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First insights into the morphological development of tarsal claws in terrestrial oribatid mites

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Original research

ABSTRACT

Mites occupy a wide range of ecological niches and are good models to investigate correlations of morphological structures and ecology in arthropods. Here we compare tarsal claw shape of three terrestrial oribatid mite species with different ecological backgrounds. By means of geometric morphometrics we describe shape, size and development of the tarsal claw of the monodactyl mite species *Lamellovertex caelatus* and *Platynothrus peltifer*, and the tridactyl *Melanozetes meridianus.* After analysis of juvenile and adult mites we can distinguish the euryoecious *P. peltifer* and the alpine *M. meridianus* with similar claw curvatures from the saxicolous *L. caelatus* with considerably less curved claws. The claw height of *P. peltifer*, on the other hand, is remarkably higher than in the other two species. Despite these differences, no correlation between claw characteristics and environmental factors can be inferred. During the development of the mites, claw curvature and shape remain constant from protonymph to adult and claw size increases direct proportionally with body growth in all studied species. Neither the monodactyl nor the tridactyl species show any specific changes in claw characteristics.

Keywords geometric morphometrics; geomorph; monodactyl; nymphs; ontogeny; tridactyl

Introduction

Tarsal claws are common attachment devices in oribatid mites, and their number can vary from having one to three on a single leg. Although the number is known for the majority of species, almost nothing is known about the specific shape and size of the claws, and how these are correlated to environmental factors. In a study of oribatid mites from a mangrove forest, it was demonstrated that littoral species occurring on the regularly flooded roots of the trees show considerably larger claws than species living on the trunk or in the canopy (Karasawa and Hijii 2004). Another study confirmed the larger size of littoral species and additionally revealed that the shape of the claws is strongly correlated with the substrate they walk on, i.e., species living on rocky shores possess more robust and stronger curved claws, while species dwelling in mangrove habitats exhibit distinctly less robust and less curved claws (Pfingstl *et al.* 2020). A subsequent investigation including juvenile stages demonstrated that claw shapes are selected early in the development, as claw curvature remains constant throughout ontogeny, while the size increased direct proportionally to increasing body size (Pfingstl and Kerschbaumer 2022). However, these littoral oribatid mites are monodactyl, which means they only possess a single claw on each tarsus, and they are subject to intense wave action and surf, therefore, a strong evolutionary selection for specific claw shapes is assumed (Pfingstl *et al.* 2020). In terrestrial oribatid mites, on the other hand, there are many species showing one, two or three claws on each leg and the knowledge about selective constraints shaping the claws is absent. Terrestrial oribatid mites occur in numerous habitats, like soil, litter, lichens, moss, trees etc. (e.g., Norton and Behan-Pelletier 2009) and thus are exposed to a variety of

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environmental factors and surface structures. If claw shape and size are correlated with these different ecological factors is completely unknown. Moreover, in two and three-clawed species there is a distinct morphological change in the tarsal claw apparatus during ontogeny, because oribatid immatures typically show a single claw, except for rare exceptions in certain primitive Oribatida (e.g., Grandjean 1954). This change in number, from one to multiple tarsal claws, could be accompanied by a change in shape or size too, because the load of the body weight is distributed differently. Ontogenetic changes in claw shapes have yet only been documented in the three-clawed oribatid *Paraleius leontonychus*, where the adults are phoretic on bark beetles using specifically curved median claws to attach to the setae of the host, while immatures remain in the galleries of the beetles and show normally curved claws (Ermilov and Khaustov 2016, Knee 2017). In this case, the change in shape is clearly a result of the different ecological habits of the stages and not of different relative body weights or characteristics. Apart from the above-mentioned studies, knowledge about claws development and their interaction with the respective environment is largely unknown for oribatid mites, especially for terrestrial representatives.

To get a first insight, we performed a geometric morphometric study of the claws of three different terrestrial species, namely *Lamellovertex caelatus*, *Platynothrus peltifer* and *Melanozetes meridianus*, including juvenile material. *L. caelatus* is known to be a saxicolous mite species, preferring temporarily dry mosses and lichens (Bernini 1976, Mahunka and Mahunka-Papp 1995, Krisper *et al.* 2002, Shtanchaeva and Netuzhilin 2003, Weigmann 2006). *P. peltifer*, on the other hand, is a euryoecious species which can be found in a wide range of habitats (Weigmann and Kratz 1981, Siepel 1990, Weigmann 2006) including very wet forests and semiaquatic habitats, like bogs and swamps (e.g., Weigmann *et al.* 2015). The third studied species, *M. meridianus*, can occur in wet mosses and forest litter (Weigmann 2006) but prefers upland bogs and other alpine biotopes (Weigmann *et al.* 2015). *L. caelatus* and *P. peltifer* are monodactyl throughout their lives, whereas *M. meridianus* shows a three-clawed (tridactyl) adult stage, with a prominent median claw and two weak lateral claws.

Aims of the present study were (i) to test if these different species are characterized by different claw shapes, (ii) to check if any ontogenetic changes occur in claw morphology, and (iii) to test if the ontogenetic change from monodactyly to tridactyly also results in a shape change of the median claw.

Material and methods

In our study claw shape data was gathered from 98 adult and juvenile mites belonging to three different oribatid mite species. Specimens were sampled in 2020 and 2022 by the authors or originated from the oribatid mite collection of the Institute of Biology, University of Graz (IBUG), Austria.

Our sample comprised 17 juveniles and 14 adults of *Lamellovertex caelatus* from dry moss on rocks (Ernstbrunn, Lower Austria, Austria); 22 juveniles and 23 *Platynothrus peltifer* adults from a population in a peatbog (Wenigzell, Styria, Austria) and a population from very humid moss (Festenburg, Styria, Austria); and 11 juveniles and 11 adult specimens of *Melanozetes meridianus* from moss cover on rock in alpine grassland (Hochwechsel, Styria, Austria).

In our analyses we only investigated the shape of the middle claw of *Melanozetes meridianus*.

For determination of juvenile developmental stage, we were working with size classes, either taken from literature (Hartenstein 1962, Seniczak 1989) or they were established within this study (*L. caelatus*). Sample information in detail is given in Table 1.

Whole specimens in a dorsal view and claws of the first leg were photographed with a digital microscope (Keyence VHX-5000). We measured body length (BL) (from tip of rostrum to posterior edge of notogaster in lateral view) and claw length (CL) from photographs using VHX-5000_900F Datenkommunikationssoftware Version 1.6.0.0. Claw shape was characterized

Table 1 Sample information with number of investigated specimens.

	Lamellovertex caelatus	*Melanozetes meridianus*	*Platynothrus peltifer*
protonymphs	3	3	1
deutonymphs	11	4	11
tritonymphs	3	4	10
adults	14	11	23

using 2D landmark-based geometric morphometrics. Landmark digitizing was done in TpsDig2 Version 2.31 (Rohlf 2017). The coordinates of three landmarks and 32 semilandmarks were recorded. Claw curvature was calculated from the raw landmark coordinates as angle between three landmarks on inner curvature of the claw (gamma). Detailed description of producing images and gathering measurements and landmarks was given in Pfingstl and Kerschbaumer (2022). All analyses were performed in R, version 4.2.2 (R Core Team 2022). Raw coordinates in tps format were imported in R and subsequent analyses were conducted using the following r-packages: "ggplot2", "geomorph", "Morpho", "shapes" (Adams *et al.* 2022, Baken *et al.* 2021, Schlager 2017, Wickham 2016). Geometric morphometrics heavily relies on Generalized Procrustes Analysis (GPA), which aligns claws onto a standardized coordinate system while controlling for differences in their position, size, and orientation. In the r-package geomorph, GPA can be performed using the gpagen function. Due to the incorporation of semilandmarks, an extra step was added to the Procrustes algorithm. This step involves sliding semilandmarks on curves along their tangent vectors until their positions are optimized to minimize shape differences between specimens as measured by the Procrustes distance (Adams and Otárola-Castillo 2013).

We performed a principal component analysis (PCA) on aligned shape coordinates of only adult specimens to visualize the claw variation among species. Furthermore, claw curvature (gamma) was compared among species. To describe claw development from different juvenile stages to adult mites we produced claw mean shapes of protonymphs, deutonymphs, tritonymphs and adults of species and compared ontogenetic shape change among species by computing regressions of shape (PC1) and log-transformed body length.

Moreover, we investigated the relationship between body size and claw length, claw curvature respectively. Therefore, we produced regressions of claw curvature and claw length to body length in juveniles and adults of investigated mite species. To examine whether the morphological disparity in claw shape among species differs between juveniles, adults and species, we quantified morphological disparity in claw shape estimated Procrustes variance (PV) for each group.

Results

Adults of the oribatid mite species *L. caelatus*, *M. meridianus* and *P. peltifer* show species-specific claws. The first PCA eigenvalue accounted for 48.11% of variation. The ordination of the specimens along the first two principal components (Figure 1a) shows that variation along PC1 is related to species affiliation. The species exhibit clearly distinct mean claw shapes, as depicted in Figure 1b. *Lamellovertex caelatus* has a slender and elongated claw, while the claws of *M. meridianus* and *P. peltifer* are more curved. Especially *P. peltifer* has a very broad and robust claw. *Melanozetes meridianus* does not stand out in its claw shape although it is a tridactyl species. Our claw curvature analysis confirms the impression of mean shape pictures that *L. caelatus* claw is much flatter than the other two species (Figure 1c). The claw curvature of *M. meridianus* and *P. peltifer* is notably lower, measuring around 80°, in comparison to *L. caelatus* which has a curvature of 97°.

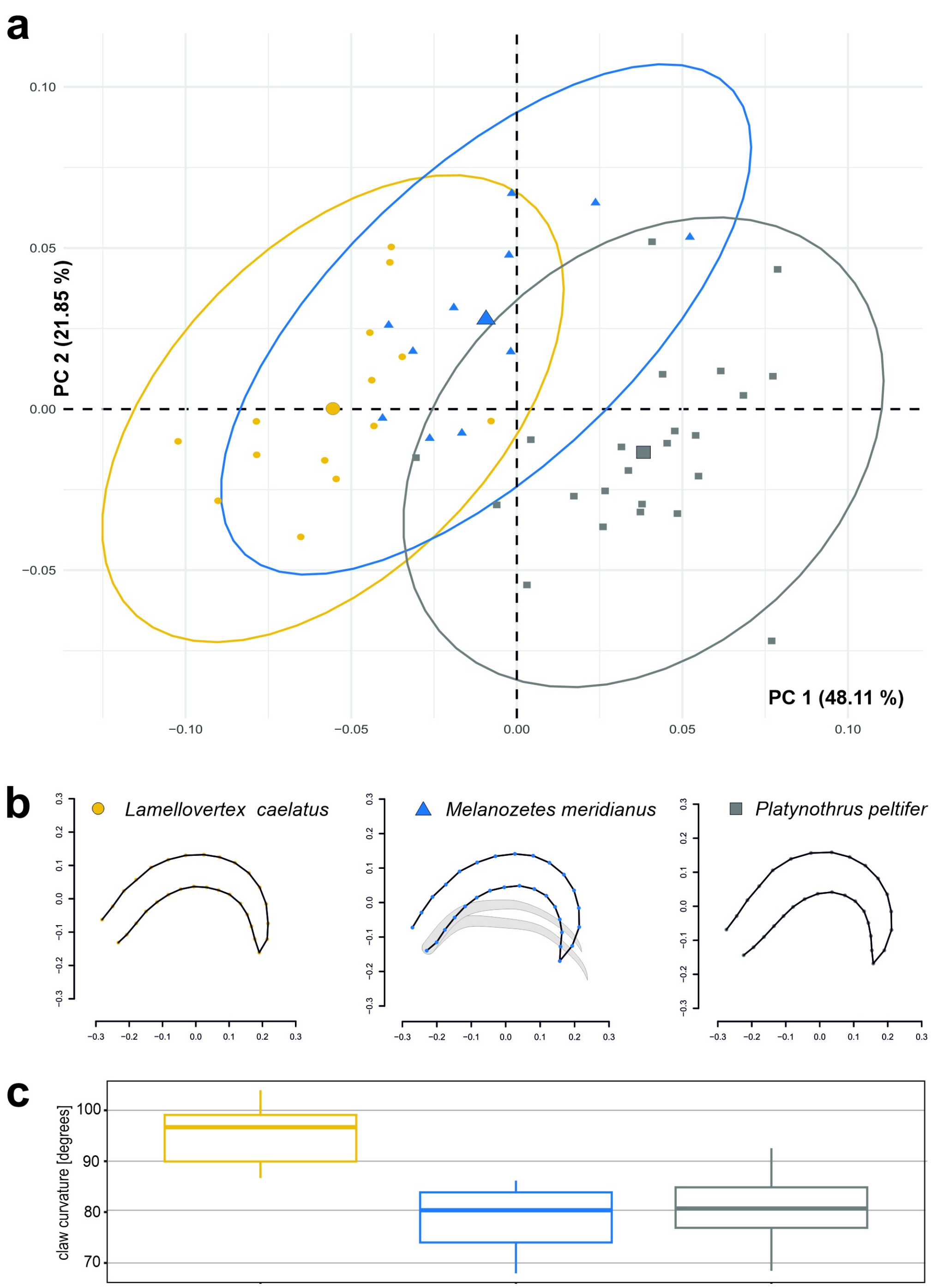

Figure 1 Claw shape of adults: a – PCA including adult individuals of the three species *L. caelatus, M. meridianus* and *P. peltifer*; b – mean shapes of species adult specimens; c – claw curvature of the three species. Box plots represent the median (central line), 25th and 75th percentiles (box), and the minimum and maximum points (whiskers).

Concerning the ontogenetic growth from protonymph to adult mite, claw shape does not change drastically among the different nymphal states in none of the species (Figure 2a–c). There are no marked differences in claw shape between the monodactyl juveniles and the middle claw of their tridactyl adults of *M. meridianus*.

There is a positive linear correlation of claw length and body length. Claws get bigger with

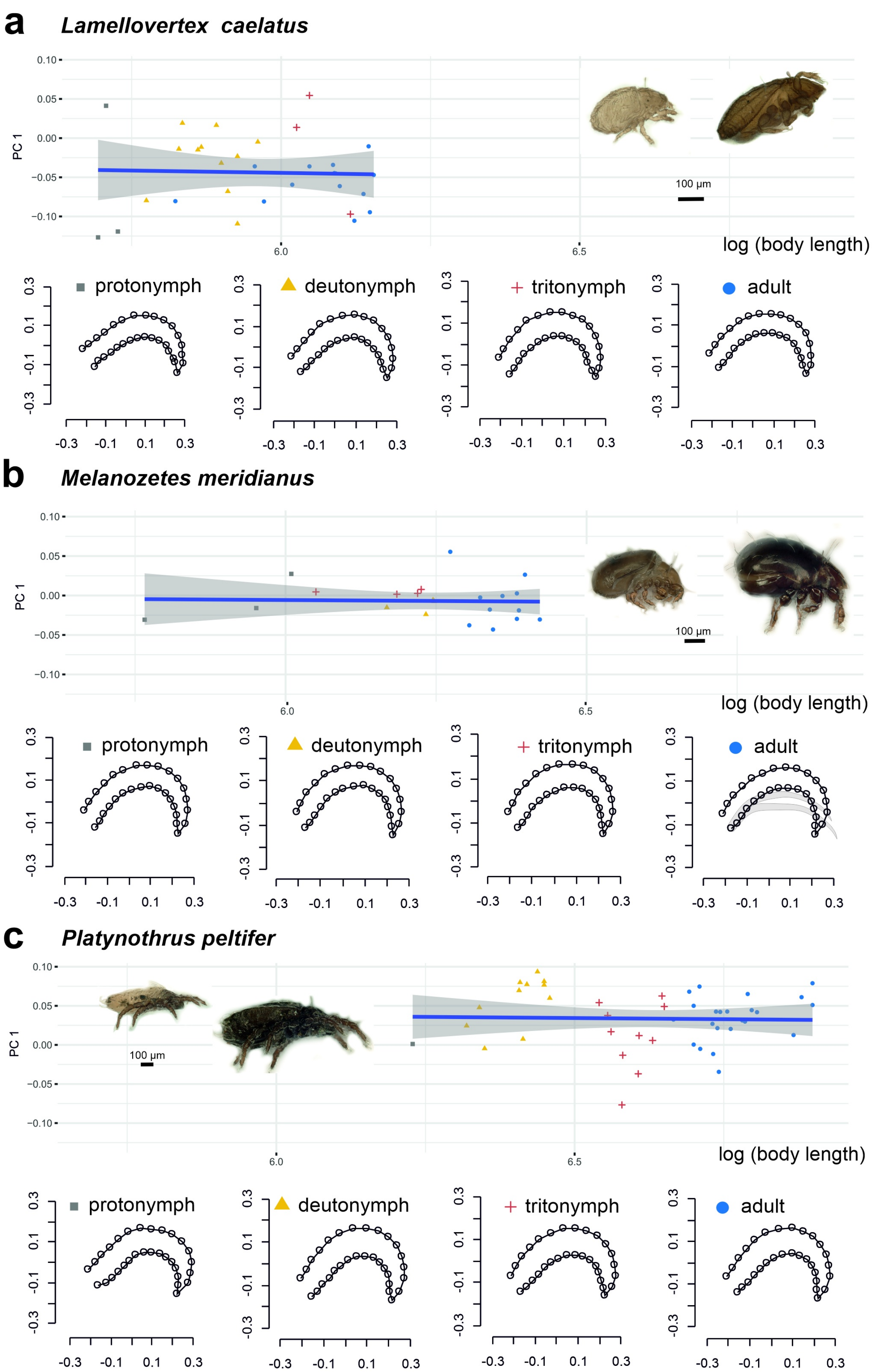

Figure 2 Development of claws: Correlation of claw shape (PC1) to body length with linear regressions. Lateral photographs of nymphal and an adult mite. Claw mean shapes of every juvenile and adult life stage in the three investigated species a – *L. caelatus*; b – *M. meridianus* and c – *P. peltifer*.

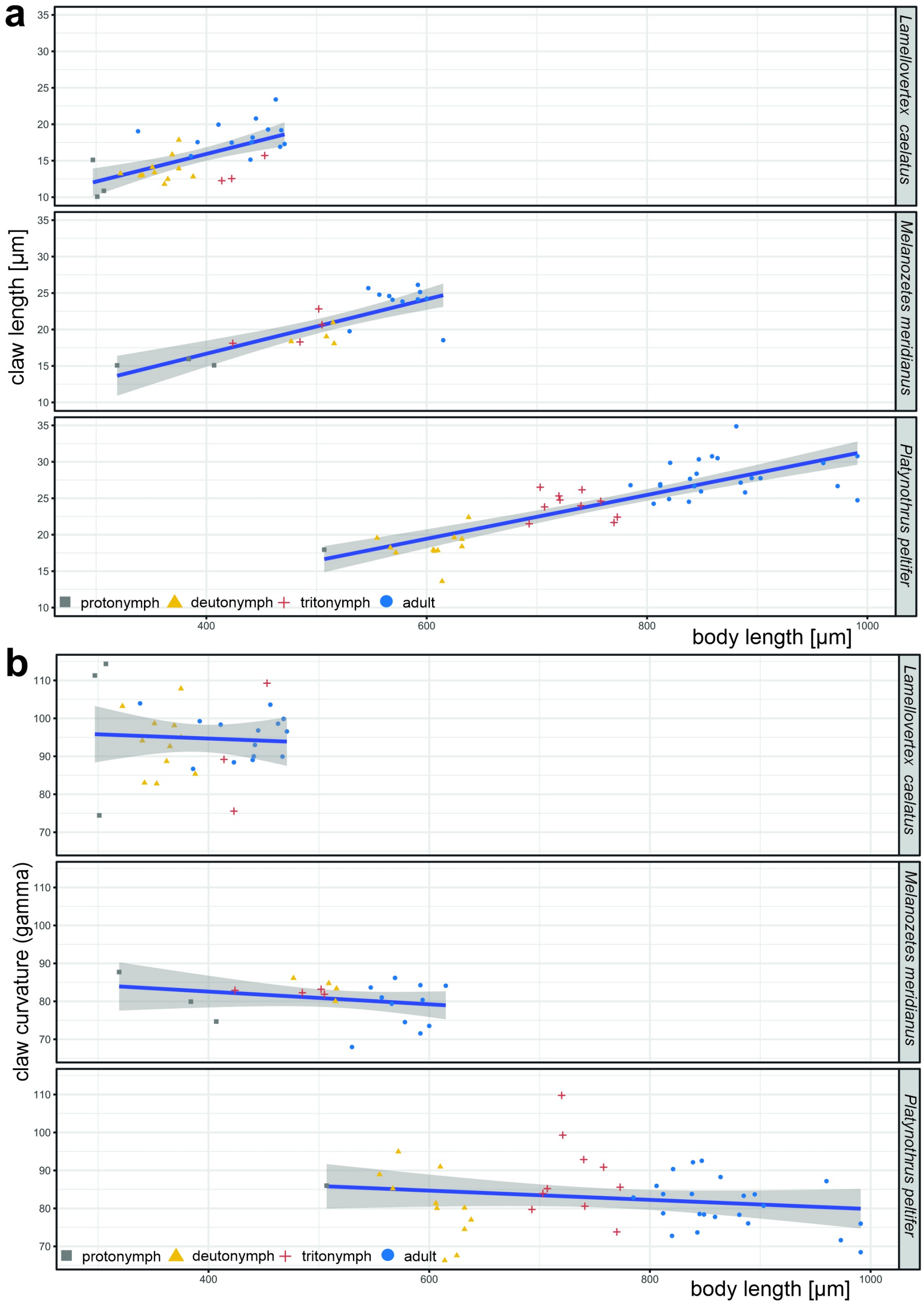

Figure 3 Claw length and curvature in ontogeny: a – Claw length and body size. Correlation of claw length to body length of specimens from larva to adult stadium in different species; b – Claw curvature and body size. Correlation of claw curvature to body length of specimens from larva to adult stadium in different species.

increasing mite size along all life stages (Figure 3a). However, claw curvature is mostly static along different life stages in all three species (Figure 3b).

Compared to *M. meridianus* and *P. peltifer,* the variation in claw shape is greatest in *L. caelatus*, expressed by the highest Procrustes variances in most immature stages as well as in adults (Table 2).

Table 2 Claw disparity. Procrustes variance of different species and stadiums.

	Lamellovertex caelatus	*Melanozetes meridianus*	*Platynothrus peltifer*
protonymphs	0.016514017	0.002992891	0.003648804
deutodymphs	0.005627859	0.003095423	0.006447517
tritonymphs	0.006638325	0.001920925	0.004848923
adults	0.006132447	0.004282586	0.003652948
juveniles	0.007727263	0.003273865	0.005593669

Discussion

In monodactyl intertidal oribatid mites there is a clear correlation between claw shape and used microhabitat (Pfingstl *et al.* 2020). Strong selection acting on these claws has resulted in the loss of phylogenetic signal (Kerschbaumer and Pfingstl 2021), which means claw shapes of closely related species are distinctly different if they inhabit different microhabitats. In the present study, the terrestrial species also show diverging claw shapes, but assigning shapes to a specific microhabitat or lifestyle is yet unfeasible. *Lamellovertex caelatus* is classified as a saxicolous species living in dry mosses and lichen (e.g. Krisper *et al.* 2002, Weigmann 2006) and shows a significantly less curved claw and higher intraspecific variation than the other two species. Claw curvature is almost the same in *M. meridianus* and *P. peltifer*. Both species belong to completely different systematic groups and their ecologies do not really match. *Platynothrus peltifer* is euryoecious and occurs in diverse grassland and forest types, *M. meridianus*, on the other hand, prefers upland bogs and alpine biotopes (Weigmann 2006, Weigmann *et al.* 2015). However, both species are generalists and are often found in very humid semiaquatic environments (Weigmann 2006, Behan-Pelletier and Eamer 2007). The claw height (dorsal to ventral edge of claw) of *P. peltifer* is considerably larger than in *M. meridianus* and higher claws are considered to be more resistant to break when vertical forces are applied (Ribas *et al.* 2004). *Platynothrus peltifer* shows a distinctly larger body size and thus may also require more robust claws. At the moment, all the above statements are pure conjecture, much more data from other species, and habitats are needed to verify. Although present data indicate that claw features do vary between species, the reasons for the different shapes remain unclear.

The inclusion of juvenile material demonstrates that claw shapes and curvatures do not significantly change during development in the investigated three terrestrial species. This conforms to the claw ontogeny of intertidal oribatid mites (Pfingstl and Kerschbaumer 2022) and indicates that there is no ecological shift between juvenile and adult stage, i.e., immatures dwell in the exact same environment and show the same lifestyle. In *Paraleius leontonychus* immatures dwell in the galleries of bark beetles while the adults use the bark beetles as transport hosts to reach new trees (e.g., Knee 2017). The change from a non-phoretic to a phoretic lifestyle is accompanied by a distinct modification of the adult claw, i.e., the normal juvenile claw is transformed into a strongly hooked claw which allows attaching to the setae of the beetle (Ermilov and Khaustov 2016). Other changes in lifestyle, as for example shown in euphthiracaroid and phthiracaroid mites, where immatures are exclusively endophagous in plant tissues but leave the tissues to forage outside as adults (Norton and Behan-Pelletier 2009), may also be linked to changes in claw morphology. In contrast to the present investigation, studies on these ecology shifting groups may reveal significant variations in claw development.

The developmental change from a single tarsal claw to three claws in the adult in *M. meridianus* does not affect the shape of the median claw, which is homologous to the single claw of the immatures (Grandjean 1941). The lateral claws of adult *M. meridianus* are fairly slender and thus probably not able to carry heavy loads. Consequently, they might help to increase friction or provide balance, but the median claw carries the weight more or less alone, and this could explain why there is no change in median claw characteristics. It is assumable that tridactyl species with weak lateral claws follow this developmental pattern, but tridactyl species with strong lateral claws, e.g. *Cymbaeremaeus cymba* or *Micreremus brevipes*, may diverge from that scheme.

The present research represents only a preliminary insight into the correlation between claws and their environment in terrestrial oribatid mites, because there is still a large diversity of habitats, ecologies and basic claw morphologies which need to be studied in detail.

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