

# **CHAPTER 5-5 TARDIGRADE DENSITIES AND RICHNESS**

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# CHAPTER 5-5

## TARDIGRADE DENSITIES AND RICHNESS



Figure 1. *Echiniscus*, the genus with the most species among mosses. Photo by Martin Mach, with permission.

### Densities and Richness

But just how common are these bryophyte-dwelling tardigrades (Figure 1)? I think the largest reported density I have found in the literature is 22,000 individuals per gram of dry moss (Mathews 1938), but that is an old number and may well have been replaced. These animals seem to be especially adapted for the bryophyte habitat (Jerez *et al.* 2002), achieving densities as great as 2,000,000 individuals per square meter of *Bryum argenteum* (Figure 2) (Brusca & Brusca 1990). (Is that greater than 22,000 per gram?) Nelson (2002) reminds us that densities of these animals are highly variable and conditions for optimum development of the population are unknown (see also Kinchin 1994). Factors such as temperature and moisture (Franceschi *et al.* 1962-1963; Morgan 1977; Briones *et al.* 1997), air pollution (Steiner 1994a, b, c, 1995), and food availability (Hallas & Yeates 1972) all influence population density. And it appears that random dispersal may be a major factor, since both population density and species diversity vary considerably between adjacent microhabitats that appear to be identical (Nelson 2002).



Figure 2. *Bryum argenteum* exhibiting the tight leaves that provide capillary spaces where tardigrades can enjoy prolonged water retention. Photo by Michael Lüth, with permission.

Among the more extensive studies is that of Kathman and Cross (1991) on Vancouver Island, British Columbia, Canada. They collected from mosses at six altitudes on five mountains and found 39 species among 37 moss species, with 13,696 individuals in all. However, as noted in Bertolani's (1983) study, the species of moss did not seem to be important.

Horning *et al.* (1978) collected from soil, fungi, algae, bryophytes, lichens, marine substrata, freshwater substrata, and litter in New Zealand and surrounding islands. They provide summaries of the tardigrade species from each bryophyte species. From their 1354 collections, they represented 577 terrestrial habitats. All 14 of the more abundant tardigrade 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, except for *Milnesium tardigradum* (Figure 3), which occurred more often among lichens. They reported the number of species on each bryophyte, but not the density of individuals. As in other studies, moisture seemed to play a major role. They considered the "plant" categories, arranged from dry to moist, to be crustose lichen > fruticose lichen > foliose lichen > liverworts & mosses. The foliose lichens and mosses served as habitat for more tardigrade species than did the liverworts, crustose lichens, or fruticose lichens. Liverworts housed 30 tardigrade species on 26 liverwort species.



Figure 3. *Milnesium tardigradum*, a moss dweller that seems to have a slight preference for lichens. Photo by Martin Mach, with permission.

Roof mosses (Figure 4) have their share of tardigrade fauna; Morgan (1977) recorded densities of four tardigrade species [*Macrobiotus hufelandi* (Figure 15), *Milnesium tardigradum* (Figure 3), *Ramazzottius oberhaeuseri* (Figure 5), *Echiniscus testudo* (Figure 6)] of up to 823 individuals per gram of the mosses *Ceratodon purpureus* (Figure 7) and *Bryum argenteum* (Figure 8) on roofs in Swansea, Wales. In total, Morgan collected 32,552 tardigrades from these two mosses on just three roof locations at the University College of Swansea.

Even new species might be abundant in many parts of the world. This is an under-collected group, as suggested by finding very common species for the first time in some countries. Kristensen *et al.* (2009) found more than 200 individuals of a new species of *Bryodelphax* (see Figure 9) in a "very small moss sample." And these were cohabiting with *Macrobiotus hufelandi* (Figure 15) and *Milnesium tardigradum* (Figure 3).



Figure 4. Moss-covered roof that has been sampled along the edge. Photo by Susan Moyle-Studlar, with permission.



Figure 5. *Ramazzottius oberhaeuseri*, a common moss-dweller, including those on roofs. Photo by Martin Mach, with permission.

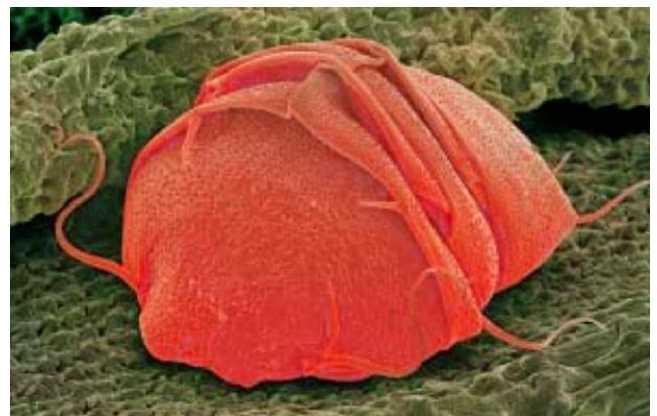


Figure 6. *Echiniscus testudo* tun on a moss leaf. Photo by Power & Syred through Creative Commons.



Figure 7. *Ceratodon purpureus*, another common roof moss that can house innumerable tardigrades. Photo by Michael Lüth, with permission.





Figure 8. *Bryum argenteum*, a common roof moss that can house innumerable tardigrades. Photo by Michael Lüth, with permission.

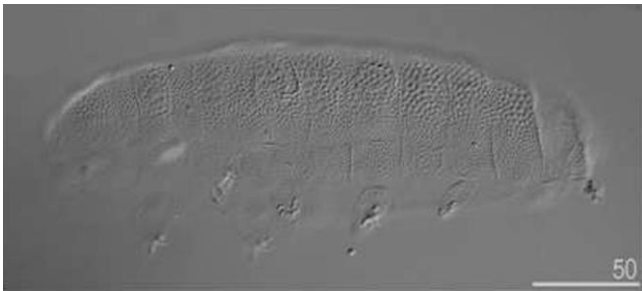
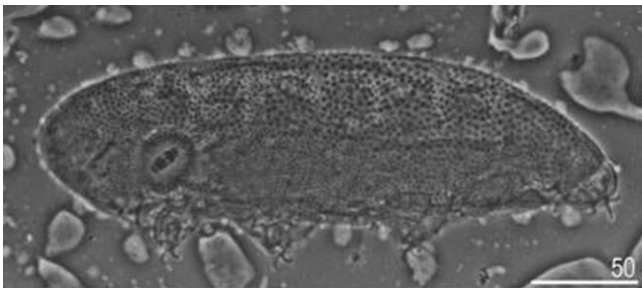


Figure 9. *Bryodelphax asiaticus*. Photo through Creative Commons.

## Europe

One might expect the knowledge of European tardigrades to be the most complete, partly because the taxonomy of the bryophytes has been known longer than in many other countries, including North America, and partly because of the interest of Europeans in natural history.

Some European mosses have abundant tardigrades: *Hypnum cupressiforme* (Figure 10), *Hylocomium splendens* (= *Hypnum parietinum*) (Figure 11), and *Sanionia uncinata* (Figure 12), as well as *Grimmia* (might include *Schistidium*; Figure 13) and *Tortula* (Marcus 1928a; probably includes *Syntrichia*; Figure 14) and may contain up to 20,000 individuals per 1 g of air-dried moss (Marcus 1928b).



Figure 10. *Hypnum cupressiforme*, home of abundant tardigrades. Photo by Michael Lüth, with permission.



Figure 11. *Hylocomium splendens*, a good habitat for tardigrades. Photo by Janice Glime.



Figure 12. *Sanionia uncinata*, a suitable tardigrade habitat. Photo by Janice Glime.





Figure 13. *Grimmia elongata* cushions. Photo by Michael Lüth, with permission.



Figure 14. *Tortula intermedia* cushion. Photo by Michael Lüth, with permission.

In a boreal forest in Sweden, Jönsson (2003) found sixteen species of tardigrades on mosses, including the widespread *Macrobiotus hufelandi* (Figure 15) as the most common. Among these, five were new to Sweden. They also found that the forest tended to have more tardigrade species than did a clear-cut area, but overall abundance within a species differed little between these two habitats.

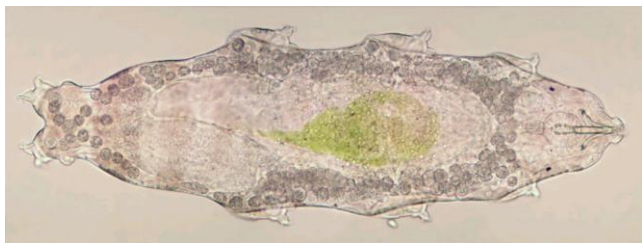


Figure 15. *Macrobiotus hufelandi*, a dominant species on *Rhytidiadelphus squarrosus* (Figure 19) in the Black Forest, Germany. Photo by Martin Mach, with permission.

In the Tihany Peninsula, Hungary, Felföldy and Iharos (1947) found modest numbers, with 38 individuals per gram of the moss *Eurhynchium swartzii* (Figure 16) and 84 per gram among clones of *Barbula* [formerly in *Didymodon*] *tophacea* (Figure 17).



Figure 16. *Eurhynchium swartzii*, a pleurocarpous moss that is known to house tardigrades. Photo by Kristian Peters through Wikimedia Commons.



Figure 17. *Barbula tophacea*, an acrocarpous moss that houses tardigrades. Photo by Michael Lüth, with permission.

Hofmann and Eichelberg (1987) found sixteen species, including two undescribed, among mosses at Lahnu, near Giessen, Germany. Maucci (1980) collected 2686 samples of bryophytes and found 23 species of tardigrades.

In Sardinia, Pilato and Sperlinga (1975) likewise found sixteen species of tardigrades among the bryophytes. These included *Macrobiotus nuragicus* and *M. arguei* as new species. *Isohypsibius pappi*, *I. sattleri* (formerly *I. bakonyiensis*), and *Hypsibius convergens* (Figure 18) were new for Sardinia. It seems that finding new species within tardigrade communities is a fairly common occurrence.



Figure 18. *Hypsibius convergens*, one of the most common of bryophyte dwellers. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.



Schuster and Greven (2007) followed the inhabitants of the moss *Rhytidiadelphus squarrosus* (Figure 19) in the Black Forest in Germany for 54 months (Table 1). They uncovered 19,909 individuals comprising 24 species. The dominant species were *Macrobiotus hufelandi* (Figure 15; 56%), *Paramacrobiotus richtersi* (Figure 20; 18%), and *Diphascon pingue* (Figure 21; 12%). In contrast to the Oregon study, the highest diversity occurred in winter, whereas the number of individuals declined in winter, then increased from spring until autumn, as in Oregon. On the other hand, *D. rugosum* (Figure 22), *Hypsibius dujardini* (Figure 23), and *H. cf. convergens* (Figure 18) exhibited peaks in winter. Water-loving species were most numerous in the moist season, whereas *euryhydric* species increased when it was relatively dry and sunny. During the course of the 54 months, 14 of the 24 species remained, whereas species succession/change occurred among the others.

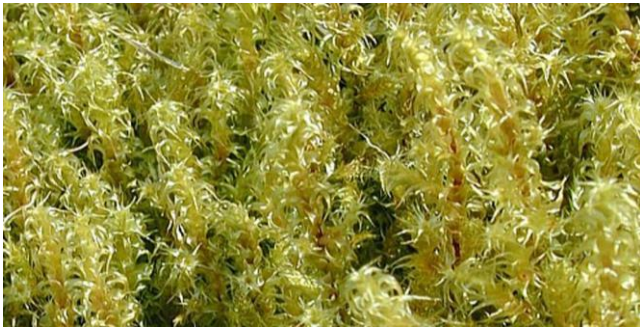


Figure 19. *Rhytidiadelphus squarrosus*, the home for 24 rotifer species in The Black Forest of Germany. Photo by Michael Lüth, with permission.



Figure 20. *Paramacrobiotus richtersi*, one of the most common and abundant of the bryophyte tardigrades. Photo by Science Photo Library through Creative Commons.



Figure 21. *Diphascon pingue*. Photo by Michael Collins, with permission.

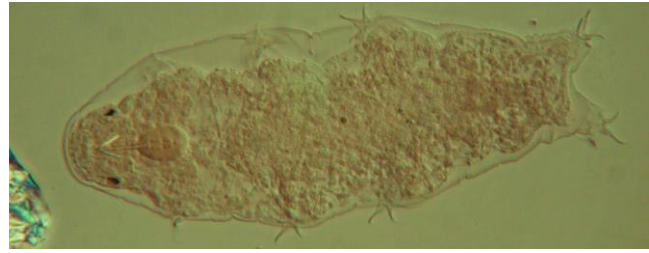


Figure 22. *Diphascon rugosum*, a tardigrade that peaks in winter in Oregon, USA. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

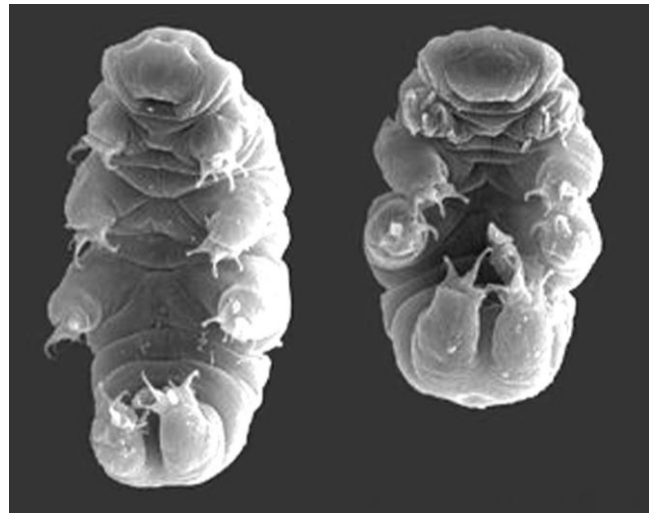


Figure 23. *Hypsibius dujardini*, a moss dweller that has its peak population in winter in the Black Forest of Germany. Photo by Bob Goldstein, with permission.

Species such as *Diphascon oculatum* (Figure 24) that had reasonable numbers on *Rhytidiadelphus squarrosus* (Figure 19), but for which no eggs were found (Schuster & Greven 2007), might deposit eggs at a different season than those sampled. It is unlikely that they would deposit eggs in a different habitat/location from that of the adults because of their limited mobility. On the other hand, rare species occurring only once, e.g. *Mesocrista spitzbergensis* (Figure 25) [note – this is a name change from *M. spitzbergense*, required to make the gender agree with that of the genus (Degma *et al.* 2010)], may have been an accidental arrival on *Rhytidiadelphus squarrosus*, or generally rare. It would be interesting to know the longevity and life cycle of rare species.



Figure 24. *Diphascon oculatum*, an inhabitant of *Rhytidiadelphus squarrosus* (Figure 19). Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

Table 1. Comparison of total number of individuals (in order of dominance), eggs in exuviae, dominances, and frequencies for each tardigrade species collected on *Rhytidiadelphus squarrosus* (Figure 19) in the Black Forest of Germany within the investigation period of 54 months. Asterisks indicate species found at least once in each year of study. From Schuster & Greven 2007.

Species	N. individuals	Eggs / Exuviae	Dominance (%)	Frequency (%)
* <i>Macrobiotus hufelandi</i> (Schultze 1833)	11118	448	55.84	100
* <i>Paramacrobiotus richtersi</i> (Murray 1911)	3600	179	18.08	100
* <i>Diphascon pingue</i> sl (Marcus 1936)	2359	170	11.85	100
* <i>Hypsibius scabropygus</i> (Cuénot 1929)	429	15	2.15	78.5
* <i>Macrobiotus patiens</i> (Pilato <i>et al.</i> 2000)	403	7	2.02	87.9
* <i>Hypsibius dujardini</i> (Doyère 1840)	390	58	1.96	72.9
* <i>Diphascon rugosum</i> (Bartos 1935)	348	22	1.75	48.6
* <i>Isohypsibius prosostomus</i> (Thulin 1928)	294	29	1.48	67.3
* <i>Hypsibius convergens</i> (Urbanowicz 1925)	246	18	1.24	46.7
* <i>Hypsibius pallidus</i> (Thulin 1911)	246	13	1.24	65.4
* <i>Hypsibius</i> cfr. <i>convergens</i>	164	8	0.82	31.8
* <i>Milnesium tardigradum</i> (Doyère 1840)	101	4	0.51	48.6
* <i>Diphascon oculatum</i> (Murray 1906)	77	0	0.39	41.1
* <i>Diphascon prorsirostre</i> (Thulin 1928)	63	1	0.32	39.3
<i>Isohypsibius pappi</i> (Iharos 1966)	24	7	0.12	16.8
<i>Hypsibius</i> sp.	12	0	0.06	2.8
<i>Diphascon nobilei</i> (Binda 1969)	8	0	0.04	2.8
<i>Minibiotus</i> cfr. <i>poricinctus</i>	8	0	0.04	3.7
<i>Minibiotus</i> cfr. <i>scopulus</i>	6	0	0.03	5.6
<i>Diphascon scoticum</i> (Murray 1905)	5	0	0.03	2.8
<i>Minibiotus intermedius</i> (Plate 1888)	5	0	0.03	3.7
<i>Diphascon bullatum</i> (Murray 1905)	1	0	0.01	0.9
<i>Diphascon higginsii</i> (Binda 1971)	1	0	0.01	0.9
<i>Mesocrista spitzbergensis</i> (Richters 1903)	1	0	0.01	0.9
Sum	19909	979	100.00	



Figure 25. *Mesocrista spitzbergensis*, an inhabitant of *Rhytidiadelphus squarrosus*. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.

In Scotland, Morgan (1976) found that bryophyte and lichen dwellers represented the highest number of tardigrades as well as having the greatest species diversity. In Wales, Morgan (1974) found tardigrades numbering  $2287 \times 10^3 \text{ m}^{-2}$  among mosses. By contrast, Hallas and Yeates (1972) found only  $12 \times 10^3 \text{ m}^{-2}$  in soil and litter in Danish forests.

Studies on abundance reveal a wide range of densities. Degma and coworkers (2003, 2006; & Pecalková 2003; *et al.* 2004, 2005) have provided us with records of tardigrades on named species of mosses in Slovakia. On *Hypnum cupressiforme* (Figure 10) in Central European

oak-hornbeam forests of Slovakia, Degma *et al.* (2005) found 3050 tardigrades [21 species in two families (*Hypsibiidae* & *Macrobiotidae*)] from 79 moss samples. As in many other studies they were unable to demonstrate any of 12 environmental variables that accounted for the distribution of the tardigrades. Rather, they found that the distribution of species was random.

Nevertheless, in his 2003 study, Degma found particular tardigrades on particular bryophytes (Figure 26-Figure 43): *Eremobiotus alicatai* on mosses *Brachythecium rutabulum* (Figure 26) and *Eurhynchium hians* (Figure 27); *Isohypsibius pappi* on these two as well as on *B. reflexum* (Figure 28), *Homalothecium sericeum* (Figure 29), *Hypnum cupressiforme* (Figure 10), *Mnium stellare* (Figure 31), and *Rhynchostegium megapolitanum* (Figure 32); *Isohypsibius josephi* on *Amblystegium serpens* (Figure 33) and *Brachythecium starkei* (Figure 34); *Diphascon iltisi* on *Campylium halleri* (Figure 35); *Astatumen trinacriae* (Figure 36) on *Brachythecium rutabulum* (Figure 26), *Homalothecium sericeum* (Figure 29), *Hypnum cupressiforme* (Figure 10), *Isothecium alopecuroides* (Figure 30), *Leskeella nervosa* (Figure 37), *Paraleucobryum longifolium* (Figure 38), and *Pterigynandrum filiforme* (Figure 39); *Isohypsibius dastychi* in unidentified moss. Degma and Pecalková (2003) reported *Diphascon belgicae* in *Brachythecium reflexum* (Figure 28); *Calohypsibius schusteri* and *Itaواسcon pawlowskii* in *Hypnum cupressiforme* (Figure 10). In 2006 Degma reported *Echiniscus* cf. *reticulatus* on *Ctenidium molluscum* (Figure 40); *Testechiniscus*



*spitsbergensis* on *Ctenidium molluscum* (Figure 40), *Distichium capillaceum* (Figure 41), *Ditrichum flexicaule* (Figure 42), and *Tortella tortuosa* (Figure 43). But are these just chance findings, or is there a preference? It is interesting that all but the last three and *Paraleucobryum longifolium* (Figure 38) are mat-forming mosses. Was this a preference of the tardigrade or the collector? Or simply a consequence of the habitat?



Figure 26. *Brachythecium rutabulum*, a mat-forming moss that is home to *Astatumen trinacriae*, *Eremobiotus alicatai*, and *Isohypsibius pappi*. Photo by Michael Lüth, with permission.



Figure 27. *Eurhynchium hians*, a mat-forming moss that is home to *Eremobiotus alicatai* and *Isohypsibius pappi*. Photo by Michael Lüth, with permission.



Figure 28. *Brachythecium reflexum*, a mat-forming moss that is home to *Diphascion belgiae* and *Isohypsibius pappi*. Photo by Michael Lüth, with permission.



Figure 29. *Homalothecium sericeum*, a mat-forming moss that is home to *Astatumen trinacriae* and *Isohypsibius pappi*. Note the branches turned to one side. Photo by Michael Lüth, with permission.



Figure 30. *Isothecium alopecuroides*, home to *Astatumen trinacriae* and *Isohypsibius pappi*. Photo by Biopix through EOL Creative Commons.



Figure 31. *Mnium stellares*, home to *Isohypsibius pappi*. Photo by Michael Lüth, with permission.



Figure 32. *Rhynchostegium megapolitanum*, home to *Isohypsibius pappi*. Note the droplets of water adhering to the leaves, making this a good limnoterrestrial habitat. Photo by Michael Lüth, with permission.





Figure 33. *Amblystegium serpens*, home to *Isohypsibius josephi*. Photo by Michael Lüth, with permission.



Figure 34. *Brachythecium starkei*, home to *Isohypsibius josephi*. Photo by Michael Lüth, with permission.

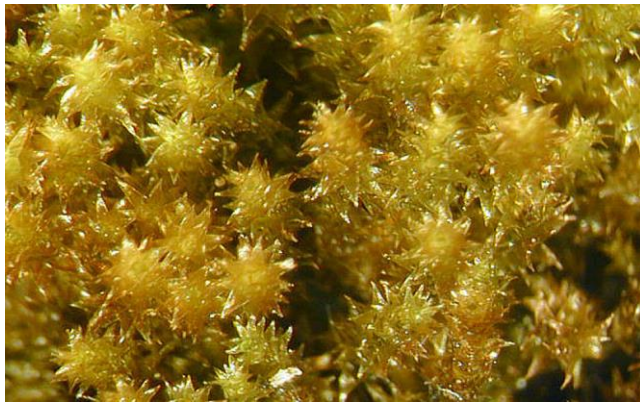


Figure 35. *Campylium halleri*, home to *Diphascon iltisi*. Photo by Michael Lüth, with permission.

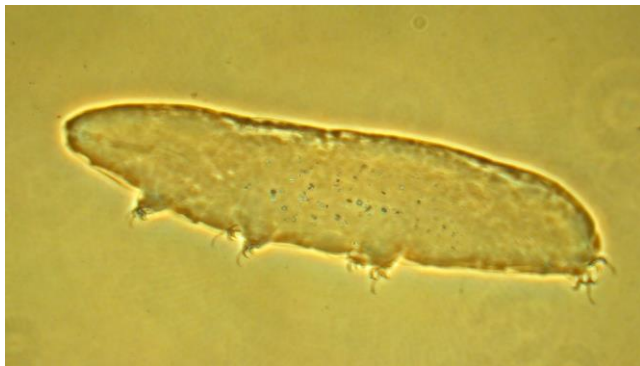


Figure 36. *Astatumen trinacriae*. Photo by Paul J. Bartels, with permission.



Figure 37. *Leskeella nervosa*, home to *Astatumen trinacriae*. Note the bulbils at the tips of branches. Photo by Michael Lüth, with permission.



Figure 38. *Paraleucobryum longifolium*, a cushion former on rocks, home to *Astatumen trinacriae*. Photo by Michael Lüth, with permission.



Figure 39. *Pterigynandrum filiforme*, home to *Astatumen trinacriae*. Photo by Michael Lüth, with permission.



Figure 40. *Ctenidium molluscum*, home to *Echiniscus cf. reticulatus* and *Testechiniscus spitsbergensis*. Photo by Michael Lüth, with permission.





Figure 41. *Distichium capillaceum*, a cushion former, home to *Testechiniscus spitsbergensis*. Photo by Michael Lüth, with permission.



Figure 42. *Ditrichum flexicaule*, exhibiting tight vertical leaves, home to *Testechiniscus spitsbergensis*. Photo by Michael Lüth, with permission.



Figure 43. *Tortella tortuosa*, a cushion former, home to *Testechiniscus spitsbergensis*. Photo by Michael Lüth, with permission.

## North America

The neglect of tardigrades has not escaped North America. Meyer (2006a) lamented that only one species of tardigrade had been reported from Florida. By sampling 47 species of mosses, liverworts, lichens, and ferns from trees and shrubs in all 67 counties of Florida, he found 20 species of tardigrades. Like other studies discussed here, he could find no association between tardigrade species and any particular bryophyte or lichen species. He did, however, find differences between species occurring on lichens and mosses in general.

It is clear that neglect of the bryophyte habitat is neglect of tardigrades in general. Based on species-area curves, Bartels and Nelson (2007) estimated the greatest species richness among bryophytes in their comparison of habitats in the Great Smoky Mountains, USA, although their actual numbers showed about equal numbers of species among the terrestrial habitats:

Aquatic	29
Soil	39
Lichen	35
Moss	37
Total	140

Among the additional species most likely to contribute to the predicted number of bryophyte dwellers are a number of species found there on other substrata, that are known from bryophytes elsewhere but not found in the necessarily limited sampling in this study.

Meyer *et al.* (2003) examined populations among a variety of habitats in central Florida and Ouichita Mountains, Arkansas, USA. They found the tardigrades to be both diverse and abundant, varying greatly within the same species among mosses on different rocks and trees. For example, in an extreme case a tree exhibited three species with numerous individuals while the adjacent tree had none. Four adjacent cores yielded from 0 to 86 individuals, totalling 5 species. This type of distribution is consistent with the patchiness discussed below and supports the hypothesis of random dispersal followed by aggregation resulting from reproduction without migration.

Paul Davison (pers. comm. 21 June 2006), working in Alabama, USA, contends that tardigrades are best found on "scrappy mosses" that occur in harsh environments. These include those on the face of concrete steps or rock and concrete walls, rooftops, or bark of city trees. In fact, some researchers have suggested that the tardigrades might require a dry period during their lives to survive. Using such mosses, drying, and crumbling them through a 0.5 cm screen over a dish pan can yield as many as 70 tardigrades in just 5 mL of processed extract.

A more modest flora was in evidence in the collections from Southwestern Virginia, USA (Riggin 1962). In 434 collections of mosses and lichens, Riggin found only 694 individual tardigrades – hardly a story of high densities on a broad scale. These were represented by 26 species. *Macrobiotus* seems to be among the most common genera on bryophytes, including North American collections where Riggin found 63% of the Virginia bryophyte (moss?) and lichen collections housing members of this genus.

In a study of both the Upper and Lower Peninsulas of Michigan, USA, Meyer *et al.* (2011) revealed 28 species of tardigrades from mosses, liverworts, lichens, and leaf litter, of which 19 were from bryophytes [*Echiniscus blumi*, *E. merokensis*, *E. virginicus*, *E. wendti*, *Pseudechiniscus facettalis*, *P. suillus* (Figure 44), *Milnesium tardigradum* (Figure 3), *Hypsibius arcticus* (Figure 45), *Ramazzottius baumanni*, *R. oberhaeuseri* (Figure 5), *Diphascion alpinum*, *D. nodulosum* (Figure 46), *Astatumen trinacriae* (Figure 36), *Macrobiotus echinogenitus*, *M. hufelandi* (Figure 15), *Minibiotus intermedius* (Figure 47), *Fractonotus caelatus*, *Paramacrobiotus areolatus* (Figure 48), *P. tonollii* (Figure 49)]. Of the 28, 18 species were considered to be cosmopolitan. They found only one new



species, and it was not a bryophyte dweller. Although Ramazzotti and Maucci (1983) reported that more than ten taxa of tardigrades can often occur in a single bryophyte sample, and the range is generally 2-6, Meyer *et al.* found diversity on Michigan bryophytes to usually be at the lower end of this range.



Figure 44. *Pseudechiniscus juanitae*. Photo by Paul J. Bartels, with permission.



Figure 45. *Hypsibius arcticus*. Photo from Smithsonian Institution through EOL Creative Commons.



Figure 46. *Diphascon nodulosum*. Photo by Michael Collins, with permission.



Figure 47. *Minibiotus intermedius*. Photo by William Miller through Flickr.



Figure 48. *Paramacrobiotus* [=Macrobiotus] *areolatus*. Photo by Martin Mach, with permission.

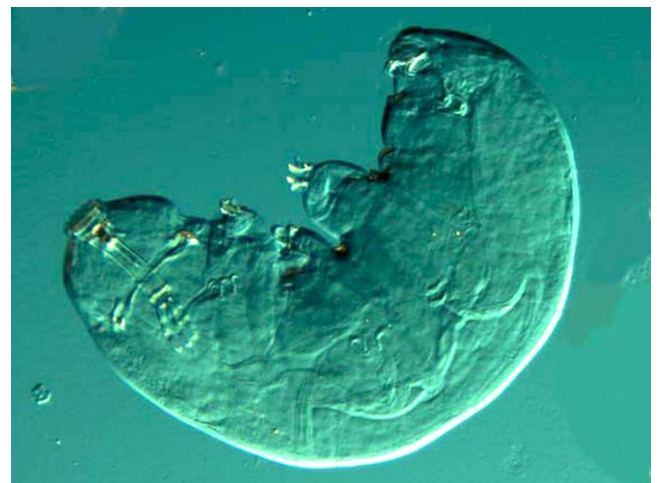


Figure 49. *Paramacrobiotus tonollii*. Photo by Paul J. Bartels, with permission.

Nelson and Hauser (2012) collected epiphytic mosses and liverworts in a natural area in Oregon, USA. Out of 1102 invertebrates collected, the tardigrades ranked second, exceeded only by the mites (*Acari*). They pointed out the need for water sampling (washing samples) to find tardigrades. These animals did not show up in the Berlese



extraction used by many collectors. Their collections reveal at least six or seven different taxa of tardigrades from each epiphytic moss water sample, a number that brings the patchy distribution of tardigrades into question. They considered the tardigrades to be well represented for a group with approximately 1000 species, compared to mites with approximately 50,000 species.

### South America and Neotropics

Numbers of species and density varies widely among tardigrade collections. Claps *et al.* (2009) found 28 species in 10 genera in a sub-Antarctic *Nothofagus* forest (18) and plateau (13) in the Rio Negro province of Argentina. In Costa Rica, Kaczmarek *et al.* (2009, 2011) found more than 7000 tardigrade individuals in 700 samples of lichens, mosses, and liverworts. These comprised 64 species in 18 genera, but the average number of species per sample was not more than three. They found altitude to be an important factor in distribution, with the highest diversity in the range of 1400-2000 m asl (35 species, 55% frequency). Only 18 species (28% frequency) occurred in the range of 2400-2800 m asl. In the range of 2000-2400 m asl the number of individuals was high. Then at 3200 m asl the frequency (70%) and abundance increased again. Surprisingly, they found a significantly higher presence in the urban and agricultural habitats than they did in natural habitats. Although 24 species had very defined habitat preferences, with the highest frequency in humid habitats, substrate and plant type were not important in their habitat choice.

### Asia

Unfortunately, much of the Asian literature is lost to the western world because of our lack of skill in reading the languages. But according to Beasley *et al.* (2006), the knowledge of tardigrades in China is meager. And ecological studies seem to be totally wanting. Many of the studies are simply reports of collections made by outsiders (*e.g.* Mathews 1937a, b; Bartos 1963; Pilato 1974; Beasley *et al.* 2006). Pilato (1974) found six species of tardigrades in Chinese bryophyte communities and identified three new species: *Bryodelphax* [= *Echiniscus*] *sinensis*, *Macrobiotus mandalae*, and *Macrobiotus mauccii*. Yang (2002) reported on tardigrades from bryophytes in Yunnan Province. Beasley *et al.* (2006) reported only 18 species from a wide geographic range (3 provinces) in China, with 12 of these species occurring on mosses [*Echiniscus nepalensis*, *Pseudechiniscus jiroveci*, *Murrayon hibernicus*, *Hypsibius pallidus*, *Isohypsibius sattleri*, *Doryphoribius flavus*, *Diphascon pingue* (Figure 21), *Diphascon scoticum* (Figure 50), *Diphascon prorsirostre*, *Mesocrista spitsbergensis* (Figure 51), *Platicrista angustata* (Figure 52), *Milnesium tardigradum* (Figure 3)] and 1 on a liverwort [*Cornechiniscus lobatus* (see Figure 53)]. Of the 18 species reported, 8 were new to China! It is likely that a much larger fauna exists but has not been explored – or translated.

In 2007, Beasley and Miller published a list of tardigrades from Xinjiang Uygur Autonomous Region, China, based on bryophyte specimens from the Missouri Botanical Garden. They found only 78 tardigrades among the 270 specimens of bryophytes, comprising 12 species. Of these 12, 7 were new to China. Several additional

species could not be identified. The best known bryophyte dweller among these was *Milnesium tardigradum* (Figure 54). *Echiniscus testudo* (Figure 6) was found among the greatest number of bryophyte species. The majority of species were in the *Heterotardigrada*, possibly due to the higher elevation of the samples and the arid nature of the habitats.



Figure 50. *Diphascon scoticum*. Photo by Łukasz Kaczmarek, with permission.



Figure 51. *Mesocrista spitsbergensis*. Photo by Björn Söhlenius Swedish Museum of Natural History, with permission.



Figure 52. *Platicrista angustata*, a species that occurs on mosses in China. Photo by Michael Sullivan, with permission.

International knowledge of the Japanese tardigrade fauna suffers from the same language barrier. Mathews, who also named a number of Chinese taxa, reported on the Japanese tardigrades in 1936/37. More recently, Ito (1999) made an ecological study on the north slope of Mt. Fuji,



sampling soil, mosses, and lichens. The number of soil tardigrades ranged 8,050 m<sup>-2</sup> to 75,500 m<sup>-2</sup>. Their density was as high as the density of soil arthropods such as mites (Acari) and springtails (Collembola). A few of these showed a relationship with altitude (950-2380 m asl), but typically the dominant species for a habitat did not change much among locations. On the other hand, they changed considerably between habitats at a single location.



Figure 53. *Cornechiniscus cornutus*. Photo by Martin Mach, with permission.

The Japanese certainly have not ignored the tardigrades. They have made important contributions to the physiology (Horikawa & Higashi 2004; Horikawa *et al.* 2006) and space biology (Horikawa 2008; Ono *et al.* 2008) of these organisms. There are also good studies on the ecology of soil species. But ecological studies on bryophyte-dwelling taxa are hard to find.

## Africa

Although little is known about them, Africa sports its share of moss-dwelling tardigrades. Pilato and Pennisi (1976) reported 21 species of tardigrades among the mosses in their collections from Cyrenaica (eastern coast of Libya), two of which represented the first members of their genera in Africa. A third, *Isohypsibius brulloi*, was a new species. Binda (1984) found thirteen species of moss-dwelling tardigrades in South Africa and Mozambique.

Meyer and Hinton (2009) found only nine species of tardigrades among mosses and lichens in KwaZulu-Natal, South Africa, bringing the total number of species from soil, mosses, and lichens to 61 in southern Africa. But aside from species records, tardigrade-bryophyte ecological studies seem to be rare or non-existent for Africa.

## Antarctic and Arctic

Unlike Asia, Africa, and South America (McInnes 1994), tardigrades are fairly well studied in polar climates, especially in the Antarctic. In the Antarctic, bryophytes, as well as lichens and algae, provide important habitats for tardigrades, rotifers, and nematodes (Utsugi & Ohyama 1991; Sohlenius *et al.* 2004). Most invertebrates decrease in abundance as one approaches the poles, but Jennings (1979) found that tardigrades actually increase in abundance in the Antarctic tundra. Peters and Dumjahn (1999) found 15 species in ten genera in their 249 cushion moss samples from Disko Island, West Greenland. On the other hand, in his moss studies on the Antarctic

Schirmacher Oasis, Mitra (1999) examined 36 sites and found only two tardigrade species.

Here they are also patchily distributed, nevertheless usually having the highest densities among these three groups of organisms. The ubiquitous and very common moss inhabitant, *Macrobiotus* sp., is present there, on the sub-Antarctic Marion Island (McInnes *et al.* 2001). Other tardigrades present include *Milnesium* cf. *tardigradum* (Figure 54) and *Echiniscus* sp. (Figure 55). Gut analysis of *M. tardigradum* revealed the presence of bdelloid rotifers and even other tardigrades (*Diphascon* sp.). Sohlenius and Boström (2006) also noted predation by tardigrades on rotifers in East Antarctica.

On the **nunataks** (mountain peaks that penetrate the ice sheet) in continental Antarctica, distribution of tardigrades is patchy, with the greatest abundance occurring within moss cushions and **guano** (accumulated excrement of seabirds and bats) from bird colonies (Swedish Museum of Natural History 2009). Nine tardigrade taxa have been identified in the Swedish studies.



Figure 54. *Milnesium tardigradum*, a cosmopolitan moss inhabitant. Photo by Yuuji Tsukii, with permission.



Figure 55. *Echiniscus*, a ubiquitous genus that occurs on mosses in the Antarctic. Photo by Martin Mach, with permission.

On Signy Island off the coast of Antarctica, Jennings (1979) found five species of tardigrades that occurred at both of the sampling sites: *Echiniscus capillatus*, *E. meridionalis*, *Hypsibius dujardini* (Figure 23), *Diphascon alpinum*, *Diphascon pingue sensu lato* (Figure 21; or may be *Diphascon polare*, *D. dastychi*, or *D. victoriae*), and *Macrobiotus furciger* (Figure 56). Other less common taxa were *Diphascon scoticum* (Figure 50), *Isohypsibius renaudi* (Figure 57), and *Isohypsibius asper* (Figure 58). Jennings conducted sampling for two years and found maximum populations of 309x10<sup>3</sup> m<sup>-2</sup> in moss communities of *Polytrichum strictum* - *Chorisodontium aciphyllum* (Figure 59-Figure 61). In the *Calliergidium austro-*



*stramineum* – *Calliergon sarmentosum* – *Sanionia uncinata* communities (Figure 12; Figure 62; Figure 63) they found a maximum of  $71 \times 10^3 \text{ m}^{-2}$ . Reproductive potential is high, with increases of 3- to 4-fold in a single year. Hallas and Yeates (1972) found they could reach as high as 10- to 20-fold increases. *Echiniscus* increased 100-fold at one Signy Island site (Jennings 1979).

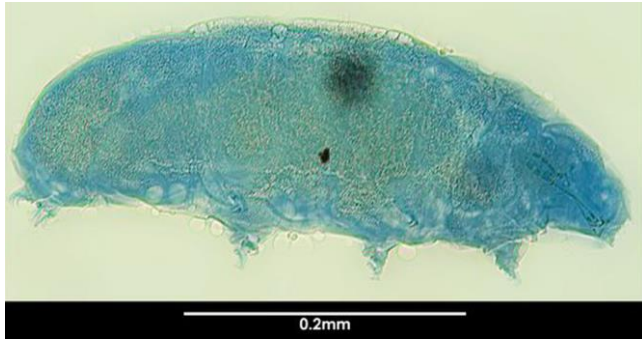


Figure 56. *Macrobotus furciger*. Photo by Smithsonian Institution through EOL Creative Commons.



Figure 57. *Isohypsibius renaudi*. Photo through EOL Creative Commons.



Figure 58. *Isohypsibius asper*. Photo by Smithsonian Institution through EOL Creative Commons.

In their Antarctic study, Utsugi and Ohyama (1989) found five species of tardigrades in 15 out of 31 samples from Ongul Island, Langhovde, Skarvsnes, Einstoingen, and Rundvagshetta, including algae, lichens, and mosses. *Hypsibius arcticus* (Figure 45) was common in all their samples. The other four species were rare.



Figure 59. *Polytrichum strictum* and *Chorisodontium aciphyllum* in the Antarctic, where Jennings (1979) found  $309 \times 10^3$  tardigrades per  $\text{m}^2$ . Photo by Tim Hooker, with permission.

In a different study on Wilkes Land, East Antarctica, Petz (1997) found tardigrades in more than 74% of the collections of fellfield mosses. These were the most abundant of the invertebrates, with 4,607 in just one gram of moss. Rotifers were the most abundant in other habitats. Ottesen and Meier (1990) likewise found that tardigrades were more abundant among mosses on South Georgia, compared to other habitats.

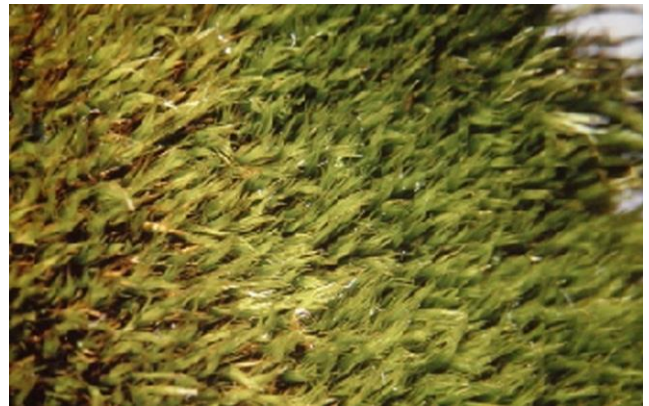


Figure 60. *Chorisodontium aciphyllum* in the Antarctic. Photo by Tim Hooker, with permission.



Figure 61. *Polytrichum strictum*, a moss habitat in the Antarctic and other cool, wet areas. Photo by Michael Lüth, with permission.





Figure 62. *Calliergon sarmentosum*, of the *Calliergidium austro-stramineum* – *Calliergon sarmentosum* – *Sanionia uncinatus* association in the Antarctic. Photo by Michael Lüth, with permission.



Figure 63. *Sanionia uncinata*, a cosmopolitan moss that provides tardigrade habitat in the Antarctic. Photo by Jan-Peter Frahm, with permission.

## Seasonal Variation

Densities may vary with seasons (Figure 66). *Hypsibius convergens* (Figure 18) exhibits temporal variation in pool and meadow moss habitats (Marcus 1929). In city mosses, the numbers of individuals of *Macrobiotus hufelandii* (Figure 15) and *Pseudechiniscus pseudoconifer* correlated with meteorological factors during a 3-month winter/early spring study (Franceschi *et al.* 1962-63). It appears that *Echiniscus* (Figure 55) and its segregate genera may commonly have seasonal variations. Jennings (1979) found that *Echiniscus* (possibly considered a segregate genus now) was the only tardigrade with seasonal variation among the eight species in his Signy Island study.

This is at least in part a reflection of changes in moisture. As already seen for *Diphascon rugosum* (Figure 22), *Hypsibius dujardini* (Figure 23), and *Hypsibius cf. convergens* (Figure 18), there were clear population peaks in winter in a carpet of the soil moss *Rhytidiadelphus squarrosus* (Figure 19) in the Black Forest, Germany (Schuster & Greven 2007). Species diversity and evenness was generally higher for the tardigrade communities in winter and least in summer (Figure 64). On the other hand, *Macrobiotus hufelandii* (Figure 15), *Diphascon pingue* (Figure 21), and to a lesser degree *Paramacrobiotus richtersi* (Figure 20), declined in winter, increasing in spring through fall (Figure 65). *Macrobiotus hufelandii* had its peaks in summer and lows in January (Schuster & Greven 2007), as shown for total tardigrades by Merrifield and Ingham (1998), but the other major species did not follow that pattern (Schuster & Greven 2007).

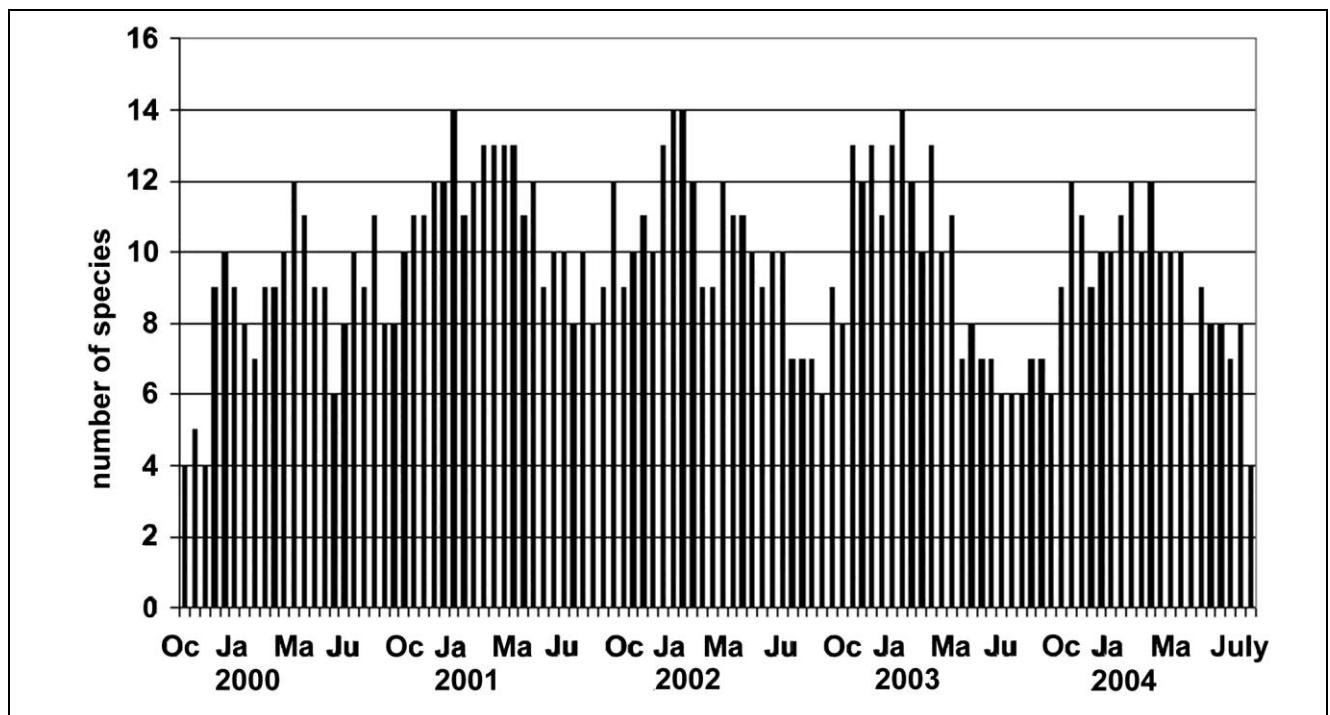


Figure 64. Seasonal changes in number of species of tardigrades found in *Rhytidiadelphus squarrosus* (Figure 19) clumps. (n = 108). Redrawn from Schuster & Greven 2007.



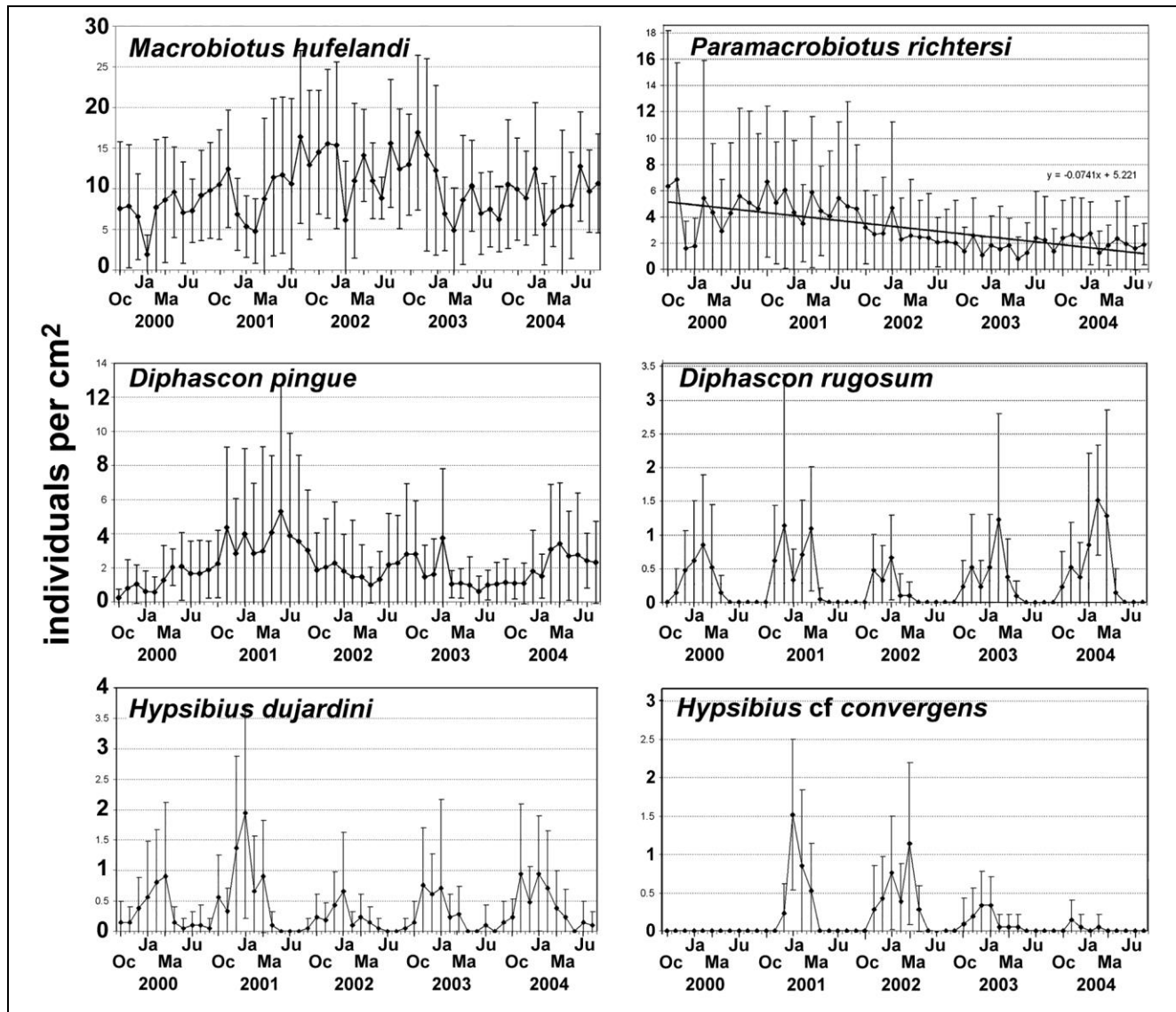


Figure 65. Seasonal changes in number of individuals of the dominant tardigrades found in *Rhytidiadelphus squarrosus* (Figure 19). *Paramacrobotus richtersi* shows a trend of decline during the sampling years, as shown by the regression line. Modified from Schuster and Greven 2007.

Using a Baermann funnel (Merrifield & Ingham 1998), Merrifield (1992) reported 5 tardigrades per gram on *Eurhynchium oregonum* (Figure 67) in Oregon, USA, from April to August, with an increase to 15 in September and October, then a crash to 1 for winter months of November through March (Figure 66). Were the bears hibernating elsewhere, or were numbers crashing in the damp Oregon winter?

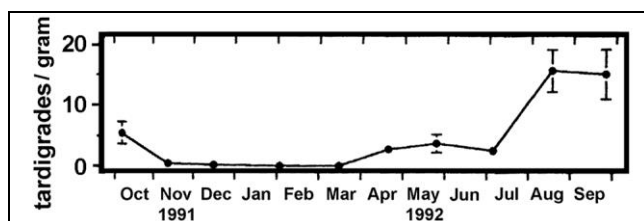


Figure 66. Seasonal changes in numbers of tardigrades on mosses at Mary's Peak, Oregon, USA. Redrawn from Merrifield & Ingham 1998.



Figure 67. *Eurhynchium oregonum*, a non-winter habitat for tardigrades. Photo from University of British Columbia bryophyte website, with permission.



Romano *et al.* (2001) attempted to determine the seasonal effects on tardigrades among mosses along Choccolocco Creek, Alabama, USA. They surveyed mosses on three trees each in six sites for 18 months and found no correlation between occurrence and season. However, they did find seasonal differences in the number of species and abundance when they pooled samples.

## Patchiness

A number of studies suggest that the distribution of tardigrades within a given area or on a particular type of substrate is patchy. Degma *et al.* (2005) actually did both cluster analysis and CCA, demonstrating that most of the differences in species diversity were the result of randomly found species and that colonization of any given substrate is a random process. It would appear that the greatest determining factor in their specific location and species composition is their dispersal to that location, a process that is as random as it is for the mosses and liverworts they sit on. Further support for this randomness is their random distribution among populations of the moss *Hypnum cupressiforme* (Figure 68), supported by a Chi-square goodness of fit test.



Figure 68. *Hypnum cupressiforme*, a ubiquitous moss that seems suitable for many taxa of tardigrades. Photo by Michael Lüth, with permission.

Degma *et al.* (2009, 2011) found that the horizontal distribution of the tardigrades on a moss clump is aggregated, but that aggregation is not related to moisture in the moss cushion. They hypothesized that once a tardigrade arrives through random recruitment it is able to establish a micro-population. From that beginning slow radiation occurs. The result is that large substrates have more tardigrades but some parts of these larger patches will lack tardigrades while other parts will house aggregations. They continued their study (Degma *et al.* 2011) using *Hypnum cupressiforme* (Figure 68) with a 5x5 matrix of circular plots and determined that there was no significant moisture gradient along that moss slope. Nevertheless, the tardigrades existed in clumps or patches. With a large number of individuals (224) in seven species [*Milnesium tardigradum* (Figure 3), *Hypsibius convergens* (Figure 18), *H. microps*, *Diphascon pingue* (Figure 21), *Astatumen trinacriae* (Figure 36), *Macrobiotus hufelandi* (Figure 15), *Minibiotus* sp. (Figure 47)], they found that species number was random, but that species distribution

was aggregated. That aggregated distribution was NOT related to moisture in the moss mat. They concluded, therefore, that the best hypothesis to explain the patchy distribution of the tardigrades within the moss cushion was that recruitment of eggs and specimens on the moss was random and that these recruits subsequently reproduced, creating micro-populations where density gradually increased over time. This hypothesis makes the assumption that tardigrades migrate little from the location of their birth. Following this reasoning on a larger scale would account for the patchy distribution observed on larger moss clumps. Larger patches of mosses are more likely to be the recipients of dispersed tardigrades or their eggs and hence are more likely to have tardigrades than would small patches. This would also account for the high degree of variation encountered in random sampling from various moss cushions in the same location. While the individuals are aggregated, the aggregations are random.

Meyer (2006b) did a careful study on the spatial variability of tardigrade populations among moss patches on trees and rocks at three locations in the USA. He examined the fauna on patches ranging 0.1 to >5 cm<sup>2</sup>. He found very high variation among the patches. One interesting discovery was that very small patches rarely had tardigrades. Could it be that they did not retain moisture long enough, or was it a matter of dispersal, with small patches having endured too short a time for colonization to be common?

Perhaps it is predictable that patchiness would characterize Antarctic moss dwellers. In the Antarctic, bryophytes, as well as lichens and algae, provide an important habitat for tardigrades, rotifers, and nematodes (Utsugi & Ohyama 1991; Sohlenius *et al.* 2004). Here tardigrades are also patchily distributed, nevertheless having the highest densities among these three groups of organisms. One might assume that bryophytes must arrive first, or that the tardigrades arrive with their bryophyte home. Hence, dispersal to the continent and its remote islands most likely plays a major role in their location.

Studies by the Swedish Museum of Natural History (2009) likewise found patchy distribution of tardigrades on the nunataks of the Antarctic. These windswept peaks emerge above the ice sheets and provide the substrate needed for bryophytes, lichens, and inhabiting tardigrades. Moss cushions and humus enriched by bird colonies provided the greatest numbers of tardigrades, with 400 samples yielding only nine tardigrade taxa. Nevertheless, 32% of the samples had tardigrades (Sohlenius & Boström 2006). The importance of the stochastic process of colonization is supported by the presence of different developmental stages in various samples, suggesting that dispersal may be a dynamic, albeit random, process occurring constantly on the windy peaks. Further population control may exist through competition with the co-occurring nematodes, whereas it appears that the poor rotifers serve as dinner for at least some of these tardigrades.

Bettis (2008) tested differences in tardigrade distribution on *Grimmia* (Figure 69) on exposed granitic outcrops vs protected seasonally riparian forms in California, USA. Again, the distribution was "very patchy" and did not support the hypothesis that more tardigrades would be on the more protected, more moist mosses.





Figure 69. *Grimmia laevigata* in Europe. Photo by Michael Lüth, with permission.

Both Meyer (2006b) (in the terrestrial system) and Romano *et al.* (2001) (in the aquatic system), emphasized the importance of accounting for this patchiness in designing a sampling strategy. Meyer suggested that the variability of a given location should be understood before determining the number of samples to take. Romano emphasized the need for a greater sampling effort.

In short, it appears that the major factor accounting for tardigrade distribution and patchiness is dispersal. If the tardigrade lands in an appropriate habitat, it is able to withstand considerable environmental variation there, and the habitat itself seems to offer little to discriminate against any tardigrade species. Rather, factors like reproductive potential may play the greater role in determining the abundance, and possibly even the diversity, once the tardigrades arrive.

I was excited to make new friends among newcomers to the bryophyte-tardigrade relationship. I hope this chapter has inspired more young researchers to include the bryophyte microcosm in their studies. Jaime Jiménez, a vertebrate zoologist, summarizes his conversion to tardigrade study in the box below:

### Statement by Jaime Jiménez

While working on the seedsnipe and geese feces with Nick [Nick Russo] and Mike [Robertson] on Navarino Island, examining for bryophytes fragments to cultivate, they found a few small water bears. Nick and Mike were my first cohort students from my IRES-NSF grant (Bernard [Goffinet] was the US co-mentor). We were all captivated to see these creature for the first time. It happened that Peter Convey (BAS that used to examine tardigrades from Antarctica) was at the lab during these days and he offered to bring these samples to Cambridge to the tardigrade world expert Sandra McInnes. She put me in contact with William Miller (KS, one of the US tardigrade experts), as she recently reviewed a paper of him on tardigrades found in bird nests. Simultaneously, with Mike, Nick and Sandra we presented a poster in Copenhagen and then in British Columbia (American Ornithological Societies conference). I invited William to

UNT, and since then we have been collaborating. As a result, I “rearranged my lab” to add microscopes, dissecting scopes and cameras to mammal traps, camera traps, mist nests and binoculars. This triggered my enthusiasm to collect many bryophytes/moss samples throughout southern Chile from which I am “hunting” tardigrades to study their biogeography and habitat associations. I also have one graduate student working on tardigrade biotic homogenization.

### Summary

Tardigrades can range in numbers from none to 22,000 individuals per gram of dry moss. More than 2 million are known from a single square meter. On Vancouver Island in Canada, 39 species have been found among bryophytes. They do not seem to prefer any particular moss, and they often occur equally as frequently on lichens and liverworts as they do on mosses. In New Zealand, 30 species are known from liverworts.

*Macrobiotus* and *Echiniscus* (and their more recent segregates) are among the most abundant tardigrades in the bryophyte fauna. Although most invertebrates decrease in numbers toward the poles, tardigrades actually increase. However, their numbers are highly variable from one place to another. Here, even more so than elsewhere, distribution of the tardigrades is patchy. Even adjacent trees in some localities are known to differ greatly in their tardigrade fauna. Yet, on Wilkes Land in the Antarctic, 74% of the fellfield mosses had tardigrades.

They are known to increase up to 100-fold, but it appears that 3- to 4-fold is more typical. Their abundance can be seasonal, with some peaking in winter and others in summer or spring/fall. Some respond to the rainy season. Others don't seem to respond to season.

Dispersal plays a large role in both geographic distribution and local patchiness. Within the cushions the tardigrades are often aggregated, but there appears to be no relationship with moisture. On the other hand, small patches seem to lack tardigrades, suggesting that moisture is important. But arrival is a major factor, and from that arrival of one tardigrade, a population develops. Since their movement is slow, they accumulate. But small patches of mosses indicate a short time in which arrival could have occurred.

### Acknowledgments

Like all of my chapters, this one is really the product of the efforts of many biologists. Roberto Bertolani provided an invaluable update to the tardigrade taxonomic names and offered several suggestions on the text to provide clarification or correct errors. Bryonettors have been wonderful in making their photographs available to me and seeking photographs from others. Paul Davison and Des Callahan have been helpful in providing suggestions and offering images. Bob Goldstein, Bjorn Sohlenius, Martin Mach, and Yuuji Tsukii have given permission to use images that illustrate the species and life



cycle stages. Łukasz Kaczmarek has provided me with references and contact information. As always, a big thank you goes to Michael Lüth for permission to use his many images and to all those who have contributed their images to Wikimedia Commons and other public domain sources for all to use. I must admit that this chapter would have been far less interesting without the help of Google to locate the tardigrade stories. I fear I have forgotten some who have helped – I have worked on this chapter for too many years. Nomenclature follows Degma *et al.* (2010).

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