

# CHAPTER 5-3

## TARDIGRADE HABITATS



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

### 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). The tropics seem unfavorable (Mathews 1938), perhaps for the same reasons that bryophytes are uncommon in tropical waters – they are warm and wet at the same time.

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 only mosses (and not also liverworts), I used the term bryophytes. I also learned that many ecologists include mosses in the category of "soil"! While this can be a useful concept for functional ecology, one needs to be aware of it when searching for bryological 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.

Yet the 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.

### Altitude

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. 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 2) was one of these "montane" species, but Dastyeh (1985) later reported it from locations between 0 and 1100 m altitude on Spitsbergen Island, Norway. Furthermore, Dastyeh (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.

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 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 *Macrobotus hufelandi* (Figure 3) was absent in the Alabama collections. These data suggest that there may be more than just chance determining the species and abundance differences.

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>Bertolanus</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>	70	318	45	7	40	27	
<i>Diphascon prorsirostre</i>	4	38	16	3	8	5	
<i>Diphascon recamieri</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>Macrobotus crenulatus</i>	1	0	0	0	0	0	
<i>Macrobotus echinogenitus</i> (Figure 4)	0	0	10	79	48	0	737
<i>Macrobotus harmsworthi</i>	177	459	284	44	8	10	
<i>Macrobotus hufelandi</i>	3039	1710	2061	1116	1586	662	
<i>Macrobotus islandicus</i>							1
<i>Macrobotus lazzaroi</i>	10	0	0	0	0	0	
<i>Macrobotus</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>Paramacrobotus</i> [=Macrobotus] <i>areolatus</i>	31	16	0	0	0	0	476
<i>Paramacrobotus</i> [=Macrobotus] <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 suillus</i>	0	0	3	0	0	0	44
<i>Ramazzottius baumanni</i>	18	44	8	7	5	3	
<i>Ramazzottius 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

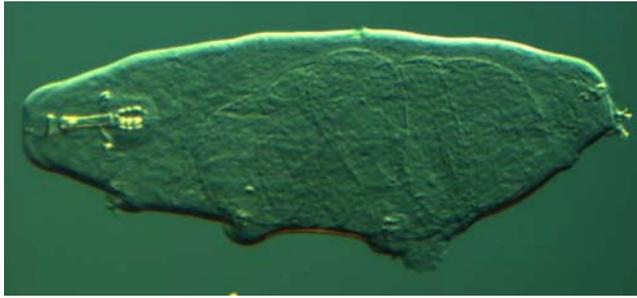


Figure 2. *Macrobiotus harmsworthi*, a common tardigrade on bryophytes and elsewhere. Photo by Paul Bartels.



Figure 3. *Macrobiotus hufelandi*, one of the most abundant tardigrades on bryophytes. Photo by Paul Bartels.



Figure 4. *Macrobiotus echinogenitus*, a tardigrade living on riparian bryophytes at Choccolocco Creek Alabama, USA. Photo by Paul Bartels.

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). 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. Dastyh (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, Dastyh (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. 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. They 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* from continental Antarctica (Figure 5), 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.

Temperature may play a role in the zonation of these Antarctic bryophytes. Bryophyte temperatures in the Antarctic can differ considerably from that 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 6. 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.



Figure 5. *Bryum* cushions in Antarctica, demonstrating the deep turfs that can house tardigrades. Photo by Catherine Beard.

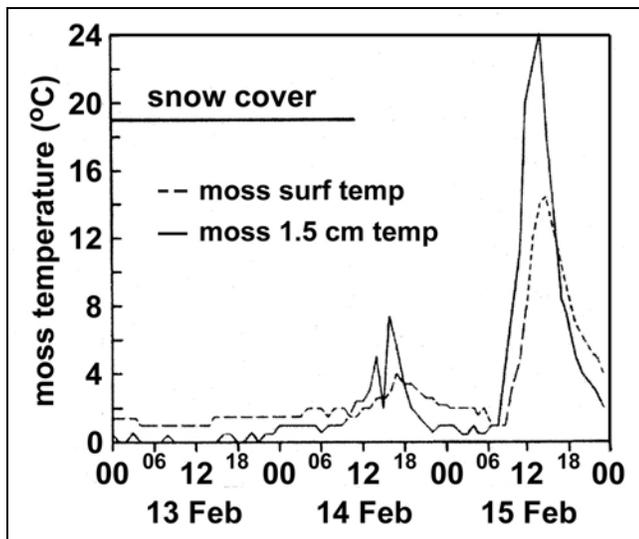


Figure 6. Comparison of moss surface temperature with that of 1.5 cm depth in moss cover on Signy Island in the Antarctic on three days in February, 1973. Redrawn from Jennings 1979.

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.

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 6).

Both *Bertolanius nebulosus* and *Richtersius coronifer* (Figure 7) endure ice formation as they proceed through the onset of freezing temperatures (Westh & Kristensen 1992). Both are able to supercool to  $-6$  or  $-7^{\circ}\text{C}$  before they succumb to freezing. These two tardigrades are common in Polar areas, as well as elsewhere. *Richtersius coronifer*

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

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  $-80^{\circ}\text{C}$  for six years and two months. They then rapidly thawed the liverwort at  $10^{\circ}\text{C}$ . You guessed it! Tardigrades survived, along with nematodes and a bdelloid rotifer. Only two individuals [*Diphasco* sp. (see Figure 8), *Hypsibius* cf. *dujardini* (Figure 9)] out of fifteen tardigrades (13%) made it, but that is still remarkable! The eleven individuals of *Macrobiotus furciger* and one of *Echiniscus* sp. did not. Nematodes fared a bit better, with 31% survival out of 159 individuals.



Figure 8. *Diphasco scoticum*, a moss-dwelling representative of a genus in which one member survived storage at  $-80^{\circ}\text{C}$  for six years! Photo by Łukasz Kaczmarek.

Sømme and Terje Meier (1995) examined *Echiniscus jenningsi*, *Macrobiotus furciger*, and *Diphasco chilense* from Mühlhlig-Hofmannfjella, Dronning Maud Land, Antarctica to ask similar winter survival questions. They compared both hydrated and dehydrated individuals. After 600 days at  $-22^{\circ}\text{C}$ , both hydrated and dehydrated

tardigrades had high survival rates. After 3040 days, the dry individuals still had a high rate of survival. However, at  $-80^{\circ}\text{C}$  hydrated *Echiniscus jenningsi* did not fare as well as the others, decreasing in survivorship as time increased from 7 to 150 days. At  $-180^{\circ}\text{C}$ , all hydrated individuals of these three species rapidly died, but all dehydrated species had good survivorship after 14 days at  $-180^{\circ}\text{C}$ .



Figure 9. *Hypsibius dujardini*, a species that survived  $-80^{\circ}\text{C}$  for six years. Photo by Rpgch Wikimedia Commons.

It is incredible that some Antarctic tardigrades can survive temperatures as low as  $-80^{\circ}\text{C}$  in a **hydrated** state (Sømme & Meier 1995; Sømme, 1996)! The ability to survive short periods in a hydrated condition just below freezing 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 them 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 their ability 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 3), collected from the Qinling Mountains in central China. They acclimated the water bears to 2 and  $22^{\circ}\text{C}$  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 animals 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 were provided at the new temperature before measurements began, lasting another 3-

5 minutes. The next question to ask is how fast can the tardigrades acclimate to a new temperature?

### 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 diana*, *Isohypsibius sattleri*, *Platicrista angustata*, *Diphascon belgicae*, *D. pingue*). 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 10) was by far the most abundant. The wet growth form seemed to harbor more tardigrades than did other bryophyte growth forms.

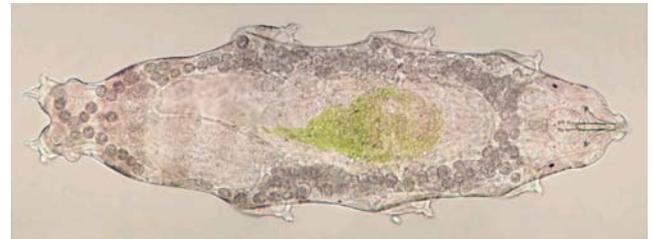


Figure 10. *Macrobiotus hufelandi*. Photo by Martin Mach.

### Epiphytes

Whereas forest floor bryophyte dwellers are protected by snow in winter, bryophytes on trees (**epiphytes**) are typically 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 *Ulotia crispa* (Figure 11) 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 10)
- Milnesium tardigradum* (Figure 12)
- Minibiotus* cf. *pustulatus*
- Paramacrobiotus tonollii*
- Pseudechiniscus*



Figure 11. *Ulota crispa*, an epiphytic moss that houses a number of tardigrade species. Photo by Michael Lüth.

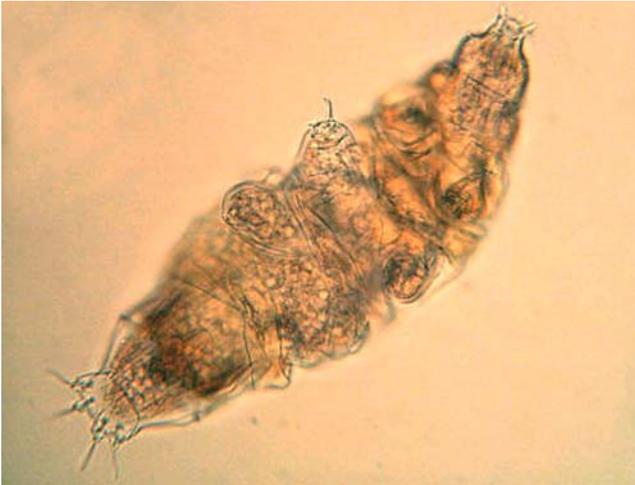


Figure 12. *Milnesium tardigradum*. A cosmopolitan bryophyte inhabitant. Photo by Martin Mach.

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 *Macrobotus* species (Figure 2 - Figure 4) 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. 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.

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 low in the Alabama, USA, riparian sites (Table 1), with only twelve species overall (Romano *et al.* 2001). Mosses included *Anomodon* (Figure 13), *Leucodon* (Figure 14), and *Schwetschkeopsis* (Figure 15), all epiphytes.



Figure 13. *Anomodon rugelii*, an epiphytic moss. Photo by Michael Lüth.



Figure 14. *Leucodon sciurooides*, an epiphytic moss that compresses and curls its branches upward when it dries. Photo by Michael Lüth.

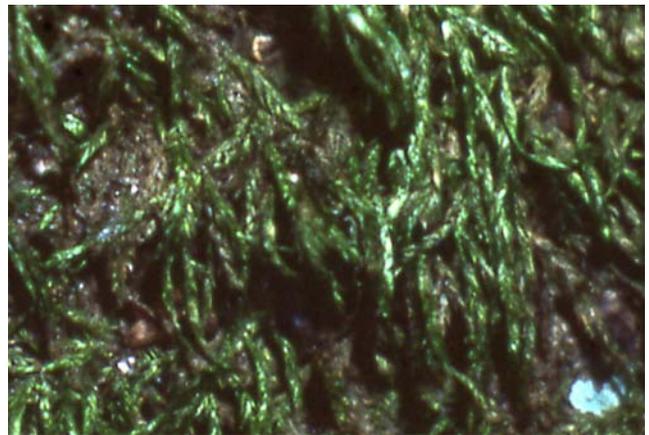


Figure 15. *Schwetschkeopsis fabronia*, an epiphyte from Asia and North America. Photo by Janice Glime.

As in the Alabama study, Jerez Jaimes (2003) found a low diversity of only seven species on the moss *Calymperes palisotii* (Figure 16) 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). Meyer also found no specificity for a particular bryophyte, but there was specificity for bryophytes as opposed to foliose lichens. 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 dry periods.



Figure 16. *Calymperes palisotii*, a moss that had the lowest tardigrade diversity on the University of Puerto Rico campus, Mayagüez. Photo by Claudio Delgadillo Moya.

*Diphascon* [= *Hypsibius*] *scoticum* (Figure 17), 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.

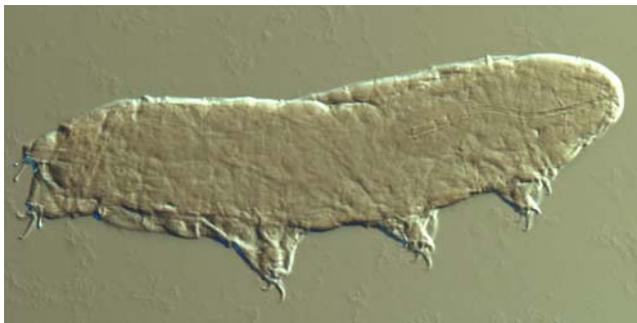


Figure 17. *Diphascon scoticum*, a very common tardigrade, one that has been found among mosses on logs. Photo by Paul Bartels.

## 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, Suren (1993) found that tardigrades were only 1.2% of the invertebrates collected among mosses in 103 streams.

In streams, flow velocity may cause tardigrades to seek refuge among mosses. Suren (1992) reported high densities of tardigrades (*Dactylobiotus* [= *Macrobiotus*] *dispar*; Figure 18 - Figure 19) associated with mosses in alpine streams of New Zealand. He suggested that the high periphyton biomass 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 (UFPM). The abundance of tardigrades on bryophytes was 10 times that found on stream gravel.

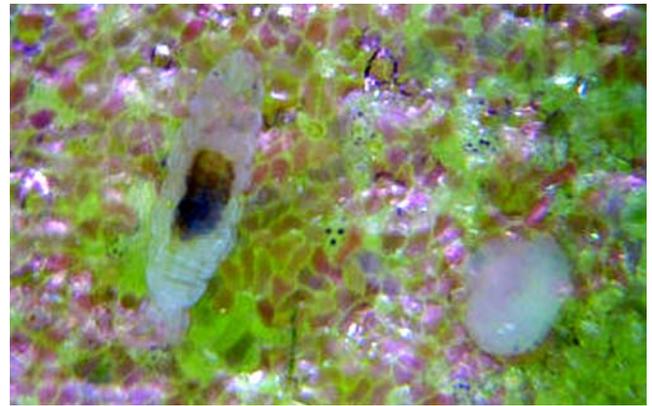


Figure 18. *Dactylobiotus* [= *Macrobiotus*] *dispar*. Photo by Martin Mach.



Figure 19. *Dactylobiotus* [= *Macrobiotus*] *dispar*. Photo by Martin Mach.

Linhart *et al.* (2002) examined scattered clumps of the aquatic moss *Fontinalis antipyretica* (Figure 20) 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 20. *Fontinalis antipyretica* in flowing water. Photo by Michael Lüth.

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 a challenging life for a tardigrade. Shcherbako *et al.* (2010) found that *Milnesium tardigradum* (Figure 12) 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 (using 22 animals), 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 19) 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.

Hingley (1993) found only two taxa in her peatland studies: *Diphascion scoticum* (Figure 17) and *Macrobiotus*. To that Pilato (2009) added *Bindius triquetrus* from *Sphagnum* 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?

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* 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).

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 21 - Figure 22), a well-known rock-forming moss, above the wet zone.



Figure 21. *Barbula* [= *Didymodon*] *tophacea*, an emergent moss known to house 84 tardigrades per gram. Photo by Michael Lüth.



Figure 22. *Barbula* [= *Didymodon*] *tophacea*, an emergent moss showing the numerous possibilities for resting in leaf axils. Photos by Michael Lüth.

### 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* 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 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 23) 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 *Macrobiotus hufelandi* (Figure 10), 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 earlier, there seems to be little or no evidence for vertical position differences or migration in mosses; only one tardigrade (*Echiniscus viridissimus*) seems more common near the upper portion of the moss (Nelson & Adkins 2001).



Figure 23. Eyespots of *Milnesium tardigradum*. Photo by Martin Mach.

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 *Rhytidiadelphus loreus* (Figure 24). 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 CO<sub>2</sub> 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 CO<sub>2</sub> kept the tardigrades from occupying lower positions and that temperature might cause migrations within the upper portion.



Figure 24. *Rhytidiadelphus loreus*. Photo by Michael Lüth.

## 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*, *Diphyscon*, 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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