



Zootaxa 4037 (1): 001–189  
www.mapress.com/zootaxa/

Copyright © 2015 Magnolia Press

# Monograph

ISSN 1175-5326 (print edition)

**ZOOTAXA**

ISSN 1175-5334 (online edition)

<http://dx.doi.org/10.11646/zootaxa.4037.1.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:670819B1-3840-4C0A-ABFF-4D5AE3A263C0>

# ZOOTAXA

4037

## The Zoogeography of Marine Tardigrada

ŁUKASZ KACZMAREK<sup>1,2,5</sup>, PAUL J. BARTELS<sup>3,6</sup>, MILENA ROSZKOWSKA<sup>1,2</sup>  
& DIANE R. NELSON<sup>4</sup>

<sup>1</sup>*Department of Animal Taxonomy and Ecology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland.  
E-mail: [kaczmar@amu.edu.pl](mailto:kaczmar@amu.edu.pl), [mil.roszkowska@gmail.com](mailto:mil.roszkowska@gmail.com)*

<sup>2</sup>*Laboratorio de Ecología Natural y Aplicada de Invertebrados, Universidad Estatal Amazónica,  
Campus Principal Km 2.1/2 via a Napo (Paso Lateral) Puyo, Pastaza, Ecuador*

<sup>3</sup>*Department of Biology, Warren Wilson College, CPO 6032, PO Box 9000, Asheville, NC 28815, USA.  
E-mail: [pbartels@warren-wilson.edu](mailto:pbartels@warren-wilson.edu)*

<sup>4</sup>*Department of Biological Sciences, East Tennessee State University, Johnson City, TN 37614, USA. E-mail [nelsond@etsu.edu](mailto:nelsond@etsu.edu)*

<sup>5</sup>*Prometeo Researcher*

<sup>6</sup>*Corresponding author*



Magnolia Press  
Auckland, New Zealand

ŁUKASZ KACZMAREK, PAUL J. BARTELS, MILENA ROSZKOWSKA & DIANE R. NELSON

**The Zoogeography of Marine Tardigrada**

(*Zootaxa* 4037)

189 pp.; 30 cm.

2 Nov. 2015

ISBN 978-1-77557-823-9 (paperback)

ISBN 978-1-77557-824-6 (Online edition)

FIRST PUBLISHED IN 2015 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: [zootaxa@mapress.com](mailto:zootaxa@mapress.com)

<http://www.mapress.com/zootaxa/>

© 2015 Magnolia Press

All rights reserved.

No part of this publication may be reproduced, stored, transmitted or disseminated, in any form, or by any means, without prior written permission from the publisher, to whom all requests to reproduce copyright material should be directed in writing.

This authorization does not extend to any other kind of copying, by any means, in any form, and for any purpose other than private research use.

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

## Table of contents

Abstract	4
Introduction	4
Materials and methods	5
List of marine tardigrade species records throughout the world	7
Phylum: Tardigrada Doyère, 1840	7
Class: Heterotardigrada Marcus, 1927	7
Order: Arthrotardigrada Marcus, 1927	7
Family: Archechiniscidae Binda, 1978	7
Genus: <i>Archechiniscus</i> Schulz, 1953a	7
Family: Batillipedidae Ramazzotti, 1962	9
Genus: <i>Batillipes</i> Richters, 1909	9
Family: Coronarctidae Renaud-Mornant, 1974	41
Genus: <i>Coronarctus</i> Renaud-Mornant, 1974	41
Genus: <i>Trogloarctus</i> Villora-Moreno, 1996	43
Family: Halechiniscidae Thulin, 1928	43
Subfamily: Dipodarctinae Pollock, 1995	43
Genus: <i>Dipodarctus</i> Pollock, 1995	43
Subfamily: Euclavarctinae Renaud-Mornant, 1983	49
Genus: <i>Clavarctus</i> Renaud-Mornant, 1983	49
Genus: <i>Euclavarctus</i> Renaud-Mornant, 1975b	49
Genus: <i>Exoclavarctus</i> Renaud-Mornant, 1983	50
Genus: <i>Moebjergarctus</i> Bussau, 1992	50
Genus: <i>Parmursa</i> Renaud-Mornant, 1984a	51
Genus: <i>Proclavarctus</i> Renaud-Mornant, 1983	51
Subfamily: Florarctinae Renaud-Mornant, 1982	52
Genus: <i>Florarctus</i> Delamare Deboutteville & Renaud-Mornant, 1965	52
Genus: <i>Ligarctus</i> Renaud-Mornant, 1982	64
Genus: <i>Wingstrandarctus</i> Kristensen, 1984	64
Subfamily: Halechiniscinae (Thulin, 1928)	67
Genus: <i>Chrysoarctus</i> Renaud-Mornant, 1984a	67
Genus: <i>Halechiniscus</i> Richters, 1908	70
Subfamily: Orzeliscinae (Schulz, 1963)	85
Genus: <i>Mutaparadoxipus</i> Gross, Miller & Hochberg, 2014	85
Genus: <i>Orzeliscus</i> du Bois-Reymond Marcus, 1952	85
Subfamily: Styraconyxinae Kristensen & Renaud-Mornant, 1983	89
Genus: <i>Angursa</i> Pollock, 1979	89
Genus: <i>Bathyechiniscus</i> Steiner, 1926	92
Genus: <i>Lepoarctus</i> Kristensen & Renaud-Mornant, 1983	93
Genus: <i>Paratanarctus</i> D'Addabbo Gallo, Grimaldi de Zio, Morone De Lucia & Troccoli, 1992	93
Genus: <i>Pleocola</i> Cantacuzène, 1951	94
Genus: <i>Raiarctus</i> Renaud-Mornant, 1981a	94
Genus: <i>Styraconyx</i> Thulin, 1942	99
Genus: <i>Tetrakentron</i> Cuénot, 1892	111
Genus: <i>Tholoarctus</i> Kristensen & Renaud-Mornant, 1983	112
Subfamily: Tanarctinae Renaud-Mornant, 1980	115
Genus: <i>Actinarctus</i> Schulz, 1935	115
Genus: <i>Tanarctus</i> Renaud-Debyser, 1959a	120
Genus: <i>Zioella</i> Renaud-Mornant, 1987b	127
Family: Neoarctidae (Grimaldi de Zio, D'Addabbo Gallo & Morone De Lucia, 1992)	127
Genus: <i>Neoarctus</i> Grimaldi de Zio, D'Addabbo Gallo & Morone De Lucia, 1992	127
Genus: <i>Renaudarctus</i> Kristensen & Higgins, 1984	128
Family: Stygarctidae Schulz, 1951	129
Subfamily: Megastygarctidinae Bello & Grimaldi de Zio, 1998	129
Genus: <i>Megastygarctides</i> McKirdy, Schmidt & McGinty-Bayly, 1976	129
Subfamily: Stygarctinae Grimaldi de Zio, D'Addabbo Gallo & Morone De Lucia, 1992	130
Genus: <i>Faroestygarctus</i> Hansen, Kristensen & Jørgensen, 2012	130
Genus: <i>Mesostygarctus</i> Renaud-Mornant, 1979b	131
Genus: <i>Neostygarctus</i> Grimaldi de Zio, D'Addabbo Gallo & Morone De Lucia, 1982a	132
Genus: <i>Parastygarctus</i> Renaud-Debyser, 1965	133
Genus: <i>Prostygarctus</i> Rubal, Veiga, Fontoura & Sousa-Pinto, 2013	139
Genus: <i>Pseudostygarctus</i> McKirdy, Schmidt & McGinty-Bayly, 1976	139
Genus: <i>Stygarctus</i> Schulz, 1951	141

Order: Echiniscoidea Richters, 1926 . . . . .	145
Family: Echiniscoididae Kristensen & Hallas, 1980 . . . . .	145
Genus: <i>Anisonyches</i> Pollock, 1975b . . . . .	145
Genus: <i>Echiniscoidea</i> Plate, 1888 . . . . .	147
Class: Eutardigrada Richters, 1926 . . . . .	159
Superfamily: Isohypsibioidea Marley, McInnes & Sands, 2011 . . . . .	159
Family: Isohypsibiidae Marley, McInnes & Sands, 2011 . . . . .	159
Genus: <i>Thulinus</i> R. Bertolani, 2003 . . . . .	162
Discussion . . . . .	162
Conclusions . . . . .	174
Acknowledgements . . . . .	175
References . . . . .	175

## Abstract

This monograph describes the global records of marine water bears (Phylum Tardigrada). We provide a comprehensive list of marine tardigrades recorded from around the world, providing an up-to-date taxonomy and a complete bibliography accompanied by geographic co-ordinates, habitat, substrate and biogeographic comments. A link is provided to an on-line interactive map where all occurrences for each species are shown. In total we list 197 taxa and their 2240 records from 39 oceans and seas and 18 Major Fishing Areas (FAO). It is hoped this work will serve as a reference point and background for further zoogeographic and taxonomic studies on marine tardigrades.

**Key words:** Arthrotardigrada, biogeography, Eutardigrada, FAO areas, Heterotardigrada, species distribution, species list, water bears

## Introduction

Members of the phylum Tardigrada are micrometazoans, generally ranging in size from 50 µm to 1 mm (although according to Guil (2008) one specimen has recently been found that reached 2 mm), with four pairs of lobopodous legs usually terminating in claws or digits. Ecdysozoans that comprise a sister group to the arthropods (Garey *et al.* 1996, 1999, Garey 2001), tardigrades are ubiquitous in marine, freshwater and terrestrial interstitial communities (Nelson & Marley 2000). They are most famous for their ability to withstand environmental extremes via cryptobiosis (for review see Welnicz *et al.* 2011, Guidetti *et al.* 2012, Rebecchi 2013), but except for a very few intertidal tardigrades this capability does not exist in marine species (see *e.g.* Clausen *et al.* 2014, Jørgensen & Møbjerg 2014). Tardigrades are a rather poorly studied taxon (*e.g.* Guil & Cabrero-Sañudo 2007) and research on marine tardigrades is severely limited (Vicente & Bertolani 2013), even though they are phylogenetically important as the basal group for the phylum (Jørgensen *et al.* 2010).

There are 197 species and subspecies of marine tardigrades described out of a total of 1220 currently known species in the phylum (Guidetti & Bertolani 2005, Degma & Guidetti 2007, Vicente & Bertolani 2013, Degma *et al.* 2009-2014). Degma *et al.* (2009-2014) list 198 marine species, but changes to that list are required for the genus *Angursa* as discussed below. Thus, marine tardigrades make up only 16% of currently known species. The marine tardigrades include all heterotardigrades in the order Arthrotardigrada, the genera *Echiniscoidea* and *Anisonyches* in the family Echiniscoididae (order Echiniscoidea) as well as four eutardigrade species in the order Parachela (*Thulinus itoi* Tsurusaki, 1980; *Halobiotus arcturulus* Crisp & Kristensen, 1983; *H. crispae* Kristensen, 1982; *H. stenostomus* (Richters, 1908)) that have been secondarily adapted to the marine environment. Described from all seas, marine tardigrades are part of the meiobenthos and occur in intertidal and subtidal areas down to the abyss (to 4690 m below sea level (bsl), Thiel 1966). Most species are interstitial, but some are algal associates and others are associated with barnacles and other invertebrates.

Research on marine tardigrades is limited due to their rarity and extremely small size, but it is also hindered by the lack of centralised information on species distributions and the absence of centralised, up-to-date diagnostic tools. This paper is an attempt to correct the first problem. The only comprehensive key to tardigrades is outdated