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# Taxonomy, systematics and ecology of the phylum Tardigrada

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Plymouth University

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# Taxonomy, systematics and ecology of the phylum Tardigrada

by

Nigel James Marley

A thesis submitted to the University of Plymouth  
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

(June 2014)

School of Marine Science and Engineering

Faculty of Science and Environment



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## **Dedication**

First I would like to dedicate this thesis to my parents, Mr. John Alan Marley and Mrs Eileen Jean Marley, whose love and support has helped me reach this goal.

My personal journey on this extended PhD journey reflects the rollercoaster in my own health, with multiple rounds of heart surgery, brain surgery and other procedures to challenge me, my family, friends and the National Health Service (NHS) all too often. I am eternally grateful to all of the surgeons, medical, nursing and other staff members within the NHS who have saved my life on a number of occasions in the last twenty years.

However, my recovery from these challenges was only possible because of the love, support and energy of my parents, sister Mrs. Liz Pollock, and older twin brother Mr. Steve Marley, who've diligently nursed my back to health each time.

I would also like to dedicate this thesis to my late great aunt Mrs. Thelma Angell, with whom I did one of my recovery stints as she also recovered from a stroke. She had a wicked sense of humour and an infectious laugh.

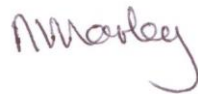
Each time I returned home to Plymouth, my amazing network of friends gave me a lot of support, even when I had forgotten who they were following the stroke! I guess it's about living life to the full and always thinking of the "glass is half full". Thank you all.

## Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

This study was predominantly self-funded but I gratefully acknowledge the organisations which have awarded me small grants to undertake specific topics, they are each cited within the grants section later in this document.

Signed...



Date...20/06/2014.....



# The taxonomy, systematics and ecology of the phylum Tardigrada

by

Nigel James Marley

## Abstract

I conducted a series of research programmes on various aspects of Tardigrada biology. The published results of which are hereby presented as part fulfilment of my submission for a PhD by publications at Plymouth University.

In this thesis my research publications are grouped into four chapters: Ecology & Faunistics, Alpha Taxonomy, Freshwater Fauna – a taxonomic challenge, and Superfamilies. In the first, I highlight my early papers which dealt with the faunistic surveys as I trained in systematics and taxonomy of the phylum. Amongst the key findings reported were the protozoan symphoriant, *Pyxidium tardigradum* van der Land, 1966, Marley and Wright (1994); a new addition to the reported fauna of the United Kingdom, Greaves & Marley(1996); and my first work on international samples from Arctic Canada, Sutcliffe *et al.*(2000).

In the second chapter, Alpha Taxonomy, I have included five papers. The first, Marley and Wright (1996), illustrates my work with one of the Royal Museums of Scotland's collections, where I updated the diagnoses of their specimens and described a new addition to the Icelandic fauna. The second paper, Russell, Marley & Hockings (2001), demonstrates how I was searching for new research methods to apply to tardigrades. It was because of similar exploration, with methods of SEM preparation, that I was invited to join the Australian-Anglo team working on sediment core samples from Antarctic freshwater lakes, Gibson *et al.* 2009. The remaining two papers in the chapter describe species new to science, *Echiniscus ollantaytamboensis* Nickel, Miller and Marley, 2001, and my first sole authored paper describing a species new to science, *Platicrista ramsayi* Marley, 2006.

The third chapter, Freshwater Fauna – a taxonomic challenge, deals with a programme of research based initially on my findings at the Royal Museums of Scotland, Edinburgh.

This then required subsequent visits to the USA and Italy to work on the taxonomic issues with original authors on their more recently described genera. I prepared the original Case for the ICZN, but this was then held by the commission for several years pending their amendments to the Code. I then rewrote the Case into the final paper, Marley, Bertolani & Nelson (2008).

The final chapter consists of two papers in which I worked on combining my expertise on the morphological characters of the buccal apparatus and claws, and combining this with new molecular dataset derived from sequencing individual specimens. My colleagues on these papers were Dr S.J. McInnes and Mr C.J. Sands, both from the British Antarctic Survey.

Overall I am including 14 published papers and 5 published conference abstracts and three online articles. The following taxa were erected during this work: *Pseudobiotus kathmanae*, *Echiniscus ollantaytamboensis*, *Platicrista ramsayi*, Ramazzottidae, Isohypsibiidae, Macrobioidea, Eohypsibioidea, Hypsibioidea, and Isohypsibioidea. Plus the following taxa were re-described, *Pseudobiotus*, *Thulinus*, *Thulinus augusti*, *Thulinus ruffoi*, and *Thulinus stephanae*.

## Chapter 1 Critical Appraisal

### The start of the research journey:

Here I explain the journey through my research experiences; illustrating the significance of these via my publications. I have grouped the papers into four chapters: Ecology & Faunistics, Alpha Taxonomy, Freshwater Fauna – a taxonomic challenge, and Superfamilies. Finally at the end of this section, I look forward at on-going research.

My journey through my PhD research has been in several phases including the acquisition of basic and advanced microscopy research skills, a thorough grounding in tardigrade taxonomy and then the synthesis and testing of new ideas. At the start of my PhD journey I had already taught myself basically how to find and mount specimens on to microscopy slides, and how to identify some species, mostly terrestrial taxa in a few large genera, i.e. *Macrobotus*, *Minibiotus*, *Hypsibius*, *Isohypsibius*, *Milnesium*, *Calohypsibius*, *Echiniscus*, *Testechiniscus*, *Pseudechiniscus* and *Bryodelphax*, to either an operational taxonomic unit or for a few taxa to species level. However my initial progress was limited due to access to specialist literature, specimen collections and expert mentors in the field. Therefore, I had to become mobile and travel to find the experts and expertise.

In those early years, I made my first visits to the Royal Museums of Scotland, Edinburgh, to review their collections including Murray's material (1904-1913) and some of the material from Morgan's material (1980's). My first transatlantic research visit to see Prof. Diane Nelson at East Tennessee State University, and then the following year to attend my first research meeting, the 6<sup>th</sup> International Tardigrade Symposium, Cambridge, UK, see list of conference presentations.

One of the outcomes from these early travels included building a relationship with the National Museums of Scotland. I was able to clarify the significance of their historic meiofauna collections, i.e. the Scottish Lakes Survey, and therefore prevented them from disposing of the bulk of the material in that collection due to local space / storage issues. Amongst the specimens I later borrowed from the museum were slides from the Morgan collection. I was able to both update the nomenclature used and to also identify specimens belonging to the Eohypsibiidae, a taxon probably unknown to Morgan at that time. See Marley & Wright (1996) in chapter 2

Another significant success from my early years was my refinement of Heinz polyvinyl alcohol mounting medium for use with tardigrades. Primarily I changed the recipe for working with mites, significantly reducing the amount of chloral hydrate. This medium is now used by a number of colleagues as it sets relatively quickly but doesn't require the slides to be ringed for many years. Specimen distortion is also reduced in comparison with Hoyer's or polyvinyl lactophenol media; see details published on the [tardigrada@mailbase.ac.uk](mailto:tardigrada@mailbase.ac.uk) list server in 2000, see Annex 1.

## **Ecology and Faunistics:**

Having begun, as previously mentioned, from a very basic starting point for both my microscopy and only having access to Morgan & King (1976), my initial progress learning how and where to find specimens went relatively well but I soon encountered issues with the lack of details contained within the single handbook. I therefore spent considerable time and effort in tracking down further references, including undertaking many visits to the library collections at the Marine Biological Association of the UK, Bristol University, Exeter University, the Natural History Museum (London) and Linnean Society of London. These national visits were always supplemented my visits to research groups abroad especially my visits to the Natural History Museum in Copenhagen, Denmark; and Prof. Nelson's laboratory at East Tennessee State University, USA.

At the starting point of my research the structure of the phylum was still relatively simple; with only 3 classes, 5 orders, 17 families, 15 subfamilies, 65 genera and about 570 described species. Whereas the latest edition of Tardigrade Checklist, version 25, published on 10/05 /2014, now contains 3 classes, 5 orders, 4 superfamilies, 26 families, 12 subfamilies, 118 genera and approximately 1150 described species. Undoubtedly the phylum's structure will continue to be re-evaluated as new techniques are utilised as tools for taxonomic descriptions, such as functional genomics research, or as new locations, habitats and substrates are explored.

In 1993 I made my first visit to Prof. Diane Nelson at East Tennessee State University, Johnson City Tennessee. In those three days I made a lot of progress, checking and correcting my basic knowledge but also realising how much more was already known about tardigrade biology. Subsequently I became a frequent visitor to Prof. Nelson's home and laboratory.

My earliest publications were primarily ecological inventory style studies, associated with the somewhat simpler taxonomic descriptions. Locally I had access to a diverse range of habitats across the city, up on to the higher, wetter habitats of Dartmoor National Park, compared to the many coastal habitats around Cornwall. These initial studies are represented by my first publication, Marley & Wright (1994) in which I reported finding the protozoan symphoriant, *Pyxidium tardigradum* Van der Land, 1966. I have received several enquires specifically about these rarely reported animals including questions from colleagues in Poland who published the first SEM images. I sent them copies of some of my work in the Electron Microscopy Centre.

Working with members of the Quekett Microscopy Club, established 1865, in London. I have attended a couple of the field days which enabled me to work with Mr Phil Greaves, with us publishing a short checklist for the Bookham Common local nature reserve, Greaves & Marley (1994). Amongst our findings was a new addition to the British fauna, which with recent taxonomic changes would now be an *Astatumen* species. This was a good result for two relatively inexperienced researchers at that time.

I have also attended several of the club's annual exhibitions held in the Natural History Museum and have been awarded the Barnard Certificate twice for my images of tardigrades using both light and SEM techniques. Entries have included the use of darkfield microscopy with the Echiniscidae Thulin, 1928; cysts of the tardigrade *Bertolanius weglaskae*; SEM images of tardigrades, which include a sculptured egg of an undescribed species from South Africa.

My work with colleagues from the Natural History Museum in London gave me access to my first sample materials from abroad. The first consisted of mosses, lichens and fragments of ancient caribou antler from the high Arctic in Canada. From those samples I extracted and identified tardigrade specimens to help build up a simple food web, Sutcliffe *et al.* 2000. Sadly I didn't see this paper for several years due to the senior author's death and my own serious illness. However I am continuing to work with many of the sample materials Dr. Sutcliffe and his wife collected during their other visits around the Russian Arctic Islands and Alaska.

With all of my travelling back and forth to the United States to work with Prof. Nelson, I was delighted to be asked to work with her on updating a paper for a special edition of Freshwater Biology. The paper was called Lotic Tardigrada, with us presenting a summary of freshwater taxa records and also highlighting interesting key facts about

their biology. I believe my main contribution that paper was to double check the initial draft by Prof. Nelson and to design the illustrations, i.e. the summaries of the claws and buccal apparatus.

### **Alpha Taxonomy:**

A second relationship with the Natural History Museum (London) was with the Young Systematists' Conference, organised by the Systematic Association. I attended two of their annual conferences to present papers on 2002 and 2004, see conferences poster presentations and conference papers lists.

Spurred on by this relationship with Natural History Museum (London), I headed up to the Royal Museums of Scotland in Edinburgh. I found great potential subjects within the museum's collections, which included some of James Murray's material from the beginning of the 20th Century, and some of Dr. Clive Morgan's materials from Scotland and Iceland collected in the early and mid-1980's. The Icelandic materials provided me with the subject for my first solo taxonomic paper, **Marley (1996)**, in which I reported a new addition to the Icelandic check-list and updated the names for all previously reported taxa.

At the 8<sup>th</sup> International Tardigrada Symposium I presented some of my findings based on specimens from Peru. Later at the same conference I saw a presentation by Mr. Nickel and Dr. Miller. I suggested at the conference that we should review our specimens, but unfortunately the other participants had not brought their specimens with them. I therefore explained, based on the presentation images we had used separately, why I believed these were the same species; I also gave them some specimens to review back in the USA. While this post-symposium confirmation was being conducted I held my original manuscript. Shortly after returning from the conference I suffered my major brain haemorrhage which incapacitated me for several years. It was over a year later that I found the other authors had added my name to their original manuscript, Nickel, Miller & Marley, 2001. I am unable to state what specific amendments they made to their original manuscript based on the copy of my presentation and description. About 5 years later Dr Michalczyk and Dr Kaczmarek contacted me with reference to their work on specimens belonging to this species group. I therefore sent example specimens from my collection to assist them because they had been unable to access any material from the Philadelphia Museum, USA or the others' in the USA.

At Plymouth University many of my colleagues organise and take part in expeditions to complete fieldwork around the world. This provides me with frequent opportunities to receive dried samples of mosses and lichens from across a range of habitat boundaries. Two such examples have come from the western side of the Andes in South America. I received some mosses and lichens collected by Dr Paul Ramsay from the Volcán Chiles, Ecuador. Within these samples I extracted a range of specimens including three animals which represented a new species to science, *Platicrista ramsayi* Marley, see Marley 2006a. This was my first sole authored new species description. Unfortunately a last minute printer's error occurred after the proofs had been corrected, and this resulted in a number of typographic errors being introduced into the published paper. After discussion with the publisher, who admitted responsibility for the error, they published a correction for the main paragraph affected, Marley 2006b.

As a result of my SEM work, probably including the award of a Barnard Certificate, from the Quekett Microscopy Club, and my illustrated presentations at the International Tardigrada symposia, I received an invitation to join an Australian universities team working on sediment cores from the bottom of Antarctic lakes. My role was to receive extracted specimen and process these to provide SEM images for publication, see **Gibson et al. 2008**. I then worked with Dr. McInnes to confirm the diagnoses of the processed eggs.

## **Freshwater Taxa – a taxonomic challenge:**

The objective for this chapter is to illustrate that rather than just undertaking alpha taxonomic studies, I have progressed to dealing with more complex matters required to unpick more complex issues. Using the Code and engaging with the ICZN.

As previously mentioned, I had specifically visited the Royal of Museums several times. During the first visit I had identified a potential error in the modern identification and description for one of the species. Despite the slides being nearly one hundred years old, the museum allowed for me to borrow a number of specimens for some comparison work with specimens in other collections. The first opportunity I had to show these specimens to my learned colleagues was at the 6<sup>th</sup> International Tardigrada Symposium. Professor Nelson and Professor Bertolani had each described new genera, *Pseudobiotus* Nelson, 1980 and *Thulinia sensu* Bertolani, 1982, later *Thulinus* Bertolani, 2003, respectively. Both were implicated in this taxonomic mix-up. We therefore agreed to follow-up the issue after the conference.

We met at Prof. Bertolani's laboratory a year later with all of the type material. Prof. Bertolani's excellent microscope enabled us to compare in detail the fine structures of the buccal apparatus. Although we all agreed that the genera would all require re-descriptions it took up a week to agree on the correct criteria. The outcome was three proposed papers; the first was a case to be sent to the ICZN for them to rule on, the second paper to redescribe *Thulinia* [now *Thulinus*] and the final one to redescribe *Pseudobiotus*.

The receipt of the ICNZ case 3017, for which I was lead author, was acknowledged, Anon. (1996), and then held by the commission for a prolonged period. The delay being due to proposed amendments to the Code.

Sadly this meant that both the other two papers were published first, Bertolani, Marley & Nelson (1999) and Nelson, Marley, & Bertolani (1999). The outcome of the review of the Code was that the Commission was no longer required to rule on cases of misidentification of the Type. Consequently the Case wasn't published or ruled on by the commission. Following a delay due to my health, I rewrote the paper and it was published, Marley, Bertolani, & Nelson (2008), to clarify the history of the misidentifications and to designate a new type species for the genus *Pseudobiotus*.

## **Superfamilies:**

The final programme of research which I am including within this thesis ran over a number of years, between me at Plymouth University and Dr. McInnes and Mr C.J. Sands at the British Antarctic Survey. During one of my visits to BAS, they explained that they were starting work on molecular analysis, initially concentrating on improving extraction and processing techniques to enable individual meiofauna specimens to be used as opposed to small groups of specimens, Sands, Convey *et al.* (2008). During our discussions we realised that between our two collections, i.e. Dr. McInnes at BAS and my collection at Plymouth University we could cover a much larger geographic range and many more taxa. From Dr. McInnes' collection and the herbarium at BAS we used samples for the Antarctic Peninsula, the sub-Antarctic islands, plus a few spot samples from Northern Hemisphere. From my sample collection we added material from around the Arctic Circle, (including the Russian Arctic Islands, Alaska, and Arctic Canada), Gambia, Japan and Australia. We both had material from Greenland and South Africa.



Dr McInnes and I concentrate on locating specimens and identifying them to operational taxonomic units. Mr. Sands, a molecular biologist, worked on extracting DNA sequences.

Once we had managed to process about one third of our specimens, for a good taxonomic coverage, Mr Sands started to compile early versions of the sequence trees. At this point, Dr McInnes and I were able to review these results and pick up on themes. I also used my knowledge of the morphology of the OTUs to help Mr Sands with some of the alignment questions, i.e. *Bryodelphax* for which we had specimens from both Polar Regions. We agreed it was important to collect further specimens from type localities and therefore Dr. McInnes and I headed to Paris, France, the type locality for a number of species.

While Mr Sands worked on the molecular data, Dr. McInnes and I worked in parallel on morphological datasets. All three of us worked on both manuscripts, with Mr Sands leading on the molecular and myself on the morphology paper. The morphology paper was submitted first but after two long delays from journal editors changing posts, it was eventually submitted to a third journal. The molecular paper therefore appeared first, and out of sequence, causing some issues with authorities for the new taxa which we were proposing.

In the Sands, McInnes et al. (2008) we introduced the superfamily rank into the Phylum, with Macrobiotoidea, Hypsibioidea, and Isohypsibioidea, and two new families, Isohypsibiidae and Ramazzottidae.

In the morphology paper, Marley et al. (2011), we were able to discuss details primarily about the apophysis for the insertion of the stylet muscles (AISM) and the structures of the claws, which were useful synapomorphies to define the superfamilies. From the morphological characters I had suggested a fourth superfamily would be required and this was eventually confirmed when some molecular data was published, (Jørgensen *et al.* 2010), with our own sequenced material waiting for further analysis.

I worked with Dr. McInnes on the morphological diagnoses. We both had strong opinions about potential diagnostics characters, although these were challenging due to the limited number of characters available. After many drafts of the morphological manuscript, I eventually proposed the compromised wording which was used in the published paper.

## General Discussion and Future Research

The overall theme behind my research has been to examine specimens from a broad range of habitats, initially for taxonomic and ecological inventory studies. With my growing personal specimen collection, and the experiences gained from visiting collections in other institutions and collecting specimens on other continents, I have been able to recognise differences in the use of commonly cited taxa names.

Many of the taxa I have focused my research efforts on, such as the freshwater groups, have according to the early literature, very broad distribution patterns. I am therefore interested in investigating these groups further to understand if this truly reflects a taxon's biogeographic distribution or our limited understanding of them, based on current morphological taxonomic studies. Hopefully with the increasing availability of molecular data, our knowledge of tardigrade biodiversity will continue to become clearer. Finally I am excited about the opportunities to integrate morphological and molecular datasets into more powerful combined datasets. Using these combined datasets to then explore questions from both a systematics and biogeography perspective.

I will be continuing this work in the immediate future with the publication of papers on the Apochela, the sister-group of the Parachela, with an evaluation of the morphological characters and taxonomic information used to describe new genera / lineages. One paper is already in submission for the above and two more will follow this summer. Secondly I will be returning to my work on the Echiniscidae, or more specifically to the *Pseudechiniscus*-line, and basal taxa such as *Hypechiniscus*.

Finally, I will be working through recently collected sample materials from Chile and the Sub-Antarctic Islands which were collected this austral summer. The brief abstract from that expedition is included at the end of this section, see Annex 2..

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**Annexes:**

**Annex 1: Email correspondence: Nigel Marley to Tardigrada Mailbase list, Mounting Media – what's yours called?**

**Subject:** [Mounting Media - what's yours called?](#)

**From:** "N Marley" <[\[log in to unmask\]](#)>

**Reply-To:** [\[log in to unmask\]](#)

**Date:** Mon, 11 Sep 2000 15:23:28 GMT

**Content-Type:** text/plain

**Parts/Attachments:**  [text/plain](#) (65 lines)

During the 8th International Symposium on the Tardigrada – (held this summer in Denmark), there was a round table discussion on techniques. This opened some interesting questions on the mountants we use, what we call them and what they contain. I thought it would be a good discussion point for the list.

Below I give details of the mounting media I use, how to make it and what its like to use.

What do other researchers use?

\*\*\*\*\*

Heinz Mounting Media (Heinz PVA)

10g Poly Vinyl Alcohol (I use low molecular weight PVA) \*\*

40ml Distilled water

10ml Glycerol

50ml phenol/distilled water solution (1.5%) \*\*

75g chloral hydrate \*\*

35ml latic acid \*\*

\*\* very nasty substance read safety instructions from supplier

Method:

- 1) Add PVA powder to water (in fume cupboard), stirring continuously, the mixture being heated in a water bath to just below boiling.
- 2) Add latic acid and stir for a few minutes. Then allow to cool until luke-warm.
- 3) Dissolve Chloral hydrate into the phenol. Add to PVA/water/latic acid solution.
- 4) Stir thoroughly and suction filter. Store in brown bottle.

My last stock bottle lasted me about 5 years. Some of the chemicals are pretty nasty and there is a lot of chloral hydrate in this preparation. Researchers in the USA will find that chloral hydrate is a restricted substance - in order to keep it you will need a licence which isn't cheap.

Specimens relax and clear very well - possibly to well. Best preparation results and longevity of slides are attained by removing almost all of the water surrounding a specimen before adding a drop of mountant. The slides become semi-hard in about 12 hours, but not completely hard for a few days. Care should be taken when using

oil techniques and cleaning the coverslips during the first month.

Overall I have found it a good mountant to use, but I am thinking of adding iodine and potassium iodine, in a similar fashion to some of the "hoyer's" mountant in circulation.

Nigel Marley  
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## **Annex 2: Systematics Research Fund 2013-2014 Report, Tardigrades of the South Shetland Islands, Antarctica, and Chile.**

### **Systematics Research Fund 2013-2014**

Expedition summary report submitted to the Systematics Research Fund for their annual report and website, (word limit = 100). [Submitted May 27th 2014]

### **Tardigrades of the South Shetland Islands, Antarctica, and Chile.**

In January-February 2014 I took part in an expedition to South Shetland Islands, Antarctica, organised by INACH. Project funding was awarded to Dr. Matthew R. Lee, Universidad de Los Lagos, Chile, and my SRF award enabled me to reach the expedition start in Punta Arenas, Chile.

I spent 37 days in Chile and Antarctica collecting samples of mosses, lichens and sediments in which to search for tardigrades. Expedition time in Antarctica was curtailed due to weather and logistics reasons. Sample processing is expected to take 18 months. Specimens of other taxa collected will be sent to other researchers.



## **Acknowledgements**

My sincere thanks to my research supervisors over the years: Dr. Don E. Wright (retired), late Dr. Andy Stevens, Dr. Pete Glynn (retired), Dr. David Bilton and Dr. Simon Rundle and to Plymouth University for enabling me to undertake this research. Sadly, I lost the advice from Dr. Andy Stevens too soon; but I have to say thank you to him for starting me working on these brilliant animals, it's taken me around the world!

To my mentors and dear friends: Dr. Diane R. Nelson, Dr. Sandra J. McInnes and the late Dr. Clark Beasley, you all share my love of everything tardigrade. We have completed ridiculous hours conducting research in laboratories from Disko Island, Greenland, to ETSU in the USA, and in various labs in the UK, Denmark, Germany, Italy, and Portugal. But no matter how long it has been between visits our friendships have never lessened! Thank you all.

To my wider family of tardigradologists, my co-authors, and the friends and students I have shared laboratories with over the years, a big thank you. It will be great not to be oldest researcher in the laboratory without a PhD finally! Thank you all.

Finally a thank you to the organisations which have awarded me grants over the years. These have enabled me to attend expeditions, courses and symposia in some amazing places. Just two more continents to go before I can say I've worked on them all! I guess that will be my next target!



## Grants

**Systematics Research Fund** (administered by the Linnean Society and the Systematics Association). Awarded: 2<sup>nd</sup> May 2013. To support participation in a Chilean expedition to Antarctica in early 2014.

**Winston Churchill Memorial Travelling Fellowship** to visit the People's Republic of China for one month in 2005. Expedition successfully completed.

**E.U. Travel & Research Grants** Improving Human Potential & Access to Infrastructure. COBICE (Copenhagen Biosystematic Center, Copenhagen, Denmark).

- November 2003. Project: "Encystment in Tardigrada."
- May & June 2001. Project: "The evaluation of cuticular sculpturing characteristics across a range of *Pseudechiniscus*-line taxa (Tardigrada), with the re-description of species."

## Small Grants

Plymouth Martine Fund - towards attending 9<sup>th</sup> International Symposium on Tardigrada, Florida, USA July 2003.

Faculty of Science, University of Plymouth - towards attending 8<sup>th</sup> International Symposium on Tardigrada, Copenhagen, Denmark August 2000.

Department of Biological Sciences, University of Plymouth - towards attending 6<sup>th</sup> International Symposium on Tardigrada, Cambridge, UK, 1994.

## Research output

### Invited Research Lectures

National University Ireland Galway, Galway, Ireland, September 2012

Xi'an Normal University, Xi'an, China, June 2007

Hong Kong University, Hong Kong, China, June 2007

### Published Papers

**Marley, N.J.**, McInnes, S.J. and Sands, C.J. (2011). Phylum Tardigrada: A re-evaluation of the Parachela. *Zootaxa*, 2819, 51–64 <http://www.mapress.com/zootaxa/2006f/zt01166p048.pdf>

**Marley, N.J.**, Bertolani, R. and Nelson, D.R. (2008) Designation of *Pseudobiotus kathmanae* Nelson, Marley & Bertolani, 1999 as the type species for the genus *Pseudobiotus* Nelson, 1980 (Tardigrada). *Zootaxa*, 1940: 41-47. <http://www.mapress.com/zootaxa/2008f/zt01940p047.pdf>

Sands, C.J., McInnes, S.J., **Marley, N.J.**, Goodall-Copestake, W., Convey, P. and Linse, K. (2008) Phylum Tardigrada: an "individual" approach. *Cladistics*, 24: 861–871. <http://onlinelibrary.wiley.com/doi/10.1111/j.1096-0031.2008.00219.x/pdf>

**Marley, N.J.** (2008). Biodiversity within the Milnesiidae (Tardigrada). *Journal of Morphology* 269 (12): 1466-1466. (Abstract) <http://onlinelibrary.wiley.com/doi/10.1002/jmor.10683/pdf>

McInnes, S., **Marley, N.J.**, and Sands, C.J. (2008). A Re-Evaluation of the Parachela (Eutardigrada: Tardigrada). *Journal of Morphology* 269 (12): 1466-1466. (Abstract) <http://onlinelibrary.wiley.com/doi/10.1002/jmor.10683/pdf>

Sands, C.J., McInnes, S.J., **Marley, N.J.**, Goodall-Copestake, W.P., Convey, P., and Linse L. (2008) Polar diversity of the Tardigrada: A combined morphological / molecular approach. Scientific Committee on Antarctic Research (SCAR), XXX, July 2008 p. 1 [http://www.uam.es/otros/cn-scar//SCAR\\_IASC\\_IPY/pdf/17167.pdf](http://www.uam.es/otros/cn-scar//SCAR_IASC_IPY/pdf/17167.pdf)

Gibson, J.A.E., Cromer, L., Agius, J.T., McInnes, S.J., and **Marley, N.J.** (2007). Tardigrade eggs and exuviae in Antarctic lake sediments: insights into Holocene dynamics and origins of the fauna. *Journal of Limnology*, 66 (Suppl. 1): 5-11. DOI: <http://dx.doi.org/10.4081/jlimnol.2007.s1.65>

**Marley, N.J.** (2006). A new species of Tardigrada, *Platicrista ramsayi* sp. nov. from the páramo of Volcán Chiles, Ecuador. *Zootaxa*, 1166: 35-48. <http://www.mapress.com/zootaxa/2008f/zt01940p047.pdf> and *Corrigenda* due to printer's error:

Zootaxa, 1762: 68. <http://www.mapress.com/zootaxa/2006f/zt01172p068.pdf>

Russell, P.M., **Marley, N.J.** & Hockings, M.E. (2001). Do confocal microscopy and tardigrades have a future together? *Zoologische Anzeiger*, 240: 543-548.

<http://www.sciencedirect.com/science/article/pii/S004452310470056X#>

DOI: <http://dx.doi.org/10.1078/0044-5231-00065>

Nickel, K., Miller, R.M. & **Marley, N.** (2001). Tardigrades of South America: Machu Picchu and Ollantaytambo, Peru. *Zoologische Anzeiger*, 240: 505-509.

<http://www.sciencedirect.com/science/article/pii/S0044523104700510>

DOI: <http://dx.doi.org/10.1078/0044-5231-00060>

Sutcliffe, A.J. & Blake, W. Jr. (plus 7 **other contributing authors**) (2000). Biological activity on a decaying caribou antler at Cape Herschel, Ellesmere Island, Nunavut, High Arctic Canada. *Polar Record*, 36: 233-246. DOI: <http://dx.doi.org/10.1017/S0032247400016491>

Nelson, D.R. & **Marley, N.J.** (2000). The biology of lotic Tardigrada. *Freshwater Biology*, 44: 93-108. DOI: <http://dx.doi.org/10.1046/j.1365-2427.2000.00586.x>

Bertolani, R., **Marley, N.J.** & Nelson, D.R. (1999). Re-description of the genus *Thulinia* (Eutardigrada, Hypsibiidae) and of *Thulinia augusti* (Murray, 1907) comb. nov.. *Zoologische Anzeiger*, 238: 139-145.

Nelson, D.R., **Marley, N.J.** & Bertolani, R. (1999). Re-description of the genus *Pseudobiotus* (Eutardigrada, Hypsibiidae) and of the new type species *Pseudobiotus kathmanae* sp. n. *Zoologische Anzeiger*, 238: 311-317.

**Marley, N.J.** & Wright, D.E. (1996). *Amphibolus weglarskae* Dastych, a new addition to the Tardigrada of Iceland with an updated checklist of Icelandic species (Eohypsibiidae, Eutardigrada). *Quekett Journal of Microscopy*, 37: 541-545.

Greaves, P.M. & **Marley, N.J.** (1994). The tardigrade fauna of Bookham Common. *The London Naturalist*, 73: 185-190.

**Marley, N.J.** & D.E. Wright (1994). *Pyxidium tardigradum* Van Der Land, a rarely record symphoriant on Waterbears (Tardigrada). *Quekett Journal of Microscopy*, 37: 232-233.

## Conference Papers

**Marley, N.J.** (2012). What do you do with a problem like Maria Milnesiidae? 12th International Symposium on Tardigrada, Vila Nova de Gaia, Portugal, July 2012.

**Marley, N.J.** (2009). The Tardigrada of Devon and Cornwall, United Kingdom, including three species new to science and seven new additions to the U.K. fauna. 11th International Symposium on Tardigrada, Tübingen, Germany, August 2009.

Ramsay, B.P.L. & **Marley, N.J.** (2009). Tardigrada communities from high-altitude forest to grassland transition in the Cordillera de Vilcanota Peru. 11th International Tardigrada Symposium, Tubingen, Germany, August 2009.

**Marley, N.J.** (2008). Biodiversity within the Milnesiidae (Tardigrada). First International Congress on Invertebrate Morphology, Copenhagen, Denmark, August 2008.

McInnes, S., **Marley, N.J.** & Sands, C.J. (2008). A Re-evaluation of the Parachela (Eutardigrada: Tardigrada). First International Congress on Invertebrate Morphology, Copenhagen, Denmark, August 2008.

Sands, C.J., McInnes, S.J., **Marley, N.J.**, Goodall-Copestake, W.P., Convey, P. and Linse, L. (2008). Polar diversity of the Tardigrada: A combined morphological / molecular approach. 3rd Scientific Committee on Antarctic research (SCAR) / International Arctic Science Committee (IASC) International Polar Year (IPY) Open Science Conference, St. Petersburg, Russia, July 2008.

**Marley, N.J.** (2006). Biodiversity within the Milnesiidae? 10th International Symposium on Tardigrada, University of Catania, Italy, June 2006.

**Marley, N.J.** (2004). Cosmopolitan taxa in the Phylum Tardigrada - Fact or Fiction? 6th Young Systematists' Forum, Natural History Museum, London, UK, December 2004.

[http://www.systass.org/ysf/6th\\_YSF.pdf](http://www.systass.org/ysf/6th_YSF.pdf)

**Marley, N.J.** (2003). Preliminary Results from a Study on Ecuadorian Tardigrada. 9th International Symposium on Tardigrada, 9<sup>th</sup> International Tardigrada Symposium, Saint Pete Beach, Florida, USA, July, 2003.

**Marley, N.J.** (2000). Tardigrade assemblages from an altitudinal transect in Venezuela. 8th International Symposium on Tardigrada, Copenhagen, Denmark August 2000.

**Marley, N.J.** (1997). Cuticular sculpturing in the *Pseudechiniscus suillus* species complex, with the description of new taxonomic characteristics. 7th International Symposium on the Tardigrada, Düsseldorf, Germany, September 1997.

Bertolani, R., **Marley, N.J.** and Nelson, D.R. (1997). Some considerations on *Thulinia* (Eutardigrada, Hypsibiidae), with the re-description of the genus and of *Thulinia augusti* (Murray,

1907) comb. n. 7th International Symposium on the Tardigrada, Düsseldorf, Germany, September 1997.

**Marley, N.J.**, & Wright, D.E. (1994). The anatomy and histology of *Amphibolus weglarskae* Dastych (Eohypsibiidae, Parachela, Eutardigrada, Tardigrada). 6th International Symposium on the Tardigrada, Cambridge, UK, August 1994.

**Marley, N.J.** & Wright, D.E. (1994). Some notes on the Arctic Tardigrada of Canada and Alaska, including a new addition to the North American fauna. 6th International Symposium on the Tardigrada, Cambridge, UK, August 1994.

## Conference Posters

**Marley, N.J.**, McInnes, S., & Sands, C.J. (2011) Morphology versus molecular: a meiofaunal conundrum resolved, Second International Congress on Invertebrate Morphology, Harvard University, Cambridge, MA, USA, June 2011.

Gibson, J.A.E., Cromer, L., Agius, J., McInnes, S.J., **Marley, N.J.** (2006). Tardigrade eggs in sediments of Antarctic lakes. 10th International Symposium on Tardigrada, University of Catania, Italy, June 2006.

**Marley, N.J.**, Bertolani, R. & Nelson, D.R. (2003). Designation of *Pseudobiotus kathmanae* Nelson (Tardigrada) as the Type Species of *Pseudobiotus* Nelson. 9<sup>th</sup> International Tardigrada Symposium, Saint Pete Beach, Florida, USA, July, 2003.

**Marley, N.J.** (2003). Tardigrades of Southwest England, United Kingdom. A Long-term, Multi-habitat Survey from the Coastal Urban Habitats to the Upland Moors. 9<sup>th</sup> International Tardigrada Symposium, Saint Pete Beach, Florida, USA, July, 2003.

**Marley, N.J.** (2002). Bear Hunting in Devon (Tardigrada). Young Systematists' Forum, Natural History Museum, London December 2002. [http://www.systass.org/ysf/4th\\_YSF.pdf](http://www.systass.org/ysf/4th_YSF.pdf)

**Marley, N.J.** (2002). Bear Hunting in Devon (Tardigrada). Joint Meeting of the British Ecological Society & the Freshwater Biological Society, Crewe August 2002.

Russell, P.M., **Marley, N.J.** & Hockings, M.E. (2000). Do confocal microscopy and tardigrades have a future together? 8th International Symposium on Tardigrada, Copenhagen, Denmark August 2000.

**Marley, N.J.** (1998). One species new to science and 8 new additions to the Tardigrada fauna of the British Isles from south west England. 10th International Meiofauna Conference (XIMCO), Plymouth, UK.

**Marley, N.J.** (1997). Redescription of the *Milnesium* claw type and the peribuccal structure of *Milnesium tetralamellatum*. 7th International Symposium on the Tardigrada, Düsseldorf, Germany, September 1997.

**Marley, N.J.** & Russell, P.M. (1994). Visualisation of the surface sculpturing of the tardigrade, *Pseudechiniscus suillus* (Ehrenberg), explored with enhanced light microscopy techniques. 6th International Symposium on the Tardigrada, Cambridge, UK, August 1994.

**Marley, N.J.** & Wright, D.E. (1994). The Eutardigrade symphoriant, *Pyxidium tardigradum* Van der Land, its European distribution and host specificity. 6th International Symposium on the Tardigrada, Cambridge, UK, August 1994.

## **Conferences organising committee membership**

**10th International Meiofauna Conference (XIMCO)**, Plymouth, UK, July 1998.

## Corrigenda to publications

The following principal taxa were cited in my papers and have subsequently been reassigned as the taxonomy and systematics of the phylum continues to evolve.

### Chapter 2:

Marley, N.J. & Wright, D.E. (1994)

- First paragraph: "*Pyxidium tardigrade*", page 232 should be "*Pyxidium tardigradum*"
- Observations first two sentences,  
"A total of eight host tardigrades were collected from both samples. The tardigrade species were *Milnesium tardigradum* (Doyère) and *Macrobiotus (Macrobiotus) hufelandi* (Schultze)." should be  
"A total of eight host tardigrades were collected from both samples. The tardigrade species were *Milnesium tardigradum* (Doyère), *R. oberhauseri* and *Macrobiotus persimilis* Binda & Pilato, 1972."

Greaves, P.M. & Marley, N.J. (1993)

- "*Hypsibius arcticus*" represented a species of the *convergens* – *microps* – *pallidus* species complex
- "*Diphascon (Adropion) scoticum*" has recently been transferred to *Adropion scoticum scoticum* (Murray, 1905) into Itaquasconinae Bartoš in Rudescu, 1964 by Bertolani *et al.* 2014
- "*Macrobiotus richtersi*" is now "*Paramacrobiotus richtersi*"
- "*Diphascon (Diphascon) pingue*" is now "*Diphascon pingue pingue* (Marcus, 1936)"
- "*Diphascon (Adropion) prorsirostre*" is now "*Adropion prorsirostre* (Thulin, 1928)"
- *Diphascon (Diphascon) pingue* is now *Diphascon pingue*
- "*Itaquascon sp.*" is now "*Astatumen sp.*"

Nelson, D.R. & Marley, N.J (2000)

- P. 94 Table 1. The genus *Milnesioides* Claxton, 1999 in the Milnesiidae was unknown to the authors at the time of our paper was accepted for publication but is accepted by both authors.

### Chapter 3:

Marley, N.J. & Wright, D.E. (1996)

- “*Amphibolus weglarskae* (Dastych, 1972)” is now “*Bertolanus weglarskae* (Dastych, 1972)”

Nickel, K., Miller, W.R. & Marley, N.

- My second initial, J., was missed off the paper submitted by the other two authors.
- In the discussion, “(*Milnesium tardigradum*, *Macrobotus areolatus*, *Macrobotus harmsworthi*, *Minibiotus intermedius*)” should be “*Milnesium* sp., *Paramacrobotus* sp., *Macrobotus harmsworthi* group sp., *Minibiotus* sp.)”

Marley, N.J. (2006)

- P42 final paragraph, “leg pair VI” should be “leg pair IV”
- P46. Printer’s errors after final proof in final paragraph:

“*P. angustata*óa” should be “*P. angustata*,”

“*P. cheleusis*óVancouver” should be “*P. cheleusis*, Vancouver”

“*P. horribilis*óMongolia” should be “*P. horribilis*, Mongolia”

“*P. itaquasconoide*óSweden” should be “*P. itaquasconoide*, Sweden”

“*P. ramsayi* **sp. nov.**óEcuador” should be “*P. ramsayi* **sp. nov.**, Ecuador”.



## Chapter 2 Publications: Ecology and Faunistics

Due to issues with copyright permission from the journals, it has not been possible to include copies of the papers in the eSubmission for the university. However the papers remain publically available from each of the journals.

**Marley, N.J.** & D.E. Wright (1994). *Pyxidium tardigradum* Van Der Land, a rarely record symphoriant on Waterbears (Tardigrada). Quekett Journal of Microscopy, 37: 232-233.

Greaves, P.M. & **Marley, N.J.** (1994). The tardigrade fauna of Bookham Common. The London Naturalist, 73: 185-190.

Nelson, D.R. & **Marley, N.J.** (2000). The biology of lotic Tardigrada. Freshwater Biology, 44: 93-108. DOI: <http://dx.doi.org/10.1046/j.1365-2427.2000.00586.x>

Sutcliffe, A.J. & Blake, W. Jr. (plus 7 **other contributing authors**) (2000). Biological activity on a decaying caribou antler at Cape Herschel, Ellesmere Island, Nunavut, High Arctic Canada. Polar Record, 36: 233-246. DOI: <http://dx.doi.org/10.1017/S0032247400016491>

### Chapter 3 Publications: Alpha Taxonomy

Due to issues with copyright permission from the journals, it has not been possible to include copies of the papers in the eSubmission for the university. However the papers remain publically available from each of the journals.

**Marley, N.J.** & Wright, D.E. (1996). *Amphibolus weglarskae* Dastych, a new addition to the Tardigrada of Iceland with an updated checklist of Icelandic species (Eohypsibiidae, Eutardigrada). *Quekett Journal of Microscopy*, 37: 541-545.

Nickel, K., Miller, R.M. & **Marley, N.** (2001). Tardigrades of South America: Machu Picchu and Ollantaytambo, Peru. *Zoologische Anzeiger*, 240: 505-509.  
<http://www.sciencedirect.com/science/article/pii/S0044523104700510>

Russell, P.M., **Marley, N.J.** & Hockings, M.E. (2001). Do confocal microscopy and tardigrades have a future together? *Zoologische Anzeiger*, 240: 543-548.  
<http://www.sciencedirect.com/science/article/pii/S004452310470056X#>

**Marley, N.J.** (2006). A new species of Tardigrada, *Platicrista ramsayi* sp. nov. from the páramo of Volcán Chiles, Ecuador. *Zootaxa*, 1166: 35-48.  
<http://www.mapress.com/zootaxa/2008/f/zt01940p047.pdf> and *Corrigenda* due to printer's error: *Zootaxa*, 1762: 68.  
<http://www.mapress.com/zootaxa/2006f/zt01172p068.pdf>

Gibson, J.A.E., Cromer, L., Agius, J.T., McInnes, S.J., and **Marley, N.J.** (2007). Tardigrade eggs and exuviae in Antarctic lake sediments: insights into Holocene dynamics and origins of the fauna. *Journal of Limnology*, 66 (Suppl. 1): 5-11. DOI:  
<http://dx.doi.org/10.4081/jlimnol.2007.s1.65>

**Marley, N.J.** (2008). Biodiversity within the Milnesiidae (Tardigrada). *Journal of Morphology* 269 (12): 1466-1466. (Abstract)  
<http://onlinelibrary.wiley.com/doi/10.1002/jmor.10683/pdf>

## Chapter 4 Publications: Freshwater Taxa - a taxonomic challenge

Due to issues with copyright permission from the journals, it has not been possible to include copies of the papers in the eSubmission for the university. However the papers remain publically available from each of the journals.

Bertolani, R., **Marley, N.J.** & Nelson, D.R. (1999). Re-description of the genus *Thulinia* (Eutardigrada, Hypsibiidae) and of *Thulinia augusti* (Murray, 1907) comb. nov.. Zoologische Anzeiger, 238: 139-145.

Nelson, D.R., **Marley, N.J.** & Bertolani, R. (1999). Re-description of the genus *Pseudobiotus* (Eutardigrada, Hypsibiidae) and of the new type species *Pseudobiotus kathmanae* sp. n. Zoologische Anzeiger, 238: 311-317.

**Marley, N.J.**, Bertolani, R. and Nelson, D.R. (2008) Designation of *Pseudobiotus kathmanae* Nelson, Marley & Bertolani, 1999 as the type species for the genus *Pseudobiotus* Nelson, 1980 (Tardigrada). Zootaxa, 1940: 41-47.

<http://www.mapress.com/zootaxa/2008/f/zt01940p047.pdf>

## Chapter 5 Publications: Superfamilies

Due to issues with copyright permission from the journals, it has not been possible to include copies of the papers in the eSubmission for the university. However the papers remain publically available from each of the journals.

Sands, C.J., McInnes, S.J., **Marley, N.J.**, Goodall-Copestake, W., Convey, P. and Linse, K. (2008) Phylum Tardigrada: an "individual" approach. *Cladistics*, 24: 861–871. <http://onlinelibrary.wiley.com/doi/10.1111/j.1096-0031.2008.00219.x/pdf>

McInnes, S., **Marley, N.J.**, and Sands, C.J. (2008). A Re-Evaluation of the Parachela (Eutardigrada: Tardigrada). *Journal of Morphology* 269 (12): 1466-1466. (Abstract) <http://onlinelibrary.wiley.com/doi/10.1002/jmor.10683/pdf>

Sands, C.J., McInnes, S.J., **Marley, N.J.**, Goodall-Copestake, W.P., Convey, P., and Linse L. (2008) Polar diversity of the Tardigrada: A combined morphological / molecular approach. *Scientific Committee on Antarctic Research (SCAR)*, XXX, July 2008 p. 1 [http://www.uam.es/otros/cn-scar//SCAR\\_IASC\\_IPY/pdf/17167.pdf](http://www.uam.es/otros/cn-scar//SCAR_IASC_IPY/pdf/17167.pdf)

**Marley, N.J.**, McInnes, S.J. and Sands, C.J. (2011). Phylum Tardigrada: A re-evaluation of the Parachela. *Zootaxa*, 2819, 51–64  
<http://www.mapress.com/zootaxa/2006f/zt01166p048.pdf>