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The interplay between claw morphology and microhabitat use in neotropical iguanian lizards

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Abstract

Traditionally, it has been suggested that variation in locomotor mode should be correlated with variation in the anatomy of the structures responsible for locomotion. Indeed, organisms can expand their ecological niche by using specialized traits of the locomotor system including hooks, claws, adhesive pads, etc. Despite the fact that claws are the most common biological mechanism of clinging in vertebrates, little is known about their function or evolutionary relationship to habitat use. The present study focuses on claw morphology in 57 species of iguanian lizards occupying different microhabitats. Qualitative differences in claw shape were explored by means of digital photographs, and quantitative measurements of the length, height and curvature of the claws of both fingers and toes were taken and correlated to information on microhabitat use obtained from the literature. Our analyses showed a strong phylogenetic component that obscured relationships between morphology and ecology. Our results also show differences in claw morphology between species that appear to be related to microhabitat use (climbing versus terrestrial species), with the best ecological descriptors being claw length and height. Performance measures and biomechanical analyses of claw function may consequently be better suited to explain the evolution of claw shape in relation to habitat use in this group.
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Introduction

Lizards exhibit a diverse suite of lifestyles and exploit a variety of habitats, ranging from rainforest to sandy deserts and even rivers and oceans. This ecological diversity is associated with variation in body size, body shape, and limb proportions (Vitt and Pianka, 1994). Some authors (Losos, 1990a, b; Feduccia, 1993; Garland and Losos, 1994; Arnold, 1998; Bonine and Garland, 1999) have shown that locomotor abilities of lizards are reflected in morphology, especially overall limb length. Lizards also show variation in the relative proportions of their limb segments and digits, which may affect their locomotor performance and ultimately their fitness

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(Jayne and Bennett, 1990; Le Galliard et al., 2004). Thus, variation in habitat use and locomotor performance should be correlated with morphology (Lundelius, 1957; Colette, 1961; Russell and Bauer, 1989; Carrillo de Espinoza et al., 1990; Colli et al., 1992; Vrcibradic and Rocha, 1996; Etheridge, 2000; Irschick et al., 2000; Zani, 2000).

Anolis lizards of the Greater Antilles (a highly diversified and species-rich group of lizards) are amongst the best studied in this context due to their specialized microhabitat use. These lizards are characterized by a variety of "ecomorphs" that define the relationship between morphology and microhabitat use. Moreover, convergently evolved morphologies appear to be strongly related to the behavior and ecology of each species (Williams, 1983; Losos, 1990a, b; Losos et al., 1998). Similar associations between morphology and habitat use have been observed for some species of chameleons (Sinervo and Losos, 1991); *Sceloropus* lizards (Losos et al., 1993), and phrynosomatids in general (Herrel et al., 2001, 2002). However, this pattern is by no means universal as no correlation was found between morphology and habitat use in *Liolaemus* species (Jaksic et al., 1980; Schulte et al., 2004; but see Etheridge, 2000), in climbing versus ground-dwelling geckos (Zaaf and Van Damme, 2001) and *Tropidurus* lizards (Kohlsdorf et al., 2001). Finally, in some groups, analyses of the relationships between morphology and ecology appear hampered by limited independent radiations into different microhabitats (i.e. phylogenetic clustering; Vanhooydonck and Van Damme, 1999).

The enlarged scales on the toes (subdigital lamellae) provide one of the most striking examples of convergent evolution and ecological equivalence among lizards in general (Williams and Peterson, 1982). These structures have evolved independently in six different families of lizards: Scincidae, Lacertidae, Phrynosomatidae, Agamidae, Gekkonidae and Polychrotidae (Williams and Peterson, 1982; Cartmill, 1985; Pough et al., 1998; Russell, 1979; Russell and Bauer, 1989). Other specialized traits often seen in lizards include sharply curved claws modified to grasp rough substrates or zygodactyly (as observed in chameleons) to accommodate grasping, and fringed toes to move across sand or water (Pianka and Vitt, 2003). Of these, claws are probably the most common biological mechanism of adhesion among vertebrates (Zani, 2000). The comparative anatomy and morphology of lizard claws has been studied in detail by diverse authors (Boas, 1894; Schmidt, 1913, 1916; Zani, 2000). For example, Mahendra (1941) showed that geckos without claws have lost the capacity to adhere to vertical surfaces. Indeed, climbing lizards (saxicolous or arboreal) in general possess traits that permit them to expand their spatial niche to occupy vertical habitats (Cartmill, 1985; Pough et al., 1998), and

most of these traits appear to be associated with the presence and use of claws (Zani, 2000).

Our focal group of lizards belongs to the genus *Liolaemus*, one of the most diverse and species-rich lizard genera of the world, including more than 200 species (Schulte et al., 2000; Morando et al., 2004, Abdala, 2007; Lobo et al., 2007; Abdala and Quinteros, 2008; Quinteros et al., 2008). These species show a variety of habitat usage, including generalized ground dwellers as well as highly specialized forms that live exclusively in very specific microhabitats (e.g. rocks, sand). However, despite this extraordinary ecological diversity, previous authors failed to detect any correlation between morphology and habitat use in *Liolaemus* species (Jaksic et al., 1980; Schulte et al., 2004). As an exception, Etheridge (2000) showed a correlation between the skeletal features and elements of scalation and habitat use in sand-dwelling *Liolaemus*. However, in previous analyses claws were not taken into account despite the fact that they can be expected to be one of the traits most directly influenced by habitat use.

Here we compare the claw anatomy of 34 species of *Liolaemus* differing in microhabitat use. Additionally, we include five *Phymaturus*, one *Anisolepis*, two *Diplolaemus*, two *Enyalius*, three *Leiosaurus*, three *Pristidactylus*, one *Urostrophus*, four *Anolis*, one *Polychrus* and one *Iguana* species for comparison. These species were selected as they often occupy very distinct and restricted microhabitats and thus allow us to test the generality of the results obtained for *Liolaemus* across iguanians in general. Our main objectives were to investigate: (i) the diversity of claw morphology across lizards occupying different microhabitats (arboreal, saxicolous, arenicolous, and generalized terrestrial); (ii) the relationship between morphology and microhabitat use, and in doing so, to test if the current ecological categories used are characterized by different claw morphologies; and (iii) to identify morphometric descriptors that indicate specializations associated with these different habitats.

Material and methods

Fifty-seven neotropical lizard species (Supplementary material) belonging to different families of iguanian lizards with different microhabitat use were used in this research. Voucher specimens from all museums are now deposited in the herpetology collection of the Fundación Miguel Lillo, Tucumán, Argentina.

Determination of microhabitat use

The assignment of microhabitat use in the lizards studied here is based on the literature data (Hirth, 1963;

Talbot, 1979; Cei, 1986; Halloy and Laurent, 1987; Etheridge and Williams, 1991; Schwartz and Henderson, 1991; Halloy et al., 1998; Etheridge, 2000; Frost et al., 2001; Cei et al., 2003; Avila et al., 2004; Lobo and Quinteros, 2005; Laspiur et al., 2007; Abdala, 2007; Pincheira-Donoso et al., 2007; Abdala and Quinteros, 2008), as well as field observations (see Table 1). The habitat use classification we used was as follows: arboreal, saxicolous, arenicolous, sand divers, and generalized terrestrial, the first two being actual climbers. Species were classified as arboreal if they regularly occur on trees; saxicolous if they are usually found on rocky boulders; arenicolous if they live in sand dunes, loose or sandy soils; sand divers if they plunge or dive head first into the sand (Halloy et al., 1998); generalist terrestrial if they use the ground routinely to move about (without burying or diving into it).

Qualitative analysis

The claws of digits III and IV from the manus and the claws of toes III, IV and V of the pes from the right side of the limbs were photographed in lateral view with a high-resolution digital camera (Sony DSC-H 5, Sony Corp., Tokyo, Japan). Each image was taken using the same magnification and from the same distance. Captured images were measured and analyzed using Image Tool 3.0 (Wilcox et al., 2002; Supplementary material). Image analysis functions included dimensional variable measurements (distance, angle, perimeter, area). Finally, we drew an outline of the claw types for illustrative purposes (Table 1) using Corel Draw 12 (Corel Corp., Ottawa, Canada).

Morphometrics

The following morphological measurements were taken for every specimen: snout–vent length (SVL); claw height (CH), claw length (CL), and claw curvature (CC) corresponding to digits III and IV of the manus, and III–V of the pes. Those digits and toes were selected because they are the longest and presumably functionally the most important ones (Teixeira-Filho et al., 2001; Vrcibradic and Rocha, 1996). All measurements were taken on the right side of the specimens. CH was measured as the vertical distance between the last dorsal and ventral toe scales (D in Fig. 1); CL was measured in two parts: claw base to mid tip length (length of inner arc from point where toe scales end to mid point of claw, A in Fig. 1) and claw mid to tip length (length of inner arc from mid point to claw tip, B in Fig. 1). CC was calculated as in Zani (2000) using the geometric relation of linear segments defined at the inner aspect of the claw (degrees of arc encompassed by claw). Measurements of SVL were taken with digital callipers (± 0.01 mm;
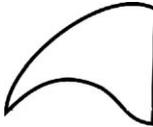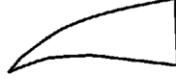
Mitutoyo Corp., Kure, Japan). We used adult and sub-adult specimens of both sexes. All morphometric variables were $\log_{10}$-transformed prior to analyses to meet requirements of normality (Zar, 1999). To remove the effects of body size from the log-transformed variables, we used residuals of regression between body size and each variable. The resultant residuals were used in a partial canonical phylogenetic ordination (Giannini, 2003) to examine size-free morphological variation and to identify the taxonomic level at which ecological variation among species occurred.

Statistical analyses

To explore the significance of phylogeny on our ecomorphological analyses, we tested the relationship between claw morphology, microhabitat use, and phylogeny by performing a partial canonical phylogenetic ordination (pCPO), a variant of the redundancy analysis (RDA). pCPO is a modification of a uni-modal canonical correspondence analysis (ter Braak, 1986) or an RDA (ter Braak and Smilauer, 1998). A pCPO was performed by adding variables successively (forward stepwise), which yielded an economic model to explain the variation in the main matrix with a minimum number of variables. Analyses such as RDA are useful when trying to relate a matrix of variables (commonly a species matrix) to another matrix (environmental matrix or explanatory variables matrix) (Legendre and Legendre, 1998). This analysis allowed us to constrain all the variation in the analysis to the explanatory variable matrix. CPO is a phylogenetically based comparative method by which the set of species is codified in a phylogenetic structure matrix (assigning 0s and 1s based on whether species belong to a monophyletic group or not). This matrix can then be employed as an external or covariate matrix in statistical tests (Giannini, 2003).

For all these analyses, calculations were done using a covariance matrix because our variables were measured in the same units (Legendre and Legendre, 1998). Additionally, we used a Monte Carlo permutation test based on 999 random permutations to calculate the statistical significance ($P < 0.05$) of every external variable (Manly, 1997). Thus, in our study the main matrix includes morphological data (claw length, height and curvature); environmental data (the five microhabitat use categories), and finally a third external matrix (the phylogenetic matrix) constructed using two different topologies based on (Nicholson, 2002; Morando et al., 2004; Lobo and Quinteros, 2005; Avila et al., 2006; Abdala, 2007). Since the phylogenetic association among *Diplolaemus*, *Leiosaurus* and *Pristidactylus* differed between Frost et al. (2001) and Schulte et al. (2003), we analyzed our data using both topologies (Fig. 2A and B, respectively) to evaluate whether the

Table 1. Microhabitat use of the species examined in this study and claw morphology illustrating qualitative differences among species with different ecological habits.

| Species	Author	Morphotype	Function	Habitat
Anisolepis longicaudus	Etheridge and Williams (1991)		Clinging ability	Arboreal
Anolis cuvieri	Schwartz and Henderson (1991)			
Anolis gundlachi	Schwartz and Henderson (1991)			
Anolis limifrons	Talbot (1979)			
Enyalius hieringi	Frost et al. (2001)			
Enyalius catenatus	Frost et al. (2001)			
Iguana iguana	Hirth (1963)			
Polychrus acutirostris	Frost et al. (2001)			
Pristidactylus valerie	Frost et al. (2001)			
Urostrophus gallardoi	Frost et al. (2001)			
Liolaemus chiliensis	Cei (1986)			
Liolaemus tenuis	Cruz, field observations			
Liolaemus pictus	Cruz, field observations			
Liolaemus dorbignyi	Quinteros et al. (2008)			Saxicolous
Liolaemus elongatus	Cei (1986)			
Liolaemus petrophilus	Avila et al. (2004)			
Liolaemus sagei	Abdala (2007)			
Liolaemus ceii	Cei (1986)			
Phymaturus spectabilis	Lobo and Quinteros (2005)			
Phymaturus excelsus	Lobo and Quinteros (2005)			
Phymaturus dorsimaculatus	Lobo and Quinteros (2005)			
Phymaturus spurcus	Lobo and Quinteros (2005)			
Phymaturus tenebrosus	Lobo and Quinteros (2005)			
Liolaemus multimaculatus	Halloy et al. (1998)		Burying in the sand	Sand diving
Liolaemus riojanus	Halloy et al. (1998)			
Liolaemus salinícola	Halloy et al. (1998)			
Liolaemus scapularis	Halloy et al. (1998)			
Liolaemus canqueli	Halloy et al. (1998)			
Liolaemus cuyanus	Etheridge (2000)		Burying in the sand	Arenicolous
Liolaemus darwinii	Etheridge (2000)			
Liolaemus fitzingeri	Etheridge (2000)			
Liolaemus laurenti	Etheridge (2000)			
Liolaemus inacayali	Abdala (2007)			
Liolaemus koslowskyi	Etheridge (2000)			
Liolaemus olongasta	Etheridge (2000)			
Liolaemus xanthoviridis	Etheridge (2000)			
Diplolaemus darwini	Scolaro (2005)		Ground dwelling	Terrestrial
Diplolaemus sexcintus	Cei et al. (2003)			
Liolaemus abaucan	Abdala (2007)			
Liolaemus albiceps	Abdala (2007)			
Liolaemus bibronii	Cei (1986)			
Liolaemus crepuscularis	Abdala and Díaz Gómez (2006)			
Liolaemus goetschi	Abdala (2007)			
Liolaemus hermannunezi	Pincheira-Donoso et al. (2007)			
Liolaemus huacahuasicus	Halloy and Laurent (1987)			
Liolaemus irregularis	Abdala (2007)			
Liolaemus lineomaculatus	Cei (1986)			
Liolaemus magellanicus	Cei (1986)			
Liolaemus multicolor	Abdala, field observations			
Liolaemus ornatus	Abdala (2007)			
Liolaemus sarmientoi	Abdala, field observations			
Leiosaurus belli	Laspiur et al. (2007)			
Leiosaurus catamarcensis	Laspiur et al. (2007)			
Leiosaurus paronae	Laspiur et al. (2007)			
Anolis humilis	Talbot (1979)			
Pristidactylus achalensis	Frost et al. (2001)			
Pristidactylus scapulatus	Frost et al. (2001)			
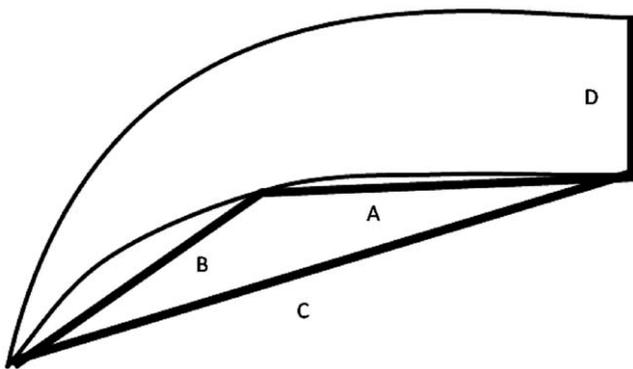
Fig. 1. Diagram illustrating the measurements taken on each claw. A = distance from the claw base to the middle of the claw; B = distance from the middle of the claw to the tip of the claw; C = claw length; D = claw height. Claw curvature = 57.296 (2 arcsine (($2 \cdot A2 \cdot B2$) + ($2 \cdot A2 \cdot C2$) + ($2 \cdot B2 \cdot C2$) ± A4 ± B4 ± C4) $0.5/(2 \cdot A \cdot B)$)) (after Zani, 2000).

tree topology had an effect on our results. All ordinations were computed using Canoco for Windows 4.5 (ter Braak and Smilauer, Plant Research International, Wageningen UR, The Netherlands) and scaling of the ordination components was done using a correlation triplot (ter Braak and Looman, 1994). Basic statistical methods followed Zar (1999) and were applied using Statistica 6.0 (StatSoft Inc., Tulsa, OK, USA). Differences were considered significant at $P < 0.05$.

Additionally, we calculated the phylogenetic signal present in our data using the randomization test described in Blomberg et al. (2003) and computed the K-statistic (an indicator of phylogenetic signal) for SVL and the claw variables included in our analysis. This analysis was implemented in Matlab v. 6.1.0 for PC (MathWorks Inc., Natick, MA, USA) using the module 'PHYSIG' (available upon request from Dr. T. Garland, University of California at Riverside). We ran all analyses using two alternative tree tolopogies (see above) and with both constant branch lengths and branch lengths transformed using an Ornstein–Uhlenbeck model of evolution. In the latter transformation we set the d-value equal to 0.2, thus creating a topology with less structure and more star-like, or equal to 0.8, resulting in a more hierarchical topology (Blomberg et al., 2003).

As both previous analyses indicated the presence of an important phylogenetic component to our data we tested for differences in claw shape among climbing and ground-dwelling lizards using a phylogenetically corrected ANOVA. Given the strong phylogenetic signal in many traits, we decided to focus here on only two groups that differ most dramatically in the physical demands during locomotion (i.e. climbers versus ground dwellers). An empirical null distribution of F-statistics that takes the phylogeny into account was generated using PDSIMUL and analyzed with PDANOVA

(Garland et al., 1993). For each variable, we ran 1000 simulations using a speciational model of evolution. The speciational model sets all branch lengths to one in PDSIMUL (Martins and Garland, 1991).

Results

Microhabitat use and claw shape

The assignment of the different species to the different habitat categories as well as a qualitative indication of claw shape is presented in Table 1. Drawings of the claws show the presence of two general morphotypes related to microhabitat use: strongly curved claws for the arboreal and saxicolous species, and non-hooked or smoothly curved claws (more than twice as long as they are high) for arenicolous, sand diving, and terrestrial forms (Table 1) suggesting differences between climbing and ground-dwelling species. Raw data are given in Supplementary material.

Partial canonical phylogenetic ordination

RDA and pCPO were performed on the microhabitat use, claw morphology, and phylogenetic matrices of the 57 species. In relation to claw shape, the RDA considered both microhabitat use and phylogeny as significant explanatory variables. The complete variance partitioning is detailed in Table 2, but only the P values corresponding to the effects of microhabitat use are indicated.

With respect to the relation between morphological variables and microhabitat use, the RDA indicates that the first two morphological axes explain 95.6% of the variance in the ecological variables (Table 2). The correlation coefficients between the first two canonical axes are 0.57 and 0.53, respectively. This analysis reveals that arboreal and saxicolous groups are defined by tall claws on fingers and toes and that there is an inverse correlation between claw height and claw curvature (Fig. 3). Arenicolous lizards including sand diving ones are characterized by long and shallow claws (Fig. 3), and terrestrial groups are generally characterized by a decrease in claw curvature (Fig. 3). The results were identical for both topologies used.

In the CPO of claw morphology and phylogenetic affinities, the first two vectors explain 90% of the variation associated with phylogeny; the third axis explains only an additional 19% (see Fig. 4). The first two canonical axes are highly correlated ($r = 0.94$ and 0.81, respectively). Monte Carlo permutations (based on 999 iterations) from the canonical ordination reveal no significant phylogenetic effect for some of the mono-

Fig. 2. Figure showing the individual groups used in canonical phylogenetic ordination in relation to microhabitat use. The tree topology in (A) differs from the topology in (B) by the placement of the species in the leiosaurid group (node N). Phylogenies A and B are composite trees based on previous work cited in Material and methods. Abbreviations for the different microhabitats: A, arboreal; S, saxicolous; Ar, arenicolous; S-D, sand diving; T, terrestrial.

Table 2. Percentage of variance explained by each ecological variable and results of Monte Carlo simulation test (999 iterations) corresponding to the redundancy analysis on canonical axes.

Explanatory variables	F ratio	P value	Explained variance (%)
Arboreal	4.72	0.014	5
Saxicolous	5.38	0.005	10
Arenicolous/ sand diving	2.26	0.09	14
Terrestrial	4.31	0.014	13

phyletic groups (i.e., all P values higher than 0.05) on the microhabitat use of the lizards.

Fourteen taxonomic groups best explain variation in the data set (Tree 1, Fig. 4A), among them Polychrotidae, *Leiosaurus*, *Phymaturus*, and *Enyalius*. Inside *Liolaemus*; climbing species tend to form a monophyletic group composed of *L. tenuis*, *L. pictus*, *L. chiliensis* among arboreal species, *L. petrophilus*, *L. ceii* and *L. elongatus* among saxicolous species. Sand-diving *Liolaemus* (Table 3, tree topology 1; Fig. 4A) also constitute a monophyletic clade. The use of an alternative topology based on Schulte et al. (2003), Tree 2 (Fig. 4B), resulted in the same major groups, but only 9 of these could be differentiated (Table 3, tree topology 2). Thus, when the phylogeny is taken into account (CPO), claw height and claw length still explain a significant proportion of the claw variation. Once both phylogenetic and ecological matrices were reduced, we performed a pCPO using the phylogenetic matrix as covariate on size-free variables. The explanatory variables of the two first axes combined retained 97.4% of the morphological variation (Table 4). According to the results of the pCPO there was a significant correlation between the shape of the claws and arboreal, saxicolous and arenicolous microhabitat use ($F = 4.34$; $P < 0.01$ and $F = 0.86$; $P < 0.001$, and $F = 1.14$; $P < 0.001$, respectively), after removing the effect of phylogeny on phenotype (i.e. employing phylogenetic variables as covariate in the regression analysis). The results using the Frost et al. (2001) topology indicate that the variance of the morphological matrix corresponding to the microhabitat use was 14%, corresponding to phylogeny 35%, and shared only 4%. The ecomorphological correlations for claw morphology and microhabitat use are shown as a triplot (Fig. 5; ter Braak and Smilauer, 1998) where the angle between vectors indicates their correlation to each axis and the lengths indicate the magnitude of influence of each variable on the canonical axis (large vectors indicate more influential variables). The species that use mainly vertical substrates had claws that were relatively high,
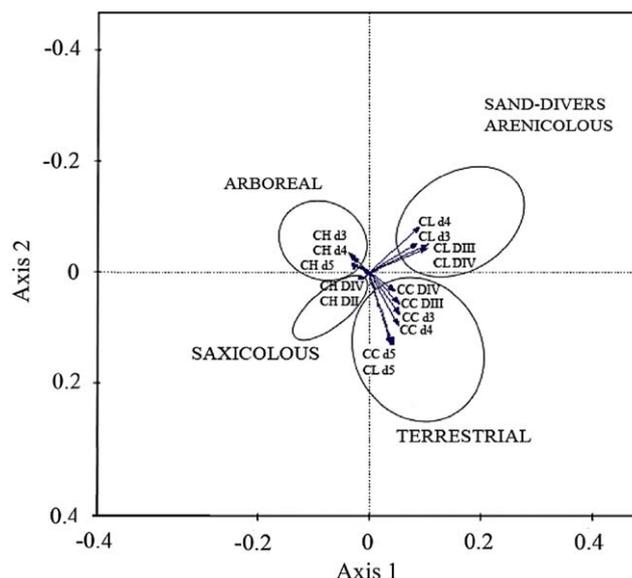

Fig. 3. RDA results showing a scatter plot in which the four groups are indicated. The RDA indicated that the first two morphological axes explained 95.6% of the variance in the ecological variables. Arboreal and saxicolous groups are defined by tall claws on both fingers and toes. There is an inverse correlation between claw height and claw curvature. Arenicolous lizards, including sand diving ones, are characterized by long and shallow claws, and terrestrial groups are generally characterized by a decrease in claw curvature. The results were identical for both topologies used (see Fig. 2A and B). Abbreviations: CH, claw height; CL, claw length; CC, claw curvature; DIII and DIV = digits three and four of the manus; d3, d4 and d5 = toes three, four and five of the pes.

especially saxicolous lizards like *Liolaemus dorbignyi* and *Liolaemus sagei* (see Table 1 and Fig. 2). In contrast, species that use horizontal substrates, especially the arenicolous ones, have relatively long and uncurved claws. Claw curvature showed a negative trend on both axes. Noticeably, and paradoxically, saxicolous species such as *L. ceii*, *L. elongatus* and *L. petrophilus* had long claws on toe 5 and generally highly curved claws on all digits. This is surprising as claw length is typically positively correlated with arenicolous habits. When the Schulte et al. (2003) topology was used, the variance of the morphological matrix corresponding to the microhabitat use was 13%, that corresponding to phylogeny 51%, and shared only 4%.

The results of our tests for the presence of phylogenetic signal in the data show that claw curvature and length typically have K-values less than one (Table 5). SVL and claw height, on the other hand, show a significant amount of phylogenetic signal. Ornstein–Uhlenbeck transformations of the branch lengths, rendering the phylogeny either more star-like or more hierarchical, strongly affect both the K-values and the significance thereof (see Table 5). The results of our phylogenetically corrected ANOVAs (Table 6) indicate
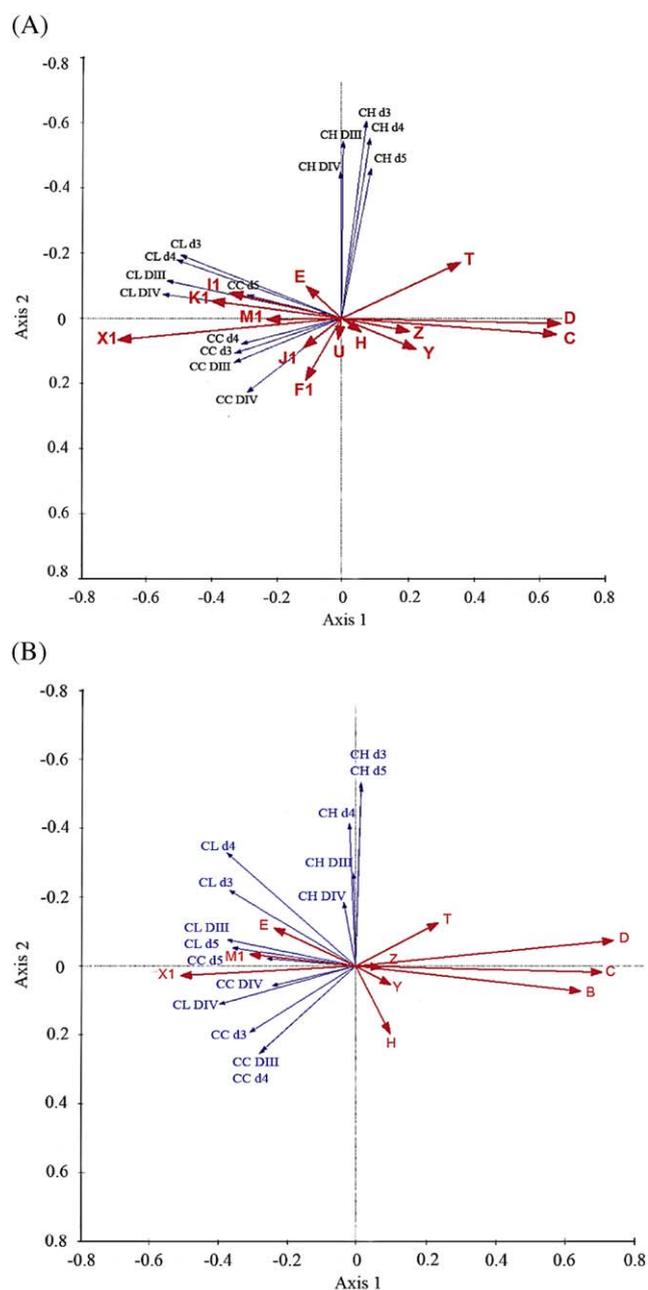
(A)

(B)

Fig. 4. Individual groups used in canonical phylogenetic ordination for microhabitat data. Letters correspond to the groups shown in Fig. 2 and to the morphological traits (CH, claw height, CL, claw length, CC, claw curvature; DIII and DIV = digits of the manus; d3, d4 and d5 = toes of the pes). (A) Tree topology 1 (data combined from Frost et al., 2001; Nicholson, 2002; Morando et al., 2004; Lobo and Quinteros, 2005; Avila et al., 2006; Abdala, 2007). (B) Tree topology 2 (data combined from Frost et al., 2001; Nicholson, 2002; Schulte et al., 2003; Morando et al., 2004; Lobo and Quinteros, 2005; Avila et al., 2006; Abdala, 2007).

high critical F-values given the topologies used in our analysis. This suggests that habitats are strongly clustered within clades and thus confirm the results

Table 3. Results of Monte Carlo simulation for individual groups (defined in Fig. 2) after CPO.

Explanatory variables	F ratio	P value	Explained variance (%)
Tree topology 1			
C	74.28	0.001	14
D	6.94	0.001	25
E	4.5	0.002	27
H	3.12	0.015	28
T	16.05	0.001	23
U	3.1	0.013	29
Y	8.65	0.001	24
Z	4.31	0.004	27
F1	4.78	0.002	28
K1	3.4	0.003	30
L1	4.31	0.003	30
M1	6.92	0.001	26
S1	2.99	0.015	32
X1	40.46	0.001	20
Tree topology 2			
B	6.36	0.001	35
C	2.76	0.04	41
D	36.06	0.001	23
E	2.21	0.001	27
H	4.32	0.007	40
T	6.65	0.001	38
Y	2.24	0.04	42
Z	4.31	0.008	27
M1	2.68	0.02	42
X1	10.34	0.001	29

The table shows the value of each variable on canonical axes. Tree topology 1: data combined from Frost et al. (2001), Nicholson (2002), Morando et al. (2004), Lobo and Quinteros (2005), Avila et al. (2006), Abdala (2007). Tree topology 2: data combined from Frost et al. (2001), Nicholson (2002), Schulte et al. (2003), Morando et al. (2004), Lobo and Quinteros (2005), Avila et al. (2006), Abdala (2007).

from the other analyses. Only the height of the claw on digit 4 of the foot was significantly different between animals occupying horizontal versus vertical habitats after taking into account the hierarchical structure of the data (Table 6).

Table 4. Phylogenetic eigenvector regression: relationships between claw morphology and explanatory variables (phylogenetic variables).

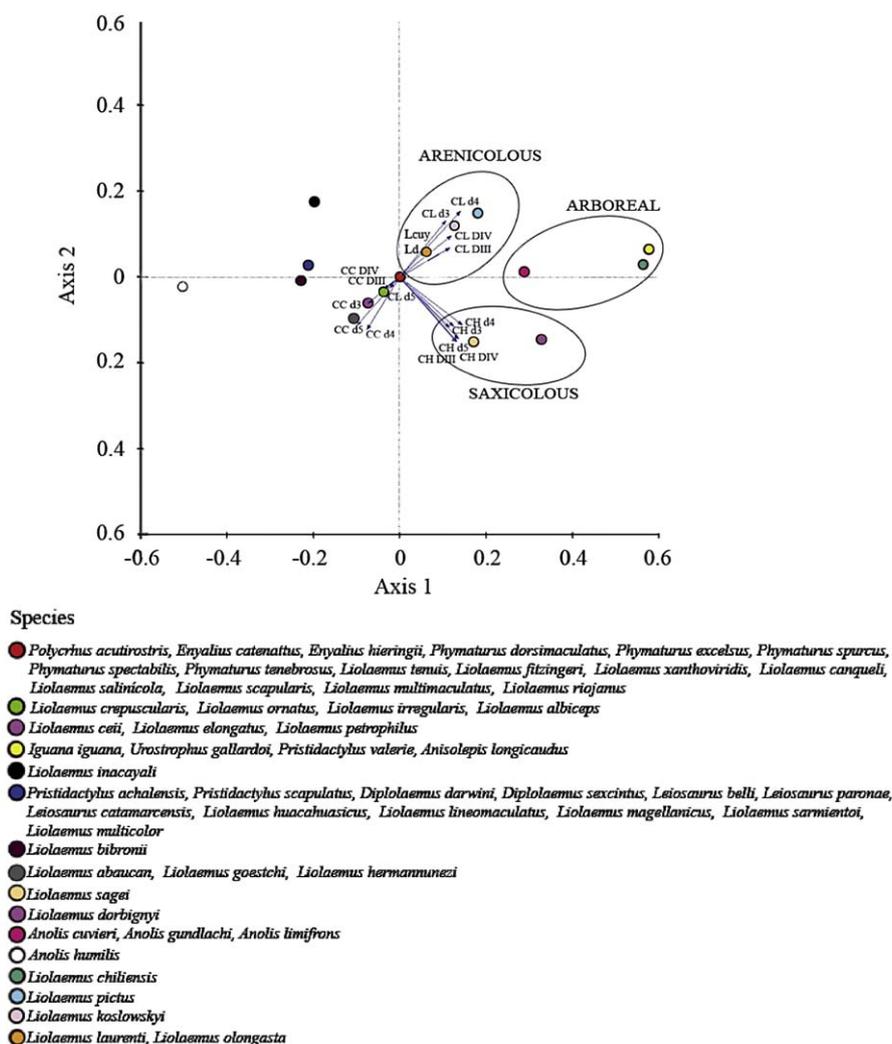| Partial CPO	Canonical axes			
	Axis 1	Axis 2	Axis 3	Total
Eigenvalue	0.094	0.024	0.003	1
Correlation between axes	0.713	0.308	0.173	
% explained variance	77.2	97.4	99.5	

Fig. 5. Triplot of factor scores from pCPO for 57 species. The pCPO used the residuals of the regression between morphological variables and snout-vent length. Abbreviations: CH, claw height, CL, claw length, CC, claw curvature; DIII and DIV = digits of the manus, d3, d4 and d5 = toes of the pes.

Discussion

Morphological claw variation among neotropical iguanian lizards can be explained by both phylogeny and ecological habits, although in different proportions (Table 5). According to our analyses, the principal variation in claw shape across *Liolaemus* lizards can be explained by common ancestry. Other attributes of claw morphology (length and curvature) may be related to microhabitat use. The main differences were observed between arenicolous (including sand divers) and climbing (arboreal and saxicolous) species. Species that occur on sandy soils tend to have longer and less curved claws. In contrast, species that are good climbers, such as arboreal and saxicolous ones, have higher and more sharply curved claws. This result generally held across all species including *Liolaemus* species. In contrast to

other studies on ecomorphological patterns in this genus (Jaksic et al., 1980; Schulte et al., 2004) where no correlation between morphology and microhabitat use was found (but see Etheridge, 2000), we show that some traits of claw morphology are associated with microhabitat use in this group of species. The discrepancy between these results may, however, be due simply to the fact that previous studies on *Liolaemus* included only three arenicolous species (*L. darwinii, L. laurenti* and *L. koslowskyi*; Schulte et al., 2004). Additionally, it is also possible that overall limb morphology is not a good predictor for microhabitat use in this group of species. Thus, focusing on claw morphology, plus an increase in the number of *Liolaemus* species and the types of habitats used has helped us to fine tune our understanding of ecomorphological relationships within the group.

　　　　M.J. Tulli et al. / Zoology 112 (2009) 379–392

Table 5. Summary of analyses calculating phylogenetic signal using two trees with different topologies (see Material and methods) and using both constant branch lengths and Ornstein–Uhlenbeck transformed branch lengths.

Variable	Tree 1		Tree 1 OU ($d = 0.2$)		Tree 1 OU ($d = 0.8$)		Tree 2		Tree 2 OU ($d = 0.2$)		Tree 2 OU ($d = 0.8$)	
	K	P	K	P	K	P	K	P	K	P	K	P
SVL	1.04	<0.0001	1.03	0.3	1.39	<0.0001	1.04	<0.0001	1.03	0.28	1.4	<0.0001
CH DIII	1.14	<0.0001	**0.99**	0.35	1.37	0.001	1.14	<0.0001	**0.99**	0.36	1.38	<0.0001
CC DIII	**0.5**	<0.0001	1.11	<0.0001	**0.76**	<0.0001	**0.5**	<0.0001	1.1	0.001	**0.76**	<0.0001
CL DIII	**0.63**	<0.0001	1.06	0.08	**0.93**	<0.0001	**0.63**	<0.0001	1.06	0.07	**0.93**	<0.0001
CH DIV	1.18	<0.0001	1.06	0.12	1.53	<0.0001	1.17	<0.0001	1.06	0.099	1.56	<0.0001
CC DIV	**0.5**	<0.0001	1.09	0.01	**0.78**	<0.0001	**0.5**	<0.0001	1.09	0.009	**0.8**	<0.0001
CL DIV	**0.65**	<0.0001	1.1	0.011	**0.96**	<0.0001	**0.65**	<0.0001	1.12	0.004	**0.97**	<0.0001
CH d3	1.73	<0.0001	**0.96**	0.91	1.95	<0.0001	1.73	<0.0001	**0.95**	0.91	1.95	<0.0001
CC d3	**0.62**	<0.0001	1.12	<0.0001	**0.95**	<0.0001	**0.62**	<0.0001	1.13	<0.0001	**0.95**	<0.0001
CL d3	**0.82**	<0.0001	1.05	0.25	1.13	0.002	**0.82**	<0.0001	1.04	0.26	1.12	<0.0001
CH d4	1.73	<0.0001	**0.98**	0.86	1.98	<0.0001	1.74	<0.0001	**0.98**	0.88	1.99	0.002
CC d4	**0.55**	0.001	1.11	0.001	**0.9**	<0.0001	**0.55**	<0.0001	1.11	<0.0001	**0.9**	<0.0001
CL d4	**0.68**	<0.0001	1.03	0.29	**0.97**	<0.0001	**0.68**	<0.0001	1.03	0.27	**0.98**	<0.0001
CH d5	1.56	<0.0001	1.07	0.61	2.07	<0.0001	1.56	<0.0001	1.08	0.59	2.08	<0.0001
CC d5	**0.45**	<0.0001	1.09	<0.0001	**0.75**	<0.0001	**0.45**	<0.0001	1.09	0.001	**0.74**	<0.0001
CL d5	**0.92**	<0.0001	1.15	0.13	1.32	<0.0001	**0.92**	<0.0001	1.16	0.12	1.32	<0.0001

Bold figures indicate significant K values (<1).
Abbreviations: OU = Ornstein–Uhlenbeck process; SVL = snout–vent length; CH = claw height; CL = claw length; CC = claw curvature; DIII and DIV = digits of the manus; d3–d5 = toes of the pes.

Table 6. Results of conventional (trad) and phylogenetically informed (phyl) ANOVAs testing for differences in claw shape between climbing (arboreal and saxicolous) and ground-dwelling lizards.

Variable	F_{trad}	P_{trad}	F_{phyl}T1	P_{phyl}T1	F_{phyl}T2	P_{phyl}T2
SVL	2.932	0.092	20.05	0.501	22.03	0.514
CH DIII	6.219	0.016	19.49	0.320	20.53	0.329
CC DIII	14.492	**<0.001**	20.83	0.113	20.98	0.123
CL DIII	1.454	0.233	20.10	0.626	19.70	0.644
CH DIV	4.175	0.046	19.35	0.409	21.58	0.436
CC DIV	6.900	0.011	19.32	0.276	21.70	0.293
CL DIV	2.103	0.153	21.43	0.571	20.63	0.110
CH d3	14.859	**<0.001**	19.19	0.098	20.63	0.110
CC d3	8.362	0.005	18.98	0.218	20.47	0.252
CL d3	0.181	0.672	19.26	0.860	19.03	0.856
CH d4	19.873	**<0.001**	20.84	0.053	19.83	**0.049**
CC d4	12.881	**0.001**	17.35	0.114	20.61	0.146
CL d4	0.027	0.871	19.88	0.953	19.81	0.954
CH d5	14.415	**<0.001**	18.18	0.098	19.75	0.101
CC d5	8.805	0.004	19.28	0.217	20.21	0.227
CL d5	0.131	0.719	19.49	0.899	21.35	0.902

Both tree topologies (T1 and T2; see Material and methods) were used. Bonferroni correction was used for conventional analyses. Bold figures indicate significant P values (<0.05).
Abbreviations: SV = snout–vent length; CH = claw height; CL = claw length; CC = claw curvature; DIII and DIV = digits of the manus; d3–d5 = toes of the pes.

Our results indicate that claw height and length are the morphological variables that are more strongly related to microhabitat use. However, our data also indicate that several of the *Liolaemus* groups characterized by a similar microhabitat usage belong to the same clade (Fig. 4, node Z). Thus, phylogenetic clustering (Vanhooydonck and Van Damme, 1999) is strong in this group. For example, the variable that defines clade Z is claw height and our analysis indicates that claw height shows a significant amount of phylogenetic signal. Thus, closely related species are more similar to each other than expected based on a Brownian motion model of evolution (Table 5). Among saxicolous lizards, *L. dorbignyi* and *L. sagei* are the only ones that belong to different clades (Fig. 2), indicating that both historical and ecological factors contribute to the evolution of claw shape in this group (Fig. 5). Based on the tree topology illustrated in Fig. 2 it can be inferred that climbing habits arose independently at least three times in the history of the *Liolaemus* genus (node Z, node C1 *L. dorbignyi*, and node I1 *L. sagei*). The clades grouping the *Phymaturus* species (Fig. 4, node T) and the *Enyalius* species (Fig. 4, node E) are also characterized by claw height. Thus, phylogeny clearly constrains "claw height evolution" within minor clades such as T and E, but since both clades do not share an immediate common ancestor, some adaptive

evolution can be inferred (see also Table 6). In fact, other distantly related lizards were similar in both morphology and ecology. Climbing species including arboreal lizards such as *Iguana iguana, Urostrophus gallardoi, Pristidactylus valerie, Anisolepis longicaudus, Liolaemus chilensis,* and arboreal *Anolis* lizards cluster together, indicating that ecological factors generally contribute to claw shape (Fig. 5). The variables claw length and claw curvature showed a $K<1$ (Table 5) suggesting adaptive variation is present, independent of the topology used. Interestingly, our results showed that rather than being sensitive to the different topologies used, the calculation of phylogenetic signal is sensitive to branch length transformations (Table 5). However, given the lack of a complete molecular phylogeny for the group of species under study and the lack of real branch lengths, conclusions regarding the phylogenetic signal present in different traits must remain preliminary.

Despite the fact that claws have received far less attention in previous studies of lizard ecomorphology, they allow lizards to climb rough substrates by using them as hooks. Climbing ability is, however, also related to the position of the center of gravity; if the center of gravity is too high, stability will be compromised. Hence, lizards that use vertical habitats (arboreal and saxicolous) tend to have shorter and especially higher claws, while species in open habitats have longer and uncurved claws as indicated by the pCPO analysis and the phylogenetically informed ANOVAs (Alexander, 1968, 1971; Losos et al., 1993; Van Damme et al., 1997; Zani, 2000; Teixeira-Filho et al., 2001; Ribas et al., 2004). Additionally, the claw feature previously suggested to contribute most to clinging ability on rough surfaces is claw height (Zani 2000), the one trait being significant in our analysis despite strong clustering of habitat use within clades. This suggests that claw height and possibly also curvature may be considered as genuine traits allowing animals to occupy an arboreal niche, as this feature is likely related to an increase in frictional grip on arboreal substrates (Cartmill, 1985). Contrary to arboreal and saxicolous species, arenicolous ones have uncurved and longer claws. Sand divers could generally not be distinguished by claw morphology from other ground-dwelling lizards, suggesting that claws may not be used during sand diving. Yet, the greater relative length of the claws of the digits could provide a better support on sandy substrates for sand dwellers in general (i.e. including sand divers) or allow for an increase in effective limb length in terrestrial species. Moreover, Teixeira-Filho et al. (2001) proposed that longer claws may provide a functional advantage in the excavation of burrows. These hypotheses, however, remain to be tested empirically.

In our data set generalist terrestrial species show an intermediate position between saxicolous and arenicolous lizards. Generalist terrestrial species have substantially less curved and shallower claws which may increase the contact with the ground. According to Teixeira-Filho et al. (2001) and Ribas et al. (2004), long claws will also improve the ability of a lizard to flee from potential predators by increasing effective limb length and thus sprint speed, will improve the excavation of burrows, and will increase their performance during locomotion in vegetated microhabitats. However, these assertions obviously need to be tested by measuring actual performance of species characterized by differences in claw shape.

In general, lizards of the genus *Liolaemus* display far less morphological variation when compared with members of the highly species-rich *Anolis* clade. Indeed, our results demonstrate the over-arching effect of phylogeny in explaining the observed morphological variation in *Liolaemus* species. This phylogenetic inertia could be responsible for the remarkable homogeneity in the general overall morphology in the genus. However, the results of our study also demonstrate that (i) the lizard taxa analyzed show qualitative and quantitative differences in claw morphology; (ii) some aspects of claw morphology are related to microhabitat use even though a major proportion of variation in claw morphology can be explained by phylogenetic relatedness; and (iii) the best predictors of habitat use seem to be variables related to claw height, despite it being affected by phylogeny. Claw curvature, on the other hand, was not particularly strongly correlated with habitat use among the species included in our analysis.

Although the proximate relationships between shape and ecology are currently still unclear, performance measures and biomechanical analyses of claw function may consequently be better suited to explain the evolution of claw shape in relation to habitat use in this group.

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Appendix 1. Supplementary Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.zool. 2009.02.001.

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