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Terrestrial and freshwater Tardigrada of the Americas

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Table of contents

Abstract	3
Introduction	3
Materials and methods	3
Results	6
Discussion	7
Acknowledgments	55
References	55

Abstract

This paper provides a comprehensive list of the freshwater and terrestrial tardigrade fauna reported from the Americas (North America, South America, Central America and the West Indies), their distribution in the Americas, and the substrates from which they have been reported. Data were obtained from 316 published references. Authors' identifications were accepted at face value unless subsequently amended. Taxa were assigned to sub-national units (states, provinces, etc.). Many areas, in particular large portions of Central America and the West Indies, have no reported tardigrade fauna.

The presence of 54 genera and 380 species has been reported for the Americas; 245 species have been collected in the Nearctic ecozone and 251 in the Neotropical ecozone. Among the tardigrade species found in the Americas, 52 are currently considered cosmopolitan, while 153 species have known distributions restricted to the Americas. Based on recent taxonomic revision of the genus *Milnesium*, the vast majority of records of *M. tardigradum* in the Americas should now be reassigned to *Milnesium tardigradum sensu lato*, either because the provided description differs from *M. tardigradum sensu stricto* or because insufficient description is provided to make a determination; the remainder should be considered *Milnesium cf. tardigradum*.

Most terrestrial tardigrade sampling in the Americas has focused on cryptogams (mosses, lichens and liverworts); 90% of the species have been collected in such substrates. The proportion of species collected in other habitats is lower: 14% in leaf litter, 20% in soil, and 24% in aquatic samples (in other terrestrial substrates the proportion never exceeds 5%). Most freshwater tardigrades have been collected from aquatic vegetation and sediment. For nine species in the Americas no substrates have been reported.

Key words: Tardigrades, Americas, biogeography, Nearctic, Neotropical

Introduction

The Americas (North America, Central America, South America, and associated islands; also known as America, the Western Hemisphere or the New World) cover 8.3% of the Earth's total surface area (28.4% of its land area) and contain about 14% of the human population (about 900 million people). Biogeographically, the Americas comprise two ecozones, the Nearctic and Neotropical.

In the Americas studies of Tardigrada, a phylum of panarthropods commonly known as water bears, date back to the mid-Nineteenth Century. Bailey (1850) reported the presence of tardigrades in the southern United States of America (USA), but identified no taxa. Packard (1873) noted the presence of two different tardigrade species from aquatic vegetation in Massachusetts and Iowa, USA. Beal (1880) found a specimen, probably a macrobiotid, in aquarium sediment from somewhere in the USA. Vanhöffen (1897) and Jensen (1928) were the first to record the presence of tardigrades in Greenland, but Richters (1911a) was the first to correctly identify species there. Plate (1889) recorded the first species from South America. Richters (1908a) and Murray (1910) published the first Canadian surveys. Heinis (1911) and May (1948) published the first records of tardigrades from Neotropical and Nearctic Mexico respectively. Tardigrades were first reported from the West Indies by du Bois-Reymond Marcus (1960) and from Central America by Riggin (1963).

Few publications contain comprehensive lists of American Tardigrada. Mathews (1938) compiled a comprehensive list of North American tardigrade species and their distributions, and Marcus (1939) did the same for South America. Nelson (1982) updated Marcus (1939) for aquatic and semi-aquatic species, while McFatter *et al.* (2007) reviewed North American freshwater Tardigrada. Rossi & Claps (1991) and Claps *et al.* (2008) reviewed the tardigrades of Argentina, Assunção (1999) listed the tardigrade species of the state of São Paulo in Brazil, Boeckner *et al.* (2005) provided a list of species found in Canada, Nickel *et al.* (2001) summarized the tardigrades

only weak support for such associations. On the other hand, Mitchell *et al.* (2009) found significant evidence for both positive and negative associations between substrates and tardigrade species. On a continental scale, Meyer & Hinton (2006) noted that most cryptogam-associated North American tardigrade species for which adequate data are available have been found in both lichens and mosses, and that few widely-collected species were found only in leaf litter or soil. This pattern holds true when the scale is expanded to include all the Americas. McFatter *et al.* (2007) found that most freshwater studies of North American tardigrades had sampled aquatic vegetation and sediment; in the Americas as a whole most freshwater tardigrades have been collected from these substrates.

Guil & Cabrero-Sañudo (2007) remarked on the preponderance of tardigrade studies carried out by scientists from the Palaearctic and Nearctic ecozones; e.g. very few of the papers on tardigrades from the Afrotropical and Indomalayan ecozones are authored by workers from those areas themselves. Although North American and European tardigradologists have played an important role in studying Neotropical tardigrades, indigenous scientists in Mexico, Costa Rica, Colombia, Argentina, Bolivia and Brazil have made significant contributions of their own.

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