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Global diversity of tardigrades (Tardigrada) in freshwater

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Abstract Tardigrada is a phylum closely allied with the arthropods. They are usually less than 0.5 mm in length, have four pairs of lobe-like legs and are either carnivorous or feed on plant material. Most of the 900+ described tardigrade species are limnoterrestrial and live in the thin film of water on the surface of moss, lichens, algae, and other plants and depend on water to remain active and complete their life cycle. In this review of 910 tardigrade species, only 62 species representing13 genera are truly aquatic and not found in limnoterrestrial habitats although many other genera contain limnoterrestrial species occasionally found in freshwater.

Keywords Tardigrada · Biogeography · Phylogeny · Distribution · Diversity

Introduction

Tardigrada is a phylum allied with arthropods. Tardigrades are generally less than 0.5 mm in size, bilaterally symmetrical, and have four pairs of legs. Their biology has been reviewed by Kinchin (1994), Nelson & Marley (2000), and Nelson (2002). Tardigrades are found in freshwater habitats, terrestrial environments, and marine sediments. The tardigrades living in terrestrial environments are the most well-known, where they live in the thin film of water found on mosses, lichens, algae, other plants, leaf litter, and in the soil and are active when at least a thin film of water is present on the substrate. Tardigrades often live alongside bdelloid rotifers, nematodes, protozoans and other animals. Aquatic freshwater tardigrades live upon submerged plants or in the sediment but are not inhabitants of the water column. Some tardigrade species can live in both aquatic freshwater and limnoterrestrial environments. In this article, the term aquatic and/or freshwater will be used to describe tardigrades that live in relatively large bodies of freshwater such as ponds, lakes, streams and rivers. The term limnoterrestrial will be used to describe tardigrades that live in the thin film of water found on mosses, algae and other plants, leaf litter, and soil.

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Most tardigrades are gonochoristic with relatively minor sexual dimorphisms that include males being slightly smaller than females. Hermaphrodism and self-fertilization has been documented in only a few, mostly aquatic species. Parthenogenesis is common and can be associated with polyploidy (Bertolani, 2001). Development from egg deposition to hatching can range from 5–40 days. Eutardigrades have direct development but heterotardigrades can display indirect development where first instar larvae lack an anus and gonopore and have fewer claws than adults. Tardigrades become sexually mature after 2–3 molts and molt 4–12 times during a lifetime of 3 or more months. Many tardigrades can undergo various forms of cryptobiosis to enter an environmentally resistant quiescent state. Examples of cryptobiosis include cryobiosis, resistance to freezing (Somme, 1996) and anhydrobiosis, in which internal water is replaced by trehalose to produce a highly resistant tun that can be revived months later (Guidetti & Jönsson, 2002).

Tardigrades have five indistinct segments; a head, three trunk segments each with a pair of lobe-like legs and a caudal segment that contains a fourth pair of legs. The legs of freshwater aquatic and limnoterrestrial tardigrades terminate in claws. The body is covered with a chitinous cuticle that also lines the fore and hind gut. Heterotardigrades are distinguished by cephalic sensory cirri lacking in eutardigrades. Many heterotardigrades are armored by the presence of thick dorsal cuticular plates. Claw structure is important in tardigrade taxonomy (Pilato, 1969). There are numerous major claw types with many recognized variations that distinguish genera. Tardigrades have a complete gut with a complex buccal-pharyngeal apparatus that is also important in taxonomy. The buccal apparatus consists of a mouth, a buccal tube, a muscular sucking pharynx, and a pair of stylets that can extend through the mouth. Most limnoterrestrial and freshwater aquatic tardigrades feed on juices sucked from moss, lichens, algae, and other plants although some tardigrades are carnivorous and consume other mesofauna such as rotifers and nematodes.

Species/generic diversity

Tardigrades are composed of two classes, four orders, at least 90 genera and 900+ species have been described to date. The most complete taxonomic reference for tardigrade species up to 1982 is that of Ramazzotti & Maucci (1983), while Bertolani (1982) focused on aquatic tardigrade species. The number of described tardigrade species has nearly doubled since 1982 (Guidetti & Bertolani, 2005). Tardigrades can be difficult to classify and in some cases the eggs are needed to discriminate among species. The true number of tardigrade species is clearly higher than the 900+ that are currently described. A few species are cosmopolitan, but most tardigrade species appear to be endemic to limited areas. Many other species once thought to be cosmopolitan are now known to be complex species groups (Pilato & Binda, 2001).

Only a few tardigrade taxa are found exclusively in freshwater aquatic habitats in the literature reviewed for this study. Table 1 lists the 62 species of tardigrades known to be exclusively aquatic. Table 2 lists the 13 genera representing five families that contain freshwater aquatic tardigrade species. Only five genera, *Carphania*, *Dactylobiotus*, *Macroversum*, *Pseudobiotus,* and *Thermozodium* were found to be exclusively aquatic in the literature reviewed for this study that included 910 species. Other genera, including *Amphibolus*, *Doryphoribius, Eohypsibius*, *Hypsibius*, *Isohypsibius*, *Mixibius*, *Murrayon* and *Thulinius* contain some species that are aquatic. Limnoterrestrial species and genera are listed in Tables 3 and 4 because limnoterrestrial tardigrades are occasionally found in aquatic habitats. The Palaearctic region has the most aquatic genera and species of tardigrades but this is likely to be a sampling artifact due to differences in the intensity of study in that area while the Oceanic Islands have the least.

Little is known of the distribution of freshwater aquatic tardigrades within a habitat. With limnoterrestrial tardigrades microhabitat can be an important factor in distribution. It has been suggested that oxygen tension, pH of the substratum, moisture content of the moss, the thickness of the moss cushion and altitude may all play a role. The extreme patchy distribution of limnoterrestrial tardigrades within seemingly homogeneous habitat has made it difficult to determine which factors cause the unevenness in their distribution. Habitat distribution studies typically do not include enough sampling to test for statistical significance and many of these studies are essentially species lists from different regions (Garey, 2006).

Table 1 Number of freshwater tardigrade species found in biogeographic regions by family. The zeroes represent either a null record (no information) or absence. See Annex 1 in the online supplemental materials for a more detailed listing. PA = Palaearctic, NA = Nearctic, NT = Neotropical, AT = Afrotropical, OL = Oriental, AU = Australasian, PAC = Pacific Oceanic islands, ANT = Antarctic

Families	PA	NA	AT	NT	OL	AU	PAC	ANT	Total freshwater species per genus	Total species per genus
Heterotardigrada										
Oreellidae	0	0	0	0	0	0	0	0	0	2
Carphaniidae	1	0	0	0	0	0	0	0	1	1
Echiniscidae	0	0	0	0	0	0	0	0	0	229
Eutardigrada										
Murrayidae	13	7	3	5	0	1	1	1	19	24
Macrobiotidae	0	0	0	0	0	0	0	0	0	226
Calohypsibiidae	0	0	0	0	0	0	0	0	0	21
Microhypsibiidae	0	0	0	0	0	0	0	0	0	7
Eohypsibiidae	2	1	0	0	0	0	0	0	2	9
Necopinatidae	0	0	0	0	0	0	0	0	0	1
(*Incertae sedis*)	0	0	0	0	0	0	0	0	0	3
Hypsibiidae	33	12	7	8	3	4	1	6	39	368
Milnesiidae	0	0	0	0	0	0	0	0	0	18
sp inquirenda	0	0	0	0	1	0	0	0	1	1
Total	49	20	10	13	4	5	2	7	62	910

Thermozodium esakii is a species of tardigrade reported from a hot spring in Japan and has been proposed to represent a third class of tardigrades known as Mesotardigrada. Neither the type specimens nor locality exist and similar specimens have not been found (Nelson 2002)

Table 2 Number of freshwater tardigrade genera found in biogeographic regions. PA = Palaearctic, NA = Nearctic, NT = Neotropical, AT = Afrotropical, OL = Oriental, AU = Australasian, PAC = Pacific Oceanic islands, ANT = Antarctic

Families	PA	NA	AT	NT	OL	AU	PAC	ANT	Total freshwater genera per family	Total genera per family
Heterotardigrada										
Oreellidae	0	0	0	0	0	0	0	0	0	1
Carphaniidae	1	0	0	0	0	0	0	0	1	1
Echiniscidae)	0	0	0	0	0	0	0	0	0	12
Eutardigrada										
Murrayidae	1	1	1	1	0	1	1	1	3	3
Macrobiotidae	0	0	0	0	0	0	0	0	0	11
Calohypsibiidae	0	0	0	0	0	0	0	0	0	5
Microhypsibiidae	0	0	0	0	0	0	0	0	0	5
Eohypsibiidae	1	1	0	0	0	0	0	0	2	2
Necopinatidae	0	0	0	0	0	0	0	0	0	1
(*Incertae sedis*)	0	0	0	0	0	0	0	0	0	1
Hypsibiidae	3	3	1	1	0	0	0	0	6	20
Milnesiidae)	0	0	0	0	0	0	0	0	0	3
sp inquirenda[a]	0	0	0	0	1	0	0	0	1	1
Biogeographic totals	6	5	2	2	1	1	1	1	13	66

[a] See footnote in Table 1

Table 3 Number of limnoterrestrial tardigrade species found in biogeographic regions by family. The zeroes indicate either a null record (no information) or absence. See Annex 2 in the online supplementary materials for a more detailed listing. PA = Palaearctic, NA = Nearctic, NT = Neotropical, AT = Afrotropical, OL = Oriental, AU = Australasian, PAC = Pacific Oceanic islands, ANT = Antarctic

Families	PA	NA	AT	NT	OL	AU	PAC	ANT	Total species per genus
Heterotardigrada									
Oreellidae	0	0	0	2	0	1	0	1	2
Carphaniidae	0	0	0	0	0	0	0	0	1
Echiniscidae	130	55	31	64	18	37	12	13	229
Eutardigrada									
Murrayidae	6	5	2	1	1	0	0	0	24
Macrobiotidae	104	35	40	47	21	51	13	14	226
Calohypsibiidae	14	7	0	5	1	1	0	2	21
Microhypsibiidae	4	5	1	1	0	1	1	0	7
Eohypsibiidae	8	3	0	0	0	0	0	0	9
Necopinatidae	1	0	0	0	0	0	0	0	1
(*Incertae sedis*)	2	0	1	0	0	1	0	0	3
Hypsibiidae	235	82	35	60	18	43	8	35	368
Milnesiidae	2	2	3	3	1	3	1	1	18
sp inquirenda	0	0	0	0	0	0	0	0	1
Total	506	194	113	183	60	138	35	66	910

See footnote in Table 1

Table 4 Number of limnoterrestrial tardigrade genera found in biogeographic regions. PA = Palaearctic, NA = Nearctic, NT = Neotropical, AT = Afrotropical, OL = Oriental, AU = Australasian, PAC = Pacific Oceanic islands, ANT = Antarctic

Families	PA	NA	AT	NT	OL	AU	PAC	ANT	Total genera per family
Heterotardigrada									
Oreellidae (1)	0	0	0	1	0	1	0	1	1
Carphaniidae (1)	0	0	0	0	0	0	0	0	1
Echiniscidae (12)	9	9	4	8	3	6	3	6	12
Eutardigrada									
Murrayidae (3)	2	1	1	1	1	1	1	1	3
Macrobiotidae (11)	8	5	5	3	4	3	2	2	11
Calohypsibiidae (5)	3	4	0	4	1	1	0	2	5
Microhypsibiidae (2)	2	2	1	1	0	1	1	0	5
Eohypsibiidae (2)	1	1	0	0	0	0	0	0	2
Necopinatidae (1)	1	0	0	0	0	0	0	0	1
(*Incertae sedis*) (1)	1	0	1	0	0	1	0	0	1
Hypsibiidae (20)	13	11	9	11	6	9	7	8	20
Milnesiidae (3)	1	1	1	1	1	3	1	1	3
sp inquirenda[a]	0	0	0	0	0	0	0	0	1
Biogeographic totals:	42	34	22	30	16	26	15	21	66

[a] See footnote in Table 1

Phylogeny and historical processes

Tardigrada is a phylum associated closely with Onychophora and Arthropoda to form Panarthropoda. Like arthropods and nematodes, tardigrades grow through ecdysis and it has been suggested that they belong to a taxon known as Ecdysozoa that contains all molting animals (Aguinaldo et al., 1997). The two groups of tardigrades known today are the heterotardigrades and the eutardigrades and both groups have marine and freshwater members. A recent family level phylogenetic analysis suggests that tardigrades adapted to freshwater aquatic habitats multiple times (Nichols et al., 2006). The present study suggests tardigrades adapted to freshwater aquatic environments at least twice, once among the heterotardigrades in the family Carphaniidae and at least once among the eutardigrades where representatives of three families (Murrayidae, Eohypsibidae, and Hypsibidae) have freshwater aquatic species.

Little is known of the factors that drive change or speciation in tardigrades. Geographic barriers, reproductive biology and substrate quality all are likely involved. It has been suggested that tardigrades evolve slowly (Pilato & Binda, 2001), aided by periods of cryptobiosis, and because of parthenogenesis, new species or populations can readily appear (McInnes & Pugh 1998). There is only weak evidence that anthropogenic forces have an effect on tardigrade evolution although it is clear that tardigrade distribution is affected by pollution (Steiner, 1994; Hohl et al., 2001).

Biogeographical studies

Figure 1 shows the data from Tables 1 and 2 summarized in the form of a biogeographical map. The northern hemisphere appears to have the most diversity, particularly the palaearctic region, which could be due to the more intensive sampling in Europe compared to other regions. Only a few biogeographical studies have been carried out on terrestrial/freshwater tardigrades (e.g., McInnes & Pugh, 1998; Pilato & Binda, 2001). Terrestrial tardigrades appear to be remarkably endemic at the continental level. One study (Pilato & Binda, 2001) found 68% of terrestrial tardigrade species were found in only one biogeographical region while only 6.8% were cosmopolitan. They also found that within

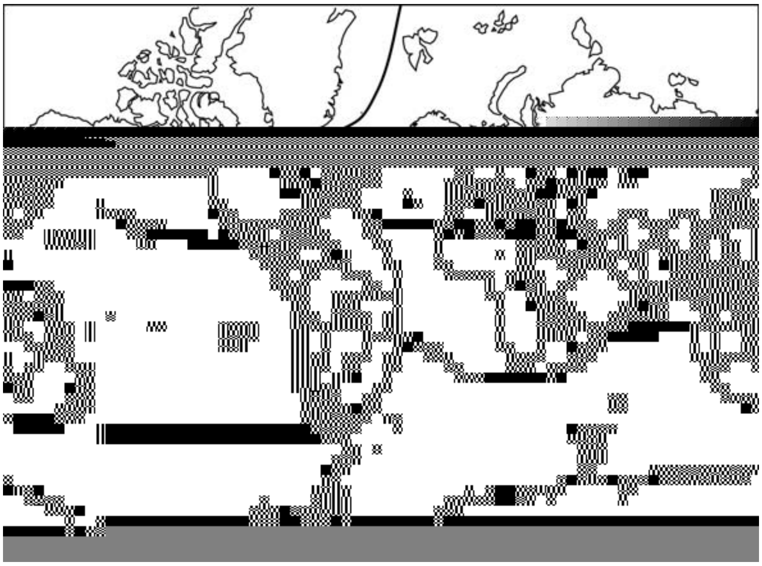

Fig. 1 Summary of the data from Tables 1 and 2 in the context of a biogeographical map. The number preceding the slash represents the number of species that are found exclusively in freshwater aquatic habitats as defined in the text. The number after the slash represents the number of genera with at least one species known to be found exclusively in freshwater aquatic habitats. PA = Palaearctic, NA = Nearctic, NT = Neotropical, AT = Afrotropical, OL = Oriental, AU = Australasian, PAC = Pacific Oceanic islands, ANT = Antarctic

a complex group of species, most often one of the species was cosmopolitan while the other species in the group were endemic to one or a few biogeographical regions. Similar results were found by McInnes & Pugh (1998) where only 22 of the ~800 species considered at that time and 10 of 51 genera were cosmopolitan. They also carried out cluster analyses of tardigrade distribution at the generic and familial level which suggest that 97% of tardigrade species and 82% of genera belong to regional clusters that can be associated with geological events. For example, their cluster analyses show that a laurasian and two gondwanan clusters correlate with the breakup of Pangaea 135 million years ago while two other clusters correspond to the division of East and West Gondwana 65 million years ago.

Economic Importance

Tardigrades have very little economic impact to humans. Their ability to undergo cryptobiosis has created an interest in the medical community and approaches to cell or organ preservation in humans have been tested. Due to the potential medical applications and their pivotal phylogenetic position, branching from the stem lineage that led to arthropods, there has been a renewed interest in the biology of tardigrades at the genomic and proteomic levels. As studies of tardigrade distribution and ecology become more complete they may yet become a useful tool for biogeography (Pilato & Binda, 2001).

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