Glime, J. M. 2017. Tardigrades: Species Relationships. Chapt. 5-4. In: Glime, J. M. Bryophyte Ecology. Volume 2. Bryological Interaction. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 18 July 2020 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology2/>.

CHAPTER 5-4 TARDIGRADES: SPECIES RELATIONSHIPS

TABLE OF CONTENTS

CHAPTER 5-4 TARDIGRADES: SPECIES RELATIONSHIPS

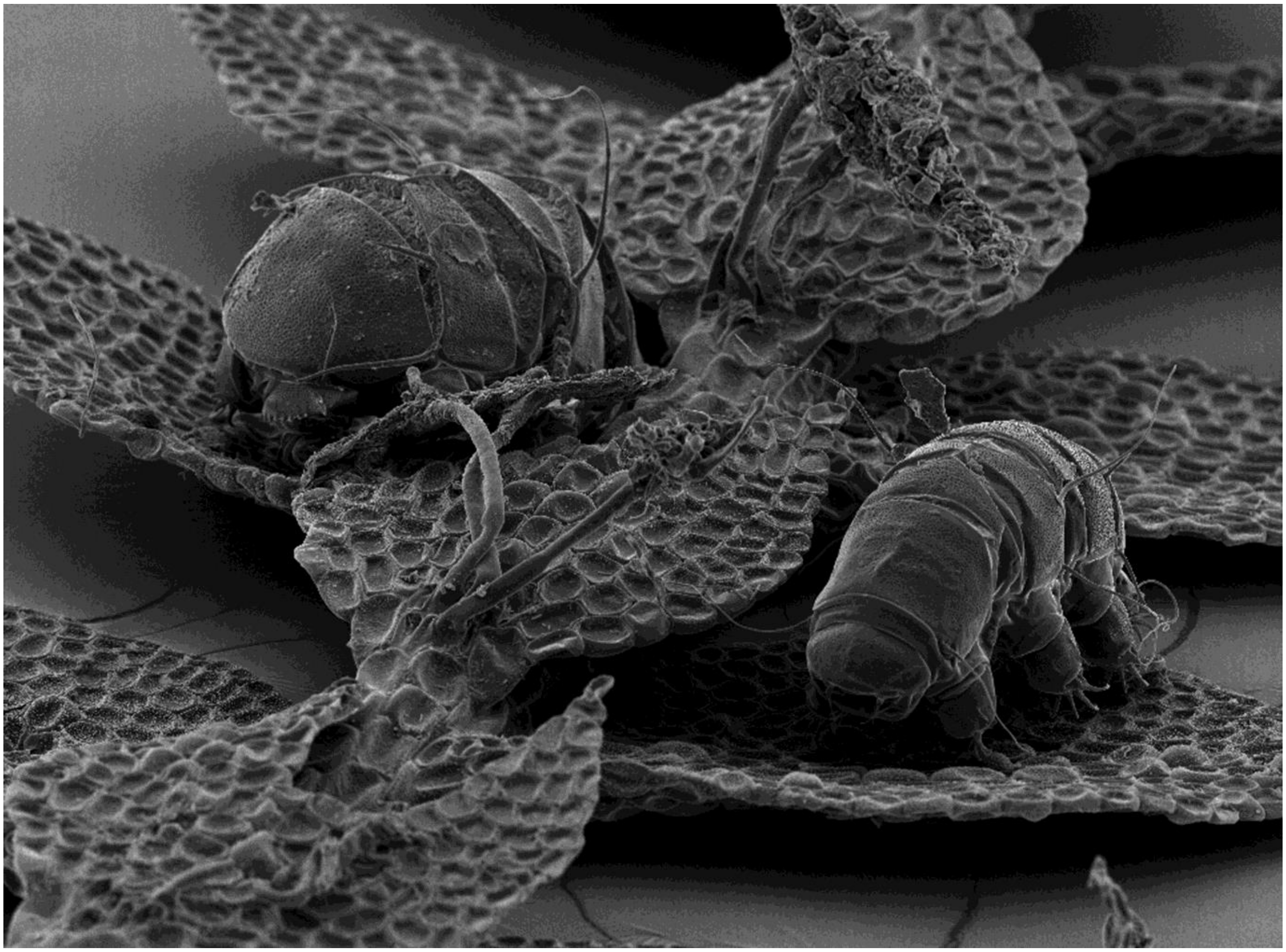

Figure 1. SEM of tardigrades on a leafy liverwort. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Species Relationships

Tardigrades occur on both mosses and liverworts (Figure 1). Since bryophytes vary widely in structure, compactness, and moisture-holding nature, one would expect that some bryophytes would be more suitable for tardigrades than others, causing specificity. But is that really the case?

Although Hofmann and Eichelberg (1987), in Lahnau near Giessen, Germany, found a correlation between species of tardigrade and degree of moisture in their preferred mosses, there seemed to be no example of a single species of tardigrade preferring a single species of moss. It appeared that species of bryophyte was not an important factor for most tardigrades.

A number of studies name the bryophytes where the tardigrades have been found, but quantitative approaches are limited. For example, Degma (2006) found ***Echiniscus reticulatus*** on the moss ***Ctenidium molluscum*** (Figure 2) and ***Testechiniscus spitsbergensis*** from the mosses ***Tortella tortuosa*** (Figure 3), ***Ctenidium molluscum*** (Figure 2), ***Distichium capillaceum*** (Figure 4), and ***Ditrichum flexicaule*** (Figure 5-Figure 6) in Slovakia.

Baxter (1979) did find differences in the tardigrades on several moss species in Ireland. These represented different life forms as well as habitats. Some of their more specific finds include stream bank mosses that had ***Diphascon oculatum*** (Figure 7). ***Polytrichum*** (Figure 8), with its more open structure, had ***Diphascon scoticum*** (Figure 9). ***Hypsibius dujardini*** (Figure 1) was abundant, accompanied by ***Isohypsibius tuberculatus***, on the turfs of ***Rhytidiadelphus squarrosus*** (Figure 10).

Figure 2. ***Ctenidium molluscum***, a moss that is home to ***Echiniscus reticulatus***, among others. Photo by Michael Lüth, with permission.

Figure 3. ***Tortella tortuosa***, a Slovakian habitat for ***Testechiniscus spitsbergensis***. Photo by Michael Lüth, with permission.

Figure 4. ***Distichium capillaceum***, a known tardigrade habitat. Photo by Michael Lüth, with permission.

Figure 5. ***Ditrichum flexicaule***, a habitat for ***Testechiniscus spitsbergensis***. Photos by Michael Lüth, with permission.

Figure 6. View inside cushion of ***Ditrichum flexicaule***, a habitat for ***Testechiniscus spitsbergensis***. Photos by Michael Lüth, with permission.

Figure 7. ***Diphascon oculatum***, an inhabitant of streambank mosses. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

Figure 8. ***Polytrichum***, a moss with spreading leaves that provide limited tardigrade habitat. Photo by Michael Lüth, with permission.

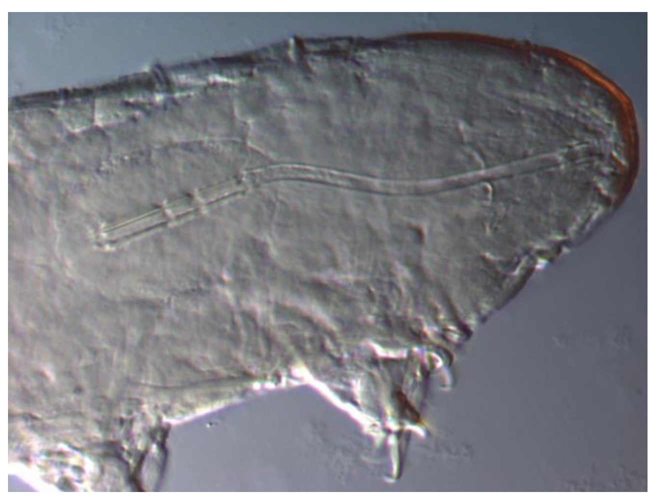

Figure 9. ***Diphascon scoticum***, a tardigrade that is able to inhabit ***Polytrichum***. Photo by Paul J. Bartels, with permission.

Figure 10. ***Rhytidiadelphus squarrosus***, where Baxter (1979) found ***Isohypsibius tuberculatus*** and ***Diphascon scoticum***. Photo by Michael Lüth, with permission.

Figure 11. ***Lembophyllum divulsum***, a home for 16 tardigrade species in New Zealand. Photo by Li Zhang, with permission.

Figure 12. ***Hypnum cupressiforme***, the moss with the most tardigrade species in the New Zealand study by Horning *et al*. (1978), shown here on rock and as a pendant epiphyte. Photos by Michael Lüth, with permission.

Horning *et al*. (1978) examined the tardigrades on 21 species of mosses in New Zealand and listed the tardigrade species on each (Table 1). Some moss species clearly had more tardigrade species than others, ranging from 1 on ***Syntrichia rubra*** to 17 on ***Hypnum cupressiforme*** (Figure 12). ***Lembophyllum divulsum*** (Figure 11) had 16 species.

Hopefully lists like the one provided by Horning *et al*. (1978) will eventually permit us to determine the characteristics that foster tardigrade diversity and abundance. Perhaps the moss ***Hypnum cupressiforme*** (Figure 12) had the most tardigrade species among the mosses in New Zealand because of its own wide habitat range there. However, Degma *et al*. (2005) found that distribution of the number of tardigrade species on this moss in their Slovakia sites was random, as supported by a Chi-square goodness of fit test. But this still does not preclude the assertion that its ubiquitous nature on a wide range of habitats in New Zealand may account for the greater number of species of tardigrades on ***Hypnum cupressiforme*** in the New Zealand study.

A kind of vertical zonation occurs among tardigrades on trees that is the reverse of that sometimes found within a moss cushion. In the Great Smoky Mountains National Park, the number of tardigrade species among epiphytes at breast height was greater than the number of species found at the base (Bartels & Nelson 2006). This may relate to the need for dry periods, but it could also relate to differences in predators and possibly even to dispersal patterns.

In their study of Chinese mosses Beasley and Miller (2007) found that **Heterotardigrada** (armored tardigrades) were better represented than were **Eutardigrada** (unarmored tardigrades), a factor the authors attribute to the **xerophilic** moss samples and the locality, which has hot, dry summers, very cold, dry winters, low summer rainfall, and high winds (Fullard 1968). The Heterotardigrada have armor, which may account for their ability to withstand the dry habitat. These tardigrades also have **cephalic** (head) appendages with a sensorial function, a character lacking in the Eutardigrada, but so far their function has not been related to a bryophyte habitat. Beasley and Miller found little specificity, but most of the mosses were xerophytic and exhibited similar moisture requirements. They did find that ***Echiniscus testudo*** (Figure 13) occurred on a wider variety of mosses than did other tardigrade species.

On Roan Mountain in Tennessee and North Carolina, Nelson (1973, 1975) found no specificity among 21 tardigrade species on 25 bryophyte species. Hunter (1977) in Montgomery County, Tennessee, and Romano *et al*. (2001) in Choccolocco Creek in Alabama, USA, again were unable to find any dependence of tardigrades upon a particular species of bryophyte in their collections.

Table 1. Tardigrade species found on the most common moss taxa in New Zealand. From Horning *et al*. 1978.

Breutelia elongata	*Macrobiotus hibiscus*
	Macrobiotus liviae
	Milnesium tardigradum
	Minibiotus intermedius
Breutelia pendula	*Diphascon prorsirostre*
	Diphascon scoticum
	Doryphoribius zyxiglobus
	Hypechiniscus exarmatus
	Macrobiotus hibiscus
	Macrobiotus liviae
	Milnesium tardigradum
Bryum campylothecium	*Hypsibius convergens*
	Isohypsibius sattleri
	Minibiotus intermedius
Bryum dichotomum	*Hypsibius wilsoni*
	Macrobiotus coronatus
	Macrobiotus liviae
Bryum truncorum	*Diphascon chilenense*
	Diphascon scoticum
	Isohypsibius sattleri
	Isohypsibius wilsoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus liviae
	Macrobiotus recens
	Paramacrobiotus areolatus
	Paramacrobiotus richtersi
	Ramazzottius oberhaeuseri
Dicranoloma billardieri	*Hypechiniscus exarmatus*
	Macrobiotus hibiscus
Dicranoloma grossialare	*Diphascon prorsirostre*
	Hypechiniscus exarmatus
	Hypsibius dujardini
	Isohypsibius cameruni
	Isohypsibius sattleri
	Limmenius porcellus
	Macrobiotus anderssoni
	Macrobiotus hibiscus
	Macrobiotus liviae
	Milnesium tardigradum
	Pseudechiniscus novaezeelandiae
Dicranoloma menziesii	*Macrobiotus hibiscus*
	Macrobiotus liviae
	Paramacrobiotus areolatus
Dicranoloma robustum	*Echiniscus bigranulatus*
	Macrobiotus anderssoni
	Macrobiotus furciger
	Macrobiotus liviae
	Milnesium tardigradum
	Pseudechiniscus juanitae
Dicranoloma trichopodum	*Echiniscus quadrispinosus*
	Echiniscus q. brachyspinosus
	Macrobiotus furciger
	Pseudechiniscus lateromamillatus
Hypnum cupressiforme	*Diphascon alpinum*
	Diphascon bullatum
	Echiniscus quadrispinosus
	Echiniscus spiniger
	Hypsibius dujardini
	Macrobiotus anderssoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus hibiscus
	Macrobiotus liviae
	Macrobiotus recens
	Milnesium tardigradum
	Oreella mollis
	Paramacrobiotus areolatus
	Pseudechiniscus novaezeelandiae
	Pseudechiniscus juanitae
	Ramazzottius oberhaeuseri
Lembophyllum divulsum	*Diphascon alpinum*
	Doryphoribius zyxiglobus
	Hypsibius convergens
	Isohypsibius sattleri
	Macrobiotus anderssoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus hibiscus
	Macrobiotus liviae
	Macrobiotus recens
	Macrobiotus subjulietae
	Milnesium tardigradum
	Minibiotus intermedius
	Paramacrobiotus areolatus
	Pseudechiniscus novaezeelandiae
	Pseudechiniscus juanitae
Macromitrium erosulum	*Macrobiotus furciger*
	Macrobiotus hibiscus
	Macrobiotus liviae
	Pseudechiniscus juanitae
Macromitrium longipes	*Doryphoribius zyxiglobus*
	Hypsibius convergens
	Macrobiotus recens
	Minibiotus intermedius
Porotrichum ramulosum	*Diphascon alpinum*
	Diphascon scoticum
	Doryphoribius zyxiglobus
	Echiniscus bigranulatus
	Hypsibius convergens
	Macrobiotus anderssoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus hibiscus
	Macrobiotus liviae
	Macrobiotus rawsoni
	Minibiotus aculeatus
	Pseudechiniscus lateromamillatus
	Pseudechiniscus novaezeelandiae
	Pseudechiniscus juanitae
Racomitrium crispulum	*Calohypsibius ornatus*
	Diphascon alpinum
	Echiniscus quadrispinosus
	Echiniscus zetotrymus
	Hebesuncus conjungens
	Hypsibius convergens
	Isohypsibius wilsoni
	Macrobiotus anderssoni
	Macrobiotus coronatus
	Macrobiotus furciger
	Macrobiotus hibiscus
	Macrobiotus orcadensis
	Milnesium tardigradum
	Oreella minor
	Paramacrobiotus areolatus
	Pseudechiniscus juanitae
Racomitrium lanuginosum	*Diphascon scoticum*
	Echiniscus quadrispinosus brachyspinosus
	Echiniscus vinculus
	Hebesuncus conjungens
	Macrobiotus furciger
	Milnesium tardigradum
	Minibiotus intermedius
	Oreella mollis
	Pseudechiniscus juanitae
Racomitrium ptychophyllum	*Echiniscus quadrispinosus*
	Echiniscus velaminis
	Hebesuncus conjungens
	Hypechiniscus exarmatus
	Hypsibius dujardini
	Macrobiotus furciger
	Milnesium tardigradum
	Minibiotus intermedius
	Oreella mollis
Syntrichia princeps	*Hypsibius convergens*
	Ramazzottius oberhaeuseri
	Isohypsibius wilsoni
	Macrobiotus coronatus
	Macrobiotus recens
	Milnesium tardigradum
	Pseudechiniscus novaezeelandiae
Syntrichia rubra	*Diphascon scoticum*
Tortula subulata var. *serrulata*	*Diphascon scoticum*
	Paramacrobiotus areolatus

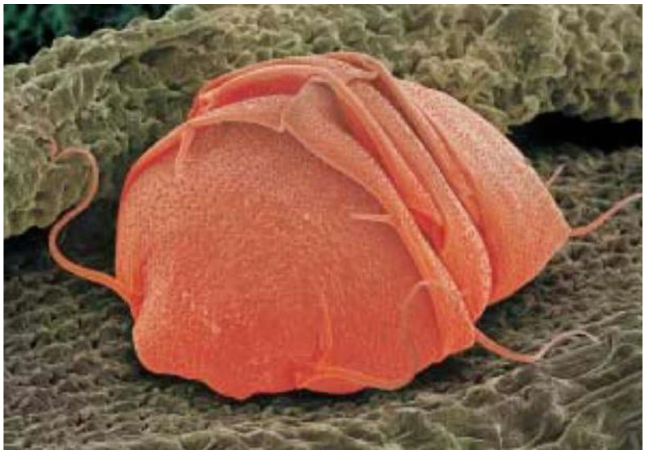

Figure 13. ***Echiniscus testudo*** tun. Photo by Power & Syred through Creative Commons.

Hofmann developed a preference coefficient:

$$P_n = (T_n/S_n) \sum_{i=1}^{n} 100(T_i/S_i)$$

where P = preference index for category n of observed factor
n = index of observed category
T = number of tardigrade populations of a single species
S = number of samples in category

The preference indices will add up to 100%. The categories can be the five bryophyte habitat groups listed by Mihelčič 1954/55, 1963; Ramazzotti 1962, and Hofmann 1987 or other groupings defined for the purpose.

Table 2. Distribution of tardigrades on specific mosses in Xinjiang Uygur Region, China, based on herbarium specimens. From Beasley & Miller 2007.

tardigrade	numb/samples	moss
Bryodelphax asiaticus	1/1	*Pseudoleskeella catenulata*
Cornechiniscus holmeni	18/5	*Grimmia tergestina* *Mnium laevinerve* *Schistidium* sp.
Echiniscus blumi	4/4	*Abietinella abietina* *Schistidium* sp.
Echiniscus canadensis	82/7	*Grimmia laevigata* *Grimmia ovalis* *Grimmia tergestina*
Echiniscus granulatus	8/3	*Grimmia longirostris* *Schistidium trichodon* *Schistidium* sp.
Echiniscus testudo	11/4	*Grimmia anodon* *Grimmia longirostris* *Grimmia tergestina* *Lescuraea incurvata* *Pseudoleskeella catenulata* *Schistidium* sp.
Echiniscus trisetosus	33/5	*Abietinella abietina* *Grimmia ovalis* *Pseudoleskeella catenulata*
Macrobiotus mauccii	2/2	*Schistidium* sp.
Milnesium asiaticum	10/4	*Grimmia anodon* *Grimmia tergestina* *Grimmia ovalis* *Schistidium* sp.
Milnesium longiungue	4/2	*Grimmia laevigata* *Grimmia ovalis*
Milnesium tardigradum	5/4	*Grimmia tergestina* *Grimmia ovalis* *Orthotrichum* sp.
Paramacrobiotus alekseevi	5/4	*Brachythecium albicans* *Schistidium* sp.

Table 3. Preference of moss species by tardigrades, using five moss species plus the remaining species combined (total = 43 species) as the habitat categories, based on 106 samples from Giessen, Germany (Hofmann 1987).

	Ceratodon purpureus	***Grimmia pulvinata***	***Bryum argenteum***	***Syntrichia ruralis***	***Syntrichia montana***	Other
samples (%)	19	9	7	7	6	52
Macrobiotus hufelandi	16	18	18	18	21	8
Ramazzottius oberhaeuseri	18	27	29	17	0	8
Milnesium tardigradum	13	23	15	20	23	6
Echiniscus testudo	11	20	20	9	34	6
mean	14.5	22.0	20.0	16.0	19.5	7.0
empty samples	25	7	9	9	11	38

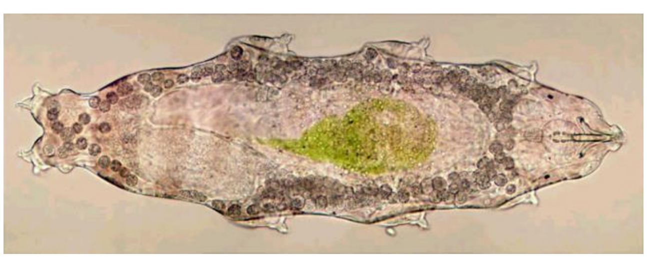

Figure 14. ***Macrobiotus hufelandi***. Photo by Martin Mach, with permission.

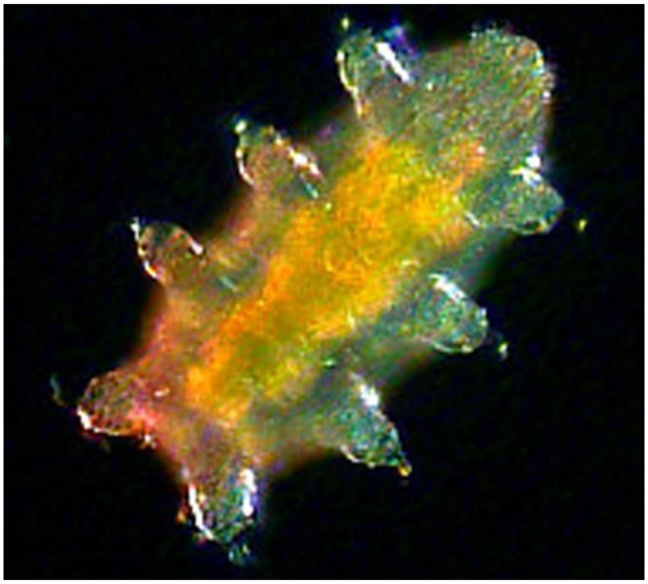

Figure 15. Adult ***Echiniscus*** sp.. Photo by Martin Mach, with permission.

Kathman and Cross (1991) found that species of bryophyte had no influence on the distribution or abundance of tardigrades from five mountains on Vancouver Island, British Columbia, Canada. In fact, Kathman and Cross (1991) were unable to find any correlation with altitude or aspect throughout a span from 150 to 1525 m. They concluded that it was the presence of bryophyte that determined tardigrade presence, not the species of bryophyte, altitude, or locality. Despite a lack of specificity among the tardigrades, 39 species inhabited these 37 species of mountain bryophytes, comprising 14,000 individuals. Several researchers contend that any terrestrial species of tardigrade can be found on any species of moss, given the "appropriate microhabitat conditions" (Bertrand 1975; Ramazzotti & Maucci 1983). If these tardigrade bryophyte specialists find no differences among the bryophytes, can we blame the ecologists for lumping all the bryophytes in their studies as well?

In collections from Giessen, Germany, the most common tardigrade species, the cosmopolitan ***Macrobiotus hufelandi*** (Figure 14), had no preference for any moss species (Hofmann 1987). But lack of influence of bryophyte species may not always be the case. Hofmann (1987) used a preference index to show that four out of sixteen tardigrades from Giessen had distinct preferences among five moss species and that they seemed to prefer cushion mosses over sheet mosses. Also contrasting with the above researchers, Bertolani (1983) found that there seemed to be a species relationship between tardigrades and coastal dune mosses. It is possible that this is again related to moisture. The moisture relationship might also explain why mosses on rotten logs seem to have few tardigrades. Could it be that they are too wet for too long?

Meyer (2006a, b, 2008) found 20 species of tardigrades among 47 species of mosses, liverworts, lichens, and ferns in Florida. There were some tardigrade species that were significantly associated with either mosses or lichens, but, as in most other studies, there was no convincing evidence for associations with any plant species substratum. Despite the lack of substrate specificity, there were three significant negative associations and one positive association between species of tardigrades. Likewise, in Georgia and the Gulf Coast, USA, Hinton and Meyer (2007) found ***Milnesium tardigradum*** (Figure 16), ***Minibiotus intermedius*** (Figure 39), and ***Minibiotus furcatus*** among mosses, whereas ***Echiniscus cavagnaroi***, ***E. kofordi*** (see Figure 15), and ***Minibiotus fallax*** were in both mosses and lichens.

Figure 16. ***Milnesium tardigradum***, an inhabitant of both mosses and liverworts. Photo by Björn Sohlenius, Swedish Museum of Natural History.

Life Forms

There is some indication that species differences may exist, based on life form. The bryophyte form can affect the moisture-holding capacity and rate of loss of moisture. That foregoing evidence suggests that the moisture-holding capacity of cushion mosses was probably a desirable trait in that habitat. On the other hand, Beasley (1990) found that more samples of clubmosses (Lycopodiaceae – tracheophytes) (75%) had tardigrades than did mosses (46%) or liverworts (0%) in Gunnison County, Colorado.

There seems to be a preference for cushions among the most common species [***Macrobiotus hufelandi*** (Figure 14), ***Ramazzottius oberhaeuseri*** (Figure 17), ***Milnesium tardigradum*** (Figure 16), and ***Echiniscus testudo*** (Figure 13)] (Hofmann 1987). But the less frequent species are commonly found among sheet mosses. The ubiquitous ***Macrobiotus hufelandi*** seems to have no preference for moss shape.

Figure 17. ***Ramazzottius oberhaeuseri***. Photo by Martin Mach, with permission.

Jönsson (2003), working in the forests of Sweden, found that wefts had more tardigrades than other moss forms. Kathman and Cross (1991) likewise found that tardigrades from Vancouver Island were more common on weft-forming mosses than on turfs, suggesting that the thick carpets of the wefts were more favorable habitat than the thinly clustered turfs with their thick rhizoidal mats and attached soil. Contrasting with some of these findings, and the preference for cushion mosses in the study by Hofmann (1987), Diane Nelson (East Tennessee State University, Johnson City, pers. comm. in Kathman & Cross 1991) found no preference for sheet or cushion mosses in her Roan Mountain, Virginia, USA study. Rather, those tardigrades were more common in thin, scraggly mosses or in small tufts than in thick cushion mosses.

Sayre and Brunson (1971) compared tardigrade fauna on mosses in 26 North American collections from a variety of habitats and substrata (Figure 18). They found that mosses of short stature in the **Thuidiaceae** (Figure 19) and **Hypnaceae** (Figure 20) had the highest frequencies of tardigrades. Other moss-dwellers were found in fewer numbers on members of the moss families **Orthotrichaceae** (epiphytic and rock-dwelling tufts; Figure 21), **Leucobryaceae** (cushions on soil and tree bases; Figure 22), **Polytrichaceae** (tall turfs on soil; Figure 23), **Plagiotheciaceae** (low mats on soil and tree bases; Figure 24), and **Mniaceae** (mats & wefts on soil; Figure 25).

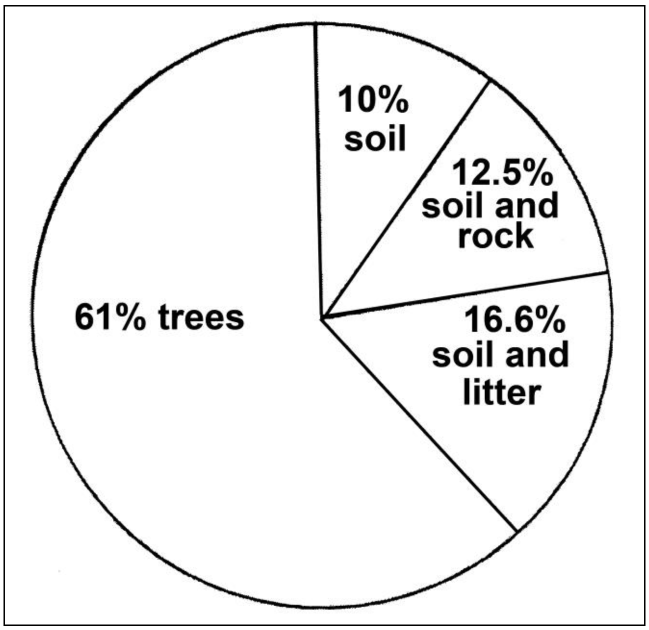

Figure 18. Relative frequency of tardigrades on bryophytes of various North American substrata. Redrawn from Sayre & Brunson 1971.

Figure 19. ***Thuidium delicatulum*** (Thuidiaceae), a low-stature moss that is a good tardigrade habitat. Photo by Michael Lüth, with permission.

Figure 20. ***Hypnum revolutum*** (Hypnaceae), representing a family that includes low-stature mosses that had among the highest frequencies of tardigrades in 26 North American collections (Sayre & Brunson 1971). Photo by Michael Lüth, with permission.

Figure 21. ***Orthotrichum pulchellum***, an epiphytic moss in the **Orthotrichaceae**. This family is among those with lower numbers of tardigrades in the North American study of Sayre & Brunson (1971) compared to families of mat-forming species. Photo by Michael Lüth, with permission.

Figure 22. ***Leucobryum glaucum***, a cushion moss in the **Leucobryaceae**. This family of mosses had lower numbers of tardigrades than those found in the mat-forming mosses in 26 North American collections (Sayre & Brunson 1971). Photo by Michael Lüth, with permission.

Figure 23. ***Polytrichum juniperinum***, a moss in the Polytrichaceae. This family of mosses tends to have low numbers of tardigrades (Sayre & Brunson 1971). The tardigrades do live among them often nestle in the leaf bases where water evaporates more slowly. Photo by Michael Lüth, with permission.

Figure 24. ***Plagiothecium denticulatum***, a low-growing soil moss in **Plagiotheciaceae**, a family with limited numbers of tardigrade dwellers (Sayre & Brunson 1971). The flattened growth habit provides few protective chambers, perhaps accounting for the lower numbers. Photo by Michael Lüth, with permission.

Figure 25. ***Plagiomnium cuspidatum***, a soil moss in the **Mniaceae**, a family with limited numbers of tardigrade dwellers (Sayre & Brunson 1971). The spreading nature of the vertical shoots and the flattened nature of the horizontal shoots would most likely not provide many protective chambers for the tardigrades. Photo by Michael Lüth, with permission.

Collins and Bateman (2001), studying tardigrade fauna of bryophytes in Newfoundland, Canada, found that rate of desiccation of the mosses affected distribution of tardigrades, and this suggests that bryophyte species and life forms that dehydrate quickly should have fewer individuals and probably different or fewer species than those that retain water longer. In different climate regimes, that rate will differ. This may explain a preference for cushions in some locations and not in others. Data are needed on humidity within the various life forms of bryophytes, correlated with tardigrade densities, to try to explain why different life forms seem to be preferred in different locations.

Liverworts

I would expect liverworts, with their flat structure, to have at least some differences in tardigrade communities (Figure 1). But reports on liverwort inhabitants are limited, at least in part due to lack of knowledge about bryophytes on the part of the tardigrade specialists and an equal lack of knowledge of tardigrades by bryologists. Hinton and Meyer (2009) found two species of tardigrades [***Milnesium tardigradum*** (Figure 16) and ***Macrobiotus hibiscus***], both also common among mosses, in samples of the liverwort ***Jungermannia*** sp. (Figure 26). In the Gulf Coast states, USA, Hinton and Meyer (2007) found ***Echiniscus virginicus*** among liverworts.

Figure 26. The leafy liverwort ***Jungermannia sphaerocarpa***, representing a genus from which tardigrades are known. Photo by Michael Lüth, with permission.

Liverworts may actually house some interesting differences as a result of their underleaves (Figure 27) and flattened life form (Figure 28). In their New Zealand study, Horning *et al*. (1978) found that among the liverworts (Table 4), ***Porella elegantula*** (Figure 27) had the most species (16). The folds and underleaves of this genus form tiny capillary areas where water is held, perhaps accounting for the large number of species. Interestingly, the tardigrade ***Macrobiotus snaresensis*** occurred on several liverwort species [4 ***Lophocolea*** species, ***Plagiochila deltoidea*** (Figure 29)], but did not appear in any moss collections. Of 150 liverwort samples (26 species), 27% had tardigrades, with a total of 16 species, mean of 2.8 species, range 1-9. In 107 samples of foliose lichens, 60.7% had tardigrades, mean 2.2 species, range 1-11.

Figure 27. ***Porella elegantula***, showing the underleaves and folds that create numerous capillary spaces. Photo by Jan-Peter Frahm, with permission.

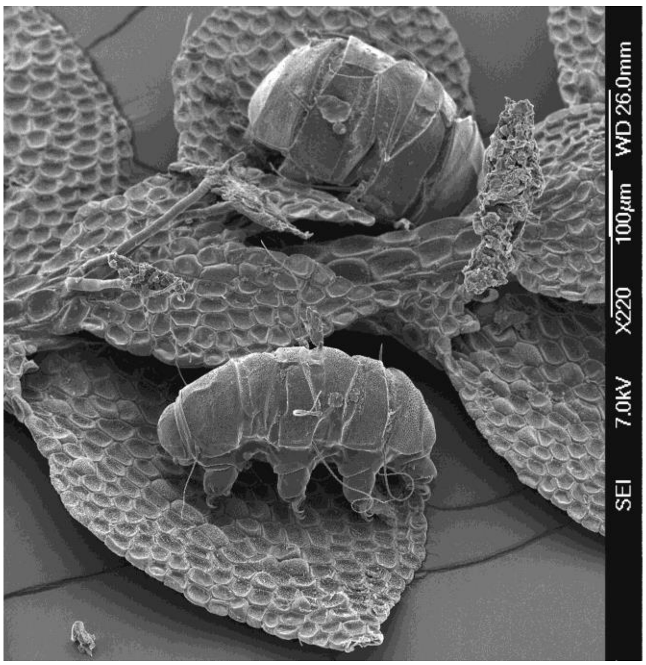

Figure 28. Underside of leafy liverwort with two tardigrades. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Figure 29. ***Plagiochila deltoidea***, a leafy liverwort that forms large patches in wet ground in New Zealand. This is a known habitat for tardigrades. Photo by Clive Shirley, Hidden Forest <http://www.hiddenforest.co.nz>, with permission.

It appears that at least some other researchers have paid attention to liverworts. Christenberry (1979) found ***Echiniscus kofordi*** and ***E. cavagnaroi*** on liverworts in Alabama, USA. Hinton and Meyer (2009) found ***Milnesium tardigradum*** (Figure 16) and ***Macrobiotus hibiscus*** in a liverwort sample from Georgia, USA. Michalczyk and Kaczmarek (2006) found a new species, ***Paramacrobiotus magdalenae*** (Figure 30, Figure 31), on liverworts in Costa Rica. Newsham *et al*. (2006) identified the tiny leafy liverwort ***Cephaloziella varians*** and used it to experiment on the effects of low temperature storage on tardigrades and other Antarctic invertebrates.

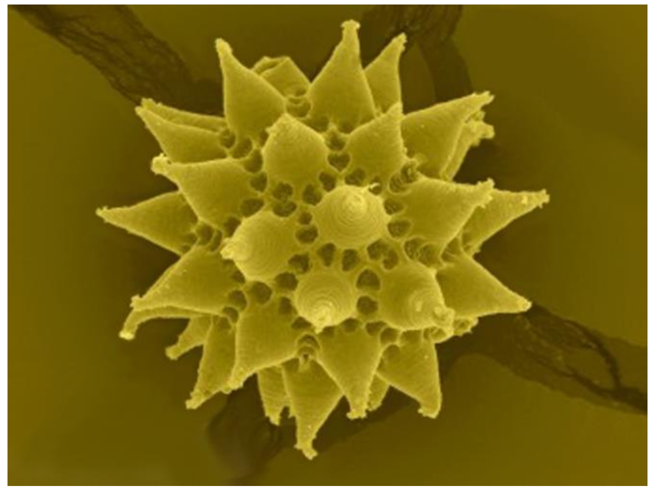

Figure 30. ***Paramacrobiotus magdalenae*** egg. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

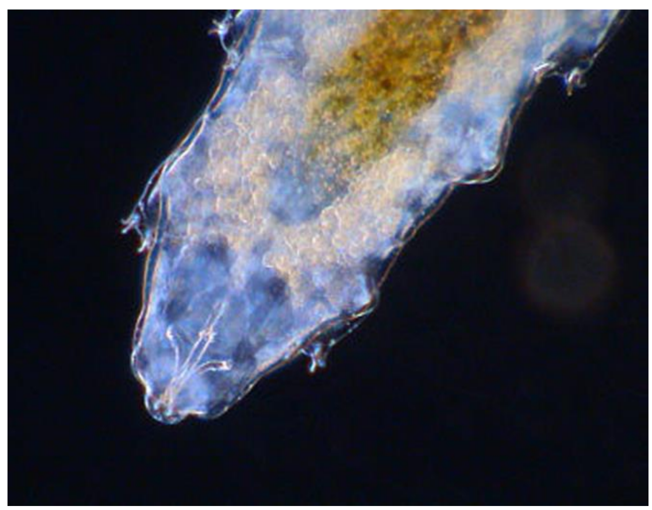

Figure 31. ***Paramacrobiotus areolatus***. Photo by Martin Mach, with permission.

Just what do we mean by "appropriate habitat conditions"? The bryophytes only occur in conditions that are appropriate for them, hence defining the conditions for the tardigrades. And the bryophytes create habitat conditions of moisture due to their morphology and substrate preference. Lack of species preference in many studies may result from methods that were insensitive to subtle differences or that failed to control for microhabitat differences. Usually no statistical tests were employed, sample sizes were small, and enumeration was often simple presence/absence data.

Table 4. Species of tardigrades found on 13 liverwort species in New Zealand and surrounding islands. From Horning *et al.* 1978.

Liverwort Species	Tardigrade Species
Lophocolea innovata	*Macrobiotus snaresensis*
Lophocolea. minor	*Macrobiotus snaresensis*
Lophocolea. subporosa	*Macrobiotus snaresensis*
Lophocolea semiteres	*Diphascon chilenense*
	Macrobiotus coronatus
Lophocolea subporosa:	*Diphascon scoticum*
	Hypsibius dujardini
	Macrobiotus snaresensis
Lophocolea sp.	*Macrobiotus liviae*
Metzgeria decipiens	*Echiniscus spiniger*
	Isohypsibius sattleri
	Paramacrobiotus areolatus)
	Macrobiotus furciger
	Macrobiotus coronatus
	Minibiotus intermedius
	Macrobiotus liviae
	Macrobiotus snaresensis
	Milnesium tardigradum
	Pseudechiniscus novaezeelandiae
Metzgeria decrescens	*Diphascon scoticum*
	Macrobiotus recens
	Macrobiotus snaresensis
	Milnesium tardigradum
Plagiochila deltoidea	*Echiniscus bigranulatus*
	Hypechiniscus exarmatus
	Hypsibius convergens
	Isohypsibius cameruni
	Macrobiotus anderssoni
	Macrobiotus liviae
	Macrobiotus recens
	Macrobiotus snaresensis
Plagiochila fasciculata	*Diphascon scoticum*
	Macrobiotus furciger
Plagiochila obscura	*Macrobiotus coronatus*
	Macrobiotus liviae
	Pseudechiniscus juanitae
Plagiochila strombifolia	*Macrobiotus anderssoni*
	Macrobiotus furciger
Porella elegantula	*Doryphoribius zyxiglobus*
	Echiniscus vinculus
	Diphascon alpinum
	Diphascon bullatum
	Diphascon prorsirostre
	Hypsibius convergens
	Isohypsibius sattleri
	Macrobiotus anderssoni
	Macrobiotus furciger
	Macrobiotus coronatus
	Macrobiotus hibiscus
	Minibiotus intermedius
	Minibiotus aculeatus
	Macrobiotus liviae
	Milnesium tardigradum
	Pseudechiniscus novaezeelandiae

Substrate Comparisons

Meyer (2006b) extended the comparison of substrata in Florida, USA, to include not only liverworts, mosses, and foliose lichens, but also ferns. He found 20 species of tardigrades on 47 species of plants and lichens. They found that some species were positively associated with mosses or with foliose lichens, but as in most other studies, there was no association with any particular plant or lichen species.

Guil *et al*. (2009a) reviewed tardigrades and their habitats (altitude, habitat characteristics, local habitat structure or dominant leaf litter type, and two bioclimatic classifications), including bryophytes and leaf litter at various elevations. They were able to show some habitat preference. Species richness was most sensitive to bioclimatic classifications of macroenvironmental gradients (soil and climate), vegetation structure, and leaf litter type. A slight altitude effect was discernible. These relationships suggest that differences among bryophyte species should exist where bryophyte species occupy different environmental types or maintain different microenvironments within a habitat. But it also suggests that within the same habitat, bryophytes of various life forms should provide different moisture regimes, hence creating species relationship differences.

In a different study in the Iberian Peninsula (extreme southwestern Europe), Guil *et al*. (2009b) found that leaf litter habitats showed high species richness and low abundances compared to rock habitats (mosses and lichens), which had intermediate species richness and high abundances. Tree trunk habitats (mosses and lichens) showed low numbers of both richness and abundances. One might conclude that the moisture of these habitats is the overall determining factor, and this should coincide with bryophyte species groups on the large scale.

Miller *et al*. (1996) found six species of tardigrades in lichen and bryophyte samples on ice-free areas at Windmill Islands, East Antarctica. The tardigrade species ***Diphascon chilenense*** (see Figure 32), ***Acutuncus antarcticus*** (formerly ***Hypsibius antarcticus***; see Figure 33), and ***Pseudechiniscus juanitae*** (=***Pseudechiniscus suillus***; Figure 34) showed a positive association with bryophytes and a negative association with algae and lichens.

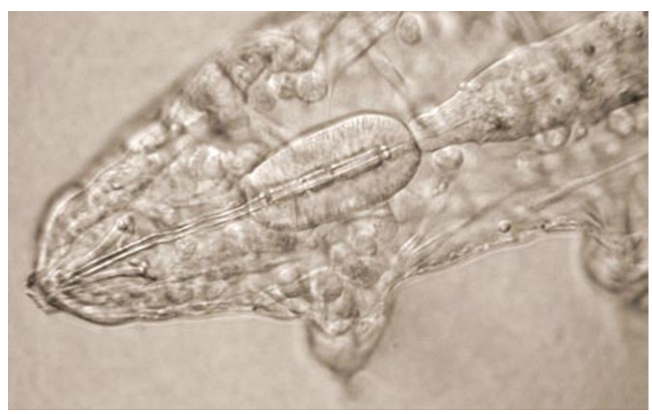

Figure 32. ***Diphascon*** sp., member of one of the most common bryophyte-dwelling genera. Photo by Martin Mach, with permission.

Meyer and Hinton (2007) reviewed the Nearctic tardigrades (Greenland, Canada, Alaska, continental USA, northern Mexico). They found that one-third of the species occur in both cryptogams (lichens and bryophytes) and soil/leaf litter (Table 5). Few tardigrades occurred exclusively in soil/leaf litter habitats. Although many occurred among both bryophytes and lichens, 18 species occurred only in bryophytes. It is likely that bryophytes offer a better moisture environment, but this has not been tested.

Figure 33. ***Hypsibius***. Photo by Yuuji Tsukii, with permission.

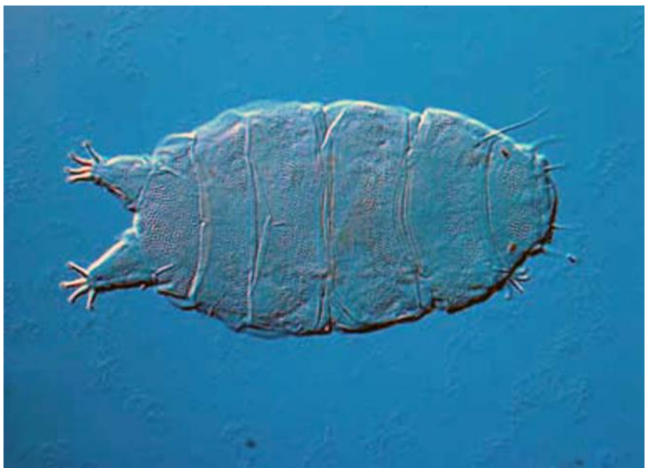

Figure 34. ***Pseudechiniscus juanitae***. Photo by Paul J. Bartels, with permission.

Table 5. Comparison of tardigrades inhabiting their primary substrates in the Nearctic realm. Only species present on that substrate in at least three sites are included. From Meyer & Hinton 2007.

Substrate category	number of species
Cryptogams only	64
Both cryptogams and soil/leaf litter	27
Soil/leaf litter only	3
Both bryophyte and lichen	50
Bryophyte only	18
Lichen only	5

Beasley (1990) conducted a similar study in Colorado, USA. Out of 135 samples of liverworts, mosses, lichens, and club mosses (Lycopodiaceae), they found 20 species in 55 samples. There were no tardigrades on liverworts (!), but they were on 46% of mosses and 43% of lichens. The big surprise is that 75% of the clubmosses had tardigrades.

In the Great Smoky Mountains National Park, Bartels and Nelson (2006) found that the number of species differed little among the substrates they sampled (soil, lichen, moss, & stream habitats). Whereas it is not unusual for the soil, lichens, and mosses to have similar fauna and richness, it seems a bit unusual for the stream habitat to be as rich. ***Amphibolus*** cf. ***weglarskae*** and ***Diphascon*** cf. ***ramazzottii*** were the only species found only on bryophytes among those four substrates.

Horning *et al*. (1978) collected from soil, fungi, algae, bryophytes, lichens, marine substrata, freshwater substrata, and litter in New Zealand and surrounding islands. From bryophyte and lichen habitats, they found that all 14 of the most abundant species occurred in at least three of the five "plant" categories (three lichen forms, liverworts, and mosses). Among these, the highest occurrence was among mosses. Although ***Milnesium tardigradum*** (Figure 16) was slightly more abundant on lichens than on mosses, the combined numbers on mosses and liverworts was still higher. Horning *et al*. identified the bryophytes and lichens and presented the species of tardigrades on each (Table 1, Table 4, Table 6). In 559 moss samples, 45.8% had tardigrades, mean of 1.8 species, range 1-8 (Table 1). Of 55 species of tardigrades known for New Zealand, 45 occurred on mosses.

Finding New Species

The common appearance of tardigrades among bryophytes causes those who seek to describe new taxa to go first to the mossy habitats. In this spirit, Kaczmarek and Michalczyk (2004a) found the new species of moss-dwelling ***Doryphoribius quadrituberculatus*** in Costa Rica. From mosses in China they described the new species ***Bryodelphax brevidentatus*** (Kaczmarek *et al*. 2005) and ***B. asiaticus*** (Figure 35; Kaczmarek & Michalczyk 2004b), as did Li and coworkers for ***Echiniscus taibaiensis*** (Wang & Li 2005), ***Isohypsibius taibaiensis*** (Li & Wang 2005), ***Isohypsibius qinlingensis*** (Li *et al*. 2005a), ***Pseudechiniscus papillosus*** (Li *et al*. 2005b), ***Pseudechiniscus beasleyi***, ***Echiniscus nelsonae***, and ***E. shaanxiensis*** (Li *et al*. 2007), and Tumanov (2005) for ***Macrobiotus barabanovi*** and ***M. kirghizicus***. Pilato and Bertolani (2005) described ***Diphascon dolomiticum*** from Italy.

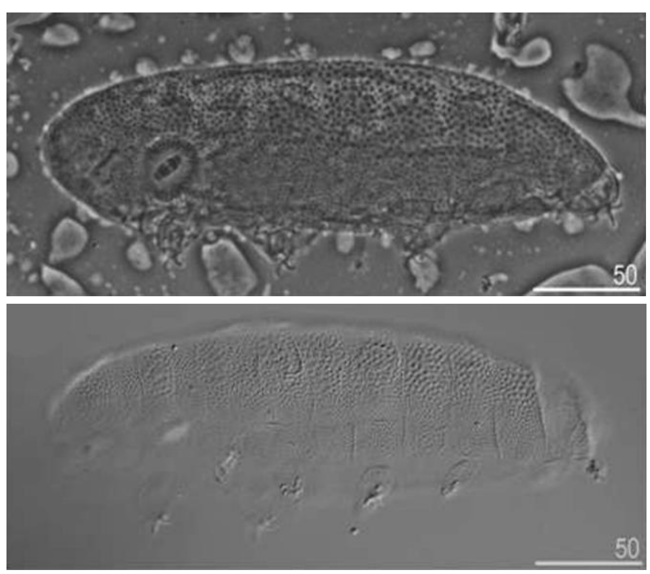

Figure 35. ***Bryodelphax asiaticus***. Photo through Creative Commons.

Table 6. Comparison of numbers of individuals and percentage of individuals of each of 14 tardigrade species on liverworts, mosses, and lichens in collections from New Zealand and surrounding islands. The remaining ones were on other non-plant substrata. Number of samples is in parentheses. From Horning *et al*. 1978.

	n	**liverworts % (150)**	**mosses % (559)**	**lichens % (239)**
Pseudechiniscus novaezeelandiae	46	8.70	56.50	23.90
Pseudechiniscus juanitae	43	6.98	44.19	27.91
Macrobiotus harmsworthi	89	5.62	55.06	34.83
Macrobiotus hibiscus	90	7.78	60.00	17.78
Minibiotus intermedius	65	7.69	41.54	32.30
Milnesium tardigradum	143	7.69	35.66	37.06
Hypsibius dujardini	32	10.53	50.00	2.63
Paramacrobiotus areolatus	58	3.45	60.34	18.97
Echiniscus bigranulatus	18	5.56	38.89	38.89
Hypechiniscus gladiator	21	19.05	61.90	9.50
Diphascon scoticum	35	11.43	65.71	11.43
Macrobiotus liviae	72	8.33	56.94	18.06
Macrobiotus anderssoni	63	11.11	42.86	22.22
Macrobiotus furciger	89	12.36	50.56	22.47

New species from South Africa are no surprise, as enumeration of small organisms in that country is barely out of its infancy. Kaczmarek and Michalczyk (2004c) described the new species ***Diphascon zaniewi*** in the Dragon Mountains there. Other species found there were more cosmopolitan: ***Hypsibius maculatus*** (previously known only from Cameroon and England), ***H. convergens*** (Figure 36), ***Paramacrobiotus*** *cf*. ***richtersi*** (Figure 37), and ***Minibiotus intermedius*** (Figure 38-Figure 39).

Figure 36. ***Hypsibius convergens***, a common moss-dweller. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

Figure 37. ***Paramacrobiotus richtersi***, a common bryophyte dweller. Photo by Science Photo Library through Creative Commons.

Figure 38. ***Minibiotus intermedius***. Photo by William Miller through Flickr.

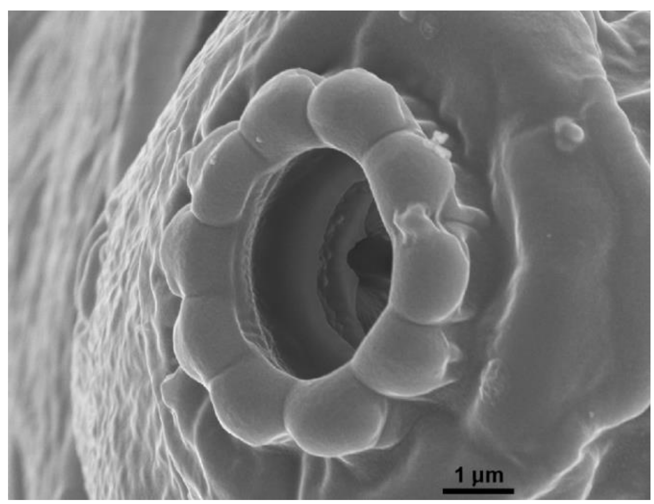

Figure 39. ***Minibiotus intermedius*** mouth. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Likewise, in South America, Michalczyk and Kaczmarek (2005) described ***Calohypsibius maliki*** as a new species from Chile; Michalczyk and Kaczmarek (2006) described ***Echiniscus madonnae*** (Figure 40) from

Peru, all from bryophytes. In Argentina they described ***Macrobiotus szeptyckii*** and ***Macrobiotus kazmierskii*** (Kaczmarek & Michalczyk 2009). In 2008 Degma *et al*. described another new species [***Paramacrobiotus derkai*** (Figure 41)] from Chile, a country where only 29 species had previously been described.

Figure 40. ***Echiniscus madonnae***, a moss dweller from Peru. Photo by Łukasz Kaczmarek & Łukasz Michalczyk, with permission.

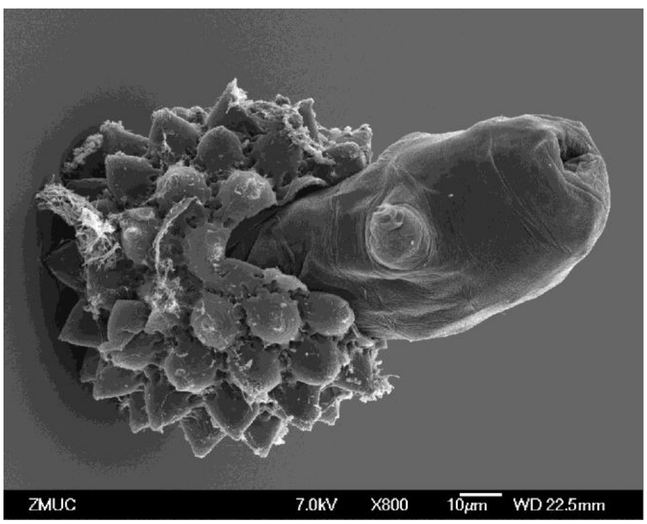

Figure 41. ***Paramacrobiotus derkai*** emerging from egg. Photo by Łukasz Kaczmarek, with permission.

In Portugal, lichens and mosses provided the new species ***Minibiotus xavieri*** to Fontoura and coworkers (2009). In Cyprus, Kaczmarek and Michalczyk (2004d) described ***Macrobiotus marlenae*** (Figure 42). ***Macrobiotus kovalevi*** proved to be a new species from mosses in New Zealand (Tumanov 2004). Clearly, mosses have been a favorite sampling substrate for tardigrade seekers (Kaczmarek & Michalczyk 2009) and most likely hold many more undescribed species around the world.

Even when new species are collected, they are not always identified or diagnosed in a timely manner. This can result in their ultimate description from multiple locations. Such is the case for ***Echiniscus viridianus*** (Figure 43), a new species described by Pilato *et al*. (2007) from Alabama and New Mexico, USA, and from the Azores Islands, all from mosses.

Figure 42. ***Macrobiotus marlenae***. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Figure 43. ***Echiniscus viridianus***. Photo by Paul J. Bartels, with permission.

Summary

Most studies indicate no correlation between bryophyte species and tardigrade species. There is limited indication that cushions may have more species, but in other studies thin mats have more than cushions. Other studies indicate they are more common on weft-forming mosses than on turfs. Open mosses like ***Polytrichum*** seem to be less suitable as homes. There may be some specificity for liverworts rather than mosses, as for example ***Macrobiotus snaresensis*** in New Zealand. Unfortunately, many researchers have not identified the bryophyte taxa in tardigrade faunistic studies. A common garden study including several bryophyte species and tardigrades of the same or different species could be revealing.

Acknowledgments

Roberto Bertolani provided an invaluable update to the tardigrade taxonomic names and offered several suggestions on the text to provide clarification or correct errors. Łukasz Kaczmarek has provided me with references, images, contact information, and a critical read of an earlier version of the text. Martin Mach and Yuuji Tsukii have given permission to use images that illustrate the species. Michael Lüth has given permission to use his many bryophyte images, and my appreciation goes to all those who have contributed their images to Wikimedia Commons for all to use. Martin Mach was kind enough to send me corrections for typos in the previous online version. Thank you to my sister, Eileen Dumire, for providing the view of a novice on the readability of the original text (it has been much expanded since then). Tardigrade nomenclature is based on Degma *et al*. 2010.

Literature Cited

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.

Baxter, W. H. 1979. Some notes on the Tardigrada of North Down, including one addition to the Irish fauna. Irish Nat. J. 19: 389-391.

Beasley, C. W. 1990. Tardigrada from Gunnison Co., Colorado, with the description of a new species of *Diphascon*. Southw. Nat. 35: 302-304.

Beasley, C. W. and Miller, W. R. 2007. Tardigrada of Xinjiang Uygur Autonomous Region, China. Proceedings of the Tenth International Symposium on Tardigrada. J. Limnol. 66(Suppl. 1): 49-55.

Bertolani, R. 1983. Tardigardi muscicoli delle dune costiere Italiane, con descrizione di una nuova specie. Atti Soc. Tosc. Sci. Nat. Mem. Ser. B 90: 139-148.

Bertrand, M. 1975. Répartition des tardigrades "terrestres" dans le massif de l'Aigoual. Vie Milieu 25: 283-298.

Christenberry, D. 1979. On the distribution of *Echiniscus kofordi* and *E. cavagnaroi* (Tardigrada). Trans. Amer. Microsc. Soc. 98: 469-471.

Collins, M. and Bateman, L. 2001. The ecological distribution of tardigrades in Newfoundland. Zool. Anz. 240: 291-297.

Degma, P. 2006. First records of two Heterotardigrada (Tardigrada) species in Slovakia. Biologia Bratislava 61: 501-502.

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., Simurka, M., and Gulanova, S. 2005. Community structure and ecological macrodistribution of moss-dwelling water bears (Tardigrada) in Central European oak-hornbeam forests (SW Slovakia). Ekologia (Bratislava) 24(suppl. 2): 59-75.

Degma, P., Michalczyk, Ł., and Kaczmarek, Ł. 2008. *Macrobiotus derkai*, a new species of Tardigrada (Eutardigrada, Macrobiotidae, *huziori* group) from the Colombian Andes (South America). Zootaxa 1731: 1-23.

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.

Fullard, H. 1968. China in Maps. George Philip & Sons, Ltd., London, 25 pp.

Guil, N., Hortal, J., Sanchez-Moreno, S. and Machordom, A. 2009a. 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.

Guil, N., Sanchez-Moreno, S., and Machordom, A. 2009b. Local biodiversity patterns in micrometazoans: Are tardigrades everywhere? System. Biodiv. 7: 259-268.

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. In: Pilato, G. and Rebecchi, L. (guest eds.). Proceedings of the Tenth International Symposium on Tardigrada. J. Limnol. 66(Suppl. 1): 72-76.

Hinton, J. G. and Meyer, H. A. 2009. Tardigrades from Fayette County, Georgia. Georgia J. Sci. 67(2): 30-32.

Hofmann, I. 1987. Habitat preference of the most frequent moss-living Tardigrada in the area of Giessen (Hessen). In: Bertolani, R. (ed.). Biology of Tardigrades. Selected Symposia and Monographs U.Z.I., Mucchi, Modena Italia, pp 211-216.

Hofmann, I. and Eichelberg, D. 1987. Faunistisch-oekologische Untersuchungen zur Habitat-praeferenz moosbewohnender Tardigraden. [Ecological investigations of the habitat preference of moss-inhabiting tardigrades.]. Zool. Beitr. 31(1): 61-76.

Horning, D. S., Schuster, R. O., and Grigarick, A. A. 1978. Tardigrada of New Zealand. N. Zeal. J. Zool. 5: 185-280.

Hunter, M. A. 1977. A study of Tardigrada from a farm in Montgomery County, Tennessee. MS Thesis, Austin Peay State University, Clarksville, TN, 61 pp.

Jönsson, K. I. 2003. Population density and species composition of moss-living tardigrades in a boreo-nemoral forest. Ecography 26: 356-364.

Kaczmarek, Ł. and Michalczyk, Ł. 2004a. First record of the genus *Doryphoribius* Pilato, 1969 from Costa Rica (Central America) and description of a new species *Doryphoribius quadrituberculatus* (Tardigrada: Hypsibiidae). Genus 15: 447-453.

Kaczmarek, Ł. and Michalczyk, Ł. 2004b. A new species *Bryodelphax asiaticus* (Tardigrada: Heterotardigrada: Echiniscidae) from Mongolia (Central Asia). Raffles Bull. Zool. 52: 599-602.

Kaczmarek, Ł. and Michalczyk, Ł. 2004c. Notes on some tardigrades from South Africa, with the description of *Diphascon* (*Diphascon*) *zaniewi* sp. nov. (Eutardigrada: Hypsibiidae). Zootaxa 576: 1-6.

Kaczmarek, Ł. and Michalczyk, Ł. 2004d. New records of Tardigrada from Cyprus with a description of the new species Macrobiotus marlenae (hufelandi group) (Eutardigrada: Macrobiotidae). Genus 15: 141-152.

Kaczmarek, Ł. and Michalczyk, Ł. 2009. Two new species of Macrobiotidae, *Macrobiotus szeptyckii* (*harmsworthi* group) and *Macrobiotus kazmierskii* (*hufelandi* group) from Argentina. Acta Zool. Cracoviensia, Seria B - Invertebrata 52: 87-99.

Kaczmarek, Ł., Michalczyk, Ł., and Degma, P. 2005. A new species of Tardigrada *Bryodelphax brevidentatus* sp. nov. (Heterotardigrada: Echiniscidae) from China (Asia). Zootaxa 1080: 33-38.

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.

Li, X.-C. and Wang, L.-Z. 2005. *Isohypsibius taibaiensis* sp. nov. (Tardigrada, Hypsibiidae) from China. Zootaxa 1036: 55-60.

Li, X.-C., Wang, L.-Z. and Yu, D. 2005a. *Isohypsibius qinlingensis* sp. nov. (Tardigrada, Hypsibiidae) from China. Zootaxa 980: 1-4.

Li, X.-C., Wang, L.-Z., and Yu, D. 2007. The Tardigrada fauna of China with descriptions of three new species of Echiniscidae. Zool. Stud. 46(2): 135-147.

Li, X.-C., Wang, L.-Z., Liu, Y., and Su, L.-N. 2005b. A new species and five new records of the family Echiniscidae (Tardigrada) from China. Zootaxa 1093: 25-33.

Meyer, H. A. 2006a. Interspecific association and substrate specificity in tardigrades from Florida, southeastern United States. Hydrobiologia 558: 129-132.

Meyer, H. A. 2006b. 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. G. 2007. Limno-terrestrial Tardigrada of the Nearctic realm. J. Limnol. 66(Suppl. 1): 97-103.

Michalczyk, Ł. and Kaczmarek, Ł. 2005. The first record of the genus *Calohypsibius* Thulin, 1928 (Eutardigrada: Calohypsibiidae) from Chile (South America) with a description of the new species *Calohypsibius maliki*. New Zeal. J. Zool. 32: 287-292.

Michalczyk, Ł. and Kaczmarek, Ł. 2006. Revision of the Echiniscus bigranulatus group with a description of a new species *Echiniscus madonnae* (Tardigrada: Heterotardigrada: Echiniscidae) from South America. Zootaxa 1154: 1-26.

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., 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.

Newsham, K. K., Maslen, N. R., and McInnes, S. J. 2006. Survival of Antarctic soil metazoans at -80ºC for six years. CryoLetters 27(5): 269-280.

Pilato, G. and Bertolani, R. 2005. *Diphascon* (*Diphascon*) *dolomiticum*, a new species of Hypsibiidae (Eutardigrada) from Italy. Zootaxa 914: 1-5.

Pilato, G., Fontoura, P., and Lisi, O. 2007. Remarks on the *Echiniscus viridis* group, with the description of a new species (Tardigrada, Echiniscidae). In: Pilato, G. and Rebecchi, L. (guest eds.). Proceedings of the Tenth International Symposium on Tardigrada. J. Limnol. 66(Suppl. 1): 33-39.

Ramazzotti, G. and Maucci, W. 1983. The phylum Tardigrada - 3rd edition: English translation by C. W. Beasley. Mem. Ist. Ital. Idrobiol. Dott. Marco de Marchi 41: 1B680.

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.

Sayre, R. M. and Brunson, L. K. 1971. Microfauna of moss habitats. Amer. Biol. Teacher Feb. 1971: 100-102, 105.

Tumanov, D. V. 2004. *Macrobiotus kovalevi*, a new species of Tardigrada from New Zealand (Eutardigrada, Macrobiotidae). Zootaxa 406: 1-8.

Tumanov, D. V. 2005. Two new species of *Macrobiotus* (Eutardigrada, Macrobiotidae) from Tien Shan (Kirghizia), with notes on *Macrobiotus tenuis* group. Zootaxa 1043: 33-46.

Wang, L.-Z. and Li, X.-C. 2005. *Echiniscus taibaiensis* sp. nov. and a new record of *Echiniscus bisetosus* Heinis (Tardigrada, Echiniscidae) from China. Zootaxa 1093: 39-45.