

## An attempt to revisit the global biogeography of limno-terrestrial Tardigrada

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### ABSTRACT

*The major increase in distribution records of limno-terrestrial tardigrades over the last ten years has enabled us to reassess the global biogeography of the Tardigrada using cluster analysis, principal components analysis and parsimony analysis of endemism (PAE). Although the new clustergram topology shows a close correlation with those we originally presented in 1998, the PAE outputs warrant a radical reinterpretation of the results as they imply that the Laurasian fauna is derived and the Gondwanan groups basal. The distribution of endemic tardigrade genera and families provides some support for this argument though the findings should be viewed with some caution as PAE has its detractors and has not been previously applied on a 'global' scale.*

*Key-words: biogeography, continental drift, dispersal, Gondwana, Laurasia, Tardigrada*

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### 1. INTRODUCTION

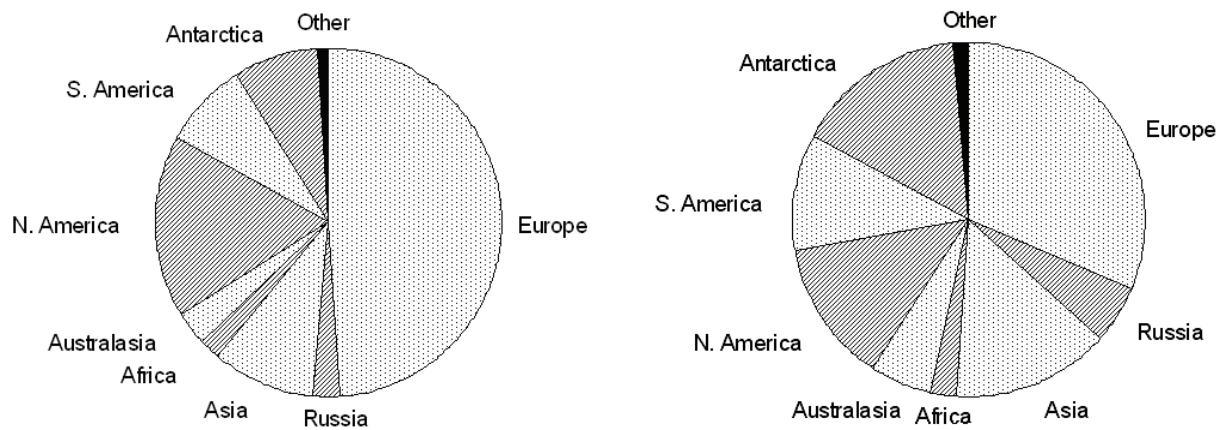
There are three important reasons for revisiting our original biogeographic analysis of non-marine Tardigrada (McInnes & Pugh 1998). First, the paper and its initial presentation were derived from an earlier database (McInnes 1994), which stimulated many tardigradologists to publish new tardigrade records. In twelve years the original database of 502 publications has expanded by 70% to 856 studies. These included a number of papers re-examining and redefining previously reported taxa as well as those recording new sites and new species. Although the data remain Eurocentric the proportion of papers discussing Russian, Asian, Australasian, South American and especially Antarctic tardigrades has increased (Fig. 1). Second, the initial approach was rather naïve in that we used a cluster algorithm not used in current multivariate analysis packages simply because we were dealing with so few records showing little spatial congruence. And, while the underlying calculations were computer generated, we manually compiled the data matrices and clustergrams. This approach provided some answers, but in less than a decade computer power has increased to a level where very large data sets can now be explored by relatively simple programmes on desktop machines, thus providing a third reason for reappraising the data.

This paper re-examines the global biogeography of limno-terrestrial tardigrades using an expanded data set and three complementary computer methods.

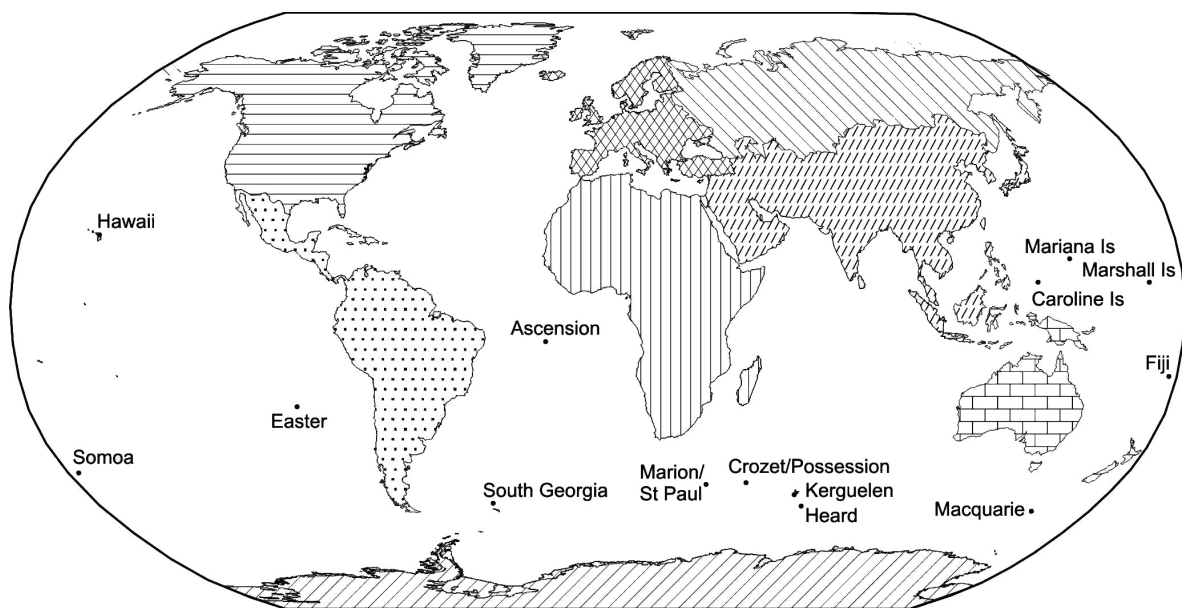
### 2. METHODS

The original Microsoft 'Word' (Microsoft Corporation, Washington, DC) database (McInnes

1994), was updated, copied and stripped down to current published systematic details (class, order, family, genus, species) and reported distribution data. We did not include any, as yet unpublished, new records or corrections currently under discussion. The data were set with tabs, exported to a Microsoft 'Excel' (Microsoft Corporation, Washington, DC) spreadsheet where geopolitical (country) distribution text records were transformed into presence - absence (1/0) digital data and collapsed into just eleven broad and pragmatic biogeographic divisions or "areas" that do not always correspond to the traditional biogeographic regions, to keep the computation times manageable. These divisions were North America (including Greenland), South America (including Central America; N.B. The geographic location and biotic affinities place Tierra del Fuego within South America not Antarctica (*sensu* Lewis Smith 1984 and Pugh & Convey 2000; cf. Sanmartín & Ronquist 2004), Europe (including Finland, Estonia, Latvia, Belarus, Ukraine and Turkey), Russia, Africa (including Madagascar), Asia (Arabian Peninsula to Japan and including Indonesia), Australasia, Antarctica and islands of the Atlantic, Pacific and Southern Oceans (Fig. 2). There were no data for the (omitted) islands of the Indian Ocean. These divisions differentiate all seven 'traditional' terrestrial biogeographic regions but separate Europe, Russia and Asia, which our analyses should combine to form a coherent 'Eurasia', or at least 'Holarctic' (with North America) cluster - regional clade, and thus provide a suitable benchmark. We copied the data onto three separate worksheets and modified each to show the distribution of (a) species, (b) genera and (c) combined species and genera. Triplicate copies of the Excel spreadsheet were produced of which one was left intact to contain data for all limno-terrestrial Tardigrada and



**Fig. 1.** Indication of the literature coverage for limno-terrestrial tardigrades in seven broad biogeographic divisions based on pre-1994 (left) and pre-2006 (right) distribution systematic papers. Note: 'Other' refers to non-systematic literature lacking any defined biogeographic attributes.



**Fig. 2.** Map showing the biogeographic divisions (see Methods). Southern Ocean Islands include: South Georgia, Marion - St. Paul, Crozet - Possession, Kerguelen, Heard and Macquarie. Pacific Ocean Islands include: Mariana Is., Marshall Is., Caroline Is., Fiji, Samoa, Easter and Hawaii. Atlantic Ocean Islands include: Ascension.

the other two reduced to Eutardigrada and Heterotardigrada.

For the purpose of this analysis 'cosmopolitan' is defined as species, genera or families found in all eleven divisions. Similarly, 'endemism', or rather 'regional-endemism' (*sensu* Rosen 1988) is defined as a species, genus or family found in a single 'biogeographic' zone. While family and genera are relatively robust, species are still subject to change indeed several 'species', e.g. *Macrobiotus hufelandi* are known to mask species groups or complexes (Biserov 1990a, b; Bertolani & Rebecchi 1993). To avoid the pitfalls of both taxon validity and species complexes we applied parsimony analysis of endemism (PAE) (Rosen 1988) as it retains endemic records at a higher taxonomic level; that is

endemic species within genus or endemic genus within family.

The Excel 'species' and 'generic' spreadsheets were exported to the Multi-Variate Statistical Package (MVSP – Kovach 1999) for cluster analysis and principal components analysis (PCA) of the distribution data. Cluster analysis applied a presence - null record (1/-) Sørensen ( $S_S$ ) coefficient (Krebs 1989) and unweighted pair-group method using arithmetic averages (UPGMA) clustering algorithm (Sokal & Sneath 1963); a more robust presence - absence (1/0) criteria would have been invalidated by missing (false absence) records. Though easy to interpret, clusters are not necessarily statistically valid (Pillar 1999), so we applied two independent benchmarks to the data. First, a minimum  $S_S > 0.1$  base-

line that is equivalent to two sites sharing one taxon from a combined total of 20 (Pugh 2004). Second, congruence with scatter-plot groups discriminated by the first three PCA axes extracted via Kaiser's Rule (Legrende & Legrende 1983) from non-transformed data.

Clusters were further verified by parsimony analysis of endemism (PAE) (Rosen 1988) by applying the method of De Grave (2001) to two bootstrapped parsimony routines within the 'PHYLIP' suite of programmes (Felsenstein 1989, 2005). The binary 'species and genera' data were used as Operational Taxonomic Units (OTUs) to conserve the data from single-site endemic taxa (Glasby & Alvarez 1999). The data were then modified by deleting taxa that were either pandemic to all eleven divisions or OGU (Operational Geographic Units) or endemic to any one OGU. Data were then row/ column transposed and exported to 'PHYLIP' as text files and, in the absence of suitable fossils, Lundberg rooted (Cracraft 1991). 'PHYLIP' input files were run through the 'SEQBOOT' programme to create 1000 pseudo-replicated 'bootstrapped' (*sensu* Felsenstein 1985) files where the 0/1 data were treated as morphological character states. 'SEQBOOT' outputs were then run through two separate parsimony programmes. First, 'MIX', a Wagner-parsimony routine that equal weights forward changes and reversals (Kluge & Farris 1969), thus providing a dispersal proxy; and second 'DOLPENNY', a Dollo-parsimony branch and bound routine, that minimises ( $1 \rightarrow 0$ ) reversal (here emigration or extinction) relative to ( $0 \rightarrow 1$ ) forward change (here immigration) (Farris 1977), providing a non-dispersal (i.e. vicariance) proxy. 'MIX' and 'DOLPENNY' outputs were compiled via bootstrapped extended majority-rule trees (Margush & McMorris 1981), input to the 'CONSENSE' routine. Consense trees with mean bootstrap values of  $<75\%$  were deemed verified though branches supported by  $<50\%$  of trees were rejected and collapsed to the next robust basal branch to yield a trifurcation. Percentage endemism and all other derived figures were calculated using 'Excel'.

### 3. RESULTS

The outputs for the dominant Eutardigrada (695 species and 50 genera) were virtually identical to those of all Tardigrada (949 and 64), while the much smaller Heterotardigrada data set of 266 species and 14 genera proved unstable with several failed (low bootstrap value) branches. Hence only the combined 'all limno-terrestrial tardigrade' data are considered here.

#### 3.1. Species (Figs 3a and 4)

PCA identifies 57.1% of variance in the first three axes (not displayed) and 100% in ten ( $n-1$  sites) axes. There is a robust 'Holarctic' (Russia, Europe and North America) ( $S_S: 0.44 < 0.50$ ) core cluster subsumed with a broader cluster including Asia, Africa and South

America ( $S_S: 0.34 < 0.50$ ) with an Australasian ( $S_S: 0.27$ ) outlier. This grouping is distinct from a more diffuse Antarctica - Southern islands ( $S_S: 0.38$ ) and Pacific islands cluster ( $S_S: 0.14 < 0.38$ ); while the Atlantic islands are discrete ( $S_S: 0.06$ ). The Holarctic (North America, Russia, Europe) cluster is also apparent as a crown regional clade under both Dollo and Wagner parsimony routines, which also identify (Antarctica, Southern island) Pacific and Atlantic island basal regional clades.

#### 3.2. Genera (Figs 3b and 5)

PCA identifies 65.4% of variance in the first three axes (not displayed) and 100% in ten ( $n-1$  sites) axes. Russia and Europe form a tight Eurasian cluster ( $S_S: 0.89$ ) but within a broader 'Holarctic' Russia, Europe, North America, Asia ( $S_S: 0.83 < 0.89$ ) group. The Holarctic cluster is allied to the West Gondwanan continents (South America and Africa) ( $S_S: 0.70 < 0.89$ ) but distinct from the remaining East Gondwanan (Antarctica, Australasia) and Southern - Pacific island ( $S_S: 0.62 < 0.78$ ) elements. The stable (Russia, Europe, North America, Asia) crown, together with the basal (Antarctica, Southern island), Pacific and Atlantic island regional clades are apparent in both Dollo and Wagner outputs.

#### 3.3. Families

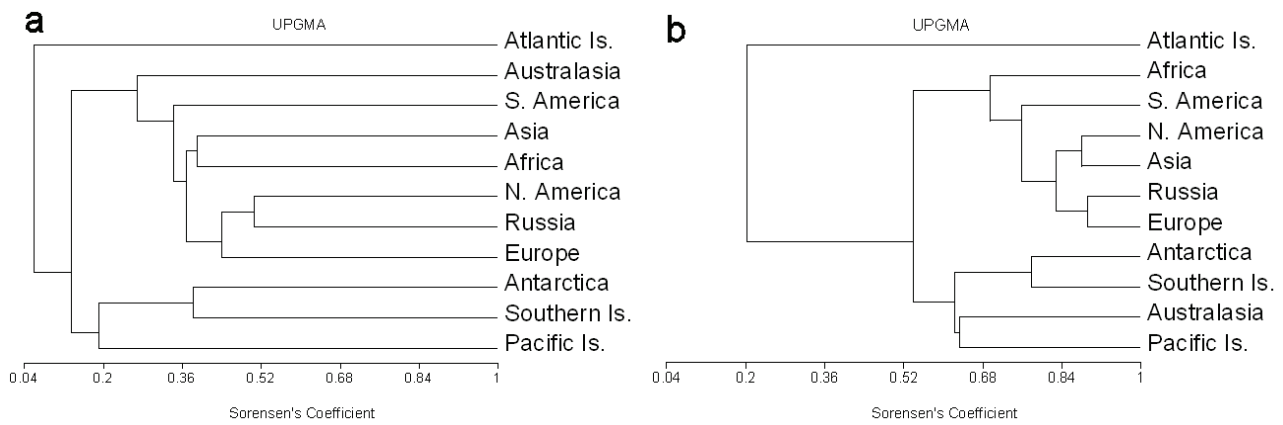
The few data points failed to provide a viable PAE output and the preponderance of widespread families make the cluster analysis invalid.

#### 3.4. Common Trends

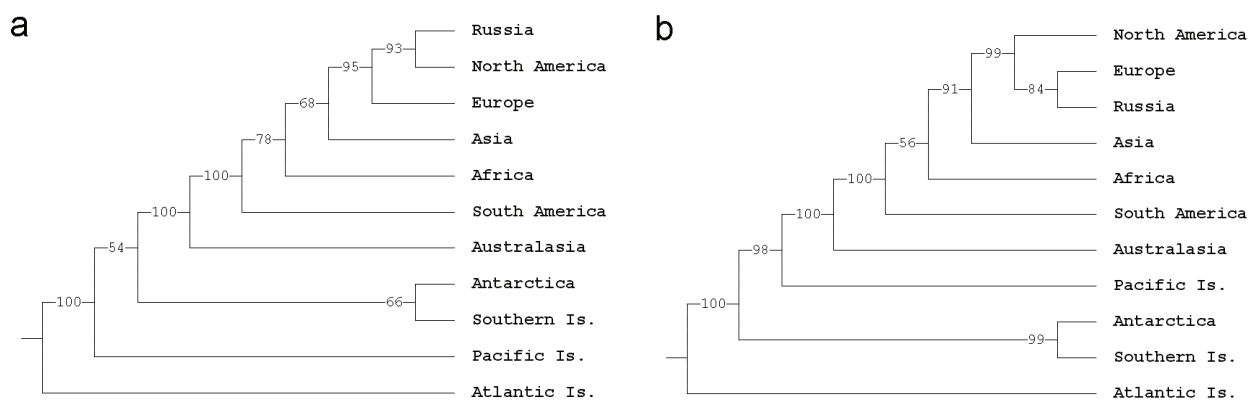
Species and generic data show very similar trends. Distinct 'Holarctic' clusters comprising Europe, Russia, North America (and Asia – genus only) is corroborated as being a relatively stable crown clade by all four PAE analyses. The robust Antarctic - Southern island cluster forms a stable basal regional outgroup along with the rather dissimilar faunas of the Pacific and Atlantic islands, while the other Gondwanan continents (Australasia, South America and Africa) form a series of intermediate regional clades.

### 4. DISCUSSION

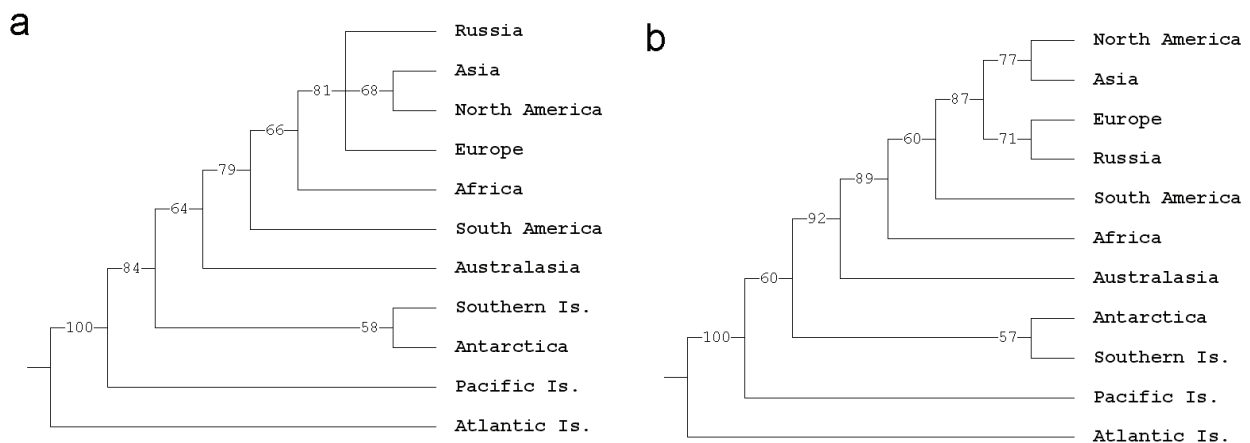
The robust Antarctic - Southern island regional clade results from a well studied regional fauna while sampling biased towards describing new, and hence largely endemic taxa has rendered the positions of the more temperate Atlantic and Pacific islands particularly 'fluid' but basal. This was verified by removing the 'island data' and re-running the analyses to yield consistent crown Holarctic - basal Antarctic regional cladogram topologies. Further evidence of sampling effort bias is evident in that our benchmark Eurasia (Europe, Russia and Asia) cluster was only apparent at the higher generic level and subsumed within a broader Holarctic fauna at species level. Even so there is clear topology congruence in both previous (McInnes & Pugh 1998) and current clustergrams, as well as regional cladograms.



**Fig. 3.** Cluster analysis of the limno-terrestrial tardigrade. **a:** Species. **b:** Genera.



**Fig. 4.** **a:** PAE regional cladogram of limno-terrestrial tardigrade species under Dollo parsimony (vicariance proxy) criteria. **b:** PAE regional cladogram of limno-terrestrial tardigrade species under Wagner parsimony (dispersal proxy) criteria. Numbers indicate percentage bootstrap consensus values of each regional clade.



**Fig. 5.** **a:** PAE regional cladogram of limno-terrestrial tardigrade genera under Dollo parsimony (vicariance proxy) criteria. **b:** PAE regional cladogram of limno-terrestrial tardigrade genera under Wagner parsimony (dispersal proxy) criteria. Numbers indicate percentage bootstrap consensus values of each regional clade.



**Tab. 1.** Endemism amongst tardigrades. # - Genera: 64 in total - excluded marine genus, but including incertae sedis.

		Europe	Russia	Africa	Asia	Indian Is.	Australasia	Pacific Is.	N. America	S. America	Atlantic Is.	Antarctica	Southern Is.
Species	Endemics	207	58	43	89	0	54	3	58	68	1	37	10
	Total	456	216	165	245	0	136	36	231	198	7	64	46
	Endemics (%)	45.4	26.9	26.1	36.3	0.0	39.7	8.4	25.1	34.3	14.3	57.8	21.7
Genera <sup>#</sup>	Endemics	4	0	1	1	0	2	0	2	1	0	0	0
	Total	47	38	31	36	0	28	14	42	36	3	18	16
	Endemics (%)	8.5	0.0	6.2	2.8	0.0	7.1	0.0	4.8	2.8	0.0	0.0	0.0

Our earlier work implied that the Antarctic - Gondwanan fauna was derived from Laurasian - Holarctic ancestors yet PAE supports an entirely contrary explanation; that is Laurasian - Holarctic tardigrades are derived from an Antarctic - Gondwanan stock. So which hypothesis is correct?

The two new phenetic analyses clearly support each other, as do their four cladistic counterparts. Indeed repeating the cluster analysis with alternative but valid cluster algorithms, such as Jaccard coefficient ( $S_j$ ) for species data and the simple matching coefficient ( $S_{SM}$ ) for more robust numerical generic data (Krebs 1989) merely corroborated the described clustergrams. Similarly replacing UPGMA clustering with single-linkage (= nearest neighbour) and complete linkage (= furthest neighbour) clustering also yielded virtually identical clustergram topologies. The cladistic data are equally robust. Removal of the species poor island groups does not alter overall regional cladogram topology which remains robust (especially at species level) if branches are collapsed to 80% bootstrap support.

There are pros and cons to both phenetic and cladistic biogeography (Rosen 1988; De Grave 2001; Brooks & van Veller 2003; Pugh 2004), and clearly this phenetic - cladistic impasse, if indeed it exists, must be resolved via an alternative approach. We could simply accept the PAE (derived Antarctic) scenario because, unlike cluster analysis, it implies direction from basal regional clade to more derived crown clade; that is 'ancient' to 'recently occupied' regions whereas cluster techniques do not. We originally proposed a Laurasia to Gondwana colonisation simply because it provided a 'better fit' with plate tectonics (McInnes & Pugh 1998).

Clustering and other phenetic techniques used to be regarded as spurious though more recent computer analysis of relatively large data sets suggest these are both useful and stable (Pugh 2004). PAE, on the other hand, has been criticised (Brooks & van Veller 2003), even damned (Morrone 2005), and this makes our analyses potentially problematic as this is both the first time that PAE has been (a) applied to a probably incomplete tardigrade database and (b) used to analyse a global distribution. The latter, and in particular the use of the Lundberg root, raises particular theoretical issues

(Rosen 1988) as it presumes the existence of a theoretical region 'outside the study area' where there are no taxa and thus the potential 'origin', which should form a basal regional outgroup to all identified regional clades. Clearly analysis of a global fauna precludes the existence of such a region, though Lundberg rooting was used here because it provided a purely mechanical, and reliable, outgroup which stabilised our regional cladograms.

PAE relies on 'shared endemism' and while Antarctica harbours only 64 species, most (58%) are endemic, yet each of the four Holarctic divisions supports much richer tardigrade faunas of 216 to 456 species but with more modest (25% to 45%) regional endemism (Tab. 1) and hence more numerous shared species thus forming a relatively stable series of crown regional clades. Endemic genera include: Europe: *Macroversum* (Muryidae), *Necopinatum* (Necopinatidae), *Carphania* (Carphaniidae), *Pseudohexapodibius* (Macrobiotidae); Africa: *Paradiphascon* (Hypsibiidae); Asia: *Famelobiotus* (Macrobiotidae); Australasia: *Milnesioides*, *Limmenius* (Milnesiidae); North America: *Haplohexapodibius* (Calohypsibiidae), *Proechiniscus* (Echiniscidae); South America: *Minilentus* (Macrobiotidae). Endemic genera are more equivocal but absent from Antarctica and the oceanic islands (Tab. 1) and the stable regional Holarctic clade results from numerous shared genera. There is further support for this derived crown clade in the distribution of the four regionally endemic families (Tab. 2) of which three (Eohypsibiidae and Necopinatidae: Eutardigrada and Carphaniidae: Heterotardigrada) are Laurasian but only one (Oreelliidae: Heterotardigrada) Gondwanan. If the Heterotardigrada is indeed older than the Eutardigrada (Kristensen 1987) then this would corroborate the PAE data with a basal Gondwanan fauna and a truly derived Laurasian regional crown clade.

It is possible to identify dispersal and non-dispersal (i.e. vicariant) elements by comparing complementary Dollo parsimony (vicariance-proxy) and Wagner parsimony (dispersal-proxy) regional cladograms (e.g. De Grave 2001). Yet our regional cladograms show similar topologies at a 50% and (not illustrated) a more robust 80% bootstrap consensus, which implies a dead end.

**Tab. 2.** Distribution of tardigrade families. \* = Endemic families; L = Laurasian; G = Gondwanan.

Family		Europe	Russia	Africa	Asia	Indian Is.	Australasia	Pacific Is.	N. America	S. America	Atlantic Is.	Antarctica	Southern Is.
Eutardigrada	Murrayidae	+	+	+	+		+	+	+	+		+	+
	Macrobiotidae	+	+	+	+		+	+	+		+	+	+
	Calohypsibiidae	+	+	+	+		+		+	+			+
	Microhypsibiidae	+	+	+	+		+	+	+	+			
	Eohypsibiidae*	L	L		L				L				
	Necopinatidae*	L											
	Hypsibiidae	+	+	+	+		+	+	+	+		+	+
	Milnesiidae	+	+	+	+		+	+	+	+		+	+
Heterotardigrada	Oreellidae*						G			G		G	
	Carphaniidae*	L											
	Echiniscidae	+	+	+	+		+	+	+	+	+	+	+
Total		10	8	7	8	0	8	6	8	8	2	7	6

But we could give precedence to the more stringent Dollo parsimony (Kluge & Farris 1969; Farris 1977; Felsenstein 2005), which invokes vicariance; that is global scale tectonic/ extinction, events.

The Miocene-Pleistocene global cooling - glaciation only ended 20,000 years ago and wiped out the majority of Arctic and Antarctic Tertiary palaeoendemic taxa (e.g. Liebherr & Schmidt 2004; Peck *et al.* 2006). Northern Hemisphere tardigrades could withdraw ahead of the glacial advance and subsequently recolonise high latitude terrain following glacial retreat (see Pugh & McInnes 1998) over a relatively 'broad front' accounting for the aforementioned shared species. But the fauna of 'island' Antarctica could not and so must be derived from a very different mechanism, either vicariant fragments of a truly pre-glacial relict fauna, post-glacial immigration across the Southern Ocean, or, a combination of both. The data are somewhat equivocal. Antarctica supports the highest proportion (37 spp. = 57.8%) of endemic species, including eight that are not yet fully taxonomically resolved. Most (31) of these endemic taxa belong to only eight common and widespread genera: *Macrobiotus*, *Minibiotus*, *Isohypsibius*, *Diphascus*, *Hebesuncus*, *Milnesium*, *Echiniscus* and *Pseudechiniscus*, and none to Antarctic endemic genera. This could, like co-occurring micro-arthropods, represent a fauna comprising disjunct relicts (Marshall & Pugh 1996; Pugh & Convey 2000) or, more likely, the products of post-glacial speciation (Stevens & Hogg 2003). Some tardigrades, unlike arachnids (Pugh & Convey 2000; Pugh 2004), have the potential for relatively long-range dispersal (Kristensen 1987; Pugh & McInnes 1998) so the Antarctic fauna could be both immigrant and very young. PAE simply interprets this paucity of shared taxa as being the result of ancient endemism rather than more recent (i.e. Quaternary glacial) extinction and recolonisation.

## 5. CONCLUSIONS

Our initial foray into the biogeography of limno-terrestrial tardigrades appeared unequivocal but was constrained by achieving a 'best fit' of clustergrams with global plate tectonics. This re-appraisal not only confirms the topology of the original clustergrams but also corroborates them at a higher (species) level. The key difference is that PAE constrains the clusters to a temporal sequence of from Antarctic - Gondwana to Holarctic - Laurasia. This 'colonisation' sequence may be an artefact resulting from much of the extant Antarctic fauna being derived from a combination of widespread (but not endemic) genera and major Quaternary extinction. These results, or rather their significance, need more careful scrutiny and verification, perhaps with new analytical tools, before we literally turn the tardigrade world on its head.

## ACKNOWLEDGEMENT

Jo Hill of Anglia Ruskin University for help with developing PAE methods.

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