

# CHAPTER 5-6

## TARDIGRADE ECOLOGY

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# CHAPTER 5-6

## TARDIGRADE ECOLOGY



Figure 1. *Echiniscus*, the genus with the most species among mosses. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

### Dispersal

As already discussed, one suggested reason for patchy distribution of tardigrades is the difficulty of dispersal for this small organism. Miller *et al.* (1994) concluded that tardigrade distribution in the Antarctic is influenced more strongly by dispersal limitations than it is by climate or habitat interactions. McInnes and Convey (2005) found a low species richness of tardigrades (6 taxa) in the South Sandwich Islands in the sub-Antarctic. They found indications that the tardigrades originated from both sub-Antarctic and maritime Antarctic populations.

Wind dispersal is considered the major means by which tardigrades move to new locations (Christenberry & Higgins 1979; Bertolani *et al.* 2009). The anhydrobiotic state is very light weight and can easily survive the various dangers of space (see below).

Faurby *et al.* (2008) suggested dispersal rate may be coupled with survival in the anhydrobiotic state. Based on these assumptions, Bromley (2009) has considered the possibilities that habitats such as rooftops with mosses serve as islands for tardigrades.

Sudzuki (1972) experimented with wind dispersal to moss mats and found that smaller micro-organisms (<10x30x50 µm) were easily blown from their location to reach the mosses 100-500 cm away. Tardigrades, on the other hand, almost never reached the mosses during two

months of experimentation with the fan-generated wind operating alternate days.

Although wind is probably the most common means, other means of dispersal may be afforded by water, insects, and other invertebrates. Resting eggs offer another dispersible propagule. Eggs of tardigrades are about the same size as a pollen grain and may similarly be dispersed by wind (Ramazzotti 1972). Many species have eggs with decorations on them (Figure 2) reminiscent of allergenic pollen grains, *i.e.*, those adapted for wind pollination.



Figure 2. Egg of *Dactylobiotus* sp. showing decorated wall similar to that of a pollen grain. Photo by Yuuji Tsukii, with permission.

Whereas tardigrades don't seem to be dispersed very easily by themselves, their dispersal as hitch-hikers on bryophytes is a more feasible means (Janiec 1996). Not only live animals, but also tuns, cysts, and eggs can be dispersed when their bryological home is dispersed. Storms, animals, wind, and water are all means by which the substrate and fauna could travel together.

Most recently, we find that a combination of seedsnipes, bryophytes, and tardigrades may contribute to their dispersal (Robertson *et al.* 2020). Robertson and coworkers demonstrated that tardigrades can live in the feces of the White-bellied Seedsnipe (*Attagis malouinus*, Figure 3). These included the tardigrades *Adropion* (Figure 4), *Isohypsibius* (Figure 26), and *Macrobiotus* (Figure 11, Figure 17, Figure 25). Since at least some of these genera are known to live among bryophytes, and *Attagis malouinus*, as well as two species of the geese *Chloephaga picta* (Figure 5) and *C. poliocephala* (Figure 6) are known to ingest bryophytes (Russo *et al.* 2020), dispersal of mosses and their adherent tardigrades might very well be dispersed by **endozoochory** – that is, dispersal by passing through the gut of the birds.



Figure 3. *Attagis malouinus* in rocky area with mosses nearby. Photo courtesy of Nick Russo.

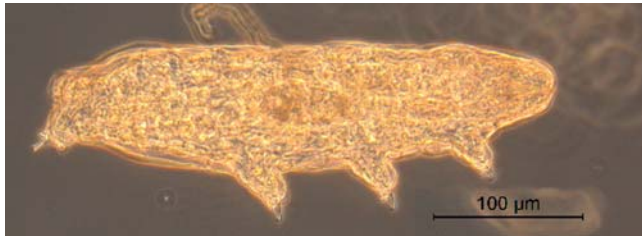


Figure 4. *Adropion scotticum*, a tardigrade found in an embryonic stage in the feces of *Attagis malouinus*. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.



Figure 5. *Chloephaga picta*, a species known to eat mosses. Female on left, male on right. Photo by Fabien Khan, through Creative Commons.



Figure 6. *Chloephaga poliocephala* adult in Patagonia, a species known to eat mosses. Female on left, male on right. Photo by Alex Proimos, through Creative Commons.

### Peninsula Effect

The **peninsula effect** postulates that the number of species will decrease as one approaches the tip of a peninsula. This presumably is the case because of the lack of opportunity for invasion of new species from the more seaward positions. Simpson (1964) suggested that there is a peninsular effect in animal distribution similar to that seen in island biogeography. Jenkins and Rinne (2008) defined the peninsula effect as "the prediction that the number of species declines from a peninsula's base to its tip." They considered whether this concept might be a "red herring" and expressed concern that most studies had not controlled for other possible explanations or from unequal sampling effort. In the Florida, USA, peninsula, they found that 82.5% of variation in freshwater microcrustacean species richness was attributed to habitat and sampling effort, and there was no peninsular effect. In fact, they suggest that the evidence previously published only supported the concept for mammals.

Taylor and Regal (1978) tested the concept of extinction and recolonization, a tenet of the peninsular effect, for rodents in Baja California and concluded that for an effective peninsular effect the habitable sites "are few and widely spaced." Brown (1987) examined the effect on butterflies (Lepidoptera) in the Baja peninsula and determined that there was no peninsular effect for that group. Likewise, Busack and Hedges (1984) found no peninsular effect for lizards and snakes on the Baja peninsula.

Taylor and Regal (1978) suggest that changes in vegetation in Florida that are due to rising water levels and climate change may account for the decline in species richness southward on that peninsula. They argue that other large peninsulas where Simpson demonstrated a peninsular effect represent major topographic changes or harsh climate gradients that could account for changes in species number.

Nevertheless, Meyer (2008) found a peninsular effect in tardigrades when bryophyte and lichen epiphytes in all 67 Florida counties were sampled, with species richness diminishing from north to south. If we combine the information gained from the above studies, it appears that Taylor and Regal (1978) may have been correct in suggesting that the peninsular effect required few and



widely spaced habitable sites. And widely spaced for one species may be a lazy day's walk for another. To put this into the perspective of bryophyte-dwelling tardigrades, isolation and difficulty of dispersal are typical, *i.e.*, widely spaced habitable sites (see dispersal discussion above), and would make tardigrades more likely to have the extinction-recolonization limits required for the peninsular shape to have a "peninsular effect." The apparent need for wind dispersal of tardigrades is further complicated by their residence within the bryophyte mat, and it seems they would most likely be dispersed only when they and their bryophyte substrate are dry and fragments to which they adhere become airborne. This dispersal limitation has been discussed earlier (Chapter 5-5 of this volume) in relation to the patchiness of populations within a given small area.

There is a possible caveat to this discussion. The definition of a peninsular effect seems to have drifted from that of Simpson (1964). He considered peninsulas to have fewer species (lower richness) than continental areas and did not treat them as having fewer species toward the tip. However, he did consider that spread of species could occur in one direction only (*i.e.*, no new mammal species were likely to arrive from the tip in the short term). He suggested that this would make them more liable to local extinctions (*i.e.*, reducing the density of species richness).

## Distribution

Tardigrades, like the protozoa, have many taxa with worldwide distributions (McInnes 1994; McInnes & Pugh 1998). With so little attention paid to this group, relative to that for the protozoa, it is difficult to draw distributional conclusions. There are hints of the "**everything is everywhere**" principle (in Wit & Bouvier 2006) for these small, lightweight creatures. (See Chapter 2-6 on Protozoa Ecology.) Their ability to become anhydrobiotic for long periods of time increases their chances for successful dispersal over great distances.

Among the moss dwellers, we find that *Doryphoribius flavus* has been found in Europe, Asia, Africa, and Central America (McInnes 1994). It is now known from Tennessee, USA (Bartels *et al.* 2007). Its original discovery was in moss subjected to desiccation (Iharos 1966). On the other hand, *Doryphoribius polynetae* had been found only in Russia in a small lake and in mosses [*Sphagnum* sp. (Figure 7), *Polytrichum juniperinum* (Figure 8)] near the lake, but was likewise recently found in Tennessee (Bartels *et al.* 2007).



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

Meyer (2008) found *Minibiotus fallax*, previously known only from Australia (Pilato *et al.* 1989), in moss and lichen collections from Florida, USA. Other surprising disjunctions are likely to appear because the group is poorly known and sampling is spotty.

Jørgensen *et al.* (2007) explored the microspecies concept in *Echiniscus testudo* (Figure 9), using DNA sequences. Their study included 13 localities on three continents. They found high haplotype diversity and low sequence diversity, suggesting that this species had haplotype evolution with distinct asexual lineages and a high dispersal, as suggested by lack of isolation by distance. Although there were geographic differences, there was low genetic diversity. *Echiniscus* (Figure 10) is the largest genus, and the authors suggest that the high number of species may result from the combination of large potential for dispersal coupled with the lack of need of a partner for reproduction. Bryologists might benefit from understanding the distribution of these organisms as bryophytes and tardigrades seem to have similar dispersal advantages and disadvantages and both are capable of asexual reproduction.



Figure 8. *Polytrichum juniperinum*. Photo by Michael Lüth, with permission.

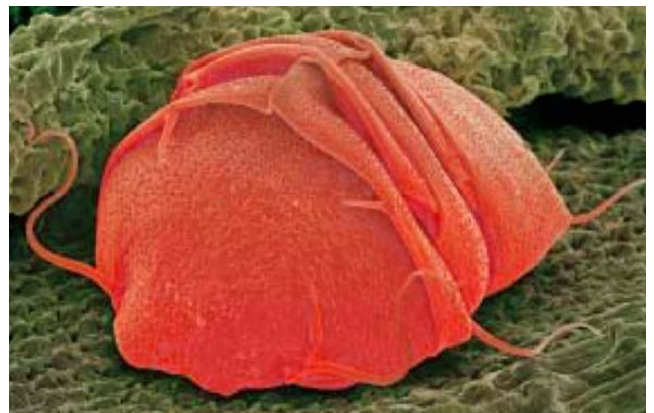


Figure 9. *Echiniscus testudo* tun. Photo by Power & Syred through Creative Commons.

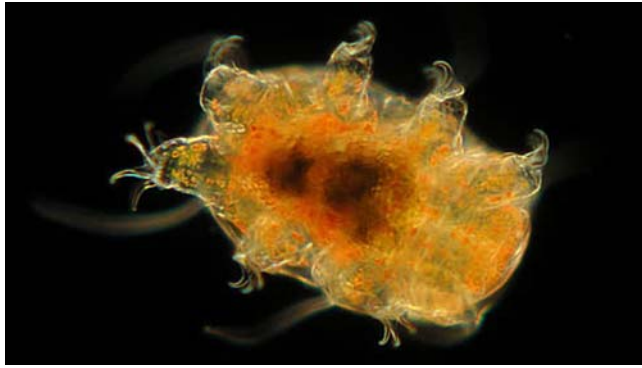


Figure 10. *Echiniscus*, the largest tardigrade genus and a common bryophyte inhabitant. Photo by Martin Mach, with permission.

Although it does not appear that *E. testudo* (Figure 9) has a large number of microspecies, it is likely that some of the more common species may actually be species complexes, further complicating our understanding of species distributions and diversity. These include taxa such as *Macrobiotus hufelandi* (Figure 11), *Minibiotus intermedius* (Figure 12), *Diphascon scoticum* (Figure 13), and *Milnesium tardigradum* (Figure 14) (Bertolani & Rebecchi 1993; Claxton 1998, 1999; Pilato 1987).



Figure 11. *Macrobiotus hufelandi*. Photo by Martin Mach, with permission.



Figure 12. SEM of *Minibiotus intermedius*. Photo by William Miller through Flickr Commons.



Figure 13. *Diphascon scoticum*. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

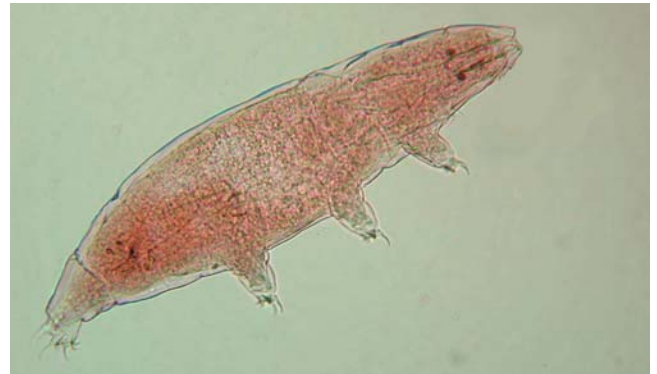


Figure 14. *Milnesium tardigradum*. Photo by Björn Sohlenius at Swedish Museum of Natural History, with permission.

Blaxter *et al.* (2004) examined the Scottish tardigrade fauna for genetic differences. They found that some **Molecular Operational Taxonomic Units (MOTU)** were shared between the two rural collections in the study, but that none were found in both the one urban and two rural sites. This lack of commonality conflicts with the generally accepted concept of ubiquity of this faunal group. They described the high variability among the specimens as representing "**taxon flocks.**" It suggests to me that once arriving at a new site, the tardigrades are likely to reproduce asexually and eventually diverge from their ancestors, creating **cryptic species**. **Genetic drift**, **Founder Principle**, and **microselection** factors could all contribute to enhancing this noted variability. I suspect we will find many similar examples among bryophytes.

Such possibilities of genetic variation without obvious morphological indicators demonstrate the folly of attempting to present a reasonable distribution pattern for the moss-dwelling tardigrades at this stage. Look for them. You will probably find a new species, or at least a new cryptic species, and certainly expand our understanding of their distributions and their ecology.

Distribution is the product of many factors, including dispersal, climate, niches available, microclimate, and attending factors such as altitude, rainfall, temperature range, and severity and length of winter or summer. Guil *et al.* (2009) sampled mosses and other vegetation to determine the effects of micro- and macro-environmental factors on the distribution of tardigrades in those habitats in the central Iberian mountain areas of Spain. They found that bioclimatic classification was the best predictor for



species richness. Altitude had a relationship, but its effects could not be separated from the macro-environmental gradients of soil, climate, vegetation type, and litter type. Within the micro-scale plots, the micro- and macro-environmental variables could explain ca 60% of the species richness, particularly litter type and vegetation type. On the other hand, abundance was not explained by the macro-environment, but rather was explained by soil composition and litter type. I have to wonder if soil composition affected the availability of bryophytes and their growth forms.

## Common Species

Among the many collections of bryophytes, species of *Echiniscus* (Figure 15), *Hypsibius* (Figure 16), *Macrobiotus* (and segregate genera; Figure 17), *Milnesium* (Figure 14), and *Ramazzottius* (Figure 18) seem particularly common.

Table 1 lists some of the taxa known from the literature, but many more exist and would be an endless task to include here. A complete list of all tardigrade names with updated nomenclature (used here) is in Degma *et al.* 2010.



Figure 15. *Echiniscus* sp., member of one of the most common genera among bryophytes. Photo by Martin Mach, with permission.



Figure 16. *Hypsibius dujardini*, member of one of the most common moss-dwelling genera of tardigrades. Photo by Bob Goldstein, with permission.

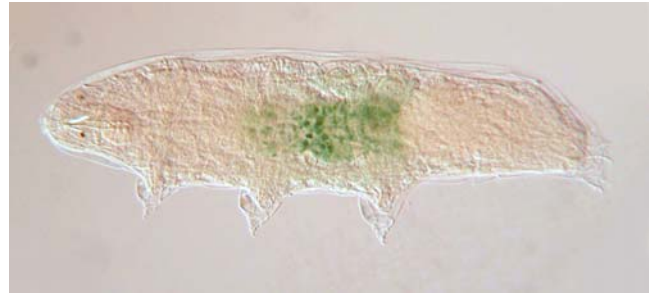


Figure 17. *Macrobiotus blocki*, an Antarctic member of one of the most common moss-dwelling genera. Photo by Martin Mach, with permission.

In Sweden, Jönsson (2003) found that *Macrobiotus hufelandi* (Figure 11) is far more common among mosses than are other tardigrade species. This species seems to be abundant in most bryophyte studies. It seems remarkable that as late as 2003, the common bryophyte dwellers *Murrayon diana*, *Isohypsibius sattleri*, *Platicrista angustata* (Figure 22), *Diphascon belgicae*, and *Diphascon pingue* (Figure 19) were recorded from Sweden for the first time (Jönsson 2003).

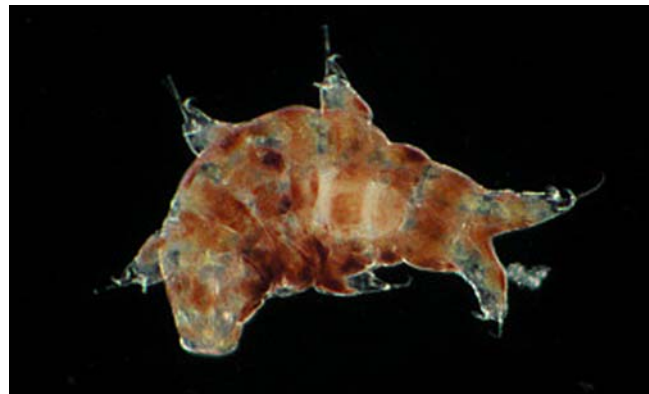


Figure 18. *Ramazzottius* sp., member of a common moss-dwelling genus. Photo by Martin Mach, with permission.



Figure 19. *Diphascon pingue*. Photo by Michael Collins, with permission.

A major problem in trying to define tardigrade distributions and habitats is the lack of sufficient study of this entire group of organisms. Guil and Cabrero-Sañudo (2000) stated that the "tardigrade species description process fails to show an asymptotic tendency." Meyer and Hinton (2007) reported that "30% of the Nearctic species have been reported from a single site!" In other words, it will be a long time before we even know most of the species in existence or even make reasonable estimates of

how many species there are. And ecological descriptions necessarily lag behind the descriptions of the species.

Beasley *et al.* (2006) lamented the difficulty of assessing diversity of tardigrades in China because of the limited data available. In their report on 18 tardigrades of Sichuan, Yunnan, and Xizang Provinces, eight were new records for China. Among the 86 species known from China, 82 are terrestrial. Among these, *Echiniscus nepalensis*, *Pseudechiniscus jiroveci*, *Murrayon hibernicus*, *Hypsibius pallidus*, *Isohypsibius sattleri*, *Doryphoribius flavus*, *Diphascon pingue* (Figure 19), *D. scoticum* (Figure 13), *D. prorsirostre* (Figure 20), *Mesocrista spitsbergensis* (Figure 21), *Platicrista angustata* (Figure 22), *Milnesium tardigradum* (Figure 14) were from mosses. Only *Cornechiniscus lobatus* (see Figure 23) was found on liverworts.

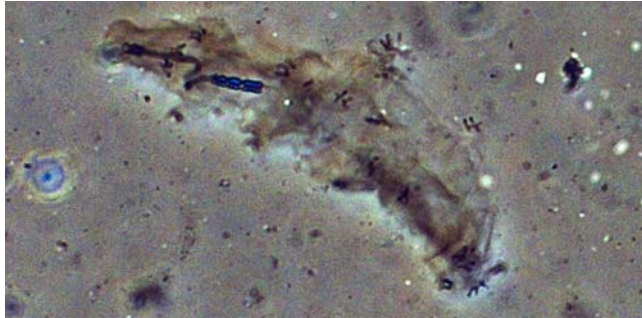


Figure 20. *Diphascon prorsirostre*. Photo by Michael Collins, with permission.



Figure 21. *Mesocrista spitsbergensis*. Photo by Björn Sohlenius, Swedish Museum of Natural History, with permission.



Figure 22. *Platicrista angustata*. Photo by Michael Collins, with permission.



Figure 23. *Cornechiniscus cornutus*. Photo by Martin Mach, with permission.

## Communities

Séméria (1982) found that a typical bryophyte-dwelling (and lichen-dwelling) tardigrade had one predator and several detritivorous or herbivorous species in its community. Typical communities of bryophyte-dwellers have 2-6 tardigrade species, and sometimes even more than ten (Ramazzotti & Maucci 1983).

Specific bryophyte communities have rarely been identified, but Miller *et al.* (1996) identified significant positive associations between the three most common of the tardigrade species and certain bryophyte species in the Antarctic. On the other hand, these same three species had a strong negative association with algae and lichens. In Britain, Wright (1991) suggested that *Milnesium tardigradum* (Figure 14) might have a selective predatory association with *Hypsibius dujardini* (Figure 16) and *Ramazzottius oberhaeuseri* (Figure 28).

Among the Florida epiphytes, Meyer (2008) typically found one predatory species [*Milnesium tardigradum* (Figure 14, Figure 50), *Paramacrobiotus richtersi* (Figure 24)], *Macrobiotus* cf. *harmsworthi* (Figure 25), or one other *Macrobiotus* species, one *Minibiotus* species, and one echiniscid species. One or more of these niches is frequently unoccupied, but when occupied the species followed this trophic hierarchy. In only one sample were there two predatory species.



Figure 24. SEM of *Paramacrobiotus richtersi*. Photo through Creative Commons.



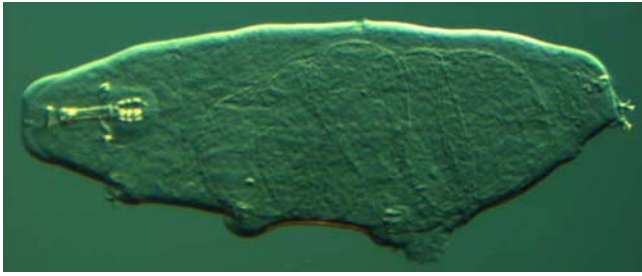


Figure 25. *Macrobiotus harmsworthi*, a common tardigrade on bryophytes and elsewhere. Photo by Paul J. Bartels, with permission.

Collins and Bateman (2001) found that *Isohypsibius prosostomus* (Figure 26) did not occur with *Diphascon scoticum* or *Minibiotus intermedius* (Figure 12) and only rarely occurred with *Diphascon pingue* (Figure 19) or *Hypsibius convergens* (Figure 27), attributing these negative associations to trophic overlap.

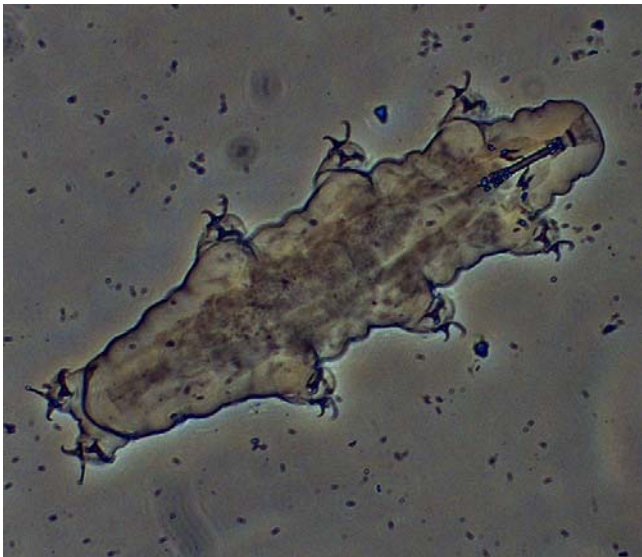


Figure 26. *Isohypsibius prosostomus*. Photo by Michael Collins, with permission.



Figure 27. *Hypsibius convergens*. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

Competitive exclusion, most likely for food, also drives community associations. Wright (1991) found that *Macrobiotus hufelandi* (Figure 11), *Paramacrobiotus richtersi* (Figure 24), and *Isohypsibius prosostomus* (Figure 26) avoid each other's company.

But food webs are not the only controlling factors. Bryophytes can play a major role through the climate they create. For example, *Macrobiotus hufelandi* (Figure 11) and *Hypsibius dujardini* (Figure 16) are absent when the habitat desiccates rapidly, making some bryophytes ideal for them (Wright 1991). *Milnesium tardigradum* (Figure 14, Figure 50) and *Ramazzottius* (formerly *Hypsibius*) *oberhaeuseri* (Figure 28) likewise avoid areas with a high rate of desiccation, as well as locations with high insolation, but also avoid poorly drained sites, excluding them from bryophytes in low-lying, wet areas. These limitations can result in predictable associations. Among these is a significant association among *Milnesium tardigradum* (Figure 14, Figure 50) – a predator – and two *Hypsibius* species among the British fauna. Further temporary community differences can be driven by the behavior of some species to migrate vertically in the moss cushion to a position of greater moisture, while other species such as *Echiniscus testudo* (Figure 9) remain behind. And of course this inability to migrate may limit the mosses it occupies in the first place.

But despite the importance of moisture in the continuing life cycle of the tardigrades, there is not always agreement on the moisture level needed. In Newfoundland, only *Hypsibius dujardini* (Figure 16) seems to follow a consistent relationship to a moisture category (Collins & Bateman 2001). It appears that rate of desiccation must be considered along with moisture level in determining the community structure.

Even on the same moss species or growth form, macrohabitat makes a difference. Jönsson (2003) found that tardigrade abundance of the same species differed between a forest and a clearcut area, with greater numbers of species in the forest. Nevertheless, abundances were similar.

## Unique Partnerships?

Despite the tiny size of this moss community, its relationships can be complex. The tardigrades *Ramazzottius oberhaeuseri* (Figure 28) and *Milnesium tardigradum* (Figure 14) both can carry the protozoan *Ptychidium tardigradum* (Figure 29) on their surface, a relationship known as that of a **symphoriont** (Morgan 1976). Morgan found both of these tardigrades with their passengers living among mosses. Van der Land (1964), who first discovered these protozoa on lichens, revived the dried tardigrades there, only to discover these protozoa that also were dormant became active after being placed in water. The accompanying rotifers and oribatid mites had no protozoan passengers, but Van der Land (1964) could not determine if these companions were alive at the time he rehydrated them. As noted earlier, this protozoan can at times be so abundant (up to 35 on a single water bear) that they slow down the tardigrade and might more appropriately be considered a parasite (Vicente *et al.* 2008). Although such symphoriont/parasitic(?) relationships have rarely been observed among the moss dwellers, we simply have not spent much time looking for them.





Figure 28. *Ramazzottius oberhaeuseri*. Photo by Martin Mach, with permission.

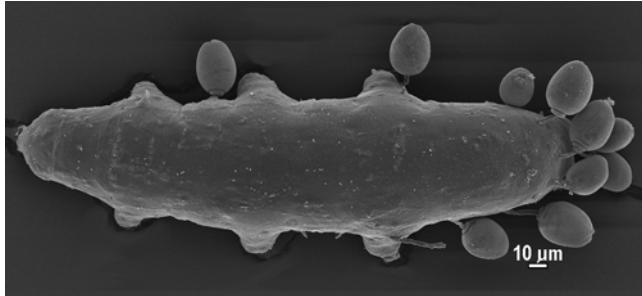


Figure 29. Tardigrade infected with the protozoan *Pyxidium* sp. Photo by Łukasz Kaczmarek and Łukasz Michalczyk, with permission.

## Bryophyte Dangers – Fungal Parasites

This wonderful bryophyte home is not without its dangers to the moss-dwelling tardigrades. The phycomycetous fungus *Catenaria anguillulae* (Figure 30) is a widespread parasite on living, senescent, and dead microscopic animals (Barron 2009). The motile zoospores are attracted to exudations from openings on the bodies of nematodes and rotifers (Jansson & Thiman 1992), and it is likely that this opportunist also occurs on tardigrades (George Barron, pers. comm. 2010). The zoospores encyst on the cuticular covering near the opening or a wound. Hence, it is typical for them to colonize around the mouth or other opening. They subsequently germinate and penetrate through the orifice or wound to attack the animal on the inside.

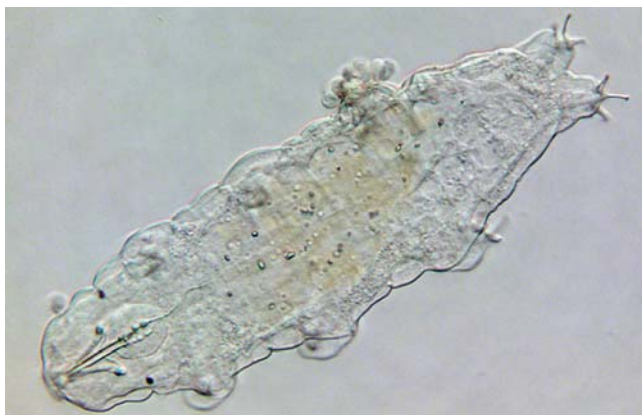


Figure 30. Tardigrade with fungus on its side. It is likely that this fungus is *Catenaria anguillulae* and that the attack location is a wound. Photo by Martin Mach, with permission.

Two fungi in the Ascomycota, *Lecophagus* [= *Cephalophora*] *muscicola* (Figure 31-Figure 32) and *Lecophagus* [= *Cephalophora*] *longispora* (Figure 33-Figure 34), capture rotifers and possibly tardigrades within the bryophytes and bryophyte-covered soil (Barron *et al.* 1990). This rather strange pair of fungi is endowed with elongate, hyaline, multiseptate, canoe-shaped conidia produced in small clusters at the apex of the conidiophores. When rotifers are present, the conidia germinate and produce one or several adhesive pegs that capture rotifers and tardigrades. Such fungal predators have been identified from moss-covered soil and forest debris in New Zealand and mosses in Canada, as well as from leaf mold in Japan, but their actual attack on tardigrades dwelling in mosses lacks documentation.

McInnes (2003) reports that the predatory fungus *Lecophagus antarcticus* attacks tardigrades that occur on cyanobacterial mats in lake sediments. Since *Lecophagus muscicola* (Figure 31-Figure 32) and *L. longispora* (Figure 33) are in the same genus and occur in wet or mossy soil (Barron *et al.* 1990; George Barron, pers. comm. 25 January 2010), it is reasonable to suggest that they might attack tardigrades in the same habitat, but can they? In fact, rotifers are attracted to the adhesive pegs of the fungus and then attach to the tip of the peg. That is their downfall, as the predator becomes the prey when the host (rotifer, nematode, or tardigrade) adheres to these adhesive pegs, possibly by lectin/carbohydrate bonding. But instead of providing a meal for the invertebrate, the fungus penetrates and parasitizes it, making it a host. Barron considers this "a stretch" to consider that the tardigrades would attack the fungi just as readily as would the rotifers. But tardigrades are known to consume other filaments such as those of algae, so it is at least a possibility.

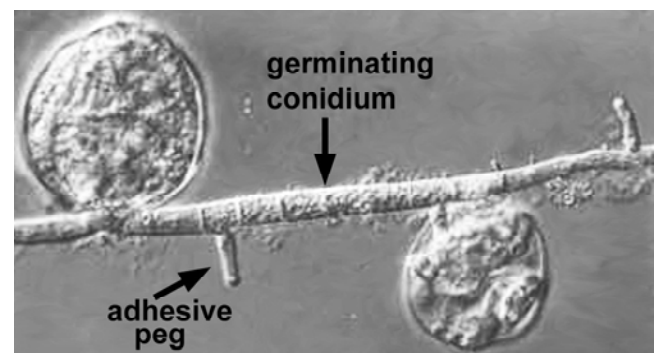


Figure 31. *Lecophagus muscicola* with two captured rotifers and two adhesive pegs. Photo by George Barron, with permission.



Figure 32. Conidia (X600) of *Lecophagus muscicola*. Photo by George Barron, with permission.



Figure 33. *Lecophagus longispora* infecting rotifers. Note also the elongate branch with terminal conidiogenous cell bearing a cluster of developing conidia. (X450). Photo by George Barron, with permission.

Several species of fungi in the genus *Ballocephala* (Zygomycota) (Figure 35-Figure 37) are known to attack tardigrades (Pohlad & Bernard 1978; Barron 2007). *Ballocephala pedicellata* was first described from individuals attacking the tardigrades *Hypsibius dujardini* (Figure 16) and the *Diphascon pingue* (Figure 19) complex living among mosses (Pohlad & Bernard 1978).

Adhesive conidia of *Ballocephala* species (Figure 35) attach to the cuticle surrounding the mouth of the tardigrade (Figure 35). These adhesive spores then encyst on the outside of their host. The spores extend long, narrow penetration pegs that are used to "snake" their way into the host, bypassing the defense mechanisms of the animal (Barron 2007). As the hyphae grow they penetrate the host and fill it with hyphae (Figure 36) that secrete extracellular enzymes to digest the tardigrade and assimilate its tissue.

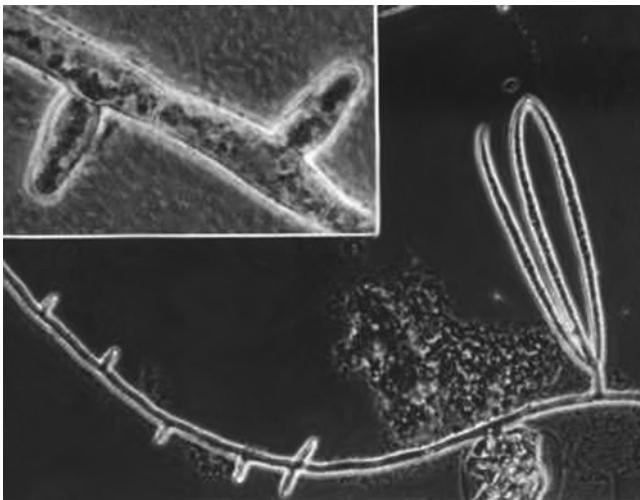


Figure 34. Hypha of *Lecophagus longispora* with a cluster of conidia and adhesive pegs, a fungus that traps rotifers and that may be a threat to some tardigrades living in mosses. Inset shows the adhesive pegs. Photos by George Barron, with permission.

Eventually the fungus breaks from the inside to the outside where it produces asexual spores (**conidiospores**) (Figure 38) that attack additional hosts. The fungus even has its own means to survive when the environment dries up and the tardigrade with it. Like many algae faced with

declining conditions, this fungus undergoes sexual reproduction and produces zygotes that in turn form a thick wall and become **zygospores** (Figure 37). These resting spores permit the fungus to survive long periods of time (weeks to years) until favorable growing conditions return. Upon germination the zygospores presumably will divide to produce conidiophores and conidia that infect later generations of the tardigrade, but so far, this event has not been witnessed.

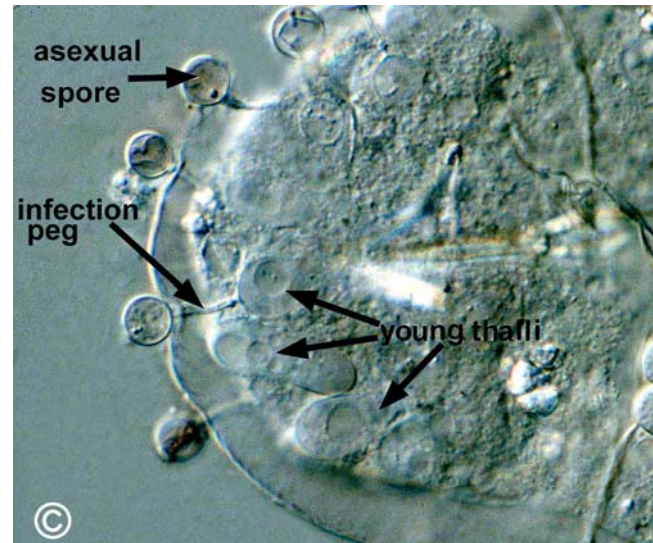


Figure 35. Spores of the fungus *Ballocephala sphaerospora* surrounding the mouth of a tardigrade. Photo by George Barron, with permission.

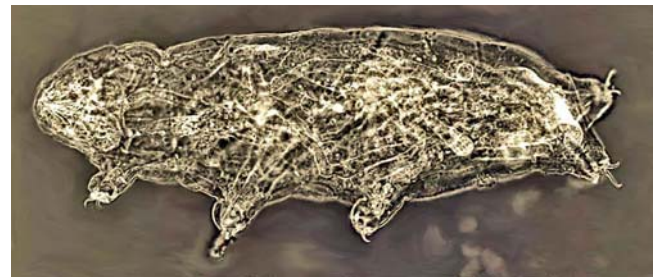


Figure 36. Tardigrade with hyphae of fungus *Ballocephala* sp. that have completely taken over its body. Photo by George Barron, with permission.



Figure 37. Zygospores of the parasitic fungus *Ballocephala sphaerospora* filling a tardigrade. The tiny balls inside the cells are oil droplets used as a reserve food supply. Photo by George Barron, with permission.



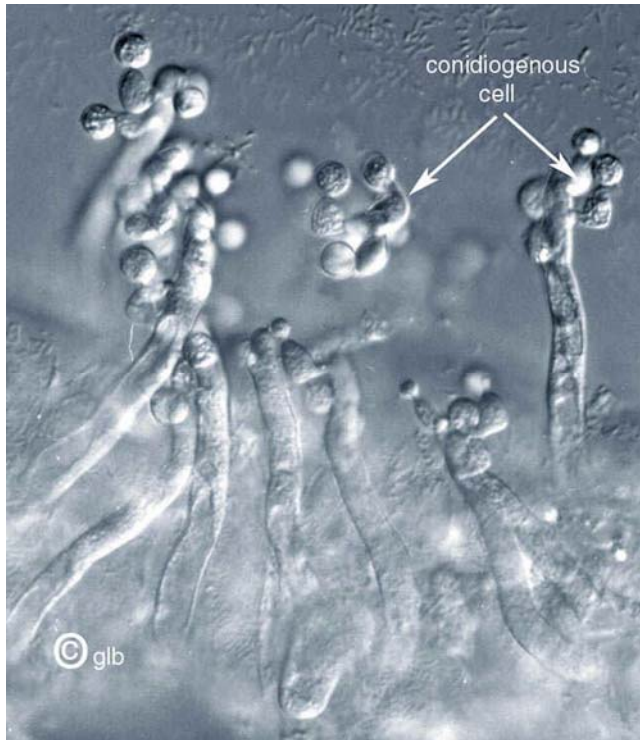


Figure 38. Conidiospores of the fungus *Ballocephala sphaerospora* on a tardigrade. Photo by George Barron, with permission.

The parasitic fungus *Haptoglossa mirabilis* (Figure 39) attacks tardigrades using the most complicated cellular mechanism known among the fungi (Robb & Barron 1982). It uses a gun-shaped attack cell that "shoots" into the host (Figure 40-Figure 41). At the anterior end of its cell is an elongated, barrel-shaped form. It is invaginated deeply into the cell, forming a bore. At the base of the bore is a walled chamber to house a missile-like attack apparatus. Robb and Barron hypothesize its mechanism:

This apparatus is able to fire the projectile at a high speed like a hypodermic needle, penetrating and injecting the host with the sporidium that infects the host. To accomplish this it has a basal vacuole with very high osmotic power. Water enters it rapidly and pumps the protoplasm and nucleus from the gun cell, through the hypodermic tube, and into the body of the host. If rotifers touch this fungus, they are hit within 0.1 second! But the proficiency of this apparatus doesn't end there. The head of this "harpoon" projectile is laminated, making it compressible. Thus, once it penetrates its host, it expands to seal the wound.

Once within the tardigrade, the fungus forms a cylindrical thallus (Figure 39) that consumes the poor tardigrade in a matter of days (Robb & Barron 1982). The hyphae eventually form zoospores. These exit through tubes and swim away to encyst. When the cysts germinate they form new clusters of gun cells. Some species can attack rotifers and nematodes as well.

George Barron (personal communication 1 March 2010) has commented to me that parasitic and predatory fungi are likely if both stylet-feeding and ingestion-feeding tardigrades coexist among mosses. But he finds it surprising that they have not yet been discovered.

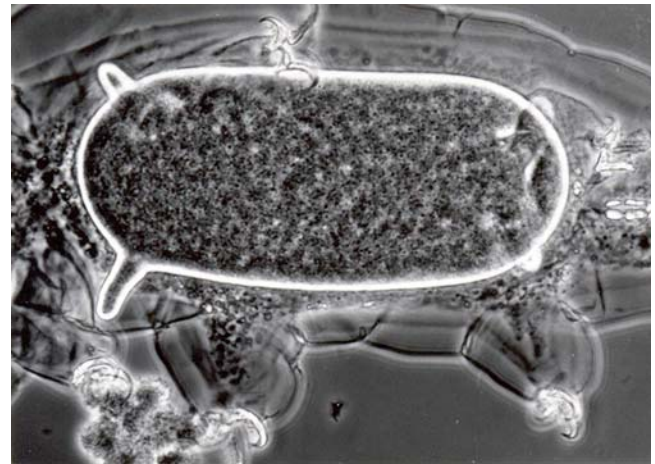


Figure 39. Fungus *Haptoglossa mirabilis* in a tardigrade, where it has formed a single thallus. Photo by George Barron, with permission.

The parasitic fungal genus *Harposporium* (Figure 42) has members that attack tardigrades (Saikawa *et al.* 1991), but the fungus must be ingested to function (George Barron, pers. comm. 25 January 2010). Barron (2008) suggests, as a hypothesis, that the spore is pumped down the oesophagus, where "it spirals and screws into the muscle fibres, thus lodging in the oesophagus."

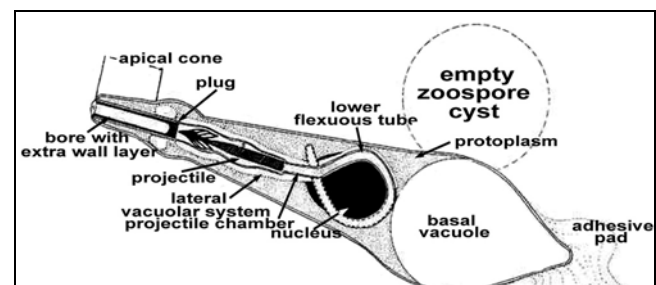
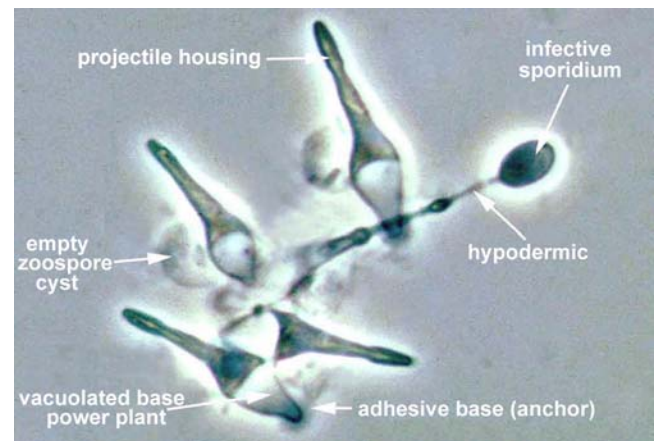


Figure 40. *Haptoglossa mirabilis* attack cells. Photo and diagram by George Barron, with permission.

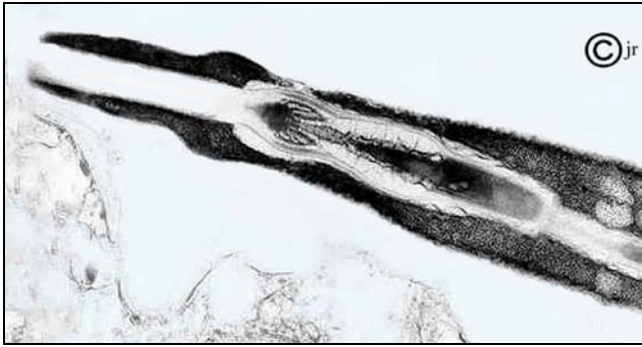


Figure 41. *Haptoglossa mirabilis* attack cell. Photo by Jane Robb and George Barron, with permission.

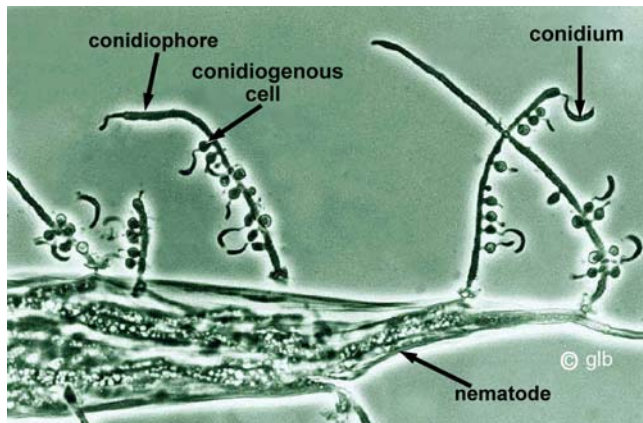


Figure 42. *Harposporium anguillulae*, a parasite on nematodes and tardigrades. Photo by George Barron, with permission.

## Role of Bryophytes in Fungal Interactions

*Milnesium tardigradum* (Figure 14) can be parasitized by a chytridiomycetous fungus, a zoosporic fungus that is common in soil (Dewel & Dewel 1987). Letcher and Powell (2002) attempted to determine the role that mosses play in the establishment of **Chytridiomycota** in four sites in the Blue Ridge and Allegheny Mountains of Virginia, USA. They first determined that frequency of **Chytridiomycota** was greatest in soil under and surrounding the rhizoids of two moss species [*Polytrichastrum* (formerly in *Polytrichum*) *ohioense* (Figure 43), *Dicranum polysetum* (Figure 44)]. They also found that random point sampling suggested differences existed in zoosporic fungal frequency between the moss-covered soil and the exposed soil adjacent to these mosses, as well as between the two taxa. Similar differences were demonstrated using linear transect sampling. But, at last, the statistical analysis of the random point samples failed to demonstrate that the differences were significant for frequency of zoosporic fungi between the exposed soil and the moss-covered soil. However, they did find a significant difference between different moss/soil complexes for the frequency of the 15 common zoosporic fungal species they identified.



Figure 43. *Polytrichastrum ohioense* males with new growth. Photo by Janice Glime.



Figure 44. *Dicranum polysetum*. Photo by Robert Klips, with permission.

One reason to suspect fungal differences under mosses compared to exposed soil is moisture. Using a scale of 0-10 (dry to saturated), Letcher and Powell found that the 48 moss-covered soil samples had a mean soil moisture content of 1.89, whereas the 24 exposed soil samples had a mean of 1.33.

## Pollution

In addition to fungal dangers, the bryophytes also become dangerous to tardigrades when they become polluted (Steiner 1994b). Vargha *et al.* (2002) found that the concentrations of metals in tardigrades bore a relationship to the concentrations in the mosses. Elevated concentrations of heavy metals correlated with a decrease in tardigrade fauna. Meininger *et al.* (1985) found that poor air quality (SO<sub>2</sub>) could reduce the number of tardigrades in otherwise suitable moisture regimes among epiphytic mosses in the area of Cincinnati, Ohio, USA (Figure 45).



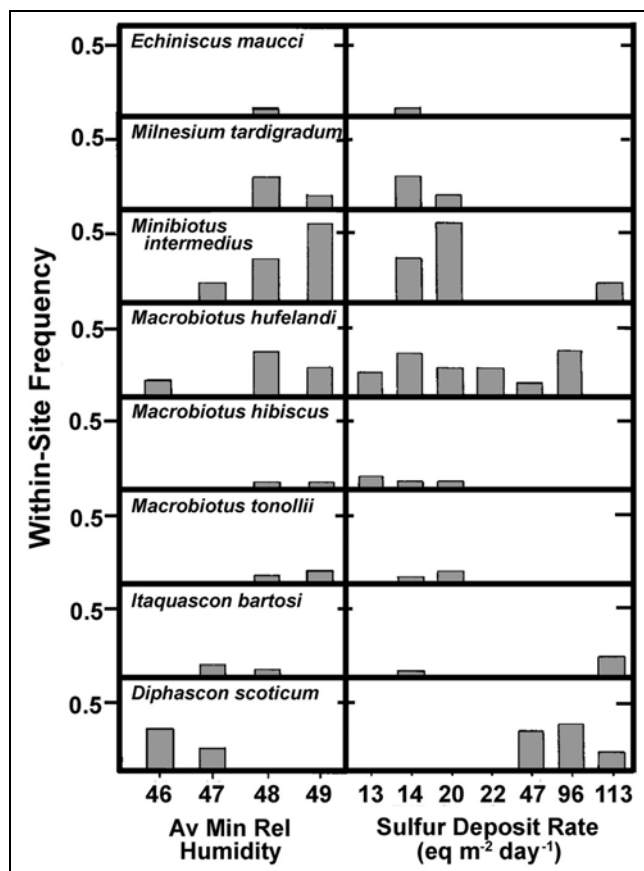


Figure 45. Effects of relative humidity and sulfur deposits from  $\text{SO}_2$  on the frequency of tardigrades inhabiting lichens and mosses on red oak (*Quercus rubra*) in the Cincinnati area of Ohio, USA.  $n=20$ . Redrawn from Meininger *et al.* 1985.

Just as bryophytes and lichens have often been used as indicators of clean air or biomonitors of air pollution, so have their tardigrade inhabitants in both aquatic (Steiner 1994a) and terrestrial (Steiner 1995) conditions. And their responses are much the same. In a study in the Cincinnati, Ohio, USA area, Meininger *et al.* (1985) found that both epiphytic (tree-dwelling) bryophytes and their tardigrade fauna had the greatest species richness in areas with high humidity and clean air. Humidity is typically depressed in urban areas, and depression is likewise more rapid there, resulting from the more open environment (fewer trees) and reradiation of heat trapped by buildings and asphalt. Two moss-dwelling tardigrades provided good indicators. *Diphascon scoticum* (Figure 13) was dominant in urban park sites with low air quality and reduced humidity. They feed on protococcal algae on the tree bark, and the low pH tolerance of this species may have played a role in its prevalence there. *Minibiotus intermedius* (Figure 12), on the other hand, occurs more often in the more humid rural sites and is apparently unable to tolerate the rapid evaporation rates that may characterize more urban environments.

Hohl *et al.* (2001) investigated tardigrades upwind and downwind of a coal-burning power plant in Missouri, USA. They found that the tardigrade density was greater upwind, but *Echiniscus* sp. was found only downwind. The more sensitive *Ramazzottius* sp. occurred only upwind. *Macrobiotus* sp., *Minibiotus* sp., and *Milnesium*

*tardigradum* occurred in both locations, but in different numbers. Although these species were mostly named only to genus, all were in genera or species known from bryophytes.

### Acid Rain, $\text{SO}_2$ , and $\text{NO}_2$

Acid rain poses a threat to at least some tardigrades. *Hypsibius dujardini* (Figure 16) has reduced activity at pH 4.0 (Bartels 2005). Even at pH 5, activity is reduced compared to controls at pH 7 (Thompson 2008). At pH 2.8 they are killed (Bartels 2005). Acevedo (2008) examined one of the most common bryophyte dwellers, *Milnesium tardigradum* (Figure 14), for its tolerance to pH, as measured by activity. Although *M. tardigradum* could survive from pH 1.54 to 12.5 for 1 minute, this species, like *Hypsibius dujardini* (Figure 16), had increased survival time as the pH approached 7. This species proved to be more sensitive at the higher pH levels.

Nevertheless, Steiner (1994a) found that neither tardigrades nor rotifers seemed to vary in abundance in response to  $\text{SO}_2$  or  $\text{NO}_2$ . But in 1995, Steiner reported that the community composition did change in response to  $\text{SO}_2$ .

In the aquatic environment, using both experiments and air quality at 12 sites, Steiner (1995) showed that changes to the tardigrade and other aquatic fauna composition correlated negatively with the  $\text{SO}_2$  concentrations. They used untreated control mosses and those subjected to concentrations of 0.025, 0.075, and 0.225 ppm  $\text{SO}_2$  for 18 months and found that the highest level caused significant decreases in the numbers of several tardigrade species.  $\text{SO}_2$  caused a significant decrease in pH in the moss cushions. The populations of *Macrobiotus persimilis* actually increased as pollution increased. Steiner (1994a) suggested that the tardigrade (and other invertebrate) fauna of epilithic moss cushions could be appropriate biomonitors for air quality.

### Urban Environment

Even if the urban habitat is not always polluted in the usual sense, it is a drastic contrast in environment to that of more natural rural areas. Cities themselves both create and hold heat. That makes them susceptible to rapid drying, a condition lethal to many tardigrades.

Johansson *et al.* (2011) compared tardigrades from 73 urban and 24 rural locations in Fresno County, California. Only 22% of the urban samples had tardigrades, whereas 74% of the rural samples had tardigrade inhabitants. The urban samples likewise had fewer species, but the densities of these species differed little from that of the rural sites. Of the 26 species found, 7 were found only in the urban samples, 16 only in rural samples, and 3 in both. The rural communities differed more among themselves than did the urban samples. Interestingly, tardigrades seemed to prefer lower pH levels in both community types. Hence, the researchers excluded acid rain as the cause of differences. It is likely that the microclimate of the city is less favorable due to greater exposure and heat, leading to more rapid drying.

Moly de Peluffo *et al.* (2006) conducted a more controlled study of urban conditions by using samples from the same tree species from the city of General Pico in Central Argentina. They included paved areas with different traffic intensities, non-paved areas, an industrial area, and a bus station. They examined 11 mm diameter

samples of lichens and mosses from the trees. Only 5 tardigrade species were collected in total [*Echiniscus rufoviridis*, *Milnesium cf. tardigradum* (Figure 14), *Ramazzottius oberhaeuseri* (Figure 28), *Paramacrobiotus areolatus* (Figure 46), *Macrobiotus* sp.]. *Milnesium cf. tardigradum* and *Ramazzottius oberhaeuseri* were the most abundant. Mean density of tardigrades was 10, but the maximum reached 50 per cm<sup>2</sup>. *Milnesium cf. tardigradum* dominated along paved streets where there was intense traffic, suggesting that it was the most tolerant species. In periurban areas, *Ramazzottius oberhaeuseri* dominated despite the high suspension dust and high sun exposure. In the Neotropical region of Santa Rosa, Argentina, Peluffo *et al.* (2006) found the same five species. Again, only *Milnesium cf. tardigradum* occurred in areas with high levels of vehicle traffic.



Figure 46. *Paramacrobiotus areolatus* head region. Photo by Martin Mach, with permission.

Dust can be a factor in tardigrade distribution. Meininger and Spatt (1988) found that both tardigrades and their bryophyte environment are affected by road dust such as that created by the trans-Alaska Pipeline haul road (Dalton Highway). In this case, the dust is calcium-rich. *Sphagnum* (Figure 7) is absent within 10 m of the road. Instead, calcium-tolerant moss species such as *Aulacomnium turgidum* (Figure 47) and *Dicranum angustum* (Figure 48) occupy these alkaline areas. The tardigrades that survive here are xeric species such as *Diphascon scoticum* (Figure 13) and *Hypsibius dujardini* (Figure 16). Farther from the road, these fungal and algal feeding species are replaced by omnivores and carnivores [*Macrobiotus hufelandi* (Figure 11) and *M. harmsworthi* (Figure 25), respectively].

## Tardigrades in Space

Imagine living through conditions of 151°C, -273°C, the vacuum of space, radiation 500 times that humans can tolerate, 2000X normal atmospheric pressure, and ten years with no water! (Ramløv & Westh 2001; Jönsson *et al.* 2008; ZAMP Wiki 2009). Tardigrades are sometimes considered to be **extremophiles**, and their ability to survive these conditions would seemingly put them among the champions. But extremophiles are organisms that *live* at extremes; tardigrades must become dormant to survive these, and the longer they are in this condition, the lower their chances of survival (Mullen 2002). These abilities to

become dormant - enter **cryptobiosis** - have made them popular animals for space travel, surviving and carrying back the evidence of the effects of space on subcellular components. And they were the first space travellers without space suits to survive.



Figure 47. *Aulacomnium turgidum*, a calcium-tolerant species, in Norway. Photo by Michael Lüth, with permission.



Figure 48. *Dicranum angustum*, a calcium-tolerant species. Photo by Jan-Peter Frahm, with permission.

The ability to shut down makes tardigrades ideally suited for space travel (Jönsson *et al.* 2008; Rebecchi *et al.* 2009a). They can survive a vacuum (Gavaret 1859) and its resulting extreme dehydration (Jönsson *et al.* 2008). They also survive both solar and cosmic radiation. They survive extreme ionizing radiation (570,000 roentgens kills only 50%; humans can be killed by 500) (May *et al.* 1964) and can return from space travel under these extremes and become active again with no reduction in survival (Jönsson *et al.* 2008; Rebecchi *et al.* 2009a). They have even survived temperature extremes from -200°C to 151°C (Doyère 1842; Rahm 1923, 1937; Becquerel 1950; Keilin 1959; Seki & Toyoshima 1998; Lindahl & Balser 1999).

*Richtersius coronifer* (Figure 49), *Milnesium tardigradum* (Figure 50) (Jönsson 2008), and *Paramacrobiotus richtersi* (Figure 24) (Rebecchi *et al.* 2009a, b) began their space adventure on 17 September 2007. They arrived back from their adventure in space on 26 September, and not only were they alive, but they could



also reproduce! *Milnesium tardigradum* did better than *R. coronifer*. About 12% of those exposed to UV-A and UV-B managed to recover, although they exhibited reduced egg production compared to the control animals that stayed on Earth. Those exposed to the full range of UV radiation only partially recovered, then died. Jönsson *et al.* (2005) suggested that during anhydrobiosis there are no biochemical protectants to protect against radiation. Rather, it appears that survival of tardigrades may be due to efficient DNA repair.



Figure 49. *Richtersius coronifer* and its close relatives have a beautiful deep yellow color. This species has been a successful space traveller. Photo by Martin Mach, with permission.

*Paramacrobiotus richtersi* (Figure 24) and *Ramazzottius oberhaeuseri* (Figure 28) were able to withstand high doses of ultraviolet radiation in both active and anhydrobiotic states (Altiero *et al.* 2011). Nevertheless, the survival rate of hydrated or desiccated specimens was inversely related to the UV doses, with *P. richtersi* tolerating the increase of UV dose better than *R. oberhaeuseri*.

The survival of *Richtersius coronifer* (Figure 49) in the adventure beginning 17 September 2007 (Jönsson 2008) was at least somewhat predictable. In the lab, this species survived instant freezing to -195.8°C and vacuum conditions with 96-100% survival (Persson *et al.* 2009). In low Earth orbit it experienced little effect from cosmic radiation or microgravity (68, 89, 82% survival). On the other hand, when Persson *et al.* (2009) subjected *R. coronifer*, *Ramazzottius oberhaeuseri* (Figure 28), and *Echiniscus testudo* (Figure 9) to desiccation on moss, the survival rate was very low (0-22.5%). They emphasized that the protocol for desiccation is important and may not have been appropriate for survival.

Another moss-dweller (among other substrata), *Hypsibius dujardini* (Figure 16), was scheduled to be travelling in space on a Russian spacecraft as I write (Milstein 2009). Following its liftoff in October 2009, it was scheduled to reside there for three years! Its habitat is a bit of polymer microcosm with conditions mimicking those of a bit of meteor rock. But, alas, technical and safety issues have caused a two-year delay before lift off (Madrigal 2009). The objective is to determine if life can survive interplanetary space travel, a test of the **Transpermian Theory**. The Transpermian Theory suggests that life might have travelled on a bit of meteoric rock from Mars or other planet and landed on Earth billions of years ago. The tough part, both for the real meteoric

rock traveller and the spacecraft test subjects may be the landing event on Earth.

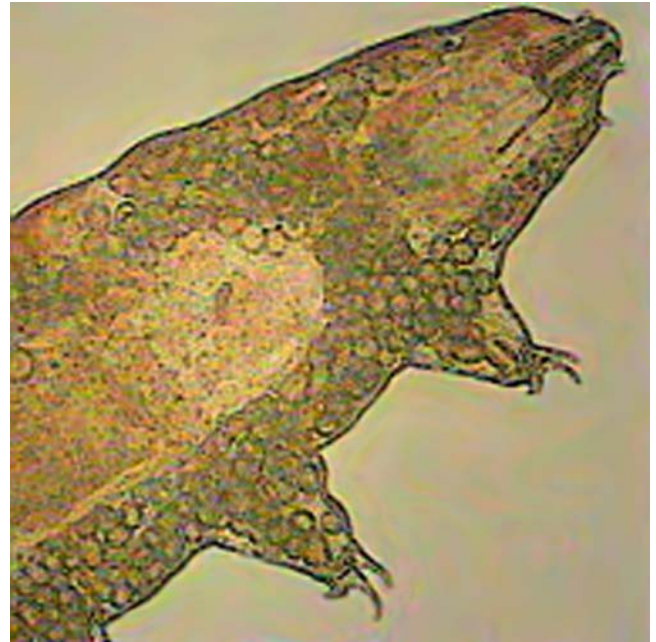


Figure 50. *Milnesium tardigradum*, a space traveller. Photo by Martin Mach, with permission.

Most tardigrades have gone on their space adventure in an anhydrobiotic state. Rebecchi *et al.* (2011) used *Paramacrobiotus richtersi* (Figure 24) to determine the effects of the anhydrobiotic state on survivorship in space. They flew these animals for twelve days in a low-earth orbit (250-290 km altitude). The desiccated animals had high survival rate (79-95%), similar to that of non-desiccated ground controls. There was no visible damage to their double-stranded DNA, but their heat shock proteins (HSP expression at 70 and 90 kDa) increased compared to ground controls.

Persson *et al.* (2011) assessed the effects of cosmic radiation on tardigrades, as well as rotifers. The tardigrades spent time in a low Earth orbit where they were exposed to cosmic radiation and microgravity. *Richtersius coronifer* (Figure 49) was dried for two years on Whatman-3 filters during its space travel. However, none of the members of this species could be revived. In a different microcosmos experiment, Persson *et al.* desiccated *R. coronifer*, *Ramazzottius oberhaeuseri* (Figure 28), and *Echiniscus testudo* (Figure 9) as well as rotifers and nematodes on a moss substrate. Species in this experiment had some, but very low, survival. Embryos of *Milnesium tardigradum* (Figure 14), on the other hand, all survived cosmic radiation from space flight. *Richtersius coronifer* also survived extreme cold and vacuum while in anhydrobiosis.

## Evolutionary Similarities to Bryophytes

What could tardigrades and bryophytes possibly have in common? Their habitat requirements, for one thing. Hence, both do well with asexual reproduction (Pilato 1979). And both do well under circumstances requiring dormancy. Pilato points out that there is marked

uniformity in both size and morphology in the four invertebrate groups of rotifers, gastrotrichs, nematodes, and tardigrades. That character does not seem to fit so well with bryophytes, but if one compares them to tracheophytes, perhaps it does. Both groups have "a less common pattern of geographic distribution than usually believed" for organisms having only passive transport. They furthermore have maintained their antiquity and have given rise to entire orders. But there are also some strong differences. Compared to tardigrades, bryophytes do not have a constant cell number, have no marine members, and are capable of regeneration. Pilato suggests that parthenogenesis would have significantly delayed evolution, a concept that has come into question for bryophytes. He furthermore suggests that by entering cryptobiosis, these invertebrate organisms escape the variability of the environment and thus escape many of the selection pressures that drive evolution.

## Sampling and Extraction

Sampling from mosses is not a very standardized procedure. The moss must first be collected from its substrate. What works for a flat mat does not work for a thick mat, wet, or tall turf. Sayre and Brunson (1971) suggested using a metal test-tube cap 2.5 cm in diameter to cut a core from the moss (see also Guil *et al.* 2009) – a technique that should work well for thin mats with stems that are not tough, but many growth forms would not sample well by this method. Since tardigrades are slow-moving, one need not worry about their escaping during the cutting procedure. However, I prefer the hand removal, followed by a dry weight of bryophyte for quantification. Fortunately, both bryophytes and tardigrades can survive such drying. A large clump could later be cut down the middle and still permit sampling of all the sub-habitats.

Fortunately, mosses need little care once collected and can easily be kept in small paper bags – the kind that was once used in the candy store (~10 x 20 cm when folded). If it is not too hot or severely dry, these will permit the mosses to dry slowly, provided they are not in the path of a fan or other drying agent. Using plastic bags can foster growth of fungi if the bag is kept for more than a day or two, and it will not permit the drying needed for both kinds of organisms. Morgan and King (1976 in Clifford 2005) suggested using an open plastic bag that would permit air drying.

Obtaining tardigrades from mosses may be a bit tedious. One method is to immerse the bryophytes in water (Claxton 1998; Guidetti *et al.* 2008) in something like a finger bowl or Petri dish. Tap water may be okay, depending on chlorine levels; if pond water is used, it should be boiled and filtered to avoid contamination. Distilled water should NOT be used because it will cause the tardigrade to take on water by osmosis and it is likely to become too extended to move. Placing the bryophyte upside down with the soil portion above the water will give the best results; muddy water makes it difficult to spot the bears (Sayre & Brunson 1971). If you are interested in vertical positioning, place aluminum foil or other cover over the container to keep it dark.

Sayre and Brunson (1971) recommend keeping the moss submerged for 24 hours at room temperature. The moss should then be removed and the absorbed water

squeezed into the dish. The water in the dish should then be stirred and poured into a counting dish. After the tardigrades have settled they can be counted with a dissecting microscope. They recommend 60X, but most dissecting microscopes don't go that high, so one might need a pair of 20X oculars. If there is too much water, they suggest decanting off the excess, but for quantitative purposes, I suspect that will lead to inaccuracies for these light-weight animals.

Nelson (1991) considered this to be a common method. She recommended letting the collected bryophytes dry in paper bags for at least several days, then placing them in water for several hours to awaken the tardigrades. The wet bryophytes are then squeezed to remove water with water bears into a Petri dish or other container. As in the Sayre and Brunson method, excess water can be decanted off and the sediment examined.

Guidetti *et al.* (2008) recommend that after immersing the bryophytes, the water should be sifted repeatedly to collect the tardigrades. From there, the animals can be extracted while observing them with a dissecting microscope.

Schuster *et al.* (1977) used a similar method. Collection material (bryophytes, soil, detritus) was swirled in water and once the dense particles settled, the water was decanted and poured through a US Standard #325 filter, pore size ~44  $\mu\text{m}$ . These were then washed from the filter into a preservation jar or onto a glass slide. Specimens can be preserved by adding 5% formalin or glutaraldehyde, or alcohol, as discussed later.

Other researchers choose to use the Baermann funnel to extract the animals (Hohberg 2006) as already described for invertebrates (Chapter 4-1 of this volume).

A slight modification of these methods is to clean a bryophyte clump of its loose soil and place it into a Petri plate upside down (Deep Data 2009). Fill the plate with water. When the bryophyte absorbs all the water, add more. Maintain a few mm of water in the plate after the bryophyte is fully hydrated. The bryophyte should be kept hydrated for several hours or overnight before examination. Remove the bryophyte from the water and examine it with a dissecting microscope at 20X or higher. Alternatively, this website also recommends squeezing out the water and examining the liquid. Look for yellow, red, or whitish animals that move "like puppies."

Nelson and Bartels (2007) used a different method when working with samples from soil, lichens, mosses, and leaf litter from the Smoky Mountains. They extracted the tardigrades using centrifugation with Ludox AM™ and mounted them on microscope slides in Hoyer's medium.

Tardigrades can be put to sleep with  $\text{MgCl}_2$  or shocked with freshwater, then decanted into a fine mesh (20-40  $\mu\text{m}$ ) net (Nelson 2002). An intriguing method is to use an aquarium air stone to bubble the tardigrades that can then be collected with a piece of paper towel laid on the surface of the water. (If that works, I doubt that decanting is good for quantitative studies.) The towel should then be rinsed through a 30-40  $\mu\text{m}$  net. For aquatic samples, water can be used from the habitat.

Clifford (2005) draws heavily on the experience of Morgan and King (1976) in his Tardigrada website. He suggests narcotizing the water bears with 20% alcohol in a volume equal to that of the bryophyte plus water. The



bears will no longer be able to cling to the bryophytes and can be more easily dislodged into the alcohol/water solution. The bryophyte and associated organisms can be removed after about 10 minutes and wrung into a Petri dish to remove the adhering water and bears. This immersion and wringing should be repeated several times, with immersion up to 15 minutes. The extracted water can be examined at about 50X magnification. (As you can see, recommendations for magnification vary from 20X to 60X. You will have to see what works for you.)

Clifford (2005) suggests that a somewhat simpler method is to flood the bryophyte with enough water to cover it for 48-72 hours. Then remove the moss to a new dish and start with the alcohol at 70%. Force the alcohol through the bryophyte clump with a pipette that has a strong bulb. A baster might work for larger mosses, but I haven't tried it. This alcohol method seems a bit cruel to the bears.

Nelson and Hauser (2012) complain that extraction from the limnoterrestrial habitats, those habitats of water adhering in spaces such as the ones among bryophytes, is often done with the Berlese funnel. They contend that this method has a strong bias toward arthropod diversity and

does not work well for relatively slow-moving or immobile animals such as tardigrades. Rather, they found much more diversity among the microscopic invertebrates such as tardigrades when they used water flooding for extraction. In fact, they found almost no taxa overlaps when comparing these two methods!

Tardigrades can be preserved in 70% alcohol, but they can be difficult to locate again, and one must check periodically to be sure the alcohol isn't about ready to dry up. A few drops of glycerine in the vial of alcohol helps when the alcohol does dry out. The preferable method seems to be to mount them in one of the standard mounting media used for bryophytes and other things. Pennak (1953) gives instructions for various media. Unfortunately (or fortunately) a number of these media have been declared carcinogenic or toxic and are no longer available.

## Checklist of Bryophyte Dwellers

I won't even pretend that I can provide a complete list of these taxa. I have not covered all the literature, and certainly many have yet to be discovered, but at least Table 1 is a start.

Table 1. Partial list of tardigrades known to inhabit bryophytes, based on literature.

### Heterotardigrada (armored tardigrades)

<i>Bryodelphax aaseae</i>	Kristensen <i>et al.</i> 2010	<i>Echiniscus spiniger</i>	Horning <i>et al.</i> 1978
<i>Bryodelphax asiaticus</i>	Kaczmarek & Michalczyk 2006	<i>Echiniscus spinulosus</i>	Guil 2002
<i>Bryodelphax brevidentatus</i>	Kaczmarek <i>et al.</i> 2005	<i>Echiniscus taibaiensis</i>	Wang & Li 2005
<i>Bryodelphax mateusi</i>	Guil 2002	<i>Echiniscus testudo</i>	Beasley & Miller 2007
<i>Bryodelphax parvulus</i>	Guil 2002	<i>Echiniscus trisetosus</i>	Kaczmarek & Michalczyk 2006
<i>Bryodelphax sinensis</i>	Pilato 1974	<i>Echiniscus velaminis</i>	Horning <i>et al.</i> 1978
<i>Bryodelphax tatrensis</i>	Guil 2002	<i>Echiniscus vinculus</i>	Horning <i>et al.</i> 1978
<i>Cornechiniscus cornutus</i>	Mach, The Water Bear	<i>Echiniscus virginicus</i>	Hooie & Davison 2001
<i>Cornechiniscus lobatus</i>	Guil 2002	<i>Echiniscus viridianus</i>	Pilato <i>et al.</i> 2007
<i>Cornechiniscus holmeni</i>	Beasley & Miller 2007	<i>Echiniscus viridissimus</i>	Nelson & Adkins 2001
<i>Cornechiniscus subcornutus</i>	Guil 2002	<i>Echiniscus wendtii</i>	Kathman & Cross 1991
<i>Echiniscus arctomys</i>	Mehlen 1969	<i>Echiniscus zetotrymus</i>	Horning <i>et al.</i> 1978
<i>Echiniscus barbarae</i>	Kaczmarek & Michalczyk 2002	<i>Hypechiniscus exarmatus</i>	Horning <i>et al.</i> 1978
<i>Echiniscus bigranulatus</i>	Horning <i>et al.</i> 1978	<i>Hypechiniscus gladiator</i>	Kathman & Cross 1991
<i>Echiniscus bisculptus</i>	Guil 2002	<i>Oreella minor</i>	Horning <i>et al.</i> 1978
<i>Echiniscus blumi</i>	Kaczmarek & Michalczyk 2006	<i>Oreella mollis</i>	Horning <i>et al.</i> 1978
<i>Echiniscus brachyspinosus</i>	Horning <i>et al.</i> 1978	<i>Parechiniscus chitonides</i>	Guil 2002
<i>Echiniscus canadensis</i>	Kaczmarek & Michalczyk 2006	<i>Parechiniscus unispinosus</i>	Guil 2002
<i>Echiniscus capillatus</i>	Jennings 1979	<i>Pseudechiniscus beasleyi</i>	Li <i>et al.</i> 2007
<i>Echiniscus cavagnaroi</i>	Christenberry 1979	<i>Pseudechiniscus brevimontanus</i>	Nelson & Bartels 2007
<i>Echiniscus ganzareki</i>	Michalczyk & Kaczmarek 2007	<i>Pseudechiniscus clavatus</i>	Guil 2002
<i>Echiniscus granulatus</i>	Kaczmarek & Michalczyk 2006	<i>Pseudechiniscus facettalis</i>	Ito 1993
<i>Echiniscus horningi</i>	Kathman & Cross 1991	<i>Pseudechiniscus goedeni</i>	Kathman & Cross 1991
<i>Echiniscus jenningsi</i>	Margulis & Chapman 1998	<i>Pseudechiniscus gullii</i>	Pilato & Lisi 2006
<i>Echiniscus kofordi</i>	Christenberry 1979	<i>Pseudechiniscus insolitus</i>	Guil 2002
<i>Echiniscus laterosetosus</i>	Ito 1993	<i>Pseudechiniscus jiroveci</i>	Kaczmarek & Michalczyk 2006
<i>Echiniscus lichenorum</i>	Guil 2002	<i>Pseudechiniscus juanitae</i>	Pilato & Lisi 2006
<i>Echiniscus madonnae</i>	Michalczyk & Kaczmarek 2006a	<i>Pseudechiniscus lateromamillatus</i>	Horning <i>et al.</i> 1978
<i>Echiniscus marinellae</i>	Guil 2002	<i>Pseudechiniscus novaezeelandiae</i>	Horning <i>et al.</i> 1978
<i>Echiniscus mauccii</i>	Kathman & Cross 1991	<i>Pseudechiniscus papillosus</i>	Li <i>et al.</i> 2005
<i>Echiniscus mediantus</i>	Guil 2002	<i>Pseudechiniscus pseudoconifer</i>	Franceschi <i>et al.</i> 1962-63
<i>Echiniscus merokensis</i>	Kaczmarek & Michalczyk 2006	<i>Pseudechiniscus spinerectus</i>	Pilato <i>et al.</i> 2001
<i>Echiniscus multispinosus</i>	Guil 2002	<i>Testechiniscus laterculus</i>	Kathman & Cross 1991
<i>Echiniscus nelsonae</i>	Li <i>et al.</i> 2007	<i>Testechiniscus meridionalis</i>	Jennings 1979
<i>Echiniscus cf. oihonnae</i>	Hooie & Davison 2001	<i>Testechiniscus spitsbergensis</i>	Kaczmarek & Michalczyk 2006
<i>Echiniscus palmai</i>	Dastych 1997		
<i>Echiniscus perarmatus</i>	Binda <i>et al.</i> 2001		
<i>Echiniscus perviridis</i>	Nelson & Adkins 2001		
<i>Echiniscus polygonalis</i>	Ito 1993		
<i>Echiniscus quadrispinosus</i>	Kathman & Cross 1991		
<i>Echiniscus reticulatus</i>	Kaczmarek & Michalczyk 2006		
<i>Echiniscus scabrospinosus</i>	Guil 2002		
<i>Echiniscus semifoveolatus</i>	Ito 1993		
<i>Echiniscus shaanxiensis</i>	Li <i>et al.</i> 2007		
<i>Echiniscus sinuloides</i> =???	Guil 2002		

### Eutardigrada (unarmored/naked tardigrades)

<i>Acutuncus antarcticus</i>	Miller <i>et al.</i> 1996
<i>Amphibolus weglarskae</i>	Bartels & Nelson 2007
<i>Astatumen trinacriae</i>	Nelson & Bartels 2007
<i>Bertolanius nebulosus</i>	Westh & Kristensen 1992
<i>Bertolanius volubilis</i>	Guidetti <i>et al.</i> 2008
<i>Bertolanius weglarskae</i>	Kathman & Cross 1991
<i>Bindius triquetrus</i>	Pilato 2009

- Biserovus bindae*  
*Calohypsibius maliki*  
*Calohypsibius ornatus*  
*Calohypsibius placophorus*  
*Calohypsibius schusteri*  
*Calohypsibius verrucosus*  
*Dactylobiotus ambiguus*  
*Dactylobiotus dispar*  
*Dactylobiotus macronyx*  
*Diphascon alpinum*  
*Diphascon belgicæ*  
*Diphascon bullatum*  
*Diphascon carolæ*  
*Diphascon chilense*  
*Diphascon dolomiticum*  
*Diphascon granifer*  
*Diphascon higginsii*  
*Diphascon iltisi*  
*Diphascon modestum*  
*Diphascon nobilei*  
*Diphascon nodulosum*  
*Diphascon oculatum*  
*Diphascon pataneii*  
*Diphascon pingue*  
*Diphascon prorsirostre*  
*Diphascon ramazzottii*  
*Diphascon recamerii*  
*Diphascon rugosum*  
*Diphascon scoticum*  
*Diphascon sexbullatum*  
*Doryphoribius flavus*  
*Doryphoribius gibber*  
*Doryphoribius huangguoshuensis*  
*Doryphoribius mexicanus*  
*Doryphoribius picoensis*  
*Doryphoribius polynetae*  
*Doryphoribius quadrituberculatus*  
*Doryphoribius zappalai*  
*Doryphoribius zyxiglobus*  
*Hebesuncus conjungens*  
*Hypsibius arcticus*  
*Hypsibius camelopardalis*  
*Hypsibius convergens*  
*Hypsibius dujardini*  
*Hypsibius maculatus*  
*Hypsibius microps*  
*Hypsibius pallidus*  
*Hypsibius roanensis*  
*Hypsibius scabropygus*  
*Insuetifurca arrowsmithi*  
*Insuetifurca xiae*  
*Isohypsibius arbiter*  
*Isohypsibius archangajensis*  
*Isohypsibius asper*  
*Isohypsibius baslovi*  
*Isohypsibius bertolanii*  
*Isohypsibius brevispinosus*  
*Isohypsibius brulloi*  
*Isohypsibius cameruni*  
*Isohypsibius josephi*  
*Isohypsibius lunulatus*  
*Isohypsibius mammillosus*  
*Isohypsibius mihelcici*  
*Isohypsibius monstrosus*  
*Isohypsibius montanus*  
*Isohypsibius pappi*  
*Isohypsibius prosostomus*  
*Isohypsibius qinlingensis*  
*Isohypsibius sattleri*  
*Isohypsibius taibaiensis*  
*Isohypsibius tuberculatus*  
*Isohypsibius wilsoni*  
*Isohypsibius woodsae*  
*Itaquascon bartosi*  
*Itaquascon mongolicus*  
*Itaquascon pawlowskii*  
*Itaquascon unguiculum*  
*Limnienius porcellus*  
*Macrobiotus almadaei*  
*Christenberry & Higgins 1979*  
*Michalczyk & Kaczmarek 2005*  
*Kaczmarek & Michalczyk 2006*  
*Guil 2002*  
*Nelson & Bartels 2007*  
*Guil 2002*  
*Guil 2002*  
*Suren 1992*  
*Guil 2002*  
*Horning et al. 1978*  
*Kathman & Cross 1991*  
*Horning et al. 1978*  
*Bartels & Nelson 2009*  
*Horning et al. 1978*  
*Pilato & Bertolani 2005*  
*Bartels & Nelson 2009*  
*Nelson & Bartels 2007*  
*Kathman & Cross 1991*  
*Kathman & Cross 1991*  
*Schuster & Greven 2007*  
*Kathman & Cross 1991*  
*Schuster & Greven 2007*  
*Nelson & Bartels 2007*  
*Kaczmarek & Michalczyk 2006*  
*Kaczmarek & Michalczyk 2006*  
*Bartels & Nelson 2007*  
*Kathman & Cross 1991*  
*Schuster & Greven 2007*  
*Kaczmarek & Michalczyk 2006*  
*Kaczmarek & Michalczyk 2006*  
*McInnes 1994*  
*Pilato & Lisi 2006*  
*Wang et al. 2007*  
*Beasley et al. 2008*  
*Fontoura et al. 2008*  
*Bartels et al. 2007*  
*Kaczmarek & Michalczyk 2004a*  
*Wang et al. 2007*  
*Horning et al. 1978*  
*Kaczmarek & Michalczyk 2006*  
*Utsugi & Ohyama 1989*  
*Guil 2002*  
*Kaczmarek & Michalczyk 2006*  
*Kaczmarek & Michalczyk 2006*  
*Kaczmarek & Michalczyk 2004b*  
*Guil 2002*  
*Kaczmarek & Michalczyk 2006*  
*Nelson & Bartels 2007*  
*Schuster & Greven 2007*  
*Kathman & Cross 1991*  
*Li 2009*  
*Binda et al. 2001*  
*Kaczmarek & Michalczyk 2006*  
*Jennings 1979*  
*Bartels & Nelson 2009*  
*Manicardi 1989*  
*Bartels & Nelson 2009*  
*Pilato & Pennisi 1976*  
*Horning et al. 1978*  
*Guil 2002*  
*Kathman & Cross 1991*  
*Guil 2002*  
*Kaczmarek & Michalczyk 2006*  
*Guil 2002*  
*Guil 2002*  
*Pilato & Sperlinga 1975*  
*Schuster & Greven 2007*  
*Li et al. 2005*  
*Kaczmarek & Michalczyk 2006*  
*Li & Wang 2005*  
*Nelson & Bartels 2007*  
*Horning et al. 1978*  
*Kathman & Cross 1991*  
*Meininger et al. 1985*  
*Kaczmarek & Michalczyk 2006*  
*Kathman & Cross 1991*  
*Pilato et al. 2002*  
*Horning et al. 1978*  
*Fontoura et al. 2008*  
*Macrobiotus anderssoni*  
*Macrobiotus arguei*  
*Macrobiotus baltatus*  
*Macrobiotus barabanovi*  
*Macrobiotus barbarae*  
*Macrobiotus blocki*  
*Macrobiotus bondavallii*  
*Macrobiotus contii*  
*Macrobiotus coronatus*  
*Macrobiotus crenulatus*  
*Macrobiotus echinogenitus*  
*Macrobiotus furciger*  
*Macrobiotus grandis*  
*Macrobiotus harmsworthi*  
*Macrobiotus hibiscus*  
*Macrobiotus hufelandi*  
*Macrobiotus islandicus*  
*Macrobiotus kazmierskii*  
*Macrobiotus kirghizicus*  
*Macrobiotus kovalevi*  
*Macrobiotus lazzaroii*  
*Macrobiotus liviae*  
*Macrobiotus lusitanicus*  
*Macrobiotus magdalenae*  
*Macrobiotus mandalae*  
*Macrobiotus marlenae*  
*Macrobiotus martini*  
*Macrobiotus mauccii*  
*Macrobiotus montanus*  
*Macrobiotus nuragicus*  
*Macrobiotus occidentalis*  
*Macrobiotus occadensis*  
*Macrobiotus pallarii*  
*Macrobiotus patiens*  
*Macrobiotus persimilis*  
*Macrobiotus polaris*  
*Macrobiotus polyopus*  
*Macrobiotus privitera*  
*Macrobiotus pseudofurcatus*  
*Macrobiotus radiatus*  
*Macrobiotus ragonesei*  
*Macrobiotus rawsoni*  
*Macrobiotus recens*  
*Macrobiotus reinhardti*  
*Macrobiotus sapiens*  
*Macrobiotus sklodowskæ*  
*Macrobiotus snaresensis*  
*Macrobiotus spectabilis*  
*Macrobiotus subjulietae*  
*Macrobiotus szepteykii*  
*Mesocrisia spitzbergensis*  
*Milnesium asiaticum*  
*Milnesium cf. euryostomum*  
*Milnesium longiungue*  
*Milnesium tardigradum*  
*Minibiotus aculeatus*  
*Minibiotus africanus*  
*Minibiotus continuus*  
*Minibiotus fallax*  
*Minibiotus gumersindoi*  
*Minibiotus hufelandioides*  
*Minibiotus intermedius*  
*Minibiotus cf. poricinctus*  
*Minibiotus pustulatus*  
*Minibiotus cf. scopulus*  
*Minibiotus weglarskæ*  
*Minibiotus xavieri*  
*Murrayon diana*  
*Murrayon hibernicus*  
*Murrayon pullari*  
*Murrayon stellatus*  
*Parhexapodibius pilatoii*  
*Paramacrobiotus alekseevi*  
*Paramacrobiotus areolatus*  
*Paramacrobiotus danielae*  
*Paramacrobiotus derkai*  
*Paramacrobiotus halei*  
*Paramacrobiotus huziori*  
*Paramacrobiotus richtersi*  
*Horning et al. 1978*  
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*Kaczmarek & Michalczyk 2006*  
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*Tumanov 2004*  
*Nelson & Bartels 2007*  
*Nelson & Bartels 2007*  
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*Kaczmarek & Michalczyk 2004c*  
*Bartels & Nelson 2009*  
*Pilato 1974*  
*Kaczmarek & Michalczyk 2006*  
*Pilato & Sperlinga 1975*  
*Guil 2002*  
*Horning et al. 1978*  
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*Guil 2002*  
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*Horning et al. 1978*  
*Michalczyk & Kaczmarek 2003*  
*Bertolani pers. comm. 2010*  
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*Horning et al. 1978*  
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*Horning et al. 1978*  
*Kaczmarek & Michalczyk 2009*  
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*Kaczmarek & Michalczyk 2006*  
*Beasley & Miller 2007*  
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*Horning et al. 1978*  
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*Pilato & Lisi 2006*  
*Claxton 1998*  
*Fontoura et al. 2008*  
*Guil 2002*  
*Kaczmarek & Michalczyk 2006*  
*Schuster & Greven 2007*  
*Hooie & Davison 2001*  
*Schuster & Greven 2007*  
*Kaczmarek & Michalczyk 2006*  
*Fontoura et al. 2009*  
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*Kaczmarek & Michalczyk 2006*  
*Guil 2002*  
*Bartels & Nelson 2009*  
*Hinton & Meyer 2009*  
*Beasley & Miller 2007*  
*Kaczmarek & Michalczyk 2006*  
*Pilato et al. 2001*  
*Degma et al. 2008*  
*Bartels & Nelson 2009*  
*Michalczyk & Kaczmarek 2006b*  
*Kaczmarek & Michalczyk 2006*



*Paramacrobrius tonollii*  
*Parhexapodibius pilatoi*  
*Platicrista angustata*  
*Platicrista cheleusis*  
*Platicrista horribilis*  
*Platicrista ramsayi*  
*Ramajendas renaudi*

Hooie & Davison 2001  
 Hinton & Meyer 2009  
 Jönsson 2003  
 Kathman & Cross 1991  
 Nelson & Bartels 2007  
 Marley 2006  
 Jennings 1979

*Ramajendas frigidus*  
*Ramazottius baumanni*  
*Ramazottius novemcinctus*  
*Ramazottius oberhaeuseri*  
*Richtersius coronifer*  
*Thulinus augusti*

Miller *et al.* 1996  
 Kathman & Cross 1991  
 Guil 2002  
 Kaczmarek & Michalczyk 2006  
 Kaczmarek & Michalczyk 2006  
 Guil 2002

## Summary

The patchy distribution of tardigrades may be due to dispersal. The tardigrades (unlike their mossy habitats) are not easily blown 100 cm by typical winds. Nevertheless, they easily survive space travel during those uncommon events of dispersal. Highly resistant eggs may be a common means of dispersal. Bryophytes and feces of bryophyte consumers may provide means of dispersal.

The most common genera are *Echiniscus*, *Hypsibius*, *Macrobiotus* and segregate genera, *Milnesium*, and *Ramazottius*. Many taxa are widespread, and many more are likely to be discovered. Cryptic species are likely.

Despite their cosmopolitan distribution and widespread occurrence in moss, lichen, and certain soil habitats, it is relatively easy to find new species anywhere in the world. Whole states in the USA (16!) lack any tardigrade records.

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