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Claw shape variation in oribatid mites of the genera *Carabodes* and *Caleremaeus*: Exploring the interplay of habitat, ecology, and phylogenetics

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Background. Claws are a commonly observed biological adaptation across a wide range of animal groups. They serve different functions and their link to evolution is challenging to analyze. While there are many studies on the comparative anatomy and morphology of claws in reptiles and birds, knowledge about arthropod claws, particularly oribatid mites, is still limited. Recent research on intertidal oribatid mites has shown that claw shape is strongly correlated with microhabitat and is subject to ecological selective pressures. However, the selective constraints shaping claws in terrestrial oribatid mites are still unknown. **Methods.** In this study, 300 specimens from 12 different species and two genera were examined. Geometric morphometrics were used to quantify claw length and curvature, and to analyze two-dimensional claw shape. In combination with molecular phylogenetic analyses of investigated populations phylogenetic signal was quantified within genera using Blomberg's K and random replicates. Additionally, ecological information on the investigated species was gathered from previous studies and compiled into tables. **Results.** The claw shapes of *Carabodes* species vary moderately, with the three species *C. reticulatus*, *C. rugosior* and *C. tenuis* deviating the most from the others. These three species are only found in a small number of habitats, which may require a more specialized claw shape. Our results show that there is a phylogenetic influence on claw shape in *Carabodes* but not in *Caleremaeus*. Additionally, habitat specificity and lifestyle were found to have ecological impact on claw shape in both genera. The present results demonstrate that characteristics of the claws of terrestrial oribatid mites are correlated with ecology, but this correlation is apparently weaker than in intertidal oribatid mites that are prone to strong external forces.

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Abstract

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Methods. In this study, 300 specimens from 12 different species and two genera were examined. Geometric morphometrics were used to quantify claw length and curvature, and to analyze two-dimensional claw shape. In combination with molecular phylogenetic analyses of investigated populations phylogenetic signal was quantified within genera using Blomberg's K and random replicates. Additionally, ecological information on the investigated species was gathered from previous studies and compiled into tables.

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Keywords – terrestrial; geometric morphometrics; phylogenetic signal; barcodes, euryoecious lifestyle

Introduction

Claws are prevalent biological adaptations found in a diverse range of animal groups, including arthropods, birds, reptiles, and large mammals. Those structures can serve various functions (Tinius & Russell, 2017). The link between claw morphology, its function and evolution are difficult to quantify, analyze, and interpret. Because claws are the most common grip mechanism in vertebrates (Zani, 2000) there are many studies about the comparative anatomy and morphology of these structures mainly in reptiles (Zani, 2000; Tulli et al., 2009; D'Amore et al., 2019; Alibardi, 2020; Mann et al., 2021, Tulli et al. 2022) and birds (Feduccia, 1993; Hahn et al., 2014).

The study of arthropod claws, on the other hand, is still at the very beginning and relatively ~~few~~ is known about these important attachment devices. Particularly knowledge about claws of oribatid mites, presents many unanswered questions regarding their function as attachment devices. Pfingstl, Kerschbaumer & Shimano (2020)~~,~~ investigated the claw shapes of numerous intertidal oribatid mites from various habitats by means of geometric morphometrics and results demonstrated that claw shape strongly correlates with the microhabitat. Species living on rocky shores have remarkably high and strongly curved claws, whereas species from mangrove habitats have significantly lower and less curved claws. Euryoecious species can dwell in a wide range of habitats and show an intermediate claw type. An additional molecular genetic investigation of intertidal species showed that there is no phylogenetic signal in claw shape, which indicates that ecology has acted as one of the primary selective forces in the diversification of claw shapes in intertidal oribatid mites (Kerschbaumer & Pfingstl, 2021). Juveniles of th~~is~~ arthropods exhibit habitat-specific claws. While claw length grows in direct proportion to increasing body size, claw curvature is almost static during development (Pfingstl & 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, Kerschbaumer & Shimano, 2020).

In terrestrial oribatid mites there are, next to monodactyl species, also species with two or three claws on each leg, and nothing is known about the selective constraints shaping these claws. Most oribatid species associated with above-ground habitats in forests are considered to have evolved from lineages associated with the forest-floor soil and litter, and thus may have evolved modifications in their morphology in relation to habitat structure and other modifications in life-history traits (e.g., Behan-Pelletier & Walter, 2000). A recent review article (Pfingstl, 2023 submitted) highlighted a huge variety of claw expressions in oribatid mites and demonstrated that almost nothing is known about the interaction of these claws with ~~the~~ specific environments. Despite ongoing research, little is currently known about the precise reasons behind the development of specific claw formations or the existence of varying numbers of claws.

In this work, we performed qualitative and quantitative analyses to explore possible links between morphological variation and both ecological factors and phylogenetic constraints that could have driven the evolution of claws of monodactyl oribatid mite species in terrestrial habitats. We examined several species from Austria belonging to the two oribatid mite genera *Carabode*s and *Caleremaeus*.

Carabodes (Acari, Oribatida Carabodidae), a morphologically characteristic oribatid mite genus was originally proposed by Koch in 1835. The type species for this genus is *Carabodes coriaceus* (Koch, 1835). Currently, the genus includes four subgenera and 135 species that are distributed worldwide (Subías 2022). These mites can be found in various habitats, including soil, litter, mosses, lichens, fungi, and on the bark of twigs, branches, and tree trunks. They can also occur on rock surfaces and in rotten wood (Reeves, 1987; Reeves & Behan-Pelletier 1998). As panphytophages, they are not specialized feeders, which accounts for their adaptability to such a wide range of habitats (Reeves, 1987). In Weigmann's (2015) work on the distribution and ecology of oribatid mites in Germany, one can discover the specific habitats and lifestyles of each *Carabodes* species. Presently, there are 14 species of *Carabodes* known to occur in Austria (Krisper et al., 2017).

The genus *Caleremaeus* has recently been reexamined by Norton & Behan-Pelletier (2020), who listed four valid species: *Caleremaeus monilipes* (Michael, 1882) from the Palaearctic region, as well as *C. retractus* (Banks, 1947), *C. arboricolus* (Norton & Behan-Pelletier, 2020) and *C. nasutus* (Norton & Behan-Pelletier, 2020) all found in North America. The palearctic species *Caleremaeus monilipes* is highly adaptable and can live in a wide range of environments. It has been observed in various habitats across Europe, including alluvial forests, alpine meadows, spruce forests, deciduous forests, dry grasslands, and scree slopes (Ayyildiz et al., 2011, Schatz, 1983). The species is known to colonize a diverse array of substrates, such as soil, litter, mosses, lichens, decaying wood, and algae. In addition to its ability to live in different habitats and substrates, *C. monilipes* has also demonstrated a remarkable vertical distribution, ranging from colline to alpine regions. In Austria, it has been recorded at elevations exceeding 2600 meters above sea level

(Schatz, 1979). In 2021, however, Lienhard & Krisper found out that *C. monilipes* in central and southern Europe indeed comprises six different species, with five species new to science: *Caleremaeus mentobellus*, *C. lignophilus*, *C. alpinus*, *C. elevatus*, and *C. hispanicus*, and all these species differ by their ecological preferences and needs.

We chose members of these two oribatid mite genera for our study because they all show a single tarsal claw, have similar lifestyles, and species of the two different genera could sometimes even be found in the same sample. Both genera might be classified as euryoecious, but certain individual species within these genera inhabit different microhabitats. We want to investigate which claw shapes exist in all these species and find out if they differ between the taxa. If differences are present, are these correlated with diverging ecologies or are they results of phylogenetic relatedness. Basically, this study should give us first insights into the interplay of claw shapes and environment in purely terrestrial oribatid mite species. What ~~shapes~~ claw~~s of~~ terrestrial species and what is the role of ecology?

Material and methods

Sample and data collection

We examined 300 specimens from 12 different species throughout the investigation (Table 1). We collected data on the genus *Caleremaeus* (Eremaoidea), including samples from three distinct species: *Caleremaeus alpinus, Caleremaeus mentobellus*, and *Caleremaeus lignophilus;* originating from nine different populations. We also gathered data on mites from the genus *Carabodes* (Carabodoidea)*,* which comprised samples from 18 populations belonging to eight different species, namely *Carabodes areolatus, Carabodes coriaceus, Carabodes labyrinthicus, Carabodes marginatus, Carabodes ornatus, Carabodes reticulatus, Carabodes rugosior* and *Carabodes tenuis.* We included two populations of the species *Odontocepheus elongatus* (Carabodoidea) as closely related outgroup in our study.

Geometric morphometrics

To perform claw morphometrics, we embedded each specimen in a microscopic slide using lactic acid and then photographed them in dorsal view with a digital microscope (Keyence VHX-5000). Subsequently, we applied pressure to crush the specimen so that the remaining legs with the claws were caught in a lateral position between the object carrier and object slide. To standardize the process, we only photographed and analyzed the claw of the first leg. Using VHX-5000_900F Datenkommunikationssoftware Version 1.6.0.0, we measured the body length and claw length from these photographs. We recorded the x,y coordinates of three landmarks (LM) and 32 semilandmarks using TpsDig2 (Vers.2.31, Rohlf, 2017). We placed 16 semilandmarks equidistantly along the claw edges dorsally between landmarks 2 and 3, and ventrally between landmarks 1 and 3. We provide a scheme for the positioning of landmarks in Pfingstl, Kerschbaumer & Shimano (2020). To enhance the analysis, we eliminated four semilandmarks that reflected positions like LM 1-3, resulting in three landmarks and 28 semilandmarks. The claw curvature was calculated from raw landmark coordinates as the angle between the three landmarks on the inner curvature of the claw (gamma). We analyzed two-dimensional claw shape in R with the package ‘geomorph’ (Baken et al., 2021). We did generalized procrustes analysis (GPA) on our landmarks and semi-landmarks (using function gpagen) and performed principal component analyses (PCA) of shape variation on aligned shapes (gm.prcomp). We tested for differences in shape disparity between populations across all species and both genera using the function morphol.disparity (in ‘geomorph’).

Phylogenetic signal

Extraction of total genomic DNA from single individuals followed the Chelex method given in Schäffer et al. (2018). Standardized protocols were applied for PCR amplification, purification and sequencing (Schäffer et al., 2010, 2018). We sequenced the standard COI barcoding region (658 bp) for one specimen of each studied population and verified all sequences by comparisons with known ones from GenBank. The two final datasets included eighteen individuals for *Carabodes* respectively, nine for *Caleremaeus*. Maximum likelihood phylogenies were obtained using IQ-TREE (Nguyen et al., 2015) on the platform PhyloSuite v.1.2.2 (Zhang et al., 2020) under Edge-linked partition model for 5000 ultrafast bootstraps (Minh et al., 2013). PartitionFinder2 (Lanfear et al., 2017) was used to select the best partitioning scheme and evolutionary models for 3 pre-defined partitions (partitioning by codons) under greedy algorithm. All calculated trees are unrooted. All alignments are available in the Supplemental Material. All sequences used in these reconstructions are available from GenBank under the accession numbers OQ970666 to OQ970692.

Based on the phylogenies generated by IQ-TREE we quantified the phylogenetic signal of claw shape within the two mite genera using Blomberg’s K (Blomberg et al., 2003) with 9999 random replicates using the R package geomorph (Adams & Otárola-Castillo, 2013) and the physignal() function.

Our raw data and R code files are available in the Supplemental Materials.

Ecological information

To get insights into ecology of the genus *Carabodes*, we created a table (Table 2b) using data of Weigmann et al. (2015), where we list the number of habitats and possible living styles for each investigated *Carabodes* species. We did the same for the genus *Caleremaeus* based on data from Lienhard & Krisper, (2021) (Table 2a).

Results

The body size of *Carabodes* species ranges from approximately 400-800 µm. The smallest species examined is *C. tenuis*, measuring around 400 µm, while the largest is *C. coriaceus*, reaching up to 800 µm (Figure 1a). Populations within each species vary slightly in size but are not significantly different. Claw size correlates well with body size in most species. The ratio of claw length to body length (cl/bl) is conspicuously higher in only two species, namely *C. coriaceus,* and *C. reticulatus*. A regression plot of the two sizes (Figure S2) shows that there is an apparent jump in claw size at a certain body size. Regarding the angle gamma, measurements range from 75 to 105 degrees. It can be observed that *C. reticulatus* and *C. marginatus* have the most widely open claws. On average, *C. rugosior* has the most curved claw with a curvature angle of around 85°. The results of the principal component analysis (PCA) conducted on the *Carabodes* dataset indicate that the first two principal components (PC1 = 30.6% and PC2 = 22.8%) account for approximately 52% of the total variation. While there is a considerable overlap between individuals of different species, species means are positioned differently in morphospace, with most species clustering around the intersection of PC1 and PC2 (Figure 1a). Notably, the meanshape of the outgroup species *O. elongatus* is located at the highest positive position on PC2, exhibiting a slightly different claw shape than the seven *Carabodes* species. The ordination of the specimens along the first two principal components shows that variation along PC2 is mainly related to species affiliation. The corresponding shape changes in the positive or negative direction of PC axis 2 show us a more compact and hunchbacked form of the species that are positioned in the positive range of PC axis two, and a slightly more elongated, drawn-out claw of the species that appear in the negative range.

The body size of *Caleremaeus* species ranges from approximately 315-400 µm, with the smallest species examined being *C. lignophilus* at around 340 µm, and the largest being *C. alpinus* (380 µm) and *C. mentobellus* with a body size of about 360 µm (Figure 2a). While populations within each species vary slightly in size, they are not significantly different. Notably, the ratio of claw length to body length (cl/bl) is lower in *C. alpinus*. In terms of the angle gamma, measurements range from 80 to 100 degrees, with no marked differences observed among the three species, only *C. alpinus* shows a slightly lower gamma in all three populations. Results of the principal component analysis (PCA) conducted on the *Caleremaeus* dataset indicate that the first two principal components (PC1 = 32.34%, PC2 = 21.38%) account for approximately 54% of the total variation. While there is considerable overlap between individuals of different species, species means are positioned differently in morphospace. *C. lignophilus* and *C. mentobellus* cluster closely together, while *C. alpinus* exhibits a different claw mean shape (Figure 2b). The corresponding shape changes in the positive or negative direction of PC axis 2 indicate a more curved form of the species that are positioned in the positive range of PC axis two, and a slightly more elongated claw of the species that appear in the negative range. There are no marked differences in claw disparity among species in both genera (Figure S1.)

Phylogenetic influence

By examining the scatterplot in Figure 3, which shows the average shapes of different populations of *Carabodes*, we can see that there are distinct groupings. When compared to the phylogenetic tree of the same populations, similarities can be seen. The populations of the species *C. marginatus*, *C. reticulatus*, *C. coriaceus*, and *C. ornatus* cluster together, while the remaining species form distinct groups. Furthermore, running the K*mult* method in R confirms presence of a phylogenetic signal in claw shape for *Carabodes* ($K= 2 \times e^{-5}$, $P=0.0036$). Despite this phylogenetic influence in claw shape it is possible to observe that there are species standing out in terms of their claw shape (Figure 1a, Figure 3). *C. rugosior*, *C. reticulatus* and *C. tenuis* exhibit claw shapes that deviate from the mean.

For *Caleremaeus* we get another picture, regarding phylogenetic influence. The phylogenetic tree of *Caleremaeus* populations demonstrates that we have distinct species, with populations of each clustering together (Figure 4). But in terms of their claw shapes, populations of the same species are not more similar to each other than they are to populations of other species, indicating the absence of a phylogenetic signal. Confirming these findings by using Blomberg's K, we find no phylogenetic signal in claw shape in the genus *Caleremaeus* ($K= 6 \times e^{-5}$, $P=0.666$).

Habitat specificity/ecological impact on claw shape

For our eight investigated *Carabodes* species we found 23 different habitat types and five types of lifestyles in the above-mentioned literature (Table 2). All species could be assigned to the lifestyle of "soil dwellers". All but one could be denoted as arboricolous, as bark dwellers. While

Carabodes labyrinthicus was found in a high number of 22 different habitats, *C. tenuis, C. reticulatus* and *C. rugosior*, with two to four different environments seem to be more specific in their choice of habitat. The investigated *Caleremaeus* species could be assigned to three different lifestyles, namely arboricolous - as bark dweller, soil dweller and epilithic – on rocks, stones and walls. *C. alpinus* was found in seven different habitats while *C. lignophilus* was exclusively found in deadwood.

When we examine all species of both genera in a principal component analysis (PCA), we see that the claw shapes of individual species and genera are not very different. (Figure 5). Although species of *Caleremaeus* are located more ~~at the edge~~, they are still within the morphospace of *Carabodes*. Based on the claw shapes of the respective species, we can see that they are very similar. Only the species *C. rugosior*, *C. reticulatus* and *C. tenuis* exhibit somehow exceptional forms. When considering habitat specificity (Table 2) a correlation between "specialized claw" and "stronger habitat specificity" can be identified for *C. rugosior*, *C. reticulatus* and *C. tenuis*.

Discussion

The two mite genera, *Caleremaeus* and *Carabodes*, can both be classified as euryoecious, but within the genus, there is some habitat specificity. In terms of habitus all investigated *Carabodes* species and the examined closely related *Odontocepheus elongatus* are easily distinguishable based on their overall morphology. The claw shape varies moderately, with *Odontocepheus elongatus* standing out due to its much more curved and compact claw than *Carabodes* species. The claw shapes of the three *Carabodes* species *C. reticulatus*, *C. rugosior* and *C. tenuis* deviate the most from the others, and interestingly these three species are only found in a small number of habitats (see table 2). This higher habitat specificity might require a more specialized claw shape but how this “specificity” looks like is not easy to define. After Weigmann et al. (2015), *C. tenuis* is restricted to bark and soil in coniferous (mixed) forests and our study samples are exclusively from deadwood taken in coniferous (mixed) forests. It is possible that this narrow niche has resulted in the strongly deviating claw shape of this species, their claws are relatively large for the small body size and show a moderate curvature. We observed a similar phenomenon for *Lamellovertex caelatus* in a former study (Kerschbaumer & Pfingstl, 2023), where the claw shape of this saxicolous species living only in dry mosses and lichens is significantly less curved than in more euryoecious species. *Carabodes reticulatus* and *C. rugosior* were sampled on bracket fungi in this study. Hågvar et al. (2014) found *C. reticulatus* only in dead sporocarps in a spruce forest. They suggest that *Carabodes* species found in fruiting bod~~y~~ of wood-decay fungi are primarily living in decomposing wood where fungal food is limited, but they use the opportunity to multiply efficiently in energy-rich sporocarps if these are available. On the other hand, *C. rugosior* was never found in sporocarps within the study of Hågvar et al. (2014) and is described as inhabitant of soil near tree bases (Sellnick & Forsslund, 1952; Weigmann, 2006). Their controverse claw shapes, with *C. rugosior* having a more curved claw (gamma difference ~10°) than *C. reticulatus*, may reflect this microhabitat difference. Interestingly, Weigmann et al. (2015) did not describe any *Carabodes* species as fungicol. The other *Carabodes* species which can be found in a noticeably wide range of different habitats (see table 2), like *C. labyrinthicus*, show claw shapes that are placed more in the center of the morphospace, i.e. they are neither strongly curved, nor extremely weakly curved, they are intermediate so to speak. The same phenomenon was observed in intertidal oribatid mites, where species with wider ecological ranges show also intermediate claw shapes (Pfingstl, Kerschbaumer & Shimano, 2020). Apparently, extreme claw shapes are not selected for if species should be able to dwell in a wider array of microhabitats. Apart from these results, we could also observe that the claws of the first leg of *Carabodes* species are basically distinctly smaller than the claws of the remaining legs. The reason for this apparent size difference is unknown and needs further detailed investigation.

However, it seems that phylogenetic relationship between species has a stronger influence on claw shape in *Carabodes* than the habitat. Species of the same genetic cluster are more similar in terms of their claw shape. We could quantify a phylogenetic signal, indicating that ecology does not play the biggest role in shaping *Carabodes* claws, as was shown for example, in oribatids of the littoral zone (Kerschbaumer & Pfingstl, 2021).

Our results concerning the genus *Caleremaeus* support the hypothesis of Lienhard & Krisper (2021), who postulate a strong association of the different *Caleremaeus* species to specific microhabitats. They found a clear genetic differentiation between species of neighboring microhabitats, but not between distant microhabitats of the same type, thus a high degree of habitat specialization is assumed. In respect of claw shapes, no apparent pattern can be found correlating this morphological structure with habitat. *Caleremaeus alpinus* which is restricted to subalpine and alpine habitats differs the most from *C. lignophilus* and *C. mentobellus* in terms of claw shape. Their claws are noticeably more curved and smaller in size, which results in a lower ratio of claw length to body length when compared to the other two species, *C. lignophilus* and *C. mentobellus* (see Figure S3). *Caleremaeus alpinus* can be found in a variety of microhabitats and therefore it is surprising that their claws are not intermediate like the claws of euryoecious *Carabodes*. But *C. alpinus* is restricted to higher altitudes and thus could be adapted to low temperatures and to a short active period and therefore claws might be shaped for faster and more effective movement. However, we have no evidence for such a correlation and need much more data in this respect. *Caleremaeus lignophilus*, on the other hand, is a clear specialist, as it can only be found in deadwood. Their claws are the least curved in comparison to the other species (*Carabodes* included) and a weaker curvature is supposed to be a feature of claws mainly used on soft substrates, at least in intertidal oribatid mites (Pfingstl, Kerschbaumer & Shimano, 2020). Dead and rotten wood is clearly a soft substrate and consequently the weaker curvature of *C. lignophilus* claws may be an adaptation to walking on this underground. Nevertheless, the comparison of only three species with partly overlapping ecologies does not allow to infer any distinct patterns of correlation between claw shape and habitat. In contrast to *Carabodes*, mapping the claw shapes onto the molecular phylogeny of populations of these *Caleremaeus* species results in a lack of a phylogenetic signal. These findings would suggest that the claw morphology of *Caleremaeus* is likely an adaptation of single species to their unique habitat and lifestyle but given the very low number of investigated species of this genus, the present lack of a phylogenetic signal must be regarded with caution.

Comparing the claw shapes of *Caleremaeus* and *Carabodes*, results in surprisingly similar shapes with relatively few divergences between these ~~far~~ distant related genera (see Figure 5). Even though single species may show large ecological variances, most of the species occupy similar habitats, and *Caleremaeus* and *Carabodes* were often found together in the exact same sample. This indicates that the overlapping habitat preferences result in similar claw shapes in these taxa originating from different superfamilies.

Conclusions

The present results demonstrate that characteristics of the claws of terrestrial oribatid mites are correlated with ecology, but this correlation is apparently weaker than in intertidal oribatid mites that are prone to strong external forces. Terrestrial habitats are less exposed to wind and water than coastal environments and falling of a lea~~ve~~ is not as dramatic for the mites as being washed away into the open ocean. Therefore, selection on claw shape may work to a lesser extent in terrestrial mites. The nature of the correlation of claws with other factors remains largely unclear due to the complex microhabitat features of terrestrial habitats. Further detailed studies on terrestrial species being specialized to certain microhabitats may reveal which claw shapes may be preferable for specific environments.

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Table 1(on next page)

Sample information

Caleremaeus	pop ID	location		habitat	date	n	leg.
Caleremaeus alpinus	CIA22	Festenburg	Seebach, forest, 1150m	moss on rock	Okt.20	6	Kerschbaumer
Caleremaeus alpinus	CIA40	Weinebene	1800m	moss on rock	Aug.20	8	Bodner
Caleremaeus alpinus	CIA76	Moschkogel	Weinebene, 1750m	alpin meadow	Jul.22	10	Fröhlich
Caleremaeus lignophilus	CIA58	Festenburg	Dorfstatt, forest ,900m	deadwood	Sep.21	10	Kerschbaumer
Caleremaeus lignophilus	CIA69	Weizklamm	Jägersteig, 600m	deadwood	Mai.22	9	Kerschbaumer/Pfingstl
Caleremaeus lignophilus	CIA74	Weizklamm	Jägersteig, 600m	deadwood	Mai.22	10	Kerschbaumer/Pfingstl
Caleremaeus mentobellus	CIA71	Weizklamm	Jägersteig, 600m	moss on rock	Mai.22	9	Kerschbaumer/Pfingstl
Caleremaeus mentobellus	CIA72	Weizklamm	Jägersteig, 600m	moss on rock	Mai.22	7	Kerschbaumer/Pfingstl
Caleremaeus mentobellus	CIA73	Weizklamm	Jägersteig, 600m	moss on rock	Mai.22	6	Kerschbaumer/Pfingstl
Carabodes	pop ID	location		habitat	date	n	leg.
Carabodes areolatus	CIA03	Graz	Lechwald, forest	deadwood	Dez.20	18	Kerschbaumer/Pfingstl
Carabodes areolatus	CIA55	Festenburg	Dorfstatt, forest	deadwood	Jun.21	9	Kerschbaumer
Carabodes areolatus	CIA56	Festenburg	Dorfstatt, forest	deadwood	Jun.21	9	Kerschbaumer
Carabodes areolatus	CIA74	Weizklamm	Jägersteig, 600m	deadwood	Mai.22	10	Kerschbaumer/Pfingstl
Carabodes coriaceus	CIA09	Vorauer Schwaig	alp, 1500m	lichen on tree	Aug.20	15	Kerschbaumer
Carabodes labyrinthicus	CIA09	Vorauer Schwaig	alp, 1500m	lichen on tree	Aug.20	10	Kerschbaumer
Carabodes labyrinthicus	CIA21	Vorauer Schwaig	alp, 1500m	lichen on tree	Okt.20	9	Kerschbaumer
Carabodes labyrinthicus	CIA45	Festenburg	Seebach, 1000 m	lichen on tree	Apr.21	10	Kerschbaumer
Carabodes labyrinthicus	CIA47	Festenburg	Seebach, 1000 m	lichen on tree	Apr.21	11	Kerschbaumer
Carabodes marginatus	CIA12	Vorauer Schwaig	alp, 1500m	moss, alpin	Aug.20	16	Kerschbaumer
Carabodes ornatus	CIA42	Weizklamm	Vogelhütte	litter	Mär.21	20	Bodner
Carabodes ornatus	CIA74	Weizklamm	Jägersteig, 600m	deadwood	Mai.22	9	Kerschbaumer/Pfingstl
Carabodes reticulatus	BF003	Puch/Paldau	Paldau	bracket fungi	Sep.22	7	Schäffer
Carabodes rugosior	CIA67	Festenburg	Dorfstatt, forest	bracket fungi	Mai.22	15	Kerschbaumer
Carabodes rugosior	CIA77	Festenburg	Dorfstatt, forest	bracket fungi	Aug.22	11	Kerschbaumer
Carabodes tenuis	CIA58	Festenburg	Dreibach,forest	deadwood	Jun.21	15	Kerschbaumer
Carabodes tenuis	CIA59	Festenburg	Greith, forest	deadwood	Sep.21	4	Kerschbaumer
Carabodes tenuis	CIA74	Weizklamm	Jägersteig, 600m	deadwood	Mai.22	11	Kerschbaumer/Pfingstl
Odontocepheus elongatus	CIA69	Weizklamm	Jägersteig, 600m	deadwood	Mai.22	8	Kerschbaumer/Pfingstl
Odontocepheus elongatus	CIA74	Weizklamm	Jägersteig, 600m	deadwood	Mai.22	8	Kerschbaumer/Pfingstl

Table 2(on next page)

Habitat specificity

(A) *Carabodes* species (B) *Caleremaeus* species and their habitats and lifestyles in literature.

(A) Carabodes	**habitats** (Weigmann et al. 2015)																							**n**	**lifestyle**					**n**
	AR	AW	AZ	E	GM	GQ	HH	LF	LR	LS	LT	MD	MH	SD	SG	UG	US	WF	WL	WM	WN	WT	WZ		ar	bo	el	ep	li	
Carabodes areolatus						x		x			x		x						x		x			7	x	x	x			3
Carabodes coriaceus								x	x			x	x					x	x		x	x		9	x	x	x	x		4
Carabodes labyrinthicus	x	x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x	x	x	x	x	22	x	x	x	x	x	5
Carabodes marginatus	x		x	x				x	x		x	x	x	x				x	x	x	x	x	x	16	x	x	x			3
Carabodes ornatus	x							x	x		x		x		x				x		x	x		10	x	x		x		3
Carabodes rugosior								x											x		x			4	x	x	x			3
Carabodes tenuis																					x			2	x	x				2
Carabodes reticulatus		x																	x		x			3		x				1
Odontocepheus elongatus		x						x	x										x		x	x		7	x	x				2

(B) *Caleremaeus*	**habitats** (sample information in Lienhard & Krisper 2021)							**n**	**lifestyle**					**n**
	alpine meadows and mats	deadwood	grass with soil	lichen	moss on stone/rock	moss	soil and litter		ar	bo	el	ep	li	
Caleremaeus alpinus	x	x	x	x	x	x	x	7	x	x	x			3
Caleremaeus lignophilus		x						1	x					1
Caleremaeus mentobellus				x	x	x	x	4		x	x			2

AR: alpine meadows and mats, AW: subalpine forests,AZ: dwarf-shrubs heathlands and tall forb stands in alpine zones,E:eurytopic (relevant occurrence in more than 3 habitat types (as S [seashore habitats], L [habitats of open non-forest landscape], W [forests and related habitats],...), GM: bogs and swamp waters, GQ: springs, spring runoff, HH: caves, LF: moist and wet grassland, LR: inland salt marshes, LS: reed beds, marshes, LT: dry grassland and scrub, MD: degraded bogs and mires, MH: raised bogs, transition mires, SD: coastal dunes, SG: salt meadows, brackish reeds, UG: constructions: buildings, walls, US: traffic areas: Railway tracks, roads, pavements, urban squares, WF: swamps forests, floodplain forests, WL: deciduous(mixed) forests on fresh soils (deciduous trees >50%), WM: bog forests WN: coniferous(mixed) forests (coniferous trees <50%),WT: deciduous (mixed) forests on dry soils (deciduous trees >50%),WZ: dwarf-shrub heathland; ar: arboricolous -bark dweller, bo: soil dweller, el: epilithic - on rocks, stones or walls, ep: epiphytic - on plants, li: limnic - in freshwater

Figure 1

Clawshape in *Carabodes*

(A) Bodylength, clawlength in relation to bodylength and claw curvature (gamma) for the different species (given in different colors, see legend 1b) and populations (different bars) of *Carabodes* and the outgroup *Odontocepheus elongatus*. (B)Scatterplot of principal component analysis showing the first two components (PC1 = 30.6% and PC2 = 22.8%). On the left-hand side, a representative photograph of *C. rugosior,* one of the *Carabodes* species, is presented, while at the right-hand side of the scatterplot shape changes associated with PC2 are shown.

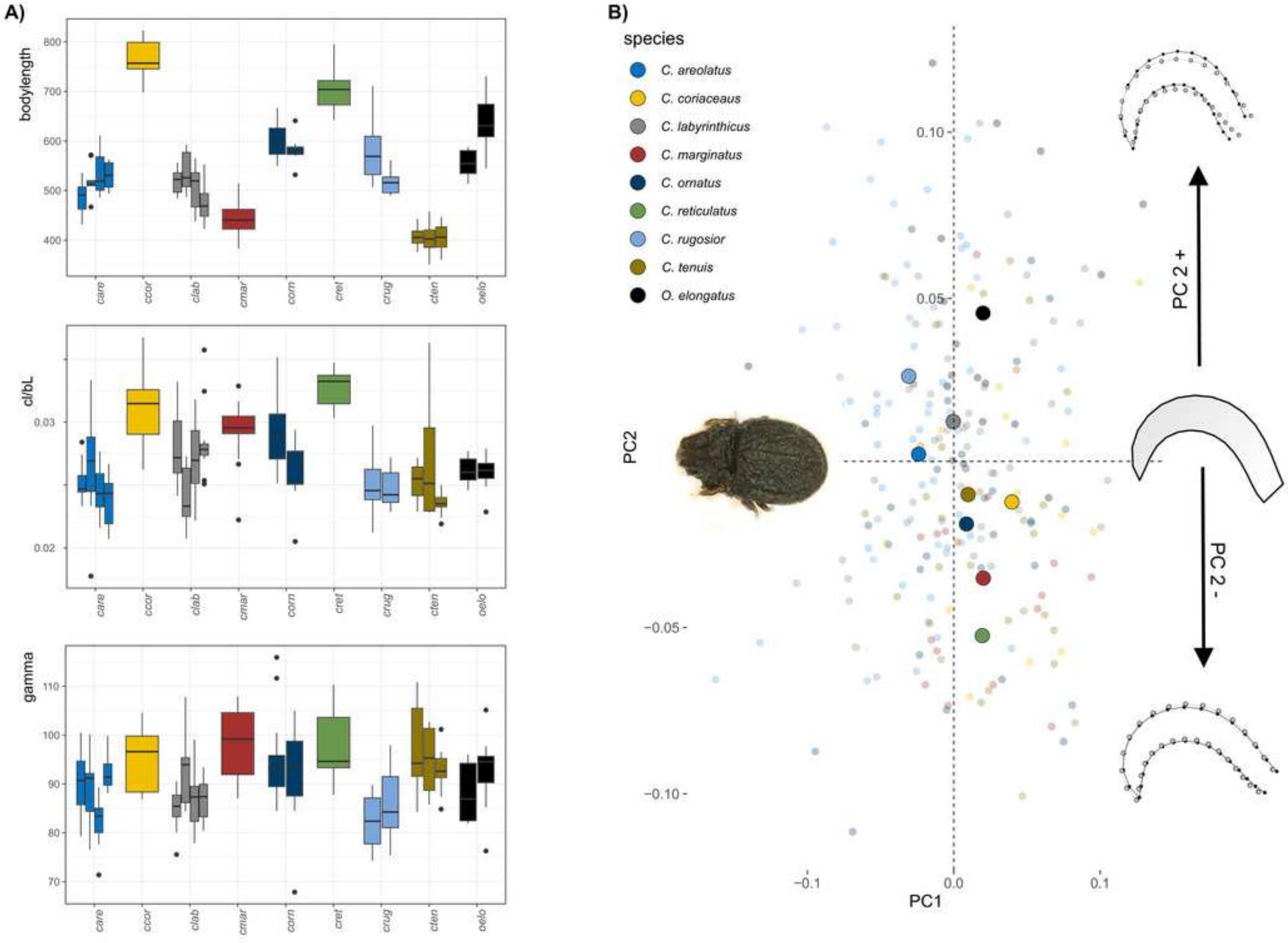

Figure 2

Clawshape in *Caleremaeus*

(A) Bodylength, clawlength in relation to bodylength and claw curvature (gamma) in different species and populations of *Caleremaeus*. (B)Scatterplot of principal component analysis showing the first two components (PC1 = 32.34%, PC2 = 21.38%). On the left-hand side, a representative photograph of *C. lignophilus,* one of the *Caleremaeus* species, is presented, while at the right-hand side of the scatterplot shape changes associated with PC2 are shown.

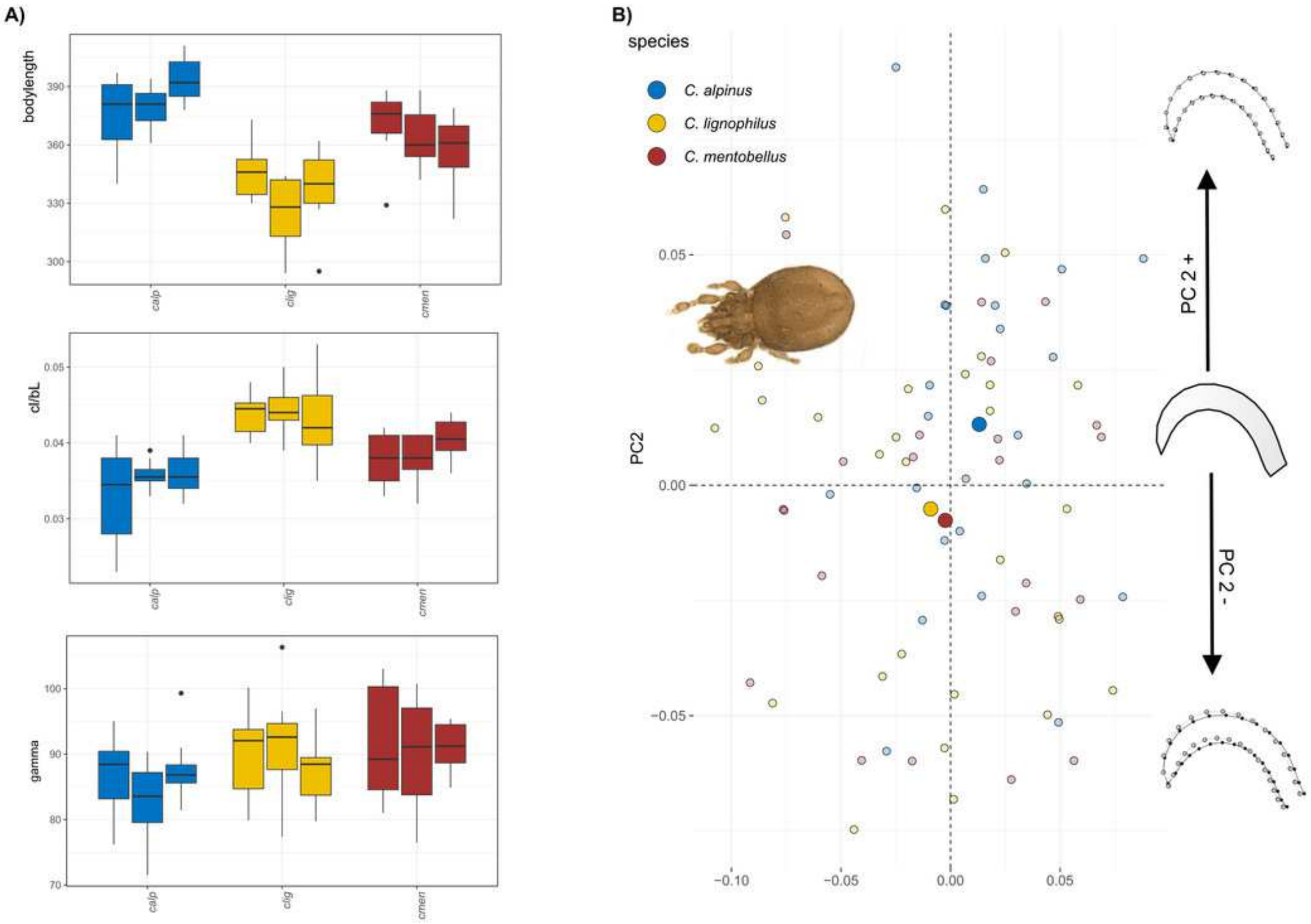

Figure 3

Clawshape and phylogeny in *Carabodes*

(A) PCA with mean shapes of all investigated *Carabodes* species and populations; (B) phylogenetic tree based on COI sequences of investigated *Carabodes* populations (colors refer to phylogenetic clades).

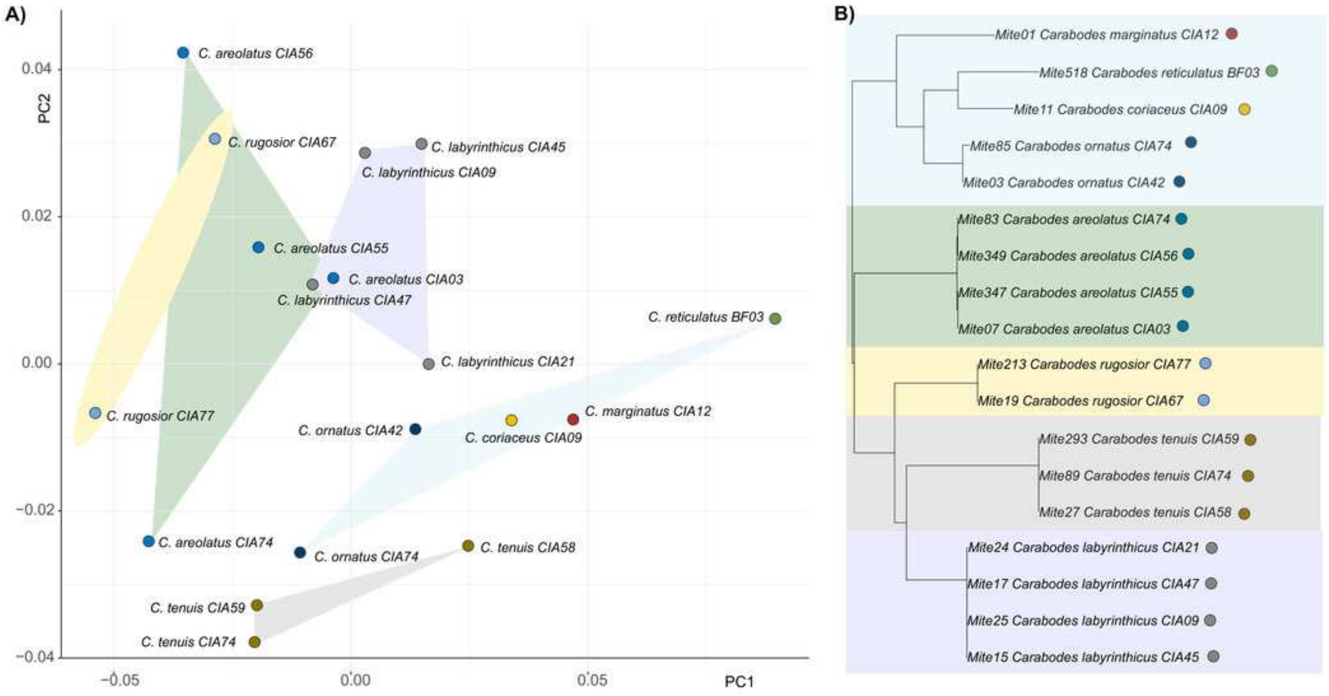

Figure 4

Clawshape and phylogeny in *Caleremaeus*

(A) PCA with mean shapes of all investigated *Caleremaeus* species and populations; (B) phylogenetic tree based on COI sequences of investigated *Caleremaeus* populations (colors refer to phylogenetic clades).

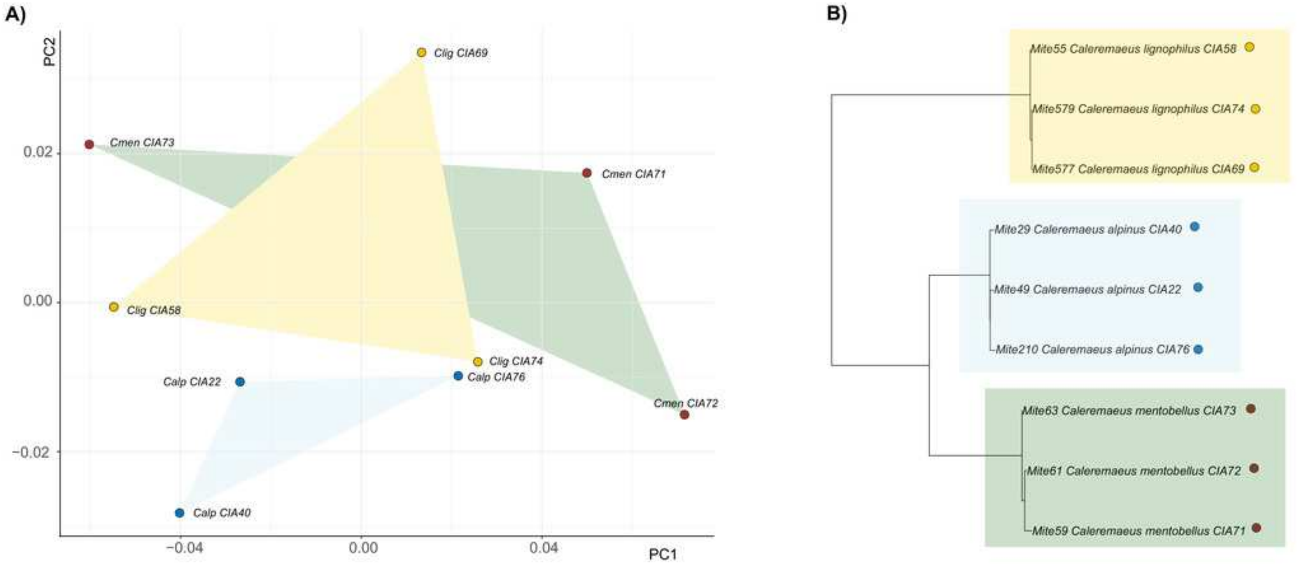

Figure 5

Principal component analysis and meanshapes of claws

Cumulative PCA on mean shapes of all investigated species from both genera *Carabodes and Caleremaeus*. Numbers within the circles representing the individual species, indicate the number of populated habitats from Table 2.