



Revisiting the Evolution of Arboreal Life in Oribatid Mites

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Abstract: Though mostly soil dwelling, oribatid mites are found in all kind of habitats, with several species exclusively living on trees. Using previously published DNA sequences and eco-morphological data available from the literature, we inferred the number of transitions between soil dwelling to a truly arboreal lifestyle in oribatid mites and the shape evolution of a particular morphological structure of a sense organ (bothridial seta (= sensillus) of a trichobothrium), the shape of which was previously reported to be associated with an arboreal lifestyle. Our data suggest that a truly arboreal lifestyle evolved several times independently in oribatid mites, but much less often than previously proposed in the past. Even though all truly arboreal species indeed seem to possess a capitate sensillus, this character is not exclusive for arboreal taxa. Nonetheless, since all truly arboreal species do have a capitate sensillus, this might be considered an important (pre-)adaptation to a life on trees. We further provide guidelines on how the term “arboreal” should be applied in future mite research and emphasize the importance of exact microhabitat characterization, as this will greatly facilitate comparisons across studies.

Keywords: lifestyle; tree related microhabitats; 18S rRNA; phylogeny; ancestral state reconstruction; sensillus

1. Introduction

Forest ecosystems harbor a strikingly large number of mite species, with particularly high biodiversity in forest soil. This tremendous species richness and adaptations to micro-environments within this ecosystem have led researchers to emphasize the potential of mites as environmental indicators [1–4].

For most tree-associated organisms, a tree is not a single, homogeneous environment. It comprises different sub-areas or regions. For example, the tree trunk itself can be divided into a basal, median, and upper part. The branches, twigs, and leaves of the canopy represent other distinct regions. The ecologically most important structures, however, are the tree-related microhabitats, which are natural, tree-borne features. They provide specific conditions and substrates, like different food resources or structures for breeding and shelter. Since different types of microhabitat support different organismic communities [5–7], they have gained considerable attention in forest management and conservation, especially in the last two decades. While nests of birds and mammals serve as home for nidicolous species, the boreholes and galleries of xylobiotic insects are important habitats and/or food sources for special communities consisting of housemates, commensals, and parasites of these xylobionts. Similar to knot-holes or holes in the trunk, which contain decaying and decomposed organic material, so-called suspended soils developed on large trees with broad branch forks contain their own, often specialized fauna.

As already shown by Wunderle [8], trees provide a habitat for several primarily soil-dwelling microarthropods, especially for oribatid mite species.

It has been known for a long time that Oribatida also occur on trees [9], and researchers soon recognized that species composition differs between soil and tree canopy [10,11]. Since then, many eco-faunistic studies targeted the diversity of oribatids on trees [12–15]. However, many previous studies provided often confusing, disparate information on individual species or species communities inhabiting trees, which indicates that abundance, distribution and diversity of tree-living species vary considerably even under presumably similar conditions. These differences in community composition can be mainly attributed to (i) habitat types (e.g., rain forest, “perpetual mist” forests, deciduous and mixed forests; [16]), (ii) tree species (e.g., [8]), or (iii) zones and age of a tree, which determines tree diameter and bark thickness and has significant impact on the number of available microhabitats [17]. Nonetheless, the diversity of tree-living oribatid mites is undoubtedly much higher than known so far. Several recent studies showed the level of cryptic diversity is high in (tree-living) oribatids, even in supposedly well known, common, and easily identifiable taxa [18–20], providing an important contribution to our knowledge of the biodiversity in forest ecosystems.

While many eco-faunistic studies dealt with tree-living oribatid communities, only one study aimed at a comprehensive analysis of arboreal lifestyle evolution in oribatids, focusing on the transition from soil dwelling to arboreal life and potentially associated phenotypic adaptations [21]. Specifically, the authors suggested that arboreal life evolved independently at least 15 times and that tree-living is more common in evolutionary younger taxa with strong sclerotization, sexual reproduction, and capitate sensilli [21].

Microhabitats are known to harbor a disproportionately high number of (likely unknown) species, not only among oribatid mites. Therefore, it is important to recognize and conserve these microhabitats [6,7]. So far, several studies have demonstrated the important role of tree-associated microhabitats for the taxonomic diversity in oribatid mites [22–27]. In all these studies, the authors use the term “arboreal” (= corticolous or arboricole), which means growing on or living in trees, to indicate that a specimen/species was collected on a tree. However, the exact use of this term differs among studies. Some use it to refer to strictly tree-living species, others apply it to more generalist species found both in soil and on trees [10,28,29]. Moreover, it is still questionable whether the species found on trees are tree or rather microhabitat specific (see also [30]). These uncertainties complicate generalizations regarding the evolution of a tree-living lifestyle in oribatid mites.

Against this background and utilizing a comprehensive phylogenetic tree based on previously published 18S rDNA sequences, the present study aims to (i) revisit the origin of a tree-living lifestyle in oribatids, (ii) test the hypothesis (according to [11]) that a capitate sensillus is a special morphological feature of arboreal life, and (iii) discuss and redefine the term “arboreal” in oribatid mites.

2. Material and Methods

2.1. Data Acquisition

We chose the 18S rRNA (18S) gene for our meta-analysis because of (i) the largest amount of sequence data available for a particular locus, covering all major groups of the oribatid mite tree of life, and (ii) its low substitution rate; the 18S gene is generally more suitable for resolving phylogenetic relationships at higher taxonomic levels. Only sequences with a minimum length of 1600 bp were obtained from GenBank. The final dataset included sequences of 165 oribatid species (see Table S1). Based on Klimov et al. [31], we used three species of Paleosomata, *Ctenacarus araneola*, *Palaeacarus hystricinus*, and *Stomacarus ligamentifer* as outgroup.

Prior to phylogenetic analysis, sequences were aligned using the MAFFT v.7 web version [32]. Poorly aligned regions were removed from the alignment using the program trimAl v1.2 [33] applying the heuristic “automated1” method (final length of dataset = 1619 bp).

Character coding of traits for ancestral state reconstruction (ASR) of lifestyle and sensillum type was primarily based on Weigmann [34] as well as on original species descriptions. Additional literature was only used in case of uncertainties or missing information (see Table S2). Ancestral character state reconstruction for lifestyle was coded as follows: soil (0), tree- and soil-living (1), exclusively tree-living (= arboreal, 2), littoral (3), mangrove (4), and limnic (5). The coding of the sensillum types followed roughly the classification scheme of Aoki [11]: no sensillum present (0), capitate and strongly clavate (1), clavate (2), slightly clavate (3), with rami (4), rod-like thin (5), and not specified (6, for details see below) (Figure 1).

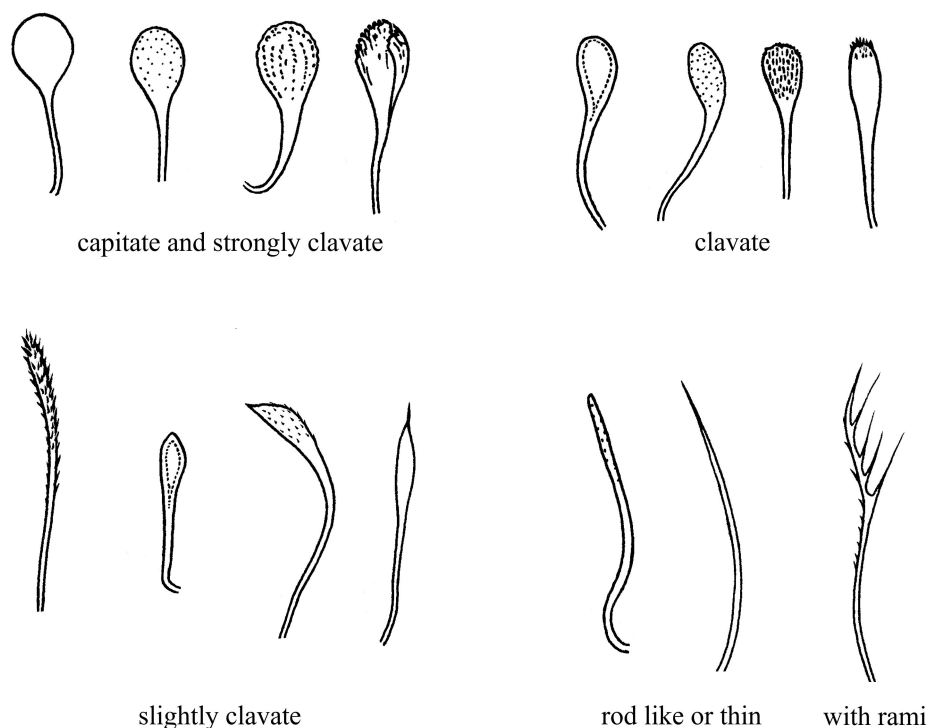


Figure 1. Drawing of sensillum types used for character coding in the present study.

2.2. Analysis

The best-fitting model of molecular evolution was selected based on the Akaike Information Criterion (AIC) in the “Smart Model Selection” tool (SMS; [35]) implemented in the PhyML 3.0 online execution ([36]; <http://www.atgc-montpellier.fr/phyml/>). Phylogenetic inference was based on Maximum Likelihood (ML), implemented in PhyML and Bayesian inference (BI), implemented in MrBayes 3.2.7 [37], applying the GTR+I+G model selected by SMS. ML analyses were run under default parameter settings and nodal support was assessed by means of bootstrapping (1000 replicates). For BI analyses, posterior probabilities were obtained from a Metropolis-coupled Markov chain Monte Carlo simulation (2 independent runs; 4 chains with 25 million generations each; trees sampled every 1000 generations). Run convergence and stationarity of parameters were checked in Tracer v1.7 ([38]; available at <http://beast.community/tracer>) and by means of the standard deviation of split frequencies (<0.01) in MrBayes. The first 12,500 (25%) trees were discarded as burn-in prior to constructing an “allcompat” consensus tree from the remaining 37,502 trees.

We traced the evolution of two characters (lifestyle, sensillum shape) over the molecular phylogeny using maximum parsimony (MP) and maximum likelihood (ML)-based reconstructions conducted in Mesquite v.3.51 [39].

We applied the “trace character over trees” option to account for topological uncertainty. The Markov k-state 1 (Mk1) parameter model was employed for the analysis of both characters, with equal probability for any particular character state. Both reconstructions were integrated over

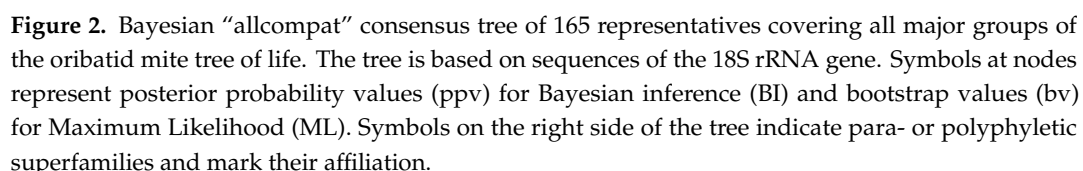
20,001 randomly selected post burn-in trees of the BI analysis and the ancestral states were summarized on the BI consensus tree.

Due to intra-generic polymorphism of sensillus shape in the genera “*Liodes*” and *Eremaeozetes* ([34] and Schatz pers. communication), we refrained from assigning a particular morphology to *Liodes* sp. (The denomination *Liodes* sp. is not a valid name for a genus of the oribatid mite family Neoliodidae [40]. It is unclear whether this record in GenBank from 1997 refers to a species of *Neoliodes* or to another genus) and *Eremaeozetes* sp. The higher-level classification of oribatids follows Schatz et al. [41].

3. Results

As both the ML and BI tree inference resulted in very similar tree topologies, only the Bayesian consensus tree is shown (Figure 2). Compared to the traditional classification, our phylogenetic tree revealed several discrepancies, for example the infraorders Parhyposomata and Mixonomata, as well as the superfamilies Plateremaeoidea, Cepheoidea, Cymbaeremaeoidea, Licneremaeoidea, Gustavioidea and Ameronothroidea appear as para- or polyphyletic, but often with only low statistical support, indicating a fair amount of topological uncertainty (which was accounted for in our ASR analyses).

ASR of lifestyle and sensillus based on ML and MP reconstructions revealed very similar results, except for some nodes that were reconstructed with greater uncertainty (equivocal) in the ML approach (Figure 3, Figure S1). Our results clearly indicate that the preconditions for colonizing tree trunks and canopies were already present in the ancestors of the higher Oribatida; e.g., *Camisia* species can be found both in soil and tree samples (Figure 3a). Nevertheless, to live nearly exclusively on trees seems to be the exception (see also [29]). However, our analysis suggests that arboreal life evolved seven times independently within the investigated taxa. Furthermore, our analysis supports a multiple independent evolution of the capitate sensillus (Figure 3b) and indicates that capitate sensilli are not restricted to arboreal species.



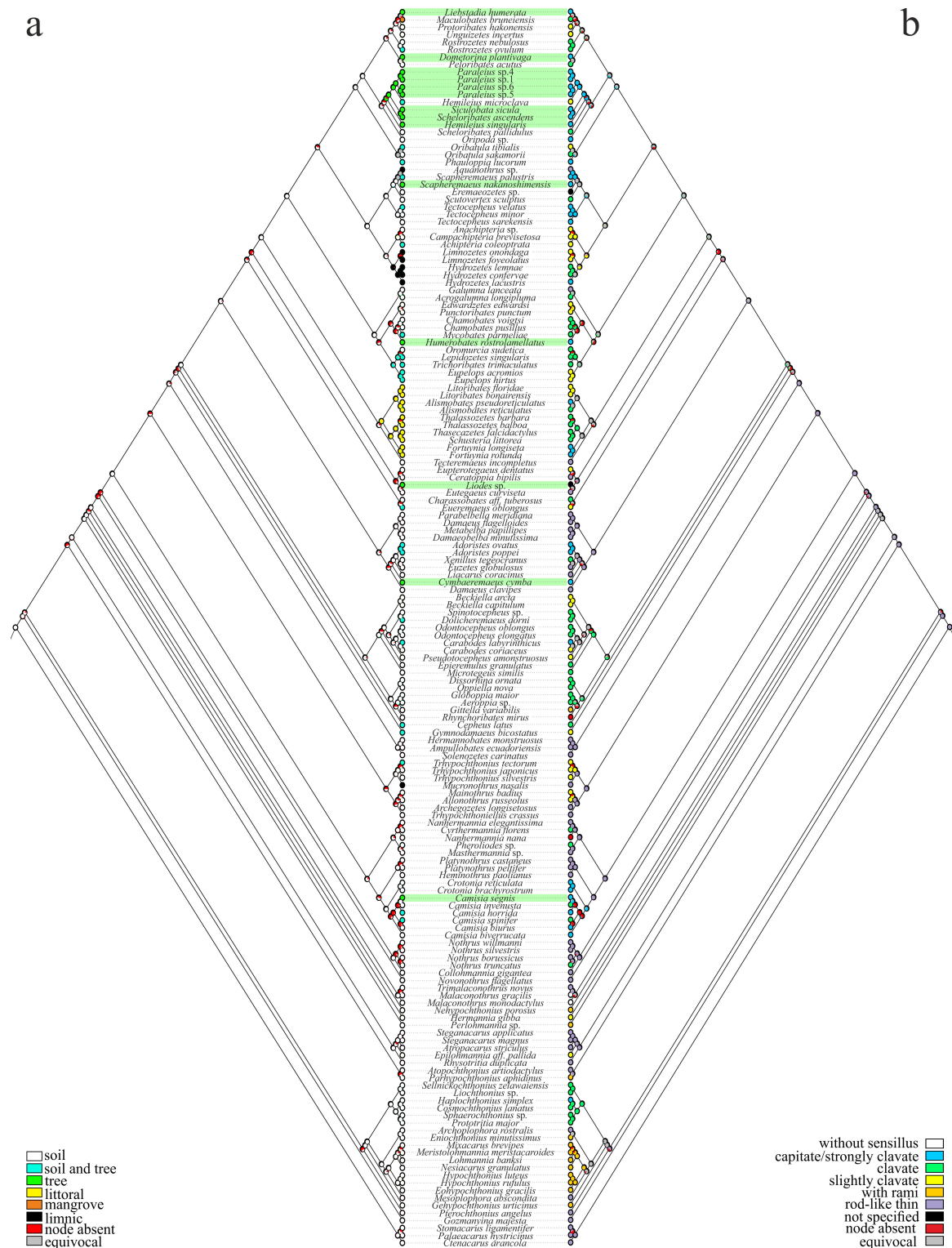


Figure 3. Ancestral state reconstructions based on likelihood of (a) lifestyle and (b) sensillus type found in oribatid mites. Tree-living taxa are highlighted in green.

4. Discussion

4.1. Revisiting the Tree-Living Lifestyle in Oribatids

Ancestral state reconstruction can give important information on the history of traits that do not fossilize, such as particular ecologies or behaviors [42]. However, consequently, inconsistent

interpretation of morphological features can lead to erroneous results and conclusions. Notwithstanding some discrepancies between our 18S phylogeny and classical taxonomy (partially apparent also in [43,44]), which is due to a lack of resolution at some inner nodes and a partly inappropriate classification scheme [45], our ancestral state reconstructions, taking topological uncertainty into account, unambiguously indicate seven transitions between soil- and tree-dwelling lifestyle in the present oribatid dataset (Figure 3a). These are much fewer transitions than inferred by a former study that proposed that life on trees evolved at least 15 times independently in oribatid mites [21], even though our study includes many more taxa. The different findings can be explained by different character coding of the lifestyle type. Whereas [21] differentiated mite species into either soil- or tree-living organisms, the majority of these taxa can be found both in soil and on trees. We used, apart from the standard classification book for oribatids [34], additional literature in cases of uncertainties (see Table S2). Moreover, we employed the character trait “tree-living” in a stricter sense, i.e., only species exclusively found on trees were assigned this character trait. As in [21], however, we can conclude that life on tree already evolved within the Crotonioidea. In this context it is also interesting to note that representatives of Enarthronota and Mixonomata, *Liochthonius* sp., and *Epilohmannia* sp. have been collected from suspended soil samples in North America [15,46], and *Liochthonius pseudolaticeps* has been found on bark of trees in Spain [47]. This suggests that the preconditions for colonizing tree trunks and canopies were already present in the early-derived oribatids, indicating a repeated independent evolution of tree life.

Many taxa included in our study are known to occur both in soil and on trees, e.g., [15]; only 14 of the 165 included species are almost exclusively tree-living. The occurrence of soil-dwelling oribatids on trees might be explained for example by so called suspended soils on trees, which provide ecological conditions similar to the forest floor [15]. Wallwork [48] and Gjelstrup [49] mentioned that mosses and lichens on rocks and trees represent such suspended soils. Thus, different kinds of suspended soils apparently facilitated the expansion of suitable habitats, especially for hemi- and epedaphic species. Most of these suspended soil dwellers are also able to survive and reproduce on the ground; therefore, many species can be found on trees as well as in soil samples. However, soil-dwelling species on trees could also be the result of introduction by other organisms. In general, colonizing a tree takes place mainly via three mechanisms: (1) the stem and suspended soils from soil and litter, (2) the upper stem and canopy by wind, and (3) the upper stem and canopy by phoresy. It has been shown that especially the transfer by birds [50,51] and by wind [52] might play an important role for the exchange of species from soil to tree.

Of course, there are many more strictly tree-living species or species occurring both in soil and on trees for which no genetic data are available so far [11,53–55]. Including an increasing number of these species in future studies will be of great importance for providing a more accurate picture of the evolution of arboreal life in oribatid mites.

4.2. Capitate Sensillus—A Special Morphological Feature of Tree-Dwelling Oribatid Mites?

Trichobothria of oribatids are complex sensory organs, highly mechanosensitive sensilli, which are of both taxonomical and functional relevance [56,57]. They are regarded as vibration receptors reacting to substrate vibrations or air currents [57]. These organs are constructed in a way that the movement of the seta (sensillus) is allowed only in two directions [57]. The shape of the sensillus has been proposed to correlate with the preferred habitat type. Aoki [11] already stated that the sensilli of arboreal taxa tend to be short capitate to strongly clavate, suggesting a function as gravity receptors. The directionality of the movement of the sensillus could be suitable to perceive the direction of gravitation, especially if the distal end of the sensillus is capitate and therefore relatively heavy. In this case, the animals would be able to “know” whether they are crawling up or down. Experimental data to verify this assumption and the hypothesized correlation of sensillus type with (micro-)habitat [57], however, are still lacking.

In general, the sensilli of oribatid mites show a broad variety in shape from filiform to club-like and globose. When the club is slender the sensillus is termed to be clavate, when the distal part broadens quickly and shows an approximately rounded or spherical club it represents a so-called capitate sensillus (see Figure 1). Clavate (large and often ornamented) sensilli were proposed to predominate in “wandering species” between soil and trees, whereas they should be capitate in arboreal species [11]. Whether an associated shortening of the stalk of the sensillus, to reduce the irritation by air currents [58]—in extreme cases the club disappears in the bothridium (e.g., in *Camisia abdosensilla* [59])—represents a further adaptation to the life on trees needs to be tested in future studies. Our study supports a multiple evolution of the capitate sensillus (Figure 3b) and indicates that capitate sensilli are found in, but are not restricted to, arboreal species, a hypothesis already discussed previously [14]. While all herein investigated arboreal species possess capitate sensilli, except for *Liodes* sp. (but see Material and Methods), the same sensillus type can also be found in soil dwellers, limnic and littoral species. Thus, even if particular sensillus types do not appear to be, associated with particular habitat types (Figure 3), the fact that all truly arboreal species seem to possess a capitate sensillus suggests that this sensillus type should indeed be considered an important (pre-)adaptation to a life on trees.

4.3. Discussing the Term “Arboreal” in Oribatid Mites

Oribatid mites can be frequently found on trees. When comparing the results of eco-faunistic studies, however, it becomes apparent that abundance, distribution and diversity of tree-living species varies considerably. Moreover, very often it is still unclear if the species found on trees are truly tree dwellers or rather wandering species in search for food, mating partner, or shelter. It is therefore necessary to clarify which species should be designated as arboreal taxa. In other words, when is a species truly arboreal?

Arboreal species *sensu stricto* are herein defined as those taxa that live on the bark of stems and branches without a layer of lichens or mosses, in the canopy, or on twigs and leaves. Furthermore, these species should undergo their whole life cycle on the tree. Among the many oribatid species (~10,000 described species [60]), only very few can be classified as arboreal *s.s.* For example, *Adhaesozetes polyphyllos* [53] as well as *Phylleremus leei* and *Ph. huntii* [61], all of which bear a short and capitate sensillus, might be considered as strictly arboreal. Unfortunately, no genetic data are available for these Australian species. All other tree-living species that also utilize different microhabitats on trees should be referred to as arboreal *sensu lato* and they should be further defined by the microhabitat they inhabit. These species are usually not found in litter and soil on the ground, except for, in rare cases, single specimens probably fallen from the tree. Some of the taxa included in our study, such as *Cymbaeremaeus cymba*, *Camisia segnis*, and *Liebstadia humerata*, can be found on stems or twigs without epiphytic layer as well as in lichens. Therefore, these species should not be defined as arboreal *s.s.* according to the above given definition. Taxa that are mainly associated with mosses or lichens on trees should be referred to as by their substrate, thus muscicolous or lichenicolous, as e.g., *Dometorina plantivaga*, which mainly occurs on lichens. All *Paraleius* species studied so far are associated with bark beetles and can be found in their galleries, where the mites live and reproduce. According to their microhabitat, *Paraleius* spp. should thus be defined as gallery-living species. Information on ecology and (micro-)habitat is available for some species, allowing for a microhabitat-based classification. This, however, is not the case for many other oribatids, which highlights the need for more detailed ecological investigations. The application of our proposed classification system has of course the consequence that only few taxa will be referred to as arboreal *sensu stricto*.

In the case of temperate and Mediterranean European forests, we suggest the application of Larrieu et al.’s [7] scheme, categorizing the tree related microhabitats into 15 main groups according to 12 substrates and four microclimatic conditions. As conditions differ among ecosystems (e.g., rainforest vs. temperate forest); however, one must also differentiate between the ecosystems. Due to different environmental conditions like moisture, temperature, or radiation, it is likely that the number of

existing microhabitats differs significantly. We expect a considerably higher number of microhabitats in rainforests, even considering the suspended soils, the variety of epiphytes or the growth of the trees. Previous studies have already shown that species found on trees are rather microhabitat specific than tree specific [24,27,30,62], pointing to the need of standardized classification schemes of microhabitats that will allow for a more straight forward and, importantly, comparable classification of tree-living taxa. This in turn will facilitate a more accurate comparison between microhabitats of different tree species, geographic areas, etc. Moreover, as mentioned at the beginning, microhabitats are important substrates contributing to the internal heterogeneity of forests [7]. Their detection and investigation will improve our knowledge about oribatid biodiversity in the future.

Reliable interpretation of evolutionary trajectories crucially depends on exact and detailed knowledge of the biological characteristics and the taxonomic classification/phylogenetic relationships of the studied taxa. Unfortunately, in many instances important information is lacking. These difficulties are exemplified by *Micreremus brevipes*, a well-known “arboreal” species, which has been reported also from Svalbard (Norway) in a permafrost and tundra habitat with litter of mosses, lichens, and vascular plants near the seashore, but definitively no trees [63]. One must assume that such different habitats show morphologically very similar, but (genetically) different species. This phenomenon of cryptic diversity might in part explain the presumed occurrence of one and the same “euryoecious species” on the ground and on trees.

Compared to their soil-living relatives, tree-living microarthropods often have to cope with markedly different climatic conditions, though this difference appears to be only minor in some ecosystems. Salavatulin [27] hypothesized that only a few oribatid mite species adapted to a life on trees. Reasons therefore would be an increased vulnerability of microhabitats to wind or solar radiation, but also a more frequent change of dryness and moisture [27]. While this holds true for habitats with extreme conditions, like forest-tundra [27] or exposed tree stands in alpine regions, drought and drought resistance should not play an important role as limiting factor in tropical and temperate rainforests. Because of the high phylogenetic age of oribatid mites, drought resistance might have been evolved in pioneer species, which colonized raw soils with changing humid conditions in ancient times. If this physiological feature is important for arboreal life, then the ability to survive dry periods should be an ancient trait. Furthermore, the food resources on virgin soils are, similar to those on the bark of trees, bacteria, algae, and lichens. The ability to feed on these food resources and the drought resistance enabled species not only to colonize litter and upper layers of soil but also to colonize trees and their different microhabitats (also see [64]).

5. Conclusions

To conclude, our analysis revealed that a truly arboreal lifestyle *sensu lato* is not particularly common, evolved several times independently in oribatid mites, but much less often than formerly proposed. We propose that only taxa that live on the bark of stems and branches without a layer of lichens or mosses, in the canopy or on twigs and leaves and undergo their whole life cycle on the tree should be regarded as “arboreal s.s.” A refined microhabitat-based classification scheme will be particularly important for future comparative ecological and evolutionary (meta-)analyses, as the different tree-associated microhabitats certainly require different phenotypic adaptations. Nonetheless, the presence of a capitatus sensillus appears to be a morphological (pre-)adaptation to life of trees (arboreal s.l.), potentially functioning as gravity receptor. Yet, it is unlikely that this is the sole adaptation to an arboreal lifestyle in oribatid mites and potential specific morphological adaptations for the life on trees should be investigated in more detail, e.g., claws and adhesive organs on legs as well as the ultrastructure and sensitivity of trichobothria.

The biodiversity of tree-living oribatid mites is undoubtedly much higher than known so far. Especially the canopies of old trees in temperate deciduous forests are not investigated thoroughly. It is well known that large old trees as well as tree-born structures represent ecologically important sites [65,66]. So-called small natural features contribute to biodiversity in a disproportionate manner

regarding their small size [67]. Therefore, a uniform classification scheme of microhabitats will be of crucial importance in mite research, as these small natural features become more and more important for preserving forest biodiversity.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/12/6/255/s1>, Table S1. Specimens, GenBank accession numbers and coding of morphological characters for the analysed samples. Table S2. Literature used for the character coding of morphological characters. Figure S1. Ancestral state reconstructions based on parsimony of (a) lifestyle and (b) sensillus type found in oribatid mites.

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References

1. Ruf, A. A maturity index for predatory soil mites (Mesostigmata: Gamasina) as an indicator of environmental impacts of pollution on forest soils. *Appl. Soil Ecol.* **1998**, *9*, 447–452. [\[CrossRef\]](#)
2. Van Straalen, N.M. Evaluation of bioindicator systems derived from soil arthropod communities. *Appl. Soil Ecol.* **1998**, *9*, 429–437. [\[CrossRef\]](#)
3. Behan-Pelletier, V.M. Oribatid mite biodiversity in agroecosystems: Role for bioindication. *Agric. Ecosyst. Environ.* **1999**, *74*, 411–423. [\[CrossRef\]](#)
4. Gergőcs, V.; Hufnagel, L. Application of oribatid mites as indicators. *Appl. Ecol. Environ. Res.* **2009**, *7*, 79–98. [\[CrossRef\]](#)
5. Kraus, D.; Büttler, R.; Krumm, F.; Lachat, T.; Larrieu, L.; Mergner, U.; Paillet, Y.; Schuck, A.; Winter, S. *Catalogue of Tree Microhabitats: Reference Field List*; European Forest Institute: Joensuu, Finland, 2016.
6. Paillet, Y.; Archaux, F.; Boulanger, V.; Debaive, N.; Fuhr, M.; Gilg, O.; Gosselin, F.; Guilbert, E. Snags and large trees drive higher tree microhabitat densities in strict forest reserves. *For. Ecol. Manag.* **2017**, *389*, 176–186. [\[CrossRef\]](#)
7. Larrieu, L.; Paillet, Y.; Winter, S.; Büttler, R.; Kraus, D.; Krumm, F.; Lachat, T.; Micheli, A.K.; Regnery, B.; Vandekerckhove, K. Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. *Ecol. Indic.* **2018**, *84*, 194–207. [\[CrossRef\]](#)
8. Wunderle, I. Die Oribatiden-Gemeinschaften (Acari) der verschiedenen Habitate eines Buchenwaldes. *Carolinae* **1992**, *50*, 79–144.
9. Travé, J. Écologie et biologie des Oribates (Acariens) saxicoles et arboricoles. *Vie et Milieu Suppl.* **1963**, *14*, 267.
10. Niedbala, W. Tree moss-mite fauna in the outskirts of Poznan. In *Oribatei and Their Role in the Process of the Soil Formation*; Lithuanian Academy of Sciences: Vilnius, Lithuania, 1970; pp. 103–112.
11. Aoki, J.I. Soil mites (oribatids) climbing trees. In *Proceedings of the 3rd International Congress of Acarology, Prague 1971*; Daniel, M., Rosický, B., Eds.; Springer: Dordrecht, The Netherlands, 1973; pp. 59–65.
12. Behan-Pelletier, V.M.; Winchester, N.N. Arboreal oribatid mite diversity: Colonizing the canopy. *Appl. Soil Ecol.* **1998**, *9*, 45–54. [\[CrossRef\]](#)
13. Winchester, N.N.; Behan-Pelletier, V.; Ring, R.A. Arboreal specificity, diversity and abundance of canopy-dwelling oribatid mites (Acari: Oribatida). *Pedobiologia* **1999**, *43*, 391–400.
14. Behan-Pelletier, V.M.; Walter, D.E. Biodiversity of oribatid mites (Acari: Oribatida) in tree canopies and litter. In *Invertebrates as Webmasters in Ecosystems*; Coleman, D.C., Hendrix, P.F., Eds.; CABI Publishing: Wallingford, UK, 2000; pp. 187–202.
15. Lindo, Z.; Winchester, N.N. Oribatid mite communities and foliar litter decomposition in canopy suspended soils and forest floor habitats of western redcedar forests, Vancouver Island, Canada. *Soil Biol. Biochem.* **2007**, *39*, 2957–2966. [\[CrossRef\]](#)
16. Arroyo, J.; Kenny, J.; Bolger, T. Variation between mite communities in Irish forest types—Importance of bark and moss cover in canopy. *Pedobiologia* **2013**, *56*, 241–250. [\[CrossRef\]](#)

17. Michel, A.K.; Winter, S.; Linde, A. The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). *Can. J. For. Res.* **2011**, *41*, 300–308. [\[CrossRef\]](#)
18. Heethoff, M.; Domes, K.; Laumann, M.; Maraun, M.; Norton, R.A.; Scheu, S. High genetic divergences indicate ancient separation of parthenogenetic lineages of the oribatid mite *Platynothrus peltifer* (Acari, Oribatida). *J. Evol. Biol.* **2007**, *20*, 392–402. [\[CrossRef\]](#)
19. Pfingstl, T.; Baumann, J.; Lienhard, A. The Caribbean enigma: The presence of unusual cryptic diversity in intertidal mites (Arachnida, Acari, Oribatida). *Org. Divers. Evol.* **2019**, *19*, 609–623. [\[CrossRef\]](#)
20. Schäffer, S.; Kerschbaumer, M.; Koblmüller, S. Multiple new species: Cryptic diversity in the widespread mite species *Cymbaeremaeus cymba* (Oribatida, Cymbaeremaeidae). *Mol. Phylogenet. Evol.* **2019**, *135*, 185–192. [\[CrossRef\]](#)
21. Maraun, M.; Erdmann, G.; Schulz, G.; Norton, R.A.; Scheu, S.; Domes, K. Multiple convergent evolution of arboreal life in oribatid mites indicates the primacy of ecology. *Proc. R. Soc. B* **2009**, *276*, 3219–3227. [\[CrossRef\]](#) [\[PubMed\]](#)
22. Seyd, E.L.; Seaward, M.R.D. The association of oribatid mites and lichens. *Zool. J. Linn. Soc.* **1984**, *80*, 369–420. [\[CrossRef\]](#)
23. André, H.M. Associations between corticolous microarthropod communities and epiphytic cover on bark. *Holarct. Ecol.* **1985**, *8*, 113–119. [\[CrossRef\]](#)
24. Nicolai, V. The bark of trees: Thermal properties, microclimate and fauna. *Oecologia* **1986**, *69*, 148–160. [\[CrossRef\]](#)
25. Root, H.T.; McGee, G.G.; Norton, R.A. Arboreal mite communities on epiphytic lichens of the Adirondack Mountains of New York. *Northeast. Nat.* **2007**, *14*, 425–438. [\[CrossRef\]](#)
26. Taylor, A.R.; Ranius, T. Tree hollows harbour a specialised oribatid mite fauna. *J. Insect Conserv.* **2014**, *18*, 39–55. [\[CrossRef\]](#)
27. Salavatulin, V. Microhabitat distribution of arboreal oribatid mites (Oribatida), associated with the Siberian pine (*Pinus sibirica*) of Western Siberia. *Exp. Appl. Acarol.* **2019**, *78*, 469–483. [\[CrossRef\]](#) [\[PubMed\]](#)
28. Vanek, J. Arboreal oribatid mites (Acari, Oribatei) in young stands of *Abies alba*. *Sbornik Vysoke Skoly Zemedelske a Lesnicke Fakulty v Praha* **1972**, *5*, 291–300.
29. Krivolutsky, D.A. Arboricular (Tree-dwelling) oribatid mites as bioindicators of environment quality. *Dokl. Biol. Sci.* **2004**, *399*, 470–473. [\[CrossRef\]](#) [\[PubMed\]](#)
30. Behan-Pelletier, V.M.; John, M.G.S.; Winchester, N. Canopy Oribatida: Tree specific or microhabitat specific? *Eur. J. Soil Biol.* **2008**, *44*, 220–224. [\[CrossRef\]](#)
31. Klimov, P.B.; O'Connor, B.M.; Chetverikov, P.E.; Bolton, S.J.; Pepato, A.R.; Mortazavi, A.; Tolstikov, A.V.; Bauchan, G.R.; Ochoa, R. Comprehensive phylogeny of acariform mites (Acariformes) provides insights on the origin of the four-legged mites (Eriophyoidea), a long branch. *Mol. Phylogenet. Evol.* **2018**, *119*, 105–117. [\[CrossRef\]](#)
32. Katoh, K.; Rozewicki, J.; Yamada, K.D. MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. *Brief. Bioinform.* **2019**, *20*, 1160–1166. [\[CrossRef\]](#)
33. Capella-Gutiérrez, S.; Silla-Martínez, J.M.; Gabaldón, T. TrimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* **2009**, *25*, 1972–1973. [\[CrossRef\]](#)
34. Weigmann, G. *Hornmilben (Oribatida)*; Goecke and Evers: Keltern, Germany, 2006.
35. Lefort, V.; Longueville, J.-E.; Gascuel, O. SMS: Smart Model Selection in PhyML. *MBE* **2017**, *34*, 2422–2424. [\[CrossRef\]](#)
36. Guindon, S.; Dufayard, J.-F.; Lefort, V.; Anisimova, M.; Hordijk, W.; Gascuel, O. New algorithms and methods to estimate Maximum-Likelihood phylogenies: Assessing the performance of PhyML 3.0. *Syst. Biol.* **2010**, *59*, 307–321. [\[CrossRef\]](#) [\[PubMed\]](#)
37. Ronquist, F.; Teslenko, M.; van der Mark, P.; Ayres, D.L.; Darling, A.; Höhna, S.; Larget, B.; Liu, L.; Suchard, M.A.; Huelsenbeck, J.P. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* **2012**, *61*, 539–542. [\[CrossRef\]](#) [\[PubMed\]](#)
38. Rambaut, A.; Drummond, A.J.; Xie, D.; Baele, G.; Suchard, M.A. Posterior summarization in Bayesian phylogenetics using Tracer1.7. *Syst. Biol.* **2018**, *67*, 901–904. [\[CrossRef\]](#) [\[PubMed\]](#)
39. Maddison, W.P.; Maddison, D.R. Mesquite: A Modular System for Evolutionary Analysis. Version 3.51. Available online: <http://www.mesquiteproject.org> (accessed on 28 June 2018).

40. Halliday, R.B.; Majka, C.G. Clarification of the status of the genus names *Leiodes* Latreille 1796 (Coleoptera), *Liodes* von Heyden 1826 (Acari) and *Neoliodes* Berlese 1888 (Acari). *Zootaxa* **2010**, *2600*, 61–65. [[CrossRef](#)]
41. Schatz, H.; Behan-Pelletier, V.M.; O'Connor, B.M.; Norton, R.A. Suborder Oribatida van der Hammen, 1968. In *Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness*; Zhang, Z.Q., Ed.; Zootaxa 3148; Magnolia Press: Auckland, New Zealand, 2011; pp. 141–147.
42. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **1999**, *401*, 877–884. [[CrossRef](#)]
43. Krause, A.; Pahl, P.; Schulz, G.; Lehmitz, R.; Seniczak, A.; Schaefer, I.; Scheu, S.; Maraun, M. Convergent evolution of aquatic life by sexual and parthenogenetic oribatid mites. *Exp. Appl. Acarol.* **2016**, *70*, 439–453. [[CrossRef](#)]
44. Pahl, P.; Lindl, A.C.; Krause, A.; Scheu, S.; Schaefer, I.; Maraun, M. The tropics as ancient cradle of oribatid mite diversity. *Acarologia* **2017**, *57*, 309–322. [[CrossRef](#)]
45. Schäffer, S.; Koblmüller, S.; Pfingstl, T.; Sturmbauer, C.; Krisper, G. Ancestral state reconstruction reveals multiple independent evolution of diagnostic morphological characters in the “Higher Oribatida” (Acari), conflicting with current classification schemes. *BMC Evol. Biol.* **2010**, *10*, 246. [[CrossRef](#)]
46. Lindo, Z.; Winchester, N.N. A comparison of microarthropod assemblages with emphasis on oribatid mites in canopy suspended soils and forest floors associated with ancient western redcedar trees. *Pedobiologia* **2006**, *50*, 31–41. [[CrossRef](#)]
47. Subías, L.S. Taxonomía y Ecología de los Oribátidos Saxícolas y Arborícolas de la Sierra de Guadarrama (Acarida, Oribatida). Ph.D. Thesis, Universidad Complutense de Madrid, Madrid, Spain, 1977; p. 375.
48. Wallwork, J.A. *The Distribution and Diversity of Soil Fauna*; Academic Press: London, UK; New York, NY, USA; San Francisco, CA, USA, 1976.
49. Gjelstrup, P. Epiphytic cryptostigmatid mites on some beech- and birch-trees in Denmark. *Pedobiologia* **1979**, *19*, 1–8.
50. Krivolutsky, D.A.; Lebedeva, N.V. Oribatid mites (Oribatei, Acariformes) in bird feathers: Non-passerines. *Acta Zool. Litu.* **2004**, *14*, 26–47. [[CrossRef](#)]
51. Krivolutsky, D.A.; Lebedeva, N.V. Oribatid mites (Oribatei, Acariformes) in bird feathers: Passeriformes. *Acta Zool. Litu.* **2004**, *14*, 19–38. [[CrossRef](#)]
52. Lehmitz, R.; Russell, D.; Hohberg, K.; Christian, A.; Xylander, W.E. Wind dispersal of oribatid mites as a mode of migration. *Pedobiologia* **2011**, *54*, 201–207. [[CrossRef](#)]
53. Walter, D.E.; Behan-Pelletier, V.M. Systematics and ecology of *Adhaesozetes polyphyllus* sp.nov. (Acari: Oribatida: Licneremaeoidea), a leaf-inhabiting mite from Australian rainforests. *Can. J. Zool.* **1993**, *71*, 1024–1040. [[CrossRef](#)]
54. Lindo, Z.; Clayton, M.; Behan-Pelletier, V.M. Systematics and ecology of the genus *Dendrozetes* (Acari: Oribatida: Peloppiidae) from arboreal habitats in Western North America. *Zootaxa* **2010**, *2403*, 10–22. [[CrossRef](#)]
55. Bayartogtokh, B.; Itioka, T.; Kitora, H.; Meleng, P.; Shimano, S. New findings of poronotic oribatid mites (Acari: Oribatida) from the high canopy of a Bornean tropical rain forest. *Int. J. Acarol.* **2020**, *46*, 73–82. [[CrossRef](#)]
56. Van der Hammen, L. *Glossary of Acarological Terminology. Vol. I. General Terminology*; Dr. W. Junk Publishers: The Hague, The Netherlands, 1980; p. 244.
57. Alberti, G.; Moreno, A.I.; Kratzmann, M. The fine structure of trichobothria in moss mites with special emphasis on *Acrogalumna lonigpluma* (Berlese, 1904) (Oribatida, Acari, Arachnida). *Acta Zool.* **1994**, *75*, 57–74. [[CrossRef](#)]
58. Norton, R.A.; Palacios-Vargas, J.G. Nueva *Belba* (Oribatei: Damaeidae) de musgos epifitos de Mexico. *Folia Entomol. Mex.* **1982**, *52*, 61–73.
59. Olszanowski, Z.; Clayton, M.R.; Humble, L.M. New species of the genus *Camisia* (Acari: Oribatida): An arboreal mite with enclosed sensilli. *Can. Entomol.* **2002**, *134*, 707–721. [[CrossRef](#)]
60. Schatz, H.; Behan-Pelletier, V. Global diversity of oribatids (Oribatida: Acari: Arachnida). *Hydrobiologia* **2008**, *595*, 323–328. [[CrossRef](#)]
61. Behan-Pelletier, V.M.; Walter, D.E. *Phylleremus* n. gen., from leaves of deciduous trees in eastern Australia (Oribatida: Licneremaeoidea). *Zootaxa* **2007**, *1386*, 1–17. [[CrossRef](#)]
62. Walter, D.E.; O'Dowd, D.J. Beneath biodiversity: Factors influencing the diversity and abundance of canopy mites. *Selbyana* **1995**, *16*, 12–20.

63. Niedbala, W. Oribatei (Acari) of Spitzbergen. *Bull. Acad. Polon. Sci. Série Sci. Biologique* **1971**, *19*, 737–742.
64. Erdmann, G.; Otte, V.; Langel, R.; Scheu, S.; Maraun, M. The trophic structure of bark-living oribatid mite communities analysed with stable isotopes (^{15}N , ^{13}C) indicates strong niche differentiation. *Exp. Appl. Acarol.* **2007**, *41*, 1–10. [[CrossRef](#)]
65. Bauer, D.M.; Bell, K.P.; Nelson, E.J.; Calhoun, A.J. Managing small natural features: A synthesis of economic issues and emergent opportunities. *Biol. Conserv.* **2017**, *211*, 80–87. [[CrossRef](#)]
66. Lindenmayer, D.B. Conserving large old trees as small natural features. *Biol. Conserv.* **2017**, *211*, 51–59. [[CrossRef](#)]
67. Hunter, M.L. Conserving small natural features with large ecological roles: An introduction and definition. *Biol. Conserv.* **2017**, *211*, 1–2. [[CrossRef](#)]



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