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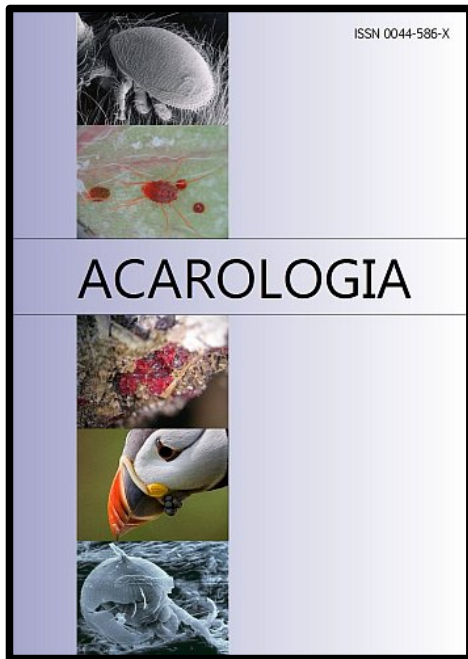
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The tropics as an ancient cradle of oribatid mite diversity

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ABSTRACT — Diversity of most animal and plant taxa increases towards the equator. The reasons for this pattern are manifold, but their relative importance is controversial. Understanding of the radiation of animal taxa is needed to uncover the mechanisms underlying latitudinal gradients in biodiversity. Species may have evolved more quickly in tropical regions, suggesting that the tropics function as cradle of diversity, or they may have survived in the tropics for longer periods of time as compared to higher latitude biomes, suggesting that the tropics function as a museum of diversity. We used oribatid mites as a model group to investigate if the high species number of this mainly soil-living taxon can be explained by the cradle or museum hypothesis. We analyzed oribatid mite communities in tropical and temperate forest ecosystems, sequenced 18S and part of the 28S rDNA of common species, and constructed phylogenetic trees using Bayesian Inference and Maximum Likelihood algorithms. Then, we mapped the distribution of species (tropical, temperate, cosmopolitan) onto the phylogenetic tree. Most tropical oribatid mite taxa formed terminal branches indicating that the high diversity of oribatid mites in tropical regions is due to recent radiation, supporting the hypothesis that the tropics function as a cradle of oribatid mite diversity. Further, the results suggest that most early-derivative oribatid mite taxa are cosmopolitan indicating that they evolved on a large ancient continent. Overall, our results support the view that oribatid mites are a very old taxon which radiated intensively in tropical regions, but their origin predates the existence of the tropical regions of today.

KEYWORDS — Acari; radiation; museum; Pangaea; Gondwana

INTRODUCTION

Species richness of many animal and plant taxa increases from temperate towards tropical regions; a phenomenon known as the latitudinal biodiversity gradient (LBG) (Rohde 1992, Roy *et al.* 1998, Willig *et al.* 2003, Hillebrand 2004, Arita & Vázquez-Domínguez 2008, Jablonski *et al.* 2013, Moreau & Bell 2013, Mannion *et al.* 2014, Rolland *et al.* 2015). Explanations for higher species diversity in the tropics as compared to high latitude biomes include biotic and abiotic factors, as niches are smaller in mature communities and climate fluc-

tuations are less pronounced. Additionally, area size may contribute to the higher species richness in the tropics as the area of tropical regions exceeds e.g., that of temperate regions (Chown & Gaston 2000). Moreover, the tropics were not glaciated during the Pleistocene, allowing more continuous radiation in low latitude biomes. Three models focus on the importance of evolutionary time for the high species diversity in tropical regions. The "cradle model" proposes higher speciation rate for tropical regions (Stebbins 1974, Stenseth 1984, Mittelbach *et al.* 2007). In contrast, the "museum model"

assumes lower extinction rates in tropical than in other regions (Stebbins 1974). The "out of the tropics model" combines these two models by postulating higher speciation rates and lower extinction rates in the tropics, with species mainly originating in the tropics and spreading to high latitude regions (Jablonski 1993; Jablonski *et al.* 2006). The LBG is well investigated in birds, reptiles, frogs, freshwater fish, termites, ants, beetles and trees (Rohde 1992, Hillebrand 2004, Abensperg-Traun & Steven 1997; Wiens *et al.* 2006). Species with contrasting diversity patterns (*i.e.*, taxa with more species in high latitude regions) such as penguins, seals and sea lions (Proches 2001) typically only occur in cold climates. However, the LBG has been little studied in below-ground living animal taxa.

Oribatid mites (Acari, Oribatida) are species-rich, highly abundant microarthropods that occur in soils and decomposing organic matter all over the world. About 10,000 species are described (Subías 2004) but more than 100,000 may exist (Walter & Proctor 2013). Oribatid mites are divided into six major phylogenetic groups (Palaeosomata, Enarthronota, Parhyposomata, Mixonomata, Desmonomata, Brachypylyna) (Subías 2004, Norton & Behan-Pelletier 2009), each including cosmopolitan, tropical and temperate species. Patterns of oribatid mite species diversity only in part match the LBG as species diversity increases from boreal to temperate regions but then little further towards tropical regions (Maraun *et al.* 2007).

Generally, oribatid mites are an ancient taxon with the first generally accepted fossil documented from the Devonian (Norton *et al.* 1988, Subías & Arillo 2002), but their origin may date back to Cambrian or even Precambrian times (Schaefer *et al.* 2010) when the Earth climate was at least episodically cold as indicated by the magnitude of sea level changes (Miller *et al.* 2005, Runkel *et al.* 2010). Due to the ancient age of the group the region where they radiated cannot be delineated easily and ascribed *e.g.*, to tropical or temperate regions, as they were relocated due to continental drift (Hammer & Wallwork 1979). The long-term evolution of oribatid mites potentially facilitated parallel radiations in different climatic regions and continents and thereby convergent evolution of traits (Pachl *et*

al. 2012).

Investigating global distribution patterns in a phylogenetic context is likely to improve understanding of factors that shaped the evolution and radiation of oribatid mites. We constructed a molecular phylogeny of oribatid mites based on two ribosomal markers (partial 18S and 28S rDNA). We used species from each of the main taxonomic groups of oribatid mites and included 28 tropical, 26 temperate and 22 cosmopolitan species. Subsequently, we mapped the current biogeographical distribution of the respective species on the phylogenetic tree and reconstructed the ancestral biogeographic distribution to evaluate which region (temperate, tropical) is the ancestral one. According to the 'museum hypothesis', tropical species should be phylogenetically early-derived with basal position in the phylogenetic tree. In contrast, a scattered and derived distribution of tropical species would support the 'cradle hypothesis'. We hypothesized that tropical regions are regions where oribatid mite speciation took place early in evolution, which would support the "tropics as museum" hypothesis.

MATERIALS AND METHODS

Taxon sampling

In total, 76 oribatid mite taxa from the six major groups and two outgroup taxa (Parasitiformes) were included in this study. In total 69 oribatid mites were identified at species level and seven at genus level. Species were collected from tropical montane rain forests in southern Ecuador (Illig *et al.* 2010), from temperate forests in central Germany (Erdmann *et al.* 2012), from the United States of America (obtained from Roy A. Norton, Syracuse, USA) and from a number of sites all over the world (Table 1). Some sequences were available from NCBI, but most were generated for this study. Animals were extracted by heat (Kempson *et al.* 1963) and determined using Balogh & Balogh (1988, 1990, 2002) and Weigmann (2006). The 18S and 28S rDNA sequences of outgroup taxa (*Amblyomma sphenodonti*, Ixodidae, and *Opilioacarus (Neocarurus) texanus*, Opilioacaridae) were taken from the NCBI databank.

Species were assigned to taxonomic groups according to the classification of Norton & Behan-Pelletier (2009). Distribution patterns (*i.e.*, cosmopolitan, tropical and temperate) of species were taken from Subías (2004). Cosmopolitan distribution refers to taxa that occur in both temperate and tropical regions, rather than to those with global distribution. Tropical oribatid mites were collected in the Neotropic (Ecuador) but many also occur in the Palaeotropic. Similarly, the temperate species were mostly collected in the Palaearctic but many of them also occur in the Nearctic. Therefore, the taxon sampling was taken to represent high and low latitude species of oribatid mites.

DNA extraction and PCR

Genomic DNA was extracted from single individuals using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) with silica membrane columns and protease K from Genaxxon (Genaxxon BioScience, Ulm, Germany). Amplification of target genes was performed in 25 µl volume. Primers for 18S rDNA were 5'-TACCTGGTTGATCCTGCCAG-3' (18Sforward) and 5'-AATGATCCTTCCGCAGGTTAC-3' (18Sreverse) (Domes *et al.* 2007a). Primers for the D3-D5 region of 28S rDNA were 5'-GACCCGTCTTGAAGCACG-3' (28Sa) and 5'-CCCACAGCGCCAGTTCTGCTTACC-3' (28Sbout) (Tully *et al.* 2006). The 18S fragment was amplified at 57°C; the 28S fragment was amplified at 49°C using standard PCR protocols. PCR products were sequenced at Göttingen Genomics Laboratory (Institute of Microbiology and Genetics, Georg August University Göttingen, Germany), using the additional sequencing primers 18S554f 5'-AAGTCTGGTGCCAGCAGCCGC-3', 18S1282r 5'-TCACTCCACCAACTAAGAACGGC-3', 18S1150f 5'-ATTGACGGAAGGGCACCACCAG-3' and 18S614r 5'-TCCAACACTACGAGCTTTTAAACC-3' (Domes *et al.* 2007a). For some species, PCR amplification of 18S rDNA was difficult and several shorter fragments were amplified using the above-mentioned primers and s6mod (Nikolaev *et al.* 2005) (modified for this study), 18S476fn (designed for this study) and

Euk516f (Lara *et al.* 2008) in the combinations 18Sforward (5'-TACCTGGTTGATCCTGCCAG-3') and 18S614r, 18S554f and 18S1282r, s6mod (5'-CCGCGGTAATTCAGCTC-3') and 18S1282r, 18S476fn (5'-GAGGTAGTGACGAAAATAACAA TACAGG-3') and 18S1282r, Euk516f (5'-GGAGGGCAAGTCTGGT-3') and 18S1282r, 18S1150f and 18Sreverse (5'-TAATGATCCTTCCGC AGGTTAC-3'). Sequences KR081601-KR081690 were generated for this study; all other sequences were obtained from NCBI.

Sequence alignment and phylogenetic analysis

Phylogenetic analysis was based on a supermatrix of the ribosomal genes 18S rDNA (1,599–2,007 bp) and partial 28S rDNA (289–350 bp). Sequences were assembled in Sequencher 5.1 (Gene Codes Corporation, Ann Arbor, Michigan, USA); ambiguous positions were corrected using the chromatograms. Two preliminary alignments were generated in ClustalX v1.8 (Thompson *et al.* 1994) using default parameters for the 18S and the 28S rDNA sequences. Sequences of the alignments were cut to the shortest sequence downloaded from NCBI. Trimmed alignments of both genes were concatenated in a single data set and a new alignment was calculated using the multiple alignment parameters gap opening 20 and gap extension 0.1. To compensate for possible long-branch attraction, a NJ tree was calculated in SeaView v4.2.3 (Gouy *et al.* 2010) and used as guide tree for a new alignment in ClustalX with the same parameters. The final alignment had a length of 2,412 bp, consisting of 2,077 bp 18S and 335 bp 28S rDNA.

The model of sequence evolution was estimated in PartitionFinder v 1.1.1. (Lanfear *et al.* 2012). Phylogenetic trees were constructed using Bayesian Inference in MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) using JK as well as GTR+I+G and Maximum Likelihood in RAxML 7.0.4 (Stamatakis 2006) GTR+I+G. MrBayes was run for 5 million generations, reaching convergence with a standard deviation of split frequencies of 0.013630 (GTR + I + G) and 0.005798 (JK). RAxML was run with 1,000 bootstraps.

TABLE 1: Species names, phylogenetic affiliation, present day distribution, and GenBank accession numbers of oribatid mite taxa and outgroups (*Amblyomma sphenodonti*, *Opilioacarus texanus*). The distribution coded for Mesquite was done on the basis of the highest available taxonomic resolution (usually species level; otherwise genus level); sequences KR081601-KR081690 were generated for this study, all other sequences were obtained from NCBI.

species/genus	Phylogenetic affiliation (after Norton & Behan-Pelletier 2009)	Distribution of the genus (after Subias 2014)	Distribution of the species (after Subias 2014)	Distribution (coded for MESQUITE)	GenBank accession nrs. 185	GenBank accession nrs. 285	Sampling location
<i>Licarus coracinus</i> (Koch, 1841)	Gustavioidae	Holarctic, Palaearctic	Palaearctic	Temperate	KR081619	KR081663	Germany
<i>Leibsdada humerata</i> Sellnick, 1928	Oripodoidea	Semioscopolitan	Holarctic, Oriental	Cosmopolitan	KR081620	KR081664	Germany
<i>Lohmannia banksi</i> (Norton et al., 1978)	Lohmannioidae	Cosmopolitan	USA	Temperate	AF022036	AY273497	USA
<i>Malaconoglia ranigera</i> Bertese, 1913	Hypochthonioidae	Pantropical, Subtropical	Pantropical, Subtropical	Tropical	JN585911	KR081665	Thailand
<i>Malaconoglia monodactylus</i> (Michael, 1888)	Crotonioidae	Cosmopolitan	Holarctic, Neotropical	Cosmopolitan	KR081621	KR081666	USA
<i>Mesoplophorida</i> Niedbala, 1988	Mesoplophoridae	Cosmopolitan	USA	Temperate	JN585912	KR081667	USA
<i>Microtegeus similis</i> Balogh & Mahunka 1980	Cepheoidea	Pantropical	Neotropical	Tropical	KR081622	KR081668	Ecuador
<i>Mitacarus brevipalps</i> (Banks, 1947)	Lohmannioidae	Cosmopolitan	USA, Costa Rica	Temperate	JN585913	KR081669	Ecuador
<i>Nanhermannia elegantissima</i> Hammer, 1958	Nanhermannioidae	Cosmopolitan	Neotropical	Tropical	KR081623	KR081670	Ecuador
<i>Nanhermannia nana</i> (Nicolet, 1855)	Nanhermannioidae	Cosmopolitan	Semioscopolitan	Cosmopolitan	KR081624	KR081671	Germany
<i>Nesiacarus granulatus</i> Hammer, 1972	Nehyphochthonioidae	Holarctic, Oriental, Australia	USA, Vietnam, Hawaii	Cosmopolitan	AF022038	AY273490	USA
<i>Nehyphochthonius porosus</i> Norton & Metz, 1980	Nehyphochthonioidae	Pantropical, Subtropical	Polynesia, Japan, Neotropical	Tropical	JN585914	KR081672	USA
<i>Nothrus vulliamii</i> Mahunka, 1983	Crotonioidae	Cosmopolitan	Neotropical	Tropical	KR081625	KR081673	Ecuador
<i>Nothrus silesstris</i> (Nicolet, 1855)	Crotonioidae	Cosmopolitan	Holarctic, Nepal, New Zealand	Temperate	EF091425	KR081674	Germany
<i>Opilioacarus (Neocarus) jezanus</i> (Chamberlin & Mulak, 1942)	Opilioacaridae (outgroup)	Cosmopolitan		Cosmopolitan	AF115375	AY626627	USA
<i>Opipella nova</i> (Oudemans, 1902)	Oripodoidea	Cosmopolitan	Cosmopolitan	Cosmopolitan	KR081626	KR081675	Germany
<i>Oribatula tibialis</i> (Nicolet, 1855)	Oripodoidea	Cosmopolitan	Holarctic	Temperate	EU439990	AY273527	Germany
<i>Palaeacarus hystrixinus</i> (Trägårdh, 1932)	Palaeacaroidae	Holarctic, Oriental	Holarctic	Temperate	EF204472	DQ090827	USA
<i>Parabellatella meridiana</i> (Norton, 1979)	Damaoidea	Holarctic, Neotropical	Chile	Temperate	KR081627	KR081676	Ecuador
<i>Parhyphochthonius aphidinus</i> Bertese, 1904	Parhyphochthonioidae	Cosmopolitan	Semioscopolitan	Cosmopolitan	EU432215	AY273493	USA
<i>Perlohmannia</i> sp. Bertese, 1916	Perlohmannioidae	Holarctica, Australia		Temperate	EU432212	KR081677	USA
<i>Pheroloides</i> sp. Grandjean, 1931	Pheroloidae	Pantropical		Tropical	KR081628	KR081678	Ecuador
<i>Phthiracarus sp. Perty, 1841</i>	Phthiracaroidae	Cosmopolitan		Cosmopolitan	KR081629	KR081679	Germany
<i>Phthiracarus castaneus</i> (Hammer, 1961)	Crotonioidae	Cosmopolitan	Neotropical	Tropical	KR081630	KR081680	Ecuador
<i>Platynothrus pelifer</i> (Koch, 1839)	Crotonioidae	Cosmopolitan	Semioscopolitan	Cosmopolitan	EF091422	KR081681	Germany
<i>Platynothrus neotropicus</i> Ermilov et al., 2013	Otocephaloidea	Subtropical, Neotropical, Oriental	Ecuador	Tropical	KR081631	KR081682	Ecuador
<i>Prochthonius angulus</i> (Bertese, 1910)	Atopochthonioidae	Holarctic, Australia, Oriental	Holarctic, Oriental	Cosmopolitan	EU432214	DQ090828	USA
<i>Rhynchobates mirus</i> Beck, 1961	Trizetoidae	Pantropical	Peru	Tropical	KR081632	KR081683	Ecuador
<i>Rhysotritia duplicata</i> (Grandjean, 1953)	Euphthiracaroidae	Cosmopolitan	Palaearctic	Cosmopolitan	EF091417	AY273491	Germany
<i>Rostratus nebulosus</i> Beck, 1965	Oripodoidea	Cosmopolitan	Neotropical	Tropical	KR081633	KR081684	Ecuador
<i>Solenozetes carinus</i> (Hammer, 1961)	Hermannelloidea	Pantropical	Neotropical	Tropical	KR081634	KR081685	Ecuador
<i>Stegacarus magnus</i> (Nicolet, 1855)	Phthiracaroidae	Cosmopolitan	Holarctic	Cosmopolitan	AF022040	KR081686	England (185) / Germany (285)
<i>Stomacarus liganififer</i> (Hammer, 1967)	Acaronychoidea	Australia, Subtropical	New Zealand	Temperate	EU433992	DQ090826	New Zealand
<i>Tectonacarus incompletus</i> Mahunka, 1988	Eremelloidea	Tropical, Palaearctic	Borneo	Tropical	KR081635	KR081687	Ecuador
<i>Tectonacarus sardensis</i> Trägårdh, 1910	Tectocephaloidea	Cosmopolitan	Cosmopolitan	Cosmopolitan	EF093776	KR081688	Germany
<i>Triphychthonius americanus</i> (Ewing, 1909)	Crotonioidae	Cosmopolitan	USA	Temperate	IQ000046	IQ000354	USA
<i>Unguizetes inertus</i> (Balogh & Mahunka, 1969)	Oripodoidea	Pantropical, Subtropical	Neotropical	Tropical	KR081636	KR081689	Ecuador
<i>Xanillus legovanus</i> (Hermann, 1804)	Gustavioidae	Holarctic, Oriental, Neotropical	Palaearctic	Temperate	KR081637	KR081690	Germany

TABLE 1: Continued.

species/genus	Phylogenetic affiliation (after Norton & Behan- Pelleter 2009)	Distribution of the genus (after Subias 2014)	Distribution of the species (after Subias 2014)	Distribution (coded for MESQUITE)	GenBank accession nrs. 185	GenBank accession nrs. 285	Sampling location
<i>Achipteria coleoptrata</i> (Linaeus, 1758)	Achipterioidea	Semioscopollitan	Holarctic	Temperate	EF091418	AY273500	Germany
<i>Amphimma spekeoides</i> Dumbleton, 1943	Isodidae (outgroup)			Cosmopolitan	DQ507238	JN86726	New Zealand
<i>Ampulabates ecuadoriensis</i> Ermilov et al., 2013	Hermannelloidea	Neotropical	Ecuador	Tropical	KR081601	IQ000356	Ecuador
<i>Anachipteria</i> sp. Grandjean, 1922	Achipterioidea	Holarctic, Oriental, Neotropical		Cosmopolitan	IQ00048	IQ000356	USA
<i>Archegozetes longistosis</i> (Aoki, 1965)	Mesoplophoroidea	Australia, Oriental		Tropical	JN585917	KR081639	Thailand
<i>Archoplophora rosstralis</i> (Willmann, 1930)	Crotonioidea	Pantropical	Pantropical	Tropical	FG661379	AY273529	Germany (culture)
<i>Atropacarus striculus</i> (Koch, 1835)	Mesoplophoroidea	Semioscopollitan	Holarctic, Oriental, Neotropical	Cosmopolitan	JN585918	DQ90830	USA
<i>Beckia capitulum</i> Balogh & Mahunka, 1978	Phthiraceroidea	Cosmopolitan	Semioscopollitan	Cosmopolitan	EF091416	KR081640	Germany
<i>Camisia segnis</i> (Hermann, 1804)	Otocephaloidea	Tropical	Cuba	Tropical	KR081602	KR081641	Ecuador
<i>Camisia spinifer</i> (C.L. Koch, 1835)	Crotonioidea	Cosmopolitan	Semioscopollitan	Cosmopolitan	EU432209	IQ000351	Germany (18S) /Russia (28S)
<i>Campachipteria brevisetosa</i> Ermilov et al., 2013	Crotonioidea	Cosmopolitan	Semioscopollitan	Cosmopolitan	EF091420	AF515422	USA
<i>Carabodes subarcticus</i> Trägårdh, 1902	Achipterioidea	Holarctic, Oriental, Neotropical	Ecuador	Tropical	KR081603	KR081642	Ecuador
<i>Chamobates voigsi</i> (Oudemans, 1902)	Carabodoidea	Semioscopollitan	Palaearctic	Temperate	EF091429	KR081643	Sweden
<i>Collobmannia elegantia</i> Sellnick, 1922	Ceratozetidae	Palaearctic, Holarctic, Palearctic	Palaearctic	Temperate	EU432189	KR081644	Germany
<i>Cosmochthonius inatus</i> (Michael, 1885)	Perlohmannioidea	Palaearctic	Palaearctic	Temperate	KR081604	KR081645	Austria
<i>Crotobia reticulata</i> Luxton, 1982	Cosmochthonioidea	Cosmopolitan	Cosmopolitan	Cosmopolitan	JN585919	IQ000348	USA
<i>Ctenacarus aranea</i> Grandjean, 1932	Crotonioidea	Cosmopolitan	New Zealand	Temperate	KR081605	KR081646	New Zealand
<i>Cythermannia florens</i> Balogh & Mahunka, 1980	Palaecaroidea	Pantropical, Subtropical	Pantropical, Subtropical	Tropical	EU432991	IQ000341	USA
<i>Danaeus (Paradanaeus) danops</i> (Hermann, 1804)	Nanhermannioidea	Pantropical, Subtropical	Neotropical	Tropical	KR081606	KR081647	Ecuador
<i>Danaeus (Epidanaeus) flagellatus</i> (Norton, 1979)	Damaoidea	Palaearctic	Palaearctic	Temperate	KR081607	KR081648	Germany
<i>Danaeus (Paradanaeus) danops</i> (Hermann, 1804)	Damaoidea	Cosmopolitan	Chile	Temperate	KR081608	KR081649	Ecuador
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Cosmopolitan	Cosmopolitan	KR081609	KR081650	Germany
<i>Etiobothrius gracilis</i> (Jacot, 1936)	Hypochthonioidea	Cosmopolitan	Pantropical, Subtropical	Tropical	EF203777	IQ000344	USA
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Neotropical	Tropical	KR081610	KR081651	Ecuador
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Neotropical	Cosmopolitan	EU432213	KR081652	Canada
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Holarctic, Oriental	Temperate	EU432211	KR081653	USA
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Holarctic	Temperate	EF091419	AY273523	Germany
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Holarctic, Neotropical	Tropical	KR081611	KR081654	Ecuador
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Australia, Neotropical, Antarctic	Temperate	EF081297	DQ90816	New Zealand
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Neotropical	Temperate	EU432994	IQ000350	USA
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Neotropical	Temperate	KR081612	KR081655	Ecuador
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Neotropical	Tropical	KR081613	KR081656	Ecuador
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Neotropical	Temperate	EU432993	KR081657	USA
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Neotropical	Temperate	KR081614	KR081658	Germany
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Holarctic	Tropical	KR081615	KR081659	Ecuador
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Semioscopollitan	Cosmopolitan	EU675634	IQ000347	USA
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Neotropical	Tropical	KR081616	KR081660	Ecuador
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Holarctic	Temperate	EF091426	AY273530	Germany
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Neotropical	Tropical	KR081617	KR081661	Ecuador
<i>Etiobothrius minutissimus</i> (Berlese, 1904)	Hypochthonioidea	Cosmopolitan	Semioscopollitan	Cosmopolitan	KR081618	KR081662	USA

Reconstruction of ancient biogeographic distribution

We used Mesquite 3.10 (Maddison & Maddison 2016) to map present day biogeographic distribution (temperate, tropical and cosmopolitan) as a character on the phylogenetic tree. Character history was traced using parsimony and likelihood to infer ancient distribution patterns. The Bayesian Inference tree (JK) provided the topology and the present day distribution of investigated species was coded as tropical, temperate or cosmopolitan. We also used the distribution extinction cladogenesis (DEC) biogeographical model (Ree & Smith 2008) for ancestral area reconstruction (implemented in BioGeoBEARS in R; Matzke 2014; R Core Team, 2014). The likelihood analysis in Mesquite (data not shown) and the DEC analysis (Fig. S3) showed a weaker resolution than the parsimony analysis; probably since we did not sample enough taxa covering the distribution of oribatid mites all over the world.

RESULTS

Tree topology

Topologies of the BI (JK; GTR + I + G) and ML trees were very similar (Fig. 1; Figs. S1; S2 in Electronic Appendix). Differences were restricted to the resolution of the backbone and node support of early-derived Enarthronota, Palaeosomata and Parhyposomata. Generally, the three trees did not contradict each other, but the ML tree had dichotomous splits with low bootstrap support (< 20) while the BI tree (GTR + I + G) had polytomies, especially in early-derivative groups (Fig. S1 in Electronic Appendix), whereas the BI tree (JK) was fully resolved with high support.

Tree topologies generally were conform to previously published phylogenies (Norton *et al.* 1993, Pachl *et al.* 2012). Brachypylina were most derived, Desmonomata and Mixonomata were intermediate and paraphyletic, and early-derivative oribatid mites (Enarthronota, Parhyposomata,

Palaeosomata) were at the basis of the tree. Ameroidea, represented by three taxa, was not resolved as a monophyletic group, as one taxon (*Haplobelba* sp.) clustered together with Ceratozetidae, Phenopelopoidea and Oripodoidea. Among middle-derived oribatid mites (Desmonomata, Mixonomata), taxonomic groups were well resolved except for *Collohmanna gigantea* and *Eulohmannia ribagai*, two Mixonomata placed within Desmonomata, and among early-derivative oribatid mites (Enarthronota, Palaeosomata, Parhyposomata) only Palaeosomata formed a monophyletic group. Enarthronota formed two monophyletic clades, and one paraphyletic cluster comprising other Enarthronota, Mixonomata and Parhyposomata.

Biogeographic distribution patterns of taxa in the phylogenetic tree

In the following we present the findings of the parsimony analysis in Mesquite (Fig. 2). Palaeosomata were represented by two temperate and one tropical species. The ancestral state for this group was temperate with one derived tropical taxon. Enarthronota formed one large cluster, including three cosmopolitan, four tropical and three temperate species. The ancestral state was cosmopolitan with derived tropical taxa in the Mesoplophoridae. Hypochthoniidae and Lohmanniidae formed a tropical group with temperate and cosmopolitan offshoots. The other Enarthronota clustered together with *Eulohmannia ribagai* (Mixonomata) and two Parhyposomata; taxa which proved problematic to resolve in previous studies (Pachl *et al.* 2012).

Mixonomata formed a large cosmopolitan clade. The three temperate members of this group were located on separate branches of the tree. In Desmonomata, the ancestral state of Nothridae was temperate with one derived tropical species. The ancestral state of Camisiidae was cosmopolitan; that of Trhypochthoniidae was temperate. Nanhermannioidea contained two tropical and one cosmopolitan species with a cosmopolitan ancestral state.

Brachypylina were the sister group to Trhypochthoniidae and *Collohmanna* sp., and their ancestral state was equivocal with an early-derived tropical taxon, Hermannielloidea. Ancestral state of derived Brachypylina (e.g., Achipteroidea, Oripodoidea) was tropical. Compared to early-derivative oribatid mites, Brachypylina had a reversed pattern with many tropical taxa and isolated, derived temperate or cosmopolitan offshoots. This pattern was prevalent in Hermannielloidea, Gymnodamaeidea, Oppioidea and Carabodoidea. However, Damaeidea and Gustavoidea within Brachypylina were temperate (Fig. 2).

DISCUSSION

Cradle or museum?

Animal and plant diversity generally increases from polar to tropical regions. This pattern is also true for soil animals, e.g. oribatid mites, though less pronounced than in plants and aboveground invertebrates (Maraun *et al.* 2007, Decaens 2010). Using oribatid mites as a model taxon, we investigated if the tropics predominantly functioned as cradle or museum for soil animal species. We hypothesized that oribatid mites from the tropics are old and experienced less climatic change than those from biomes at higher latitudes, thereby functioning as museum of diversity. The results suggest that this hypothesis has to be rejected. As indicated by molecular phylogeny of temperate and tropical oribatid mite species tropical taxa more intensively diversified in 'recent' times (*i.e.* ~ 250 mya, million years ago) as compared to temperate taxa (which evolved in Cambrian or even Precambrian times; Schaefer *et al.* 2010). This was especially true for the derived Brachypylina, supporting the view that radiation in the tropics surpasses that in temperate regions, and suggesting that the tropics function as cradle of oribatid mite diversity.

For understanding why the tropics function as cradle rather than museum of oribatid mite diversity the time scale of the radiations needs to be considered. Oribatid mites are an evolutionary very old group. Fossils are known from the Devonian

(Norton *et al.* 1988), and trace fossils have been recovered from the Carboniferous (Labandeira *et al.* 1997); however, molecular clock estimations place the origin of oribatid mites into Cambrian or even Precambrian times (Schaefer *et al.* 2010). Therefore, early-derived lineages of oribatid mites experienced an exceptionally wide range of environmental conditions including those during the major mass extinction events. Further, irrespective of where they originated they were exposed to massive environmental changes due to plate tectonics. Certainly, a great number of lineages went extinct; however, a number of present day lineages must have survived all these changes.

Food relationships of early- and middle-derived taxa (Enarthronota, Desmonomata) indicates that ancient lineages of oribatid mites lived as decomposers or fungal feeders, contrasting the derived Brachypylina which include many species feeding on lichens and algae, and also predatory species (Maraun *et al.* 2011). Feeding on dead organic matter and association with thick organic layers is typical for oribatid mites of temperate and boreal regions where they reach maximum densities (Maraun & Scheu 2000). In contrast, in the tropics the density of oribatid mites is much lower than in high latitude forests suggesting that they suffer from fast decomposition of organic matter (Illig *et al.* 2010). High density of oribatid mites at high latitudes likely contributed to the survival of ancient lineages in temperate and boreal regions as the risk of extinction declines with population density, and the opposite likely is true for tropical regions. Present day occurrence of species of virtually all old lineages of oribatid mites in temperate biomes suggests that they survived in high latitude biomes and evolved there as detritivore animals. Many of the present day species of old lineages occurring in the tropics therefore may actually have colonized the tropics from high latitude biomes and thereby potentially widened their trophic niche.

Results of the present study suggest that the most diverse and derived lineage of oribatid mites, the Brachypylina, evolved in tropical regions. According to molecular clock dating this radiation started about 300 mya (Schaefer *et al.* 2010). This

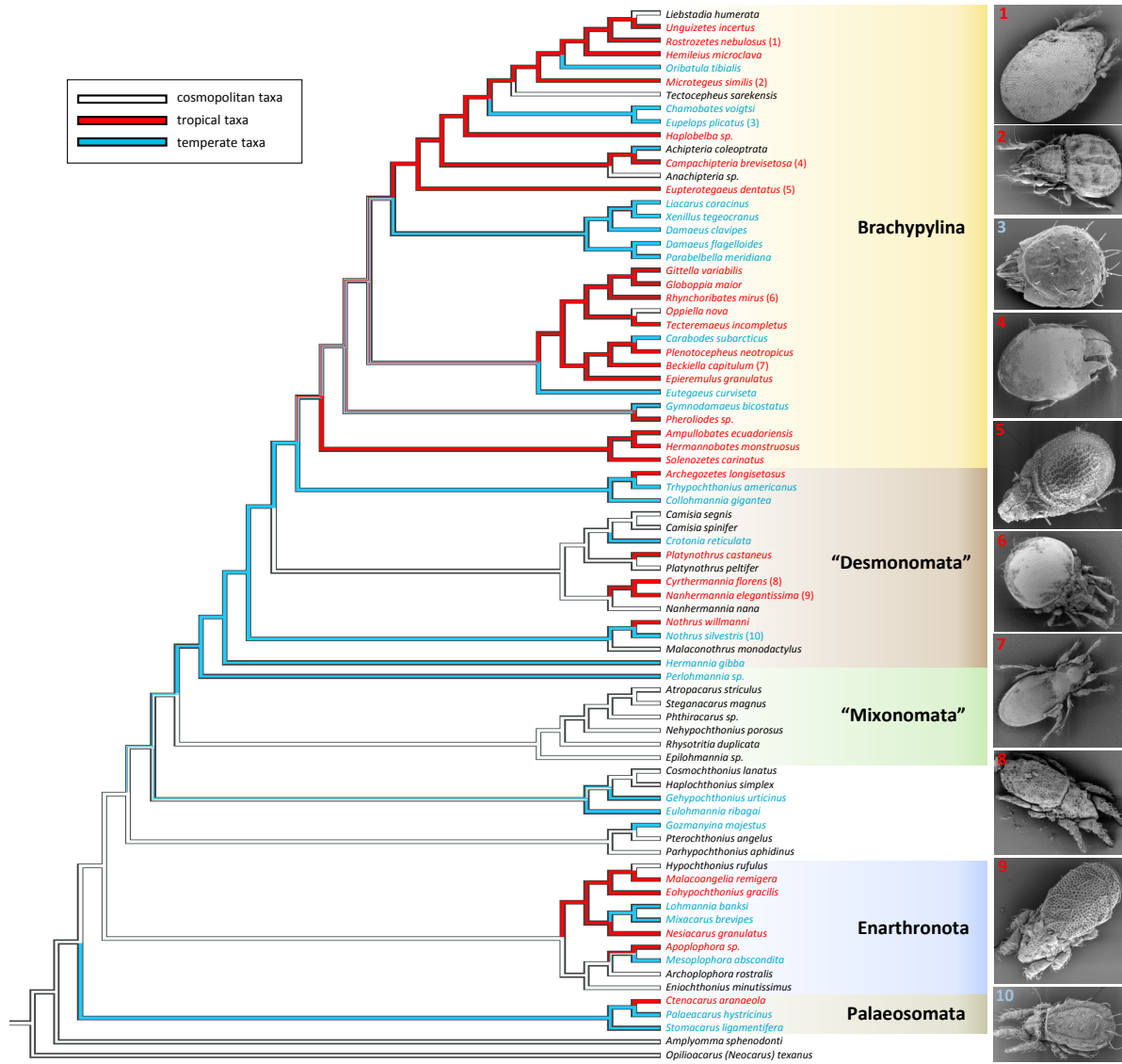


FIGURE 2: Ancestral biogeographic reconstruction of tropical, temperate and cosmopolitan occurrence of oribatid mites as reconstructed with ancestral character state mapping in Mesquite 3.10 using parsimony algorithms. See text for details. The tree is based on the BI phylogeny of the 18S rRNA and partial 28S rDNA (see Fig. 1).

suggests that radiation started on the super continent Pangea where oribatid mites were exposed mainly to tropical climate (Retallack & German-Heins 1994). Therefore, tropical regions of Pangea may be viewed as the 'cradle' of diversity of Brachypylina. In fact, as documented by our analysis and proposed earlier (Maraun *et al.* 2008, de Moraes *et al.* 2011, Mumladze *et al.* 2015), Brachypylina dominate oribatid mite communities of extant tropical and subtropical regions. Compared to other taxa for which the tropics function as cradle of diversity, such as beetles (McKenna & Farrell 2006), the radiation of tropical oribatid mite species is much older and the tropics therefore may be viewed as an 'ancient cradle' of Brachypylina.

Our conclusion that early-derived lineages of oribatid mites evolved at conditions resembling those of temperate and boreal regions is supported by the fact that at times of their radiation tropical forests did not exist. Oribatid mites presumably evolved in the Cambrian or earlier (Schaefer *et al.* 2010), and warm forest-like vegetation resembling tropical forests of today only started to evolve about 360 mya. The evolution of tropical swamp forests, which covered Pangea around 300 mya (Retallack & German-Heins 1994), may then have triggered the radiation of tropical oribatid mites. Notably, early radiation of oribatid mite lineages in the Cambrian or earlier coincides with cold conditions after warming of snowball earth (Kirschvink 1992) suggesting that early-derived oribatid mite lineages in fact evolved at cold climatic conditions matching the fact that they flourish today in high latitude biomes.

Origin of oribatid mites

Results of our study suggest that many of the early-derivative oribatid mite taxa currently have a cosmopolitan distribution. Similarly, Hammer & Wallwork (1979) suggested a cosmopolitan distribution of early- and middle-derived oribatid mite species supporting the view that oribatid mites are an old taxon that evolved prior to the split up of the today continents. In Cambrian times or earlier, oribatid mite species that colonized land likely were confronted with nutrient-poor habitats but, similar

to today, they may have fed on organic material and fungi (Schaefer *et al.* 2010). Many oribatid mite species of those ancient taxa, such as Palaeosomata and Enarthronota, today still live as generalists in habitats such as sandy soils where they mainly consume fungi (Lehmitz & Maraun 2016). This narrow niche may have hampered radiation of these taxa indicating that resource-poor sandy soils act as a 'museum' for early-derivative oribatid mites.

The pattern that recently evolved oribatid mites such as Brachypylina dominate in the tropics, whereas more ancient taxa, such as Enarthronota, Desmonomata and Mixonomata flourish in high latitude forests is not without exceptions. A number of Brachypylina species occur in temperate forests (e.g., in our study *Eupelops plicatus*, *Xenillus tegeocranus*, *Gymnodamaeus bicostatus*) and many middle-derived oribatid mite taxa, such as *Crotonia reticulata*, *Nanhermannia elegantissima* and *Lohmannia banksi*, occur in tropical regions. These exceptions complicate general conclusions on the biogeographic origin of oribatid mites. However, they may be explained by ecological factors; e.g., *Crotonia* and *Nanhermannia* predominantly occur in microsites in the tropics, i.e. on the bark of trees (*Crotonia*) (Domes *et al.* 2007b) or at high altitude (*Nanhermannia*) (Maraun *et al.* 2013), resembling habitats of high latitude forests. Similarly, Brachypylina species of temperate forests, such as *Eupelops plicatus* and *Gymnodamaeus bicostatus*, also predominantly colonize trees (rather than soil). In fact, there is increasing evidence that at least in high latitude forests the bark of trees forms a unique habitat for oribatid mites with little overlap to species in soil (Skubała & Marzec 2013, Bluhm *et al.* 2015).

Limitations, conclusions and perspectives of this study

This study aimed at improving the understanding of processes responsible for the current diversity and distribution of oribatid mites. Oribatid mites are highly diverse and the taxon sampling of our study necessarily is limited. Therefore, the biogeographic inferences made in this paper need further proof based on a wider taxon sampling including species from other biogeographic regions.

Overall, oribatid mites likely originated in Cambrian or Precambrian times on a large ancient landmass as indicated by their present day cosmopolitan distribution. Those species probably were mainly decomposers and fungal feeders (as many of them still are today) adapted to cold climatic conditions. Parallel to the origin of tropical ecosystems around 300 mya and also parallel to the formation of Pangaea, oribatid mites (especially Brachyopylina) radiated in tropical regions and split up into thousands of species. The tropics therefore might be viewed as "ancient cradle" of oribatid mite diversity. In contrast, cold habitats at high latitude where early-derived oribatid mites flourish might be viewed as "museum" of cold adapted early-derived oribatid mites which appear to have radiated much less than the (younger) tropical lineages.

Our findings, at least in part, also reject the "out of the tropics" hypothesis (origin and higher speciation but lower extinction rates in the tropics) since the tropics are evolutionary younger than oribatid mites which necessarily places the origin of oribatid mites in pre-tropical times. However, our data do not exclude the possibility that speciation rates in the tropics are higher in tropical oribatid mites than in oribatid mite taxa from temperate regions since species numbers of oribatid mites in the derived (and often tropical) Brachyopylina are much higher than those of the early-derivative 'Macropylina'. Investigating speciation rates in oribatid mites remains a challenge for future studies.

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SUPPLEMENTARY MATERIALS

Supplementary materials are available online (<http://www1.montpellier.inra.fr/CBGP/acarologia/article.php?id=4148>).

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