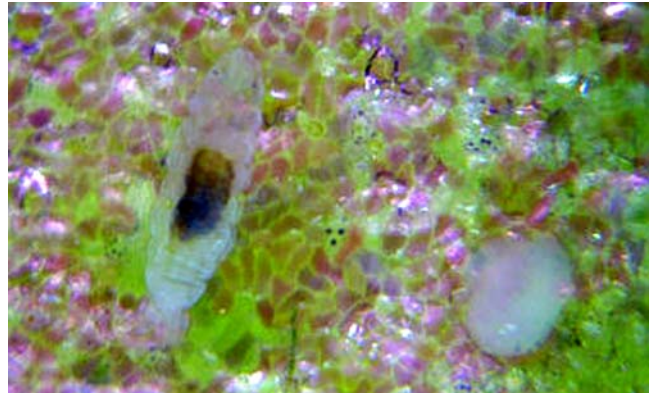


Figure 30. *Dactylobiotus* [= *Macrobotus*] *dispar*. Photo by Martin Mach, with permission.



Figure 31. *Dactylobiotus* [= *Macrobotus*] *dispar*. Photo by Martin Mach, with permission.



Figure 32. *Fissidens rigidulus* from New Zealand, a good tardigrade habitat. Photo by Bill and Nancy Malcolm, with permission.



Figure 33. *Bryum blandum* from New Zealand, where tardigrade density is greater than that on artificial mosses. Photo by Jan-Peter Frahm, with permission.

Suren (1992) reported densities of 3120 and 8160 per m² on the mosses in two trials, whereas they reached only 1760 and 1600 on the artificial substrata. He suggested that the high periphyton biomass among mosses provided a good food source that made this a good habitat for the tardigrades. This suggestion is supported by the largest percentage of variation (24.2%) being explained by the ultra-fine particulate matter (UFPOM). The abundance of tardigrades on bryophytes was 10 times that found on stream gravel.

Linhart *et al.* (2002) examined scattered clumps of the aquatic moss *Fontinalis antipyretica* (Figure 34) and found that whereas several groups of invertebrates were distributed among the clumps in relation to stream flow, this was not the case for tardigrades. Even though the researchers showed that fine organic matter trapped within the moss mat was determined by flow velocity, this did not seem to be a determining factor in tardigrade distribution.



Figure 34. *Fontinalis antipyretica* in flowing water. Photo by Michael Lüth, with permission.

In the Italian Alps *Borealibius zetlandicus* occurred on *Warnstorfia exannulata* (Figure 35; Rebecchi *et al.* 2009). This tardigrade species is known only from boreo-alpine areas, where it typically occurs in sediment, submerged aquatic mosses, or *Sphagnum* (Figure 5). But like many other tardigrades, this one has a wide habitat range, including the Barents Sea and terrestrial mosses and soil that rarely dry out. This boreal habitat distribution for this species is possible because this species is able to survive freezing. But the populations of the species studied are unable to survive desiccation.



Figure 35. *Warnstorfia exannulatus*, home for the tardigrade *Borealibius zetlandicus* in the Italian Alps. Photo by Michael Lüth, with permission.

Suren (1992) also considered the possibility that the mosses offered shelter from the rapid flow of water elsewhere. These tiny organisms are often in the leaf axils of the mosses, where they have almost no effect from the strong flow, yet the oxygen diffusion could be fairly rapid. But as yet, no data seem to support cause and effect of flow velocity and tardigrade distribution.

Living in a stream is challenging for a tardigrade. Using 22 animals, Shcherbako *et al.* (2010) found that *Milnesium tardigradum* (Figure 21) could manage in water with a mean velocity of 23.3 mm/h, moving at a mean speed of 19.8 mm/h in the light and 29 mm/h in the dark, making snails look like track stars! Bryophytes provide a safe refuge from fast-moving waters. Eles and Repas (2009) described the stream tardigrades as having faster motion and longer claws than their terrestrial counterparts.

In New Zealand, Suren (1992) found that the tardigrade *Dactylobiotus dispar* (Figure 31) represented about 6.6% of the fauna on mosses in unshaded streams compared to 0.6% on gravel. In shaded streams they occupied only 5.3% of the bryophyte fauna compared to 0.4% on gravel. But not all wet habitats seem to be very suitable for tardigrades.

Kaczmarek (pers. comm. 29 January 2010) has reminded me that most of the water-dwelling tardigrades are in fact marine. Those that are truly freshwater aquatic species live on algae or plants (including bryophytes), in the sand, or in sediments. The genus *Murrayon* (Figure 36) is unusual among the water-dwelling tardigrades in that some aquatic individuals lay their eggs in the shed shells of cladocerans (Bertolani *et al.* 2009).



Figure 36. *Murrayon dianeae*, an aquatic tardigrade. Photo by Michael Collins, with permission.

Emergent bryophytes may be especially comfortable for some species of tardigrades. One of the more "friendly" environments is in association with *Barbula* [= *Didymodon*] *tophacea* (Figure 37-Figure 38), a well-known rock-forming moss, above the wet zone.

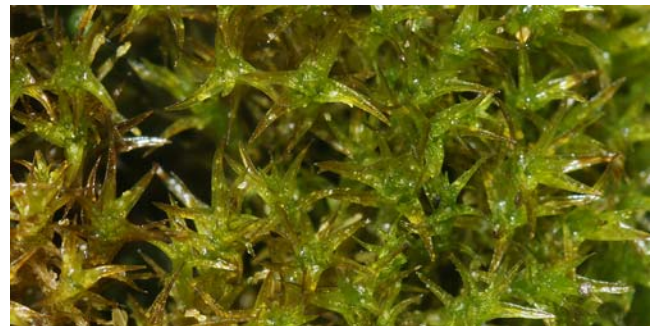


Figure 37. *Barbula* [= *Didymodon*] *tophacea*, an emergent moss known to house 84 tardigrades per gram. Photo by Barry Stewart, with permission.

The aquatic habitat is also sometimes hospitable to hygrophilous species that are more typical among moist mosses or species with a wide tolerance range for moisture conditions (Nelson & Marley 2000). On the other hand, *Hypsibius dujardini* (Figure 13) is known from moist mosses, but it is primarily aquatic (McFatter *et al.* 2007). *Parhexapodibius pilato* was found among mosses on a stream bank in central Georgia (McFatter *et al.* 2007), but otherwise is known only from Michigan (Bernard 1977).



Figure 38. *Barbula* [=*Didymodon*] *topacea*, an emergent moss showing the numerous possibilities for resting in leaf axils. Photos by Michael Lüth, with permission.

Dry Habitats

Although collectors looking for a rich bryophyte flora would most likely ignore the desert, some bryophytes depend on its predominately dry nature. The cryptogamic crust of prairies and deserts has its own tardigrade fauna (Brantley & Shepherd 2002). In this habitat of bryophytes, lichens, Cyanobacteria, and algae, long dry periods are guaranteed. The occasional wet periods make it a suitable tardigrade habitat.

As already discussed, Meininger and Spatt (1988), working along Dalton Highway in the tundra adjacent to the trans-Alaska Pipeline, found that road dust had a major impact on both the mosses and the tardigrades. The mosses near the road represented xerophytic species tolerant of high calcium. Consequently, the tardigrades likewise were taxa tolerant of drier conditions. Because of the moisture limitations on other kinds of taxa, the tardigrades near the road were mostly fungivorous and algal feeders; those farther from the road, where *Sphagnum* (Figure 5) was able to grow, tended to be more omnivorous and carnivorous. These habitat differences caused differences in tardigrade fauna between roadside bryophytes and more distant *Sphagnum* species.

Vertical and Horizontal Distribution

It seems likely that some vertical distribution within the bryophyte mat should occur. These could be defined by light levels. The presence of eyespots (Figure 41) in at least some members of Tardigrada was reported by Greven (2007), with responses to light varying from none to both positive and negative. Beasley (2001) reported negative photokinesis in the common tardigrade *Macrobotus hufelandi* (Figure 19), a common moss dweller. Rather than being attracted to or from the light, they increased

their rate of movement. Since light indicates sun intensity, it also is an indicator of the likelihood of drying, making the response to move quickly away from light an adaptive one. Vertical differences in tardigrade distribution are known from soil (Leatham *et al.* 1982). Nevertheless, as noted elsewhere, there seems to be little evidence for vertical position differences or migration of tardigrades in mosses; only one tardigrade (*Echiniscus viridissimus*) seems more common near the upper portion of the moss (Nelson & Adkins 2001). Wright (1991) found that in xeric habitats this species does not migrate vertically to the C zone as the moss dehydrates, even though other species do at the same time.

Data from the Antarctic suggest that temperature may play a role in the vertical positioning of tardigrades there. On Signy Island, 80% of the tardigrades occurred in the upper 6 cm of moss, and usually 70% were in the top 3 cm (Jennings 1979). One factor that contributes to this limited distribution is that the turf below 7-8 cm is **anaerobic** (lacking oxygen), making it inhospitable for the tardigrades. In moss-dominated flushes near the Canada Glacier in southern Victoria Land, Antarctica, the invertebrates, including tardigrades, occurred at a mean depth ranging 5-10.83 mm (Schwarz *et al.* 1993). As discussed above, the relative number of organisms increased near the surface in post-melt mosses. This is not necessarily a direct temperature response; it could result from changes in light or humidity associated with the melt.

Schuster *et al.* (2009) examined the microclimate within a cushion of the moss *Rhytidiadelphus loreus* (Figure 39). They found that the deep layers had lower daytime and higher nighttime temperatures than **ambient** (in this case, air temperature). Oxygen was similar throughout the cushion, but CO₂ increased greatly with depth. The six species of tardigrades were concentrated in the green-brown layer of the moss. The authors suggested that light and oxygen had little impact on the distribution but that CO₂ kept the tardigrades from occupying lower positions and that temperature might cause migrations within the upper portion.



Figure 39. *Rhytidiadelphus loreus*. Photo by Michael Lüth, with permission.

Differences in horizontal distribution may be the result of microhabitat differences such as shade vs sun or distance from water. But they can also be a simple result of passive, random dispersal and the slow-moving nature of the animal. Degma *et al.* (2011) sampled *Hypnum cupressiforme* (25 samples; Figure 40) to try to determine

the causes of horizontal positioning of tardigrades on that species. They found 224 tardigrades in the species *Milnesium tardigradum* (Figure 41), *Hypsibius convergens* (Figure 42), *H. microps*, *Diphascon pingue* (Figure 17), *Astatumen trinacriae* (Figure 43), *Macrobiotus hufelandi* (Figure 7), and *Minibiotus* sp. (Figure 44) They found no significant moisture gradient among the moss plants. The distribution of the tardigrade species was aggregated, but the number of species (richness) was random. There was no relationship of tardigrade species distribution to moisture.



Figure 40. *Hypnum cupressiforme*, home of seven species of tardigrades. Photo by Michael Lüth, with permission.



Figure 41. Eyespots of *Milnesium tardigradum*. Photo by Martin Mach, with permission.



Figure 42. *Hypsibius convergens*. Photo by Łukasz Kaczmarek, with permission.

But even these species may not be able to tolerate desiccation. *Macrobiotus hufelandi* (Figure 7) and *Hypsibius dujardini* (Figure 13) are unable to live in habitats that desiccate quickly, perhaps explaining their association with the slow-drying bryophytes (Wright 1991). Other bryophyte dwellers [*Milnesium tardigradum* (Figure 41) and *Ramazzottius* (formerly *Hypsibius*) *oberhaeuseri* (Figure 3)] may not tolerate constant moisture, but these two species avoid high insolation and rapid desiccation, again making bryophytes a suitable habitat.

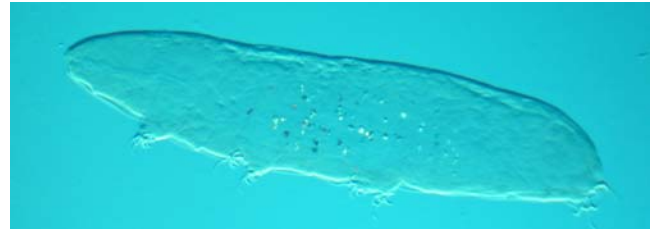


Figure 43. *Astatumen trinacriae*. Photo by Paul J. Bartels, with permission.

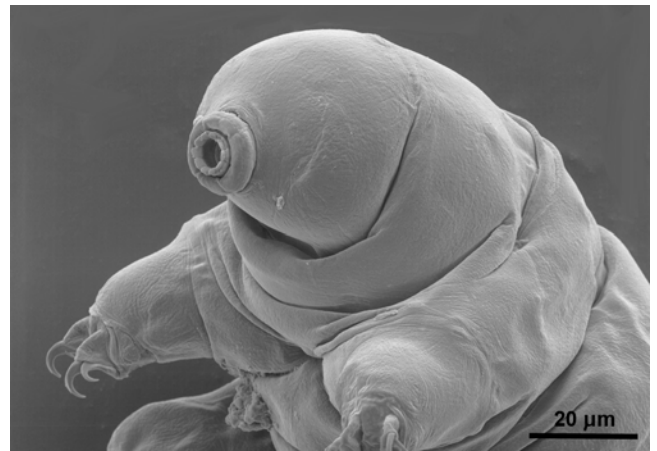


Figure 44. *Minibiotus intermedius*. Photo by William Miller, through Flickr.

Competition and food relations are often determinants of the species assemblages. For example, *Milnesium tardigradum* (Figure 41) may be found with two *Hypsibius* species that it can use for food (Wright 1991). Competition may account for the negative associations among *Macrobiotus hufelandi* (Figure 7), *Paramacrobiotus richtersi* (Figure 45), and *Isohypsibius prostostomus* (see Figure 46) in xeric habitats.



Figure 45. *Paramacrobiotus richtersi*. Photo through Creative Commons.

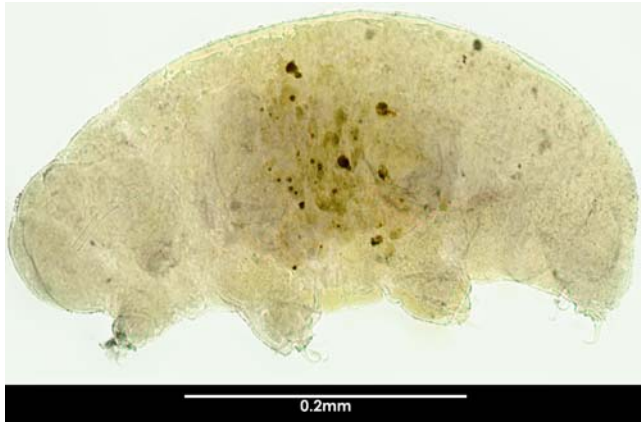


Figure 46. *Isohypsibius asper*. Photo by Smithsonian Institution through EOL Creative Commons.

Summary

Tardigrades live on both terrestrial and aquatic bryophytes, with the lowest numbers in the tropics. Epiphytic mosses seem to be especially suitable for them. Altitude is influential on species and numbers in some cases, but in others researchers were unable to find any differences. There are indications that the greatest numbers on higher mountains occur at mid elevations. Latitude, scale, and moisture availability most likely play a role.

Numbers of species in most studies are modest. In forests, studies reported herein range 7-42 species. In one study, the number of species was greater in the pine forest, but the number of individuals differed little from that of clearcut areas. *Macrobiotus hufelandi* seems to be the most common species just about everywhere. The most common genera are *Echiniscus*, *Macrobiotus*, *Diphascion*, and *Hypsibius*, and the genera recently segregated from them. Tardigrades comprised only 1.2% of the invertebrates in an expansive New Zealand study and Hingley found only two taxa in peatlands. Dry habitats may pose food limitations; constantly wet ones may be unfavorable to their longevity.

Although mosses get wet and dry on top first, it appears that tardigrades have little ability to migrate and do not even seem to be arranged in vertical assemblages. But, they have eyespots, indicating that light may play some role in their locations.

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Literature Cited

- Bartels, P. 2005. "Little known" water bears? *ATBI Quart.* 6(2): 4.
- Bartels, P. J. and Nelson, D. R. 2006. A large-scale, multihabitat inventory of the phylum Tardigrada in the Great Smoky Mountains National Park, USA: A preliminary report. *Hydrobiologia* 558: 111-118.
- Beasley, C. W. 1981. Some Tardigrada from Puerto Rico. *Tex. J. Sci.* 33: 9-12.
- Beasley, C. W. 1988. Altitudinal distribution of Tardigrada of New Mexico with the description of a new species. *Amer. Midl. Nat.* 120: 436-440.
- Beasley, C. W. 2001. Photokinesis of *Macrobiotus hufelandi* (Tardigrada, Eutardigrada). *Zool. Anz.* 240: 233-236.
- Beasley, C. W., Kaczmarek, Ł., and Michalczyk, Ł. 2006. New records of tardigrades from China, with zoogeographical remarks. *Biol. Lett.* 43(1): 13-20.
- Bernard, E. C. 1977. A new species of *Hexapodibius* from North America, with a redescription of *Diphascion belgicæ* (Tardigrada). *Trans. Amer. Microsc. Soc.* 96: 476-482.
- Bertolani, R. and Rebecchi, L. 1996. The tardigrades of Emilia (Italy). II. Monte Rondinaio. A multihabitat study on a high altitude valley of the northern Apennines. *Zool. J. Linn. Soc.* 116: 3-12.
- Bertolani, R., Altiero, T., and Nelson, D. R. 2009. Tardigrada (water bears). Chapter 188. In: Likens, G. E. (ed.). Volume 2. *Encyclopedia of Inland Waters*. Elsevier, Oxford, pp. 443-465.
- Bertrand, M. 1975. Répartition des tardigrades "terrestres" dans le massif de l'Aigoual. *Vie Milieu* 25: 283-298.
- Bettis, C. J. 2008. Distribution and abundance of the fauna living in two *Grimmia* moss morphotypes at the McKenzie Table Mountain Preserve, Fresno County, California. M.S. Thesis, California State University, Fresno, CA, 65 pp.
- Brantley, S. and Shepherd, U. 2002. Microarthropods on different types of cryptobiotic crusts in pinyon-juniper habitat. Abstracts of the 87th Annual Meeting of the Ecological Society of America and the 14th Annual International Conference of the Society for Ecological Restoration, 4-9 August, 2002, Tucson, AZ.
- Briones, M. J. I., Ineson, P., and Pearce, T. G. 1997. Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. *Appl. Soil Ecol.* 6: 117-134.
- Collins, M. and Bateman, L. 2001. The ecological distribution of tardigrades in Newfoundland. *Zool. Anz.* 240: 291-297.
- Crum, H. 1976. Mosses of the Great Lakes Forest, revised edition. Contributions from the University Herbarium, Univ. Mich., Ann Arbor. Vol. 10, 404 pp.
- Dastyh, H. 1980. Tardigrades from the Tatra National Park. *Polska Akademia Nauk Zakład Zoologii Systematycznej i Doswiadczalnej. Monografie Fauny Polski* Vol. 9. 232. pp.
- Dastyh, H. 1985. West Spitsbergen Tardigrada. *Acta Zool. Cracov.* 28(3): 169-214.
- Dastyh, H. 1987. Altitudinal distribution of Tardigrada in Poland. In: Bertolani, R. (ed.). *Selected Symposia and Monographs U.Z.I.*, 1, Mucchi, Modena, pp. 45-56.
- Dastyh, H. 1988. The Tardigrada of Poland. *Monografie Fauny Polski*. Vol. 16. Institute of Systematics and Evolution of

- Animals, Polish Academy of Sciences, Kraków, Poland, pp. 1-255.
- Degma, P., Bertolani, R., and Guidetti, R. 2010. Actual checklist of Tardigrada species (Ver. 11:26-01-2010). Accessed 18 June 2010 at <<http://www.tardigrada.modena.unimo.it/miscellanea/Actual%20checklist%20of%20Tardigrada.pdf>>.
- Degma, P., Stanislav, K., and Sabatovicova, L. 2011. Horizontal distribution of moisture and Tardigrada in a single moss cushion. *J. Zool. Syst. Evol. Res.* 49 (Suppl 1): 71-77.
- Eles, A. and Repas, L. 2009. New dates and new methods for research of freshwater Tardigrada fauna of city Szekesfeharvar. In: Greven, H., Hohberg, K., and Schill, R. O. 11th International Symposium on Tardigrada. Conference Guide. Tübingen, Germany, 3-6 August 2009, pp. 56-57.
- Elgmork, K. and Sæther, O. R. 1970. Distribution of invertebrates in a high mountain brook in the Colorado Rocky Mountains. *Univ. Colorado Studies Ser. Biol.* 31: 3-55.
- Fontoura, P., Pilato, G., Morais, P., and Lisi, O. 2009. *Minibiotus xavieri*, a new species of tardigrade from the Parque Biológico de Gaia, Portugal (Eutardigrada: Macrobiotidae). *Zootaxa* 2267: 55-64.
- Garey, J. R., McInnes, S. J., and Nichols, P. B. 2008. Global diversity of tardigrades (Tardigrada) in freshwater. *Hydrobiologia* 595: 101-106.
- Gray, N. F., Wyborn, C. H. E., and Smith, R. I. L. 1982. Nematophagous fungi from the maritime Antarctic. *Oikos* 38: 194-201.
- Greven, H. 2007. Comments on the eyes of tardigrades. *Arthropod Struc. Dev.* 36: 401-407.
- Guil, N., Hortal, J., Sánchez-Moreno, S., and Machordom, A. 2009. Effects of macro and micro-environmental factors on the species richness of terrestrial tardigrade assemblages in an Iberian mountain environment. *Landscape Ecol.* 24: 375-390.
- Hingley, M. 1993. Microscopic Life in *Sphagnum*. *Naturalists' Handbook* 20. [i-iv]. Richmond Publishing Co. Ltd., Slough, England, pp. 1-64. 58 fig. 8 pl.
- Hinton, J. G., and Meyer, H. A. 2007. Distribution of limnoterrestrial Tardigrada in Georgia and the Gulf Coast states of the United States of America with ecological remarks. *J. Limnol.* 66(Suppl. 1): 72-76.
- Hinton, J. G. and Meyer, H. A. 2008. Tardigrades from Fayette County, Georgia. *Georgia J. Sci.* 66: 30-32.
- Hofmann, I. 1987. Habitat preference of the most frequent moss-living Tardigrada in the area of Giessen (Hessen). In: Bertolani, R. (ed.). *Selected Symposia and Monographs U.Z.I., 1, Mucchi, Modena*, pp. 211-216.
- Hooie, A. K. and Davison, P. G. 2001. Tardigrade diversity in the moss *Ulota crispa* from tree canopies in the Great Smoky Mountains National Park – A preliminary report. *J. Alabama Acad. Sci.* 72: 91. Abstract.
- Ito, M. 1999. Ecological distribution, abundance and habitat preference of terrestrial tardigrades in various forests on the northern slope of Mt. Fuji, central Japan. *Zool. Anz.* 238: 225-234.
- 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.
- Jennings, P. G. 1979. The Signy Island terrestrial reference sites: X. Population dynamics of Tardigrada and Rotifera. *Brit. Antarct. Surv. Bull.* 47: 89-105.
- Jerez Jaimes, J. H., Narváez, E. X., and Restrepo, R. 2002. Tardigrados en musgos de la Reserva el Diviso (Santander, Colombia). *Revista Colombiana de Entomología* 28(2): 199-206.
- Jönsson, K. I. 2003. Population density and species composition of moss-living tardigrades in a boreo-nemoral forest. *Ecography* 26: 356-364.
- Kaczmarek, L., Gołdyn, B., Welnicz, W., and Michalczyk, L. 2011. Ecological factors determining Tardigrada distribution in Costa Rica. *J. Zool. Syst. Evol. Res.* 49: 78-83.
- Kathman, R. D. and Cross, S. F. 1991. Ecological distribution of moss-dwelling tardigrades on Vancouver Island, British Columbia, Canada. *Can. J. Zool.* 69: 122-129.
- Leetham, J. W., McNary, T. J., Dodd, J. L., and Lauenroth, W. K. 1982. Response of soil nematodes, rotifers and tardigrades to three levels of season-long sulfur dioxide exposures. *Water Air Soil Pollut.* 17: 343-356.
- Li, X.-C. and Wang, L.-Z. 2005. Effects of temperature and thermal acclimation on locomotor performance of *Macrobiotus hufelandi* Schultzze (Tardigrada: Macrobiotidae). *Current Zool.* (formerly *Acta Zoologica Sinica*) 51: 516-520.
- Linhart, J., Vlcková, S., and Uvíra, V. 2002. Moss-dwelling meiobenthos and flow velocity in low-order streams. *Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium (2001-2002) Biologica* 39/40: 111-122.
- Mathews, G. B. 1938. Tardigrada of North America. *Amer. Midl. Nat.* 19: 619-627.
- McFatter, M. M., Meyer, H. A., and Hinton, J. G. 2007. Nearctic freshwater tardigrades: A review. In: Pilato, G. and Rebecchi, L. (guest eds.). *Proceedings of the Tenth International Symposium on Tardigrada*. *J. Limnol.* 66(Suppl. 1): 84-89.
- Meininger, C. A. and Spatt, P. D. 1988. Variations of tardigrade assemblages in dust-impacted Arctic mosses. *Arct. Alp. Res.* 20: 24-30.
- Meininger, C. A., Uetz, G. W., and Snider, J. A. 1985. Variation in epiphytic microcommunities (tardigrade-lichen-bryophyte assemblages) of the Cincinnati, Ohio area. *Urban Ecol.* 9(1): 45-62.
- Meyer, H. A. 2006. Small-scale spatial distribution variability in terrestrial tardigrade populations. *Hydrobiologia* 558: 133-139.
- Meyer, H. A. 2008. Distribution of tardigrades in Florida. *Southeast. Nat.* 7: 91-100.
- Meyer, H. A. and Hinton, J. 2007. Limno-terrestrial Tardigrada of the Nearctic Realm. In: Pilato, G. and Rebecchi, L. (eds.). *Proceedings of the Tenth International Symposium on Tardigrada*. *J. Limnol.* 66(Suppl. 1): 97-103.
- Mihelcic, F. 1954/55. Zur Ökologie der Tardigraden. *Zool. Anz.* 153: 250-257.
- Mihelcic, F. 1963. Moose als Lebensstätten für Tardigraden. *Der Schlern* 37: 179-181.
- Miller, W. R. and Heatwole, H. 1995. Tardigrades of the Australian Antarctic Territories: The Mawson Coast, East Antarctica. *Invert. Biol.* 114(1): 27-38.
- Miller, W. R., Miller, J. D., and Heatwole, H. 1996. Tardigrades of the Australian Antarctic Territories: The Windmill Islands, East Antarctica. *Zool. J. Linn. Soc.* 116: 175-184.
- Nelson, D. R. 1973. Ecological distribution of tardigrades on Roan Mountain, Tennessee – North Carolina. Ph. D. dissertation, University of Tennessee, Knoxville.
- Nelson, D. R. 1975. Ecological distribution of Tardigrada on Roan Mountain, Tennessee – North Carolina. In: Higgins, R. P. (ed.). *Proceedings of the First International*

- Symposium on Tardigrades. Mem. Ist. Ital. Idrobiol., Suppl. 32: 225-276.
- Nelson, D. R. and Adkins, R. G. 2001. Distribution of tardigrades within a moss cushion: Do tardigrades migrate in response to changing moisture conditions? Zool. Anz. 240: 493-500.
- Nelson, D. R. and Marley, N. J. 2000. The biology and ecology of lotic Tardigrada. Freshwat. Biol. 44: 93-108.
- Newsham, K. K., Maslen, N. R., and McInnes, S. J. 2006. Survival of Antarctic soil metazoans at -80°C for six years. CryoLetters 27(5): 269-280.
- Pilato, G. 2009. *Bindius triquetrus* gen. nov. sp. nov. (Eutardigrada, Hysibiidae) from Sicily (Italy). Zootaxa 2058: 62-68.
- Ramazzotti, G. 1962. Il Phylum Tardigrada. Mem. Ist. Ital. Idrobiol. 14: 1-595.
- Ramazzotti, G. 1972. Phylum Tardigrada (Seconda edizione aggiornata). Vol. II. Mem. Ist. Ital. Idrobiol. 28: 1-732.
- Ramazzotti, G. and Maucci, W. 1983. Il Phylum Tardigrada. [The phylum Tardigrada - 3rd edition: English translation by C. W. Beasley.]. Mem. Ist. Ital. Idrobiol. 41: 1-1011.
- Rebecchi, L., Boschini, D., Cesari, M., Lencioni, V., Bertolani, R., and Guidetti, R. 2009. Stress response of a boreo-alpine species of tardigrade, *Borealibius zetlandicus* (Eutardigrada, Hysibiidae). J. Limnol., 68(1): 64-70.
- Riggin, G. T. Jr. 1962. Tardigrada of Southwest Virginia: With the Addition of a Description of a New Marine Species from Florida. Technical Bull. 152, Virginia Agricultural Experiment Station, Blacksburg, VA. 145 pp.
- Rodriguez-Roda, J. 1951. Algunos datos sobre la distribucion de los Tardigrados españoles. Bol. Real Soc. Esp. Hist. Nat. Secc. Biol. 49: 75-83.
- Romano, F. A. III., Barreras-Borrero, B., and Nelson, D. R. 2001. Ecological distribution and community analysis of Tardigrada from Choccolocco Creek, Alabama. Zool. Anz. 240: 535-541.
- Schuster, R. and Greven, H. 2007. A long-term study of population dynamics of tardigrades in the moss *Rhytidiadelphus squarrosus* (Hedw.) Warnst. J. Limnol. 66: 141-151.
- Schuster, R., Spiertz, I., Lösch, R., and Greven, H. 2009. Microclima and vertical distribution of tardigrades in a moss cushion. In: Greven, H., Hohberg, K., and Schill, R. O. 11th International Symposium on Tardigrada. Conference Guide. Tübingen, Germany, 3-6 August 2009, p. 59.
- Schwarz, A.-M. J., 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.
- Shcherbako, D., Schill, R. O., Brümmer, F., Nissen, M., and Blum, M. 2010. Movement behaviour and video tracking of *Milnesium tardigradum* Doyère, 1840 (Eutardigrada Apochela). Contrib. Zool. 79: 33-38.
- Sohlenius, B. and Boström, S. 2006. Patch-dynamics and population structure of nematodes and tardigrades on Antarctic nunataks. Eur. J. Soil Biol. 42(Suppl. 1): S321-S325.
- Somme, L. 1996. Anhydrobiosis and cold tolerance in tardigrades. Eur. J. Entomol. 93: 349-357.
- Somme, L. and Terje Meier, T. 1995. Cold tolerance in Tardigrada from Dronning Maud Land, Antarctica. Polar Biol. 15: 1432-2056.
- Suren, A. M. 1991a. Bryophytes as invertebrate habitat in two New Zealand alpine streams. Freshwat. Biol. 26: 399-418.
- Suren, A. M. 1991b. Assessment of artificial bryophytes for invertebrate sampling in two New Zealand alpine streams. N. Z. J. Marine Freshwat. Res. 25: 101-112.
- Suren, A. M. 1992. Enhancement of invertebrate food resources by bryophytes in New Zealand alpine headwater streams. N. Z. J. Marine Freshwat. Res. 26: 229-239.
- Suren, A. 1993. Bryophytes and associated invertebrates in first-order alpine streams of Arthur's Pass, New Zealand. New Zeal. J. Marine Freshwat. Res. 27: 479-494.
- Utsugi, K., Hiraoka, T., and Nunomura, N. 1997. On the relations between tardigrade fauna and bryophyte flora in Toyama Prefecture. Bull. Toyama Sci. Mus. 20: 57-71.
- Venkataraman, K. 1998. Studies on Phylum Tardigrada and Other Associated Fauna, South Polar Skua and Bird and Mammal Logging During 1994 - 1995 Expedition. Fourteenth Indian Expedition to Antarctica, Scientific Report, 1998. Department of Ocean Development, Technical Publication No. 12: 221-243.
- Vlcková, S., Linhart, J., and Uvíra, V. 2001/2002. Permanent and temporary meiofauna of an aquatic moss *Fontinalis antipyretica* Hedw. Acta Univers. Palack. Olom. Biol. 39-40: 131-140.
- Westh, P. and Kristensen, R.-M. 1992. Ice formation in the freeze-tolerant eutardigrades *Adorybiotus coronifer* and *Amphibolus nebulosus* studied by differential scanning calorimetry. Polar Biol. 12: 693-699.
- Wright, J. C. 1991. The significance of four xeric parameters in the ecology of terrestrial Tardigrada. J. Zool. 224: 59-77.