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Multiple convergent evolution of arboreal life in oribatid mites indicates the primacy of ecology

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Frequent convergent evolution in phylogenetically unrelated taxa points to the importance of ecological factors during evolution, whereas convergent evolution in closely related taxa indicates the importance of favourable pre-existing characters (pre-adaptations). We investigated the transitions to arboreal life in oribatid mites (Oribatida, Acari), a group of mostly soil-living arthropods. We evaluated which general force—ecological factors, historical constraints or chance—was dominant in the evolution of arboreal life in oribatid mites. A phylogenetic study of 51 oribatid mite species and four outgroup taxa, using the ribosomal 18S rDNA region, indicates that arboreal life evolved at least 15 times independently. Arboreal oribatid mite species are not randomly distributed in the phylogenetic tree, but are concentrated among strongly sclerotized, sexual and evolutionary younger taxa. They convergently evolved a capitate sensillus, an anemoreceptor that either precludes overstimulation in the exposed bark habitat or functions as a gravity receptor. Sexual reproduction and strong sclerotization were important pre-adaptations for colonizing the bark of trees that facilitated the exploitation of living resources (e.g. lichens) and served as predator defence, respectively. Overall, our results indicate that ecological factors are most important for the observed pattern of convergent evolution of arboreal life in oribatid mites, supporting an adaptationist view of evolution.

Keywords: convergent evolution; adaptation; ecological niche; pre-adaptation; oribatid mites; constraints

1. INTRODUCTION

Convergent evolution is the development of similar traits in different evolutionary lineages. Famous examples of convergence are the similar body forms and lifestyles of marsupial and eutherian mammals, camera eyes in vertebrates and cephalopods, and electrogeneration (and perception) in the platypus and in a number of fishes, but myriad evolutionary convergences have been discovered in molecules, physiological traits and complex morphological adaptations (Morris 2003). The haemoglobins in animals, plants, protists and prokaryotes probably have an independent evolutionary origin (Hardison 1996), echolocation call design evolved convergently in bats (Jones & Teeling 2006) and eusociality evolved convergently in insects, shrimps and mammals (O'Riain *et al.* 2000). However, despite the large number of observed cases of convergent evolution, its importance and implications are subjects of intense debate.

For many, convergence derives from frequent and independent adaptations and thereby points to the importance of ecological factors during evolution (Sinclair *et al.* 2003; Langerhans & DeWitt 2004; Zhang 2006; Marks 2007). In this view, convergent evolution indicates the limits of potential evolutionary pathways, such that different evolutionary trajectories resulted in similar solutions to the same ecological problem. For example, Morris (2003) used convergent evolution as evidence for directed evolution resulting in similar endpoints, although this teleological view has been criticized (Lenski 2003). Convergent evolution may also be a product of chance, as there can be more than one optimum for a trait (Gould & Lewontin 1979; Doolittle 1981; Gould 1989; Zhang & Kumar 1997; Marks 2007). An ecological challenge could have been solved in a similar way by two or more species through chance alone. Further, convergent evolution may result from historical contingencies of certain groups of organisms. Taxa may have certain pre-existing conditions, i.e. pre-adaptations, that result in fast radiation when environmental conditions change or when new habitats are colonized.

Oribatid mites may serve as model organisms to study the hypothesis of the relative importance of adaptation versus chance during evolution. They are an evolutionarily old group that probably has existed for at least 380 million years (Norton *et al.* 1988), and they slowly but continuously radiated to a large number of species; about 10 000 species are described but overall 100 000 may exist (Walter & Proctor 1999; Schatz 2002).

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We investigated whether independent adaptations (caused by ecological factors), pre-adaptations or chance events were the important factors for the evolution of arboreal life in oribatid mites by examining how often, and in which taxonomic groups, arboreal life evolved. Oribatid mites are primarily soil-living organisms, but numerous taxa include species with an arboreal lifestyle. Oribatid mites on trees live in particular arboreal microhabitats such as bark or lichens, on both trunks and twigs (Proctor *et al.* 2002; Lindo & Winchester 2006; Behan-Pelletier *et al.* 2007; Erdmann *et al.* 2007). Because arboreal oribatid mite species permanently live on trees, they probably share morphological or behavioural traits (Walter & Behan-Pelletier 1999; Karasawa & Hijii 2004) including sexual reproduction (Behan-Pelletier & Winchester 1998; Erdmann *et al.* 2006). In contrast to oribatid mites on trees, of which in temperate forests 95 per cent of all individuals reproduce sexually (Erdmann *et al.* 2006), parthenogenetic reproduction dominates in soil-living taxa; in soils of temperate forests, about 80 per cent of the individuals are parthenogenetic (Maraun *et al.* 2003; Cianciolo & Norton 2006; Domes *et al.* 2007*a*). In soil, both oribatid mites with cuticles hardened by sclerotization or mineralization and soft-bodied species coexist, whereas on trees species with soft-bodied adults are virtually absent. Soil oribatid mites are characterized by a large and often ornamented sensillus, whereas in tree-living species a capitate sensillus predominates (Aoki 1973). Further, in contrast to soil-living oribatid mites, many tree-living oribatid mite species feed on lichens (Seyd & Seaward 1984; Erdmann *et al.* 2007).

Using a large collection of oribatid mite taxa representing most of the known tree-living taxa, we investigated how often oribatid mites independently colonized trees. A molecular phylogeny was constructed using the ribosomal 18S region (18S rDNA). We also tested whether tree-living in oribatid mites is correlated with the traits noted above, sexual reproduction, a capitate sensillus and strong sclerotization, using information from the literature (e.g. Seyd & Seaward 1984; Weigmann 2006; Erdmann *et al.* 2007; B. Fischer 2007, unpublished data).

2. MATERIAL AND METHODS

(a) *Species and gene selection*

For covering all major lineages of oribatid mites, we investigated members of five out of six commonly recognized groups (table 1): Palaeosomata (three spp. included), Enarthronota (three spp.), Mixonomata (three spp.), Desmonomata (12 spp.) and Brachypylina (30 spp.) (Grandjean 1969; Weigmann 2006); the species-poor Parhyposomata were not sampled. The middle-derivative Desmonomata and the higher Brachypylina (=Circumdehiscentiae) were most heavily sampled. All specimens were collected from the field and determined to species level. Habitat (soil or bark), reproductive mode, feeding mode and type of sensillus were extracted from the literature (Seyd & Seaward 1984; Cianciolo & Norton 2006; Weigmann 2006; Erdmann *et al.* 2007) or determined by us (table 1). The degree of sclerotization was estimated from the darkness of the cuticle of mature adults. Outgroup taxa, necessary for the rooting of the tree, included members of Araneae, Ricinulei (an arachnid lineage often linked to Acari), Opilioacariformes and Ixodidae (Parasitiformes). Their sequences were obtained from GenBank (see table 1 for accession numbers).

(b) *Sample preparation, PCR and sequencing*

DNA was extracted from single individuals. Each mite was placed in an Eppendorf tube, frozen in liquid nitrogen and crushed with a plastic rod. Total DNA was extracted using Qiagen DNeasy Kit for animal tissues according to the manufacturer's protocol (elution was performed in 30 μl instead of 400 μl; Qiagen, Germany).

Amplifications were performed using the primers 18Sforward (5′-TACCTGGTTGATCCTGCCAG-3′) and 18Sreverse (5′-TAATGATCCTTCCGCAGGTTCAC-3′) (modified after Turbeville *et al.* 1991) in 25 μl volumes containing 0.5–0.7 μl of each primer (100 pmol μl^{-1}), 5–8 μl DNA and 12.5 μl HotStarTaq Mastermix (1.25 U HotStarTaq polymerase, 100 μM of each dNTP and 7.5 mM $MgCl_2$ buffer solution; Qiagen). PCR conditions were as follows: initial activation at 95°C for 15 min, 34 amplification cycles (95°C for 45 s, 57°C for 1 min and 72°C for 1 min); final elongation at 72°C (10 min).

PCR products were visualized on 1 per cent agarose gels and purified using QIAquick PCR Purification Kit (Qiagen); PCR products were directly sequenced by Macrogen Inc. (Seoul, South Korea) using the additional primers 18S554f (5′-AAGTCTGGTGCCAGCAGCCGC-3′), 18S1282r (5′-TCACTCCACCAACTAAGAACGGC-3′), 18S1150f (5′-ATTGACGGAAGGGCACCACCAG-3′) and 18S614r (5′-TCCAACTACGAGCTTTTTAACC-3′) (modified after Turbeville *et al.* 1991). All sequences are available at GenBank (see table 1 for accession numbers).

(c) *Alignment and phylogenetic analyses*

DNA sequences of the ribosomal 18S region were aligned using the default settings in CLUSTALX (Thompson *et al.* 1994, 1997); the alignment was modified by eye since gaps occurred. The evolutionary model parameters were determined with MODELTEST 3.7 (Posada & Crandall 1998) using a hierarchical likelihood ratio test. The model of evolution was GTR + I + G (Tamura & Nei 1993) with base frequencies $A = 0.2567$, $C = 0.2246$, $G = 0.2611$, gamma distribution shape parameter $\alpha = 0.5050$ for four categories of among-site variation and fraction of invariant sites $I = 0.4170$. Substitution rates were estimated as $A–C = 1.1382$, $A–T = 2.4404$, $C–G = 0.6364$ and $G–T = 1.0$, $A–G = 3.0285$ and $C–T = 4.8970$. This model of evolution was used to construct the neighbour joining (NJ) and maximum-likelihood (ML) trees.

To test whether there is a phylogenetic signal in the dataset, we carried out the permutation tail probability (PTP) test (Faith & Cranston 1991) using PAUP* 4b10 (Swofford 1999) with 10 000 replicates. The use of the PTP test has been questioned (Peres-Neto & Marques 2000), but the test is still used in a number of recent studies (e.g. Simmons & Weller 2002).

Phylogenetic trees were constructed using NJ, maximum parsimony (MP) and ML as implemented in PAUP* 4b10. MP and ML trees were constructed with a heuristic search of 100 random additions, and the tree bisection–reconnection branch-swapping algorithm with the option to collapse zero branch length. Reliability of the branches was ascertained by bootstrap analyses for NJ (100 000 replicates), MP (1000 replicates) and ML (100 replicates) in PAUP* 4b10. Bayesian phylogenetic analysis was performed with MRBAYES v. 3.1.2 (Huelsenbeck & Ronquist 2001) using prior settings nst = 6 and rates=invgamma with four independent runs of 3 000 000 generations and five chains each; rate matrix,

Table 1. Phylogenetic affiliation, full species name, fragment length, GenBank accession numbers, reproductive mode, type of sensillus and degree of sclerotization of oribatid mite taxa studied and outgroups (bark-living taxa in bold). Sequences other than those labelled 'a' were obtained from GenBank (http://www.ncbi.nlm.nih.gov/GenBank).

	taxa	fragment length (bp)	GenBank accession number	reproductive mode	type of sensillus	degree of sclerotization
outgroups						
Araneae	*Liphistius bicoloripes* (Ono 1988)	1617	AF007104	sexual	—	—
Ricinulei	*Pseudocellus pearsei* (Chamberlin & Ivie 1938)	1619	PPU91489	sexual	—	—
Ixodidae	*Amblyomma sphenodonti* (Dubleton 1943)	1621	DQ507238	sexual	—	—
Opilioacaridae	*Opilioacarus texanus* (Chamberlin & Mulaik 1942)	1619	AF124935	sexual	—	—
Enarthronota						
Hypochthoniidae	*Hypochthonius rufulus* (C. L. Koch 1835)	1664	EF091427	thelytokous	non-clavate	weak
Eniochthoniidae	*Eniochthonius minutissimus* (Berlese 1903)	1643	EF091428	thelytokous	non-clavate	weak
Lohmanniidae	*Lohmannia banksi* (Norton *et al.* 1978)	1676	AF022036	thelytokous	non-clavate	weak
Palaeosomata						
Acaronychidae	*Stomacarus ligamentifer* (Hammer 1967)	1620	EU433992	sexual	non-clavate	weak
	Zachvatkinella sp. (Lange 1954)	1619	EF203776	sexual	non-clavate	weak
Palaeacaridae	*Palaeacarus hystricinus* (Trägardh 1932)	1618	EF204472	thelytokous	non-clavate	weak
Mixonomata						
Phthiracaridae	*Steganacarus magnus* (Nicolet 1855)	1616	AF022040	sexual	non-clavate	strong
	Atropacarus striculus (C. L. Koch 1835)	1625	EF091416	thelytokous	non-clavate	strong
Euphthiracaroidea	*Rhysotritia duplicata* (Grandjean 1953)	1624	EF091417	thelytokous	non-clavate	strong
Desmonomata						
Camisiidae	***Camisia biurus* (Koch 1839)**	**1624**	**EF081302**	**thelytokous**	**clavate**	**strong**
	***Camisia horrida* (Hermann 1804)**[a]	**1624**	**EU432207**	**thelytokous**	**clavate**	**strong**
	Camisia invenusta (Michael 1888)[a]	1624	EU432208	thelytokous	clavate	strong
	***Camisia segnis* (Hermann 1804)**[a]	**1624**	**EU432209**	**thelytokous**	**clavate**	**strong**
	***Camisia spinifer* (C. L. Koch 1835)**	**1624**	**EF091420**	**thelytokous**	**clavate**	**strong**
	Platynothrus peltifer (C. L. Koch 1839)	1624	EF091422	thelytokous	non-clavate	strong
Crotoniidae	***Crotonia brachyrostrum* (Hammer 1966)**	**1624**	**EF081303**	**sexual**	**clavate**	**strong**
Malaconothridae	*Malaconothrus gracilis* v.d. (Hammen 1952)	1624	EF091424	thelytokous	no sensillus	weak
	Trimalaconothrus sp. (Berlese 1916)[a]	1624	EU432210	thelytokous	no sensillus	weak
Nothridae	*Nothrus silvestris* (Nicolet 1855)	1624	EF091425	thelytokous	non-clavate	strong
Trhypochthoniidae	*Archegozetes longisetosus* (Aoki 1965)	1631	AF022027	thelytokous	non-clavate	intermediate
	***Trhypochthonius tectorum* (Berlese 1896)**	**1623**	**AF022041**	**thelytokous**	**clavate**	**intermediate**
Brachypylina (non-Poronota)						
Carabodidae	*Carabodes subarcticus* (Trägardh 1902)	1623	EF091429	sexual	clavate	strong
	***Odontocepheus elongatus* (Michael 1879)**[a]	**1625**	**EU432200**	**sexual**	**clavate**	**strong**

(*Continued.*)

Table 1. (*Continued.*)

	taxa	fragment length (bp)	GenBank accession number	reproductive mode	type of sensillus	degree of sclerotization
Ceratoppiidae	*Ceratoppia bipilis* (Hermann 1804)[a]	1624	EU432204	sexual	clavate	intermediate
Cepheidae	*Cepheus latus* (Koch 1835)[a]	1624	EU432206	sexual	clavate	strong
Cymbaeremaeidae	***Cymbaeremaeus cymba* (Nicolet 1855)**[a]	**1624**	**EU432201**	**sexual**	**clavate**	**strong**
	***Scapheremaeus palustris* (Sellnick 1924)**	**1640**	**EU433989**	**sexual**	**clavate**	**strong**
Eremaeidae	***Eueremaeus oblongus* (Koch 1835)**[a]	**1624**	**EU432205**	**sexual**	**clavate**	**strong**
Eutegaeidae	*Eutegaeus curviseta* (Hammer 1966)	1624	EF081297	sexual	non-clavate	strong
Liacaridae	*Adoristes poppei* (Oudemans 1906)[a]	1624	EU432202	sexual	clavate	strong
Neoliodidae	***Liodes* sp. (Heyden 1829)**	**1625**	**AF022035**	**sexual**	**clavate**	**strong**
	***Poroliodes farinosus* (Koch 1839)**	**1624**	**EF203779**	**sexual**	**clavate**	**strong**
Xenillidae	***Xenillus discrepans* (Grandjean 1936)**[a]	**1624**	**EU432203**	**sexual**	**clavate**	**strong**
Brachypylina (Poronota)						
Achipteriidae	*Achipteria coleoptrata* (Linnaeus 1758)	1624	EF091418	sexual	non-clavate	strong
Ceratozetidae	*Oromurcia sudetica* (Willmann 1939)[a]	1625	EU432194	sexual	non-clavate	strong
	***Trichoribates trimaculatus* (Koch 1835)**[a]	**1625**	**EU432195**	**sexual**	**clavate**	**strong**
Chamobatidae	*Chamobates pusillus* (Berlese 1895)[a]	1624	EU432188	sexual	non-clavate	strong
	Chamobates subglobulus (Oudemans 1900)[a]	1624	EU432190	sexual	non-clavate	strong
	Chamobates voigtsi (Oudemans 1902)[a]	1624	EU432189	sexual	non-clavate	strong
Eremaeozetidae	***Eremaeozetes* sp. (Berlese 1913)**[a]	**1639**	**EU432187**	**sexual**	**clavate**	**strong**
Galumnidae	*Galumna lanceata* (Oudemans 1900)[a]	1625	EU432197	sexual	non-clavate	strong
Humerobatidae	***Humerobates rostrolamellatus* (Grandjean 1936)**[a]	**1624**	**EU432196**	**sexual**	**clavate**	**strong**
Hydrozetidae	*Hydrozetes lacustris* (Michael 1882)	1624	EU433987	thelytokous	non-clavate	intermediate
Oribatulidae	***Phauloppia lucorum* (Koch 1841)**[a]	**1648**	**EU432198**	**sexual**	**clavate**	**strong**
	Oribatula tibialis (Nicolet 1855)	1651	EU433990	sexual	non-clavate	strong
Phenopelopsidae	***Eupelops acromios* (Hermann 1804)**[a]	**1624**	**EU432192**	**sexual**	**clavate**	**strong**
	Eupelops plicatus (Koch 1835)	1623	EF091419	sexual	non-clavate	strong
Punctoribatidae	***Mycobates parmeliae* (Michael 1884)**[a]	**1624**	**EU432191**	**sexual**	**clavate**	**strong**
Symbioribatidae	***Scheloribates ascendens* (Weigmann & Wunderle 1990)**[a]	**1627**	**EU432199**	**sexual**	**clavate**	**strong**
Tectocepheidae	*Tectocepheus velatus* (Michael 1880)	1628	EF093781	thelytokous	clavate	intermediate
Tegoribatidae	***Lepidozetes singularis* (Berlese 1910)**[a]	**1625**	**EU432193**	**sexual**	**clavate**	**strong**

[a]Species sequenced for this study.

base frequencies and branch lengths were estimated and trees were sampled every 300 generations. A majority consensus tree was generated using a burn-in of 2000. Posterior probabilities were calculated based on the topology of the Bayesian tree.

History and the ancestral state of character evolution were reconstructed using parsimony algorithms of the StochChar package in MESQUITE 2.5 (Maddison & Maddison 2008). A step matrix for each character was constructed under the following assumptions: the colonization of bark from soil-living oribatid mites is more likely than the reverse; the capitate sensillus is probably evolved from a non-capitate sensillus; sex is the ancestral mode of reproduction and was frequently lost, and the sclerotization of oribatid mites evolved from weaker to stronger sclerotized species.

We investigated whether tree living is correlated with the type of sensillus, the reproductive mode or the degree of sclerotization using PHYLOCOM (Webb *et al.* 2008). Independent pairwise contrasts between tree living and the three traits, i.e. type of sensillus, mode of reproduction and degree of sclerotization, were calculated (Garland *et al.* 1999) with default values for number of randomizations (999 replicates).

3. RESULTS

Phylogenetic analyses of the ribosomal 18S rDNA region were based on 1699 base pairs and 55 taxa in total. Of the 1699 positions, 1113 were conserved and 586 were variable with 379 positions being parsimony informative. Variable positions of the ingroup (four outgroup taxa excluded) were 474 with 278 parsimony informative positions. The average pairwise ML distance of the whole dataset averaged 7.8 per cent with a maximum value of 33 per cent (the model used to calculate the ML distance was the same as that used to construct the ML tree).

As each of the tree topologies of the phylogenetic algorithms, NJ, MP, ML and Bayesian methods, were almost identical, only the Bayesian tree is shown (figure 1). Bayesian inference has been shown to be most robust against model violations and recovers (known) correct trees in nearly all cases (Mar *et al.* 2005). The PTP test indicates that there is a strong phylogenetic signal in the dataset ($p < 0.0001$). Arboreal oribatid mite species were not randomly distributed in the phylogenetic tree but dominated among evolutionarily younger taxa, especially in the Poronota. Enarthronota (*Eniochthonius minutissimus*, *Hypochthonius rufulus* and *Lohmannia banksi*) were paraphyletic except in the ML analysis, where *Hypochthonius* and *Lohmannia* were sister taxa. Enarthronota were followed by Palaeosomata (*Stomacarus ligamentifer*, *Palaeacarus hystricinus* and *Zachvatkinella* sp.) and Mixonomata (*Atropacarus striculus*, *Steganacarus magnus* and *Rhysotritia duplicata*). The middle-derivative Desmonomata included 12 species, of which *Trhypochthonius tectorum*, *Crotonia brachyrostrum* and four species of the genus *Camisia* are arboreal. The Brachypylina (=Circumdehiscentiae) were always monophyletic with high statistical support. Basal in Brachypylina were the two arboreal species of Neoliodidae, *Poroliodes farinosus* and *Liodes* sp., followed by *Cepheus latus* and two Carabodidae, *Carabodes subarcticus* and *Odontocepheus elongatus*; most groups had high bootstrap and posterior probability support. The phylogenetic positions of the soil-living species *Ceratoppia bipilis*, *Eutegaeus curviseta*, *Adoristes poppei* and of the arboreal species *Eueremaeus oblongus*, *Cymberemaeus cymba*, *Xenillus discrepans* varied among different phylogenetic analyses, but were identical in the Bayesian and ML tree. Poronota s.l. (including *Scapheremaeus palustris* and *Eremaeozetes* sp.) were monophyletic with high bootstrap support and posterior probabilities and included the arboreal species *Scheloribates ascendens*, *Phauloppia lucorum*, *Scapheremaeus palustris*, *Eremaeozetes* sp., *Eupelops acromios*, *Trichoribates trimaculata*, *Lepidozetes singularis*, *Mycobates parmeliae* and *Humerobates rostrolamellatus*. Among arboreal oribatid mites, lichen feeding evolved at least four times, in the genus *Camisia* and in *Cymberemaeus cymba*, *Phauloppia lucorum* and *Mycobates parmeliae* (figure 1).

Ancestral character state reconstruction indicated that arboreal life evolved at least 15 times among the studied oribatid mites, (figure 2*a*). All studied arboreal (and very few soil living) oribatid mite species possess a clavate sensillus (figure 2*b*); the studied soil-living oribatid mites possess a non-clavate sensillus (e.g. pectinate, fusiform, setiform, bacilliform or ciliate) and two genera (*Malaconothrus* and *Trimalaconothrus*) have no sensillus at all (table 1). All studied arboreal oribatid mites, except the four species of *Camisia*, reproduce sexually (figure 2*c*; table 1). Furthermore, sclerotization is usually strong in arboreal and soil living species, except in phylogenetically older soil-living species, most of which are only weakly sclerotized (Enarthronota and Palaeosomata; figure 2*d*; table 1).

Bark living was strongly correlated with a capitate sensillus (correlation coefficient $R = 0.68$) but only weakly correlated with a strong sclerotization ($R = 0.21$) and even less with sexual reproduction ($R = 0.12$), as indicated by the test for independent contrasts using PHYLOCOM.

4. DISCUSSION

The aim of this study was to investigate whether ecological factors, pre-adaptations or chance were responsible for the convergent evolution of arboreal life in oribatid mites. Phylogeny and model-based reconstruction of ancestral states indicated that arboreal life evolved at least 15 times in oribatid mites. As not all arboreal genera and species of oribatid mites were included, arboreal life certainly evolved more often. The arboreal oribatid mite taxa are not randomly distributed in the phylogenetic tree but cluster among the more derived Brachypylina, suggesting that higher oribatid mites may be pre-adapted to colonize trees.

High correlation of bark living and a capitate sensillus indicates that the sensillus co-evolved with the arboreal lifestyle of oribatid mites. Most arboreal oribatid mite species possess a capitate sensillus that is most probably an adaptation for arboreal life (Aoki 1973; Alberti *et al.* 1994). Presumably, this typical sensillus is an air-current receptor (anemoreceptor) that has this typical shape to avoid overstimulation (Norton & Palacios-Vargas 1982). The compact shape could limit the sensitivity of the receptor under the higher air flow of exposed situations when compared with soil. Sensilli of soil species are usually thinner and longer; they often have cilia or other ornamentations that increase sensitivity to air currents. Alternatively, the large distal ball and thin stalk of capitate sensilli could serve as a gravity receptor in arboreal species (Alberti *et al.* 1994). This idea is supported by the fact that capitate sensilli in some arboreal

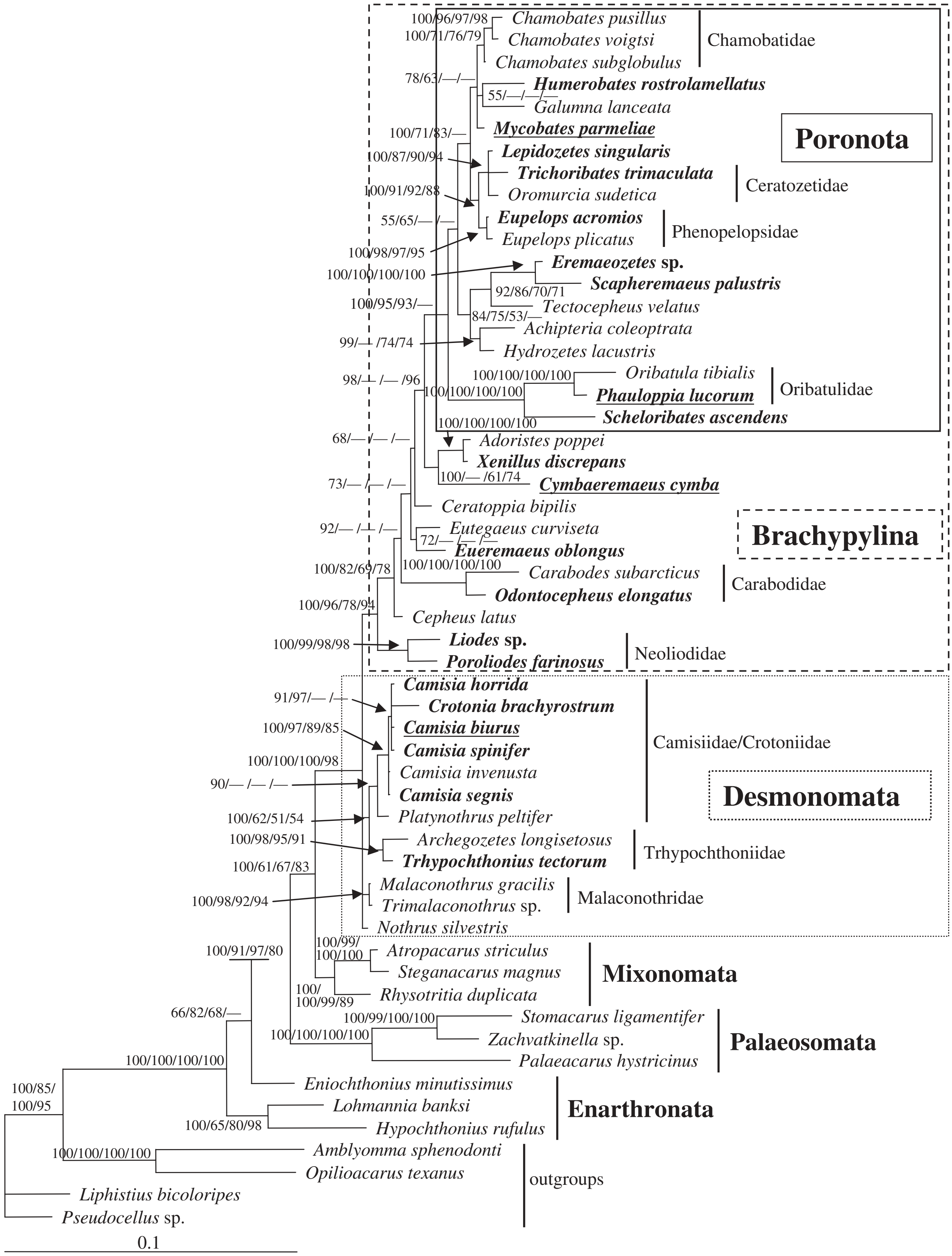

Figure 1. Bayesian phylogeny of oribatid mites based on the ribosomal 18S gene using GTR + I + G as an evolutionary model. Numbers at nodes, respectively, represent Bayesian posterior probabilities and bootstrap support values for NJ, MP and ML. Arboreal oribatid mite species are in bold face and italics; lichen-feeding species on trees are additionally underlined.

species (Crotoniidae and *Camisia abdosensilla*; Olszanowski *et al.* 2002) are entirely protected from air currents by being almost completely enclosed in a covered bothridium.

A capitate sensillus is not characteristic of all derived oribatid mites, indicating that it evolved several times in taxa that permanently colonized trees. In contrast to sexual reproduction and strong sclerotization (which were pre-adaptations of oribatid mites *before* they colonized the trees; see below), the capitate sensillus evolved convergently *after* the trees were colonized and is therefore a true adaptation to arboreal life.

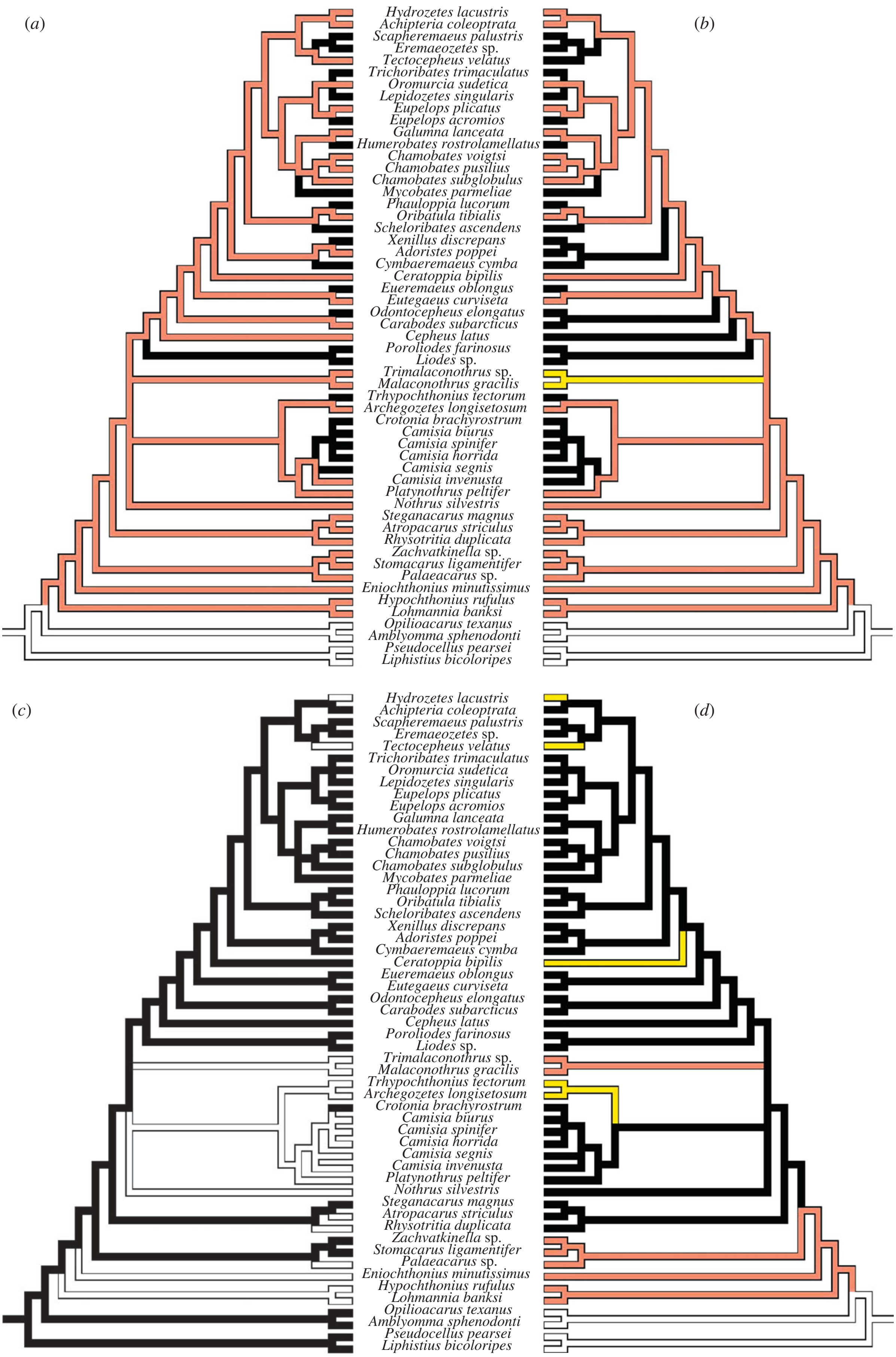

Figure 2. Ancestral character state reconstruction of (*a*) living mode, (*b*) sensillus type, (*c*) reproductive mode and (*d*) degree of sclerotization as reconstructed with MESQUITE 2.5 using parsimony algorithms. Bark living and a clavate sensillus are strongly correlated, whereas bark living is not strongly correlated with sexual reproduction and strong sclerotization. See text for details. (*a*) Black, bark; orange, soil; white, outgroups. (*b*) Black, clavate; orange, non-clavate; yellow, no sensillus; white, outgroups. (*c*) Black, sexual; white, thelytokous. (*d*) Black, strong; orange, weak; yellow, intermediate; white, outgroups.

The low correlation of bark living with sexual reproduction as well as strong sclerotization indicates that these traits already existed before the trees were colonized. The most important pre-adaptation for arboreal life in Brachypylina probably was the sexual mode of reproduction. In contrast to basal oribatid mite lineages, Brachypylina are predominantly sexual. The importance of the reproductive mode for arboreal oribatid mites can be inferred from the arboreal genus *Crotonia* that re-evolved sexual reproduction from a previously soil-living and parthenogenetic taxon, the Camisiidae/Crotoniidae (Domes *et al.* 2007*b*). It is not known why sexual reproduction is advantageous for arboreal species but it is probably related to food resources. While soil-living taxa predominantly feed on little defended food substrates, such as dead organic material, arboreal species predominantly feed on algae and lichens that at least in part are heavily defended (Seyd & Seaward 1984; Erdmann *et al.* 2007). Sexual reproduction therefore may be necessary for the co-evolutionary arms race between predators and prey (Red Queen hypothesis; Hamilton 1980).

The second important pre-adaptation of tree living oribatid mites probably was the strongly sclerotized body of the adults. Most adult oribatid mites are sclerotized, but the sclerotization of arboreal taxa is often even stronger. The strong sclerotization of bark-living oribatid mite species probably functions as predator defence. This also applies to oribatid mites in soil and litter (Sanders & Norton 2004), but this feature is probably less important in soil than on the bark of trees owing to the opaqueness of the soil habitat, which renders prey location more difficult. This hypothesis is supported by the stronger sclerotization of juvenile oribatid mite species living on the bark of trees when compared with juveniles of soil-living species. While many oribatid mites are sclerotized, Brachypylina are unique among them in possessing an extensive tracheal system, which may be evolutionarily linked to the difficulty of respiring through a sclerotized cuticle (Norton & Alberti 1997). The combination of a hard cuticle, a water-resistant epicuticle and an internalized respiratory surface could have been an effective pre-adaptation of Brachypylina to life in desiccating environments such as tree bark.

Oribatid mite species have a number of morphological characters that can be used to test whether arboreal species are really *adapted* to arboreal life or just colonized the trees permanently without evolving specific adaptations. The bark of trees is a permanent habitat for a large number of (mainly sexual) oribatid mite species (Proctor *et al.* 2002; Erdmann *et al.* 2006; Lindo & Stevenson 2007). Only a few ubiquitous parthenogenetic species such as *Tectocepheus velatus* and *Oppiella nova* live on the bark of trees and also in soil. This indicates a clear niche differentiation between soil and arboreal oribatid mite species.

Overall, our data indicate that the frequent convergent evolution of arboreal life in oribatid mites was driven in part by chance, as the arboreal species cluster randomly in higher taxa. However, the major driving force for the colonization of trees by oribatid mites was the ecological factor supporting the adaptionist view of evolution (Johannesson 2003; Morris 2003, 2006). Pre-adaptations such as sexual reproduction and strong sclerotization presumably facilitated the arboreal life of oribatid mites, and characters such as the clavate sensillus evolved later during tree colonization. We conclude that ecological forces swamp chance events such as drift and historical contingencies during evolution, supporting the 'adaptionist programme'.

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