

The comparative evolution of lizard claw and toe morphology and clinging performance

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Abstract

In this study, I utilize the expected functional relationships between claw and toe morphology and clinging performance as a basis for examining evolutionary trends across 85 lizard taxa from 13 families. After controlling for body size and phylogeny, multivariate comparisons indicate that several aspects of claw and toe morphology are correlated with clinging performance. Specifically, evolutionary increases in claw curvature, toe width and adhesive lamella number are correlated with increases in clinging performance on smooth substrates. Furthermore, evolutionary increases in claw height and decreases in toe length are correlated with increases in clinging performance on rough substrates. Sensitivity analyses revealed that changes in both branch lengths and procedural order of correction for body size and phylogeny do not generally have an effect on phylogenetic comparisons. These results demonstrate that the evolution of claw and toe morphology is correlated with the evolution of clinging performance across a wide range lizard taxa.

Introduction

There is a growing body of literature that has identified the functional relationships between morphology and performance (for review see Wainwright & Reilly, 1994). These relationships stem from the idea that an organism's phenotype influences fitness via ecologically relevant measures of performance (Arnold, 1983). Such functional relationships have been observed both within (Mullaney & Gale, 1996; Wainwright, 1996) and between species (Losos, 1990a,b; Emerson, 1991; Reilly, 1994; see also Emerson & Arnold, 1989). However, such studies have usually focused on relatively small taxonomic groups and there are very few studies that have examined large-scale relationships between morphology and performance (e.g. Emlet, 1994; Zani, 1996; Wainwright & Turingan, 1997). In addition, previous studies have examined a relatively narrow range of functional relationships, focusing primarily on either locomotion (Ricklefs & Travis, 1980; Miles & Ricklefs, 1984; Norberg

& Rayner, 1987; Emerson & Koehl, 1990; Garland & Losos, 1994) or feeding biology (Werner, 1977; Wainwright, 1987, 1988; Reilly & Lauder, 1988, 1991). In this paper, I conduct a large comparative analysis of the evolutionary relationships between morphology and performance of clinging by lizards. I test the general hypothesis that evolutionary changes in claw and toe morphology are related to changes in organismal performance.

Focusing on clinging by animals offers an ideal opportunity for testing the functional relationships between morphology and performance because of the perceived importance of clinging. In most of the previous literature on clinging, specialized morphological traits for clinging have been viewed as adaptations that allow organisms to expand their niche space beyond terrestrial habitats (Cartmill, 1985; Pough *et al.*, 1998, p. 260). These specialized traits include hooks or claws (e.g. Richardson, 1943; Bock & Miller, 1959; Feduccia, 1993), adhesive toe pads (e.g. Gillett & Wigglesworth, 1932; Edwards, 1962; Emerson & Diehl, 1980; Russell, 1986) or other adhesive patches of skin (e.g. Pasteur, 1964; Cartmill, 1979; Haffner, 1998), as well as other releasable attachments (Nachtigall, 1974). Claws are perhaps the most common

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biological mechanism of attachment, particularly in vertebrates. Mahendra (1941) experimentally tested the importance of claws for climbing by removing claws from lizards. He found that clawless geckos lost their ability to adhere to very rough surfaces. This result suggests that claws are necessary for clinging in lizards. The comparative anatomy and morphology of animal claws has been studied in greater detail by previous authors as well (Boas, 1894; Schmidt, 1913, 1916). These studies found that the basic design of vertebrate claws is similar among species, which allows for cross-species comparisons.

Adhesive toe pads offer a second, often complementary mechanism by which animals can cling. Numerous insects (Gillett & Wigglesworth, 1932; Edwards, 1962), frogs (Green, 1979; Emerson & Diehl, 1980) and lizards (Ernst & Ruibal, 1967; Williams & Peterson, 1982; Peterson, 1983) have various adhesive structures associated with their toes. These structures allow animals to produce traction force that can be used to counter the effects of gravity. Previous work has noted the positive relationship between aspects of the toe pad (pad area, number of subdigital lamella [toe-pad subdivisions]) and clinging ability in frogs (Emerson & Diehl, 1980; Emerson, 1991) as well as lizards (Losos, 1990a; Irschick *et al.*, 1996). However, work by Mahendra (1941) demonstrated that adhesive toe pads alone do not allow lizards to adhere to very rough surfaces and that the action of claws and toe pads together may be necessary for clinging by lizards with adhesive toe pads.

In the studies reviewed above there is an often an untested assumption that morphological adaptations alter the performance ability of organisms and allow them to expand their ecological niches. In this paper, I utilize lizard claw and toe morphology and clinging performance to test portions of this assumption. I focus on lizards as the study group because they are diverse not only taxonomically, but also ecologically and morphologically. To begin, I characterize the multivariate evolutionary patterns associated with lizard claws and toes in an attempt to identify the general relationships between morphology and performance. I follow this with a set of sensitivity analyses in which I vary branch lengths and the procedural order for body size and phylogeny correction. I use these analyses as a test of the statistical robustness of the results of this study. Together, results from these experiments should help identify the overall evolutionary trends present within lizards as a group, as well as the sensitivity of these results to changes in statistical conditions.

Materials and methods

Sampling

Lizards used for this study were collected from February 1993 through July 1996 at various localities

in Brazil, Ecuador, Nicaragua and the United States. Data on individual lizards were collected by walking through the habitat both during the day and at night. In this way, I was able to sample 85 populations representing 68 species and 13 families of New World lizards.

In order to assay performance and morphology, lizards were captured alive in the field. In most cases I used a monofilament thread slip-knot attached to the end of a 2-m fibreglass pole. This slip-knot was gently manoeuvred over the head of the lizard and tightened by raising the pole. Lizards were immediately removed by hand from the slip-knot and placed in individual cloth bags. The weight of the lizard was generally sufficient to tighten the slip-knot without harming the animal. However, lizards weighing less than about 1 g (e.g. many gekkonids and gymnophthalmids) typically did not cause the slip-knot to tighten. For these taxa, I captured lizards by quickly placing a hand over the animal to immobilize it. Immobilized animals were then picked up by the other hand and placed in a cloth bag. For species too wary to be captured by either of these techniques (e.g. most teiid species), wire-mesh funnel traps were used (see Zani & Vitt, 1995). These traps were usually baited with large insects (e.g. tettigoniids, gryllids) or spiders and placed in an open location with the top covered by opaque plastic to shield from direct sunlight. When in operation, I checked these traps for ensnared lizards every 1–2 h.

Performance and body size data (see Table 1) were collected from 14.8 ± 0.97 and 19.4 ± 1.34 individuals of each species, respectively. Claw and toe traits were also measured on 8.2 ± 0.35 individuals per species. For most species, only adults or large subadults were included in performance and morphology measures to minimize the confounding effects of intraspecific allometric variation. In all analyses, I included animals of both sexes, except for the unisexual species *Leposoma percarinatum* and *Cnemidophorus flagellicaudus*.

The taxonomic relationships between several tropical populations and species used in this study are not clear. For example, the two populations of *Neusticurus* included here undoubtedly belong to the *eupleopus* species group, but whether they are the same or separate species is not known (T. C. S. Avila-Pires, personal communication). In light of this problem, voucher specimens for tropical species (except *Coleodactylus amazonicus*) were killed using a lethal injection of nembutal. These animals were then preserved in 10% formalin and stored in 70% ethanol following the methods of Pisani (1973). All preserved specimens were deposited in the Museo de la Universidad Católica del Ecuador in Quito, the Museo Nacional de Nicaragua in Managua, the Museu Goeldi in Belém, Brazil, or the Oklahoma Museum of Natural History in Norman. The remaining animals were released at the site of capture.

Trait	Definition
Body size:	
Snout-vent length	from tip of snout to cloacal aperture (vent)
Tail length	from vent to tail tip (excluding regenerated tails)
Mass	total body mass
Hind-limb length	left limb length from anterior point of insertion in body wall to tip of long toe
Fore-limb length	left limb length from posterior point of insertion in body wall to tip of long toe
Hind claw and toe:	
	measured on left long toe
Claw base-to-mid length	length of inner arc from point where toe scales end to mid-point of claw (see Fig. 1)
Claw mid-to-tip length	length of inner arc from mid-point to claw tip (see Fig. 1)
Claw height	vertical distance where toe scales end (see Fig. 1)
Claw curvature	degrees of arc encompassed by claw (see Fig. 1)
Toe length	length from base to tip of toe
Toe width	width at widest point of toe
Adhesive lamella number	total number of adhesive, subdigital divisions from tip of expanded toe disc to base of toe
Performance:	
	force required to pull horizontal lizard laterally from:
Rock clinging	rock surface
Wood clinging	wooden surface
Plexiglas clinging	Plexiglas surface

Table 1 List of traits measured on each of 85 lizard taxa.

Procedures

Performance measures

As an index of clinging performance, I measured the capacity of lizards to adhere to an experimental surface by placing a small slip-knot attached to a Pesola spring-loaded balance around the waist of the animal. The lizard was then placed on a flat, horizontal substrate. After allowing the animal to assume a resting posture, I slowly (approximately 0.5 m s^{-1}) drew the balance horizontally away from the posterior of the animal and recorded the maximum force required to pull the stationary animal from the substrate. This procedure was performed three times per experimental substrate in an attempt to measure maximum clinging ability of each individual; the largest value from the three trials was used in statistical tests. I excluded performance trials in which lizards failed to cling (as indicated by disproportionately small clinging force), appeared to give up, or used only some limbs to cling. I also excluded trials in which lizards ran, jumped or bit during the trial. Only lizards with three acceptable trials were included. With the exception of *Sauromalus obesus*, *Coleonyx variegatus* and *Sceloporus magister*, I tested animals for clinging within 3–4 h of capture; otherwise, animals were maintained such that they had access to an incandescent lamp for thermoregulation and were given *ad libitum* access to water and food for approximately 3 weeks prior to testing.

Each species was tested near its mean activity temperature because the locomotor ability of lizards is maximal near their preferred body temperature (Huey, 1983; Bennett & John-Alder, 1984; Marsh & Bennett,

1986). Activity temperature was determined by measuring body temperatures of 12.1 ± 2.69 field-active individuals for each taxa. Body temperatures were recorded at the time of capture for most individuals used in performance testing using a Miller and Weber quick-reading cloacal thermometer. Cloacal-temperature measurements of 3.9 ± 0.12 individuals per taxa taken prior to performance trials ensured that lizards were tested near each species' activity temperature. Although performance at activity temperature may differ from optimal performance temperature, measuring performance at activity temperature most closely approximates the thermal state at which lizards are likely required to perform in nature.

Three experimental substrates were used for performance measures. Individuals were tested on each of the three substrates in random order. Substrates included: rock (cinder block; $15 \times 10 \text{ cm}$ for small lizards, $30 \times 15 \text{ cm}$ for large lizards), wood (roughcut tropical hardwood, *Dinisia escelsa*; $30 \times 15 \text{ cm}$), and Plexiglas ($30 \times 20 \text{ cm}$). These three substrates were fairly uniform in their composition and were meant to encompass the breadth of variation of natural substrates encountered by lizards: rock and wood are naturally occurring rough surfaces; Plexiglas simulates smooth surfaces, such as leaves. Although actually measuring performance on leaves would have been preferable to Plexiglas, it was impossible to obtain an appropriate, standardized leaf surface from all localities sampled. Preliminary trials using *Musa* and *Heliconia* leaves showed that clinging performance was remarkably similar on Plexiglas and smooth leaves. Performance

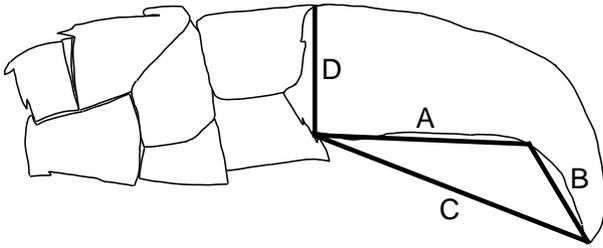


Fig. 1 Diagram of the measurements taken from claws. Claw length = total length of segments A + B; Claw height = length of segment D; Claw curvature = $57.296 * (2 * \arcsine(((2 * A^2 * B^2) + (2 * A^2 * C^2) + (2 * B^2 * C^2) - A^4 - B^4 - C^4)^{0.5} / (2 * A * B)))$.

measures obtained for Plexiglas represent the animal's ability to cling in the absence of claws (claws are not able to penetrate Plexiglas). To determine whether lizards without adhesive toe pads were able to cling to Plexiglas, I used lizard body mass times the experimental rate of acceleration (0.5 m s^{-1}) to predict actual performance in a regression analysis. For taxa that lack adhesive toe pads, actual performance should not exceed the predicted value, and the slope of this regression should not be greater than one. With few exceptions, I found that lizards lacking adhesive toe pads were unable to cling to Plexiglas (slope = 0.88, $r = 0.917$). To determine if there were effects due to microheterogeneity of the three experimental substrates, I performed separate repeated-measures analyses of variance (with clinging trial [1, 2, 3] as the factor) on 10 randomly chosen taxa. In all cases no statistical differences between the three trials were observed (P values > 0.05).

Morphological measures

I measured a number of morphological traits that are likely to be relevant to clinging performance (Table 1, Fig. 1). These include lizard snout-vent length, tail length, body mass, hind- and fore-limb length, claw length, claw height, claw curvature, toe length, toe width and adhesive lamella number. In most cases these were measured on the same individuals used for measuring performance, but for *Sauromalus obesus*, *Coleodactylus amazonicus* and *Coleonyx variegatus*, I used museum specimens from nearby localities. Claw characteristics (Fig. 1) were assayed using either preserved specimens or ink imprints of claws. Ink imprints were recorded by first pressing the claw onto an ink pad, followed by pressing it to a field notebook. I measured claw traits using both preserved specimens and ink imprints for *Gambelia wislizeni*, *Crotaphytus bicinctores*, *Uta stansburiana*, *Sceloporus occidentalis* and *Cnemidophorus tigris*. In all cases, mean claw curvatures based on both techniques were within two degrees of one another ($r = 0.933\text{--}0.975$).

Phylogenetic correction

To consider relationships among evolutionary changes in morphology, performance and ecology, I used Felsenstein's (1985) method of independent contrasts as implemented in the computer package COMPARE (Martins, 1996). This method requires information on phylogenetic relationships that is independent of the characters under study. Not only does one need to assume the position of species on a phylogenetic tree (topology), but also the relative distances between nodes on the phylogeny (branch lengths) in units of expected amount of character change.

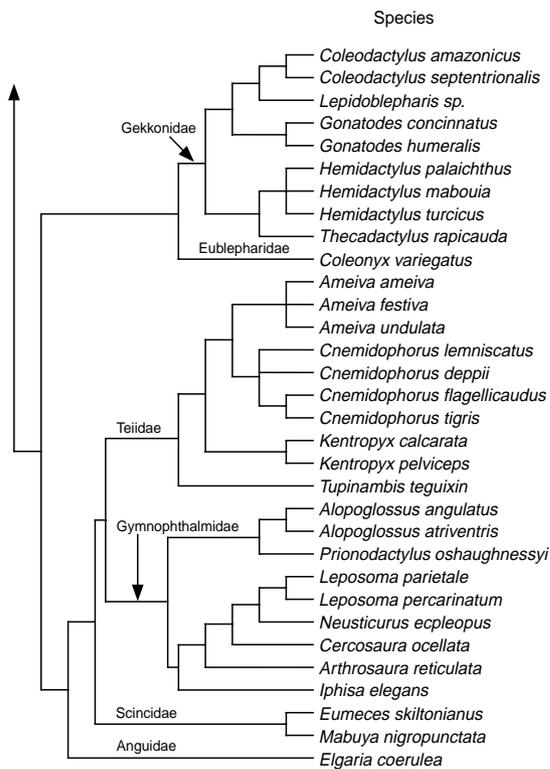
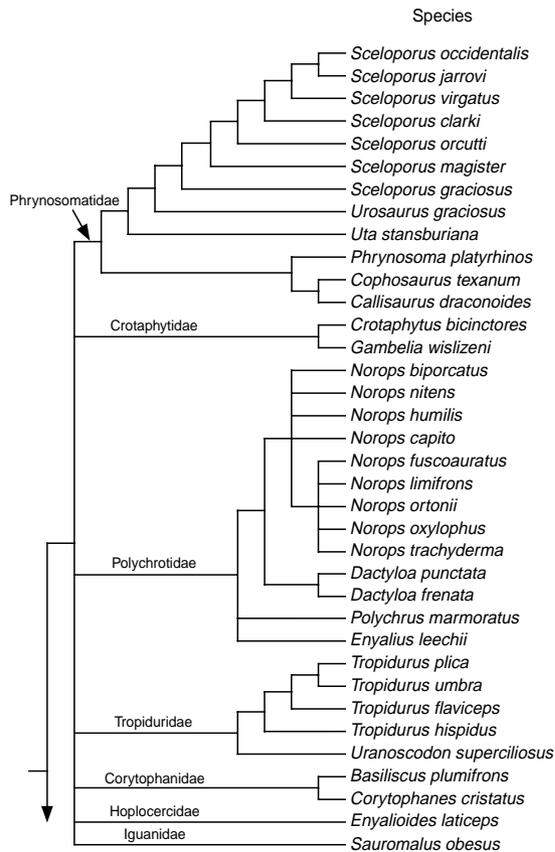
Topology

I used a phylogenetic hypothesis (Fig. 2) based on a number of sources: Estes *et al.* (1988; based on 130 osteological and 18 soft-anatomy characters); Frost & Etheridge (1989; 67 osteology and soft anatomy); Frost (1992; 77 osteology and soft anatomy); Guyer & Savage (1986, 1992; karyology, albumin immunology, and 15 osteology); Kluge (1987; 44 karyology, osteology, and soft anatomy); Presch (1974, 25 osteology) and Presch (1980, 26 osteology and soft anatomy); Reeder & Wiens (1996; 60 scalation, 55 osteology, 15 coloration, 9 behaviour, 9 myology, 4 karyology, 2 protein electrophoresis, 779 bp rRNA); Wright (1993; karyology). Taxonomy for Amazonian lizards follows Avila-Pires (1995), except for tropidurids (Frost, 1992) and polychrotids (Guyer & Savage, 1986, 1992). While it is possible to combine these multiple sources to obtain a reasonable hypothesis for phylogenetic topology, determining appropriate branch lengths is more problematic.

Branch lengths

The actual branch lengths for my phylogenetic hypothesis (Fig. 2) were not known. Therefore, I used a common way to assign unknown branch lengths in which all branches are set equal to one another (Martins & Garland, 1991). This model (herein 'speciational branches') assumes that evolutionary change occurs only at speciation events (Rohlf *et al.*, 1990). Several groups of lizards are depicted in Fig. 2 as unresolved polytomies. In these cases, I used an arbitrary branching pattern and set internodal distances equal to zero (Felsenstein, 1985), thereby treating these as rapid radiations or 'hard' polytomies. Multiple populations of a single species were also treated as an arbitrary-branching polytomy and were separated by zero branch lengths.

Upon computing independent contrasts, it is helpful to determine if data have been adequately standardized to ensure that they receive equal weighting in subsequent analyses (Garland *et al.*, 1992). To accomplish this, I plotted the absolute value of contrasts vs. their standard deviations (i.e. square roots of sums of branch lengths) following Garland *et al.* (1992). Significant linear or nonlinear trends from these plots indicate inadequate



standardization of the contrasts. In all cases, no trends were observed in my data, indicating that standardization using speciation branch lengths was adequate (P values > 0.05).

Statistical analyses

The statistical analyses described below were conducted on all 85 taxa for which I collected data (54 species represented by a single population; 13 represented by two populations; one represented by four populations) using the programs in COMPARE (Martins, 1996) and then STATVIEW 4.51 (Abacus Concepts, 1995). I began by computing Felsenstein (1985) contrasts of the trait means. This procedure transposes each variable into a phylogenetically relevant set of statistically independent, homoscedastic numbers that conform to the assumptions of most standard statistical tests.

Because body size can considerably affect the measurement of phenotypic values (see LaBarbera, 1989), I also statistically controlled for body size where applicable. To do this, I conducted a principal-component analysis (PCA) on independent contrasts of several traits that contribute to lizard size: snout-vent length, tail length, mass, and hind- and fore-limb lengths. Since body mass scales to approximately the cube of linear measurements, I used the cube root of body mass. All of these traits loaded very heavily on the first principal component (factor loadings >0.9). I then regressed independent contrasts of all morphological and performance traits against the first body size principal component (size PC1) and computed residuals from these regressions to be used in subsequent analyses. Residuals of lamella number and claw curvature were not taken as these were not significantly related to body size.

Correlations

To consider how morphology and performance are interrelated, I conducted two separate PCAs on contrasts to generate components corresponding to hind claw and toe morphology and clinging performance (Table 2). For these analyses I utilized speciation branch lengths (all equal 1). I interpret here those components that explain 70% of the total variation. The resulting orthogonal factor scores were used to compute correlation coefficients (forced through origin as required; Felsenstein, 1985; Garland *et al.*, 1992) between the variables describing morphology and performance. These statistical associations are the amount of correlated evolution between characters. Due to the multiple comparisons conducted in this study, one would expect a few spurious

Fig. 2 Hypothesis of phylogenetic relationships for 68 lizard species based on data from numerous sources (see 'Topology' section in Materials and methods).

Table 2 Orthogonal PCA loadings conducted on independent contrasts of morphology and performance from 85 lizard taxa.

Character	Component		
	I	II	III
Hind claw and toe:			
Claw base-to-mid length	-0.153	-0.428	0.720
Claw mid-to-tip length	-0.106	0.173	0.877
Claw height	0.010	0.859	0.136
Claw curvature	0.666	0.422	0.033
Toe length	-0.049	-0.718	0.449
Toe width	0.789	-0.004	-0.184
Lamella number	0.900	-0.091	-0.096
Eigenvalue	2.438	1.473	1.205
% variation explained	34.8	21.0	17.2
Performance:			
Rock clinging	0.891	-0.030	-
Wood clinging	0.848	0.209	-
Plexiglas clinging	0.087	0.989	-
Eigenvalue	1.615	0.929	-
% variation explained	53.8	31.0	-

Factors explaining 70% of the variance are included.

correlations to arise by chance alone. There are numerous ways to correct for this problem of multiple comparisons, but the approach I take is to consider $P > 0.01$ to be statistically insignificant, $P \leq 0.01$ to be significant and $P \leq 0.001$ to be highly significant.

Sensitivity analyses

I conducted two sets of analyses to determine the sensitivity of correlations to statistical conditions. For the first set of analyses, as a test of the assumption that the branch lengths did not unduly bias results, I conducted correlation analyses in which the data were standardized using a phylogenetic hypothesis with extreme branch lengths. The first test involved lengthening the branches at the base of the tree (branches from the tree root to individual lizard families) so that they were 100 times that of nontransformed length (i.e. 1). This method (herein 'nonindependent branches') forces most of the hypothesized divergence to occur near the root of the tree. The second test involved lengthening the branches at the tips of the tree (branches from each species to the tree tip) 100 times that of nontransformed length. This method (herein 'independent branches') forces most of the hypothesized divergence to occur near the tips of the phylogenetic tree. The null hypothesis in these tests is that the analysis using speciation branch lengths approximates the actual amount of divergence along any given branch. By testing extreme forms of branch lengths and examining results for differences, one can determine the validity of this hypothesis. Detecting

qualitative differences using these extreme branch lengths would disprove the null hypothesis and indicate that the real branch lengths are important in determining significance of results. In addition to these extreme branch lengths, I also conducted statistical analyses in which no phylogenetic correction was employed (herein 'raw data').

For the second set of sensitivity analyses, I examined the influence of the procedural order for statistical comparisons. Some researchers have reserved phylogenetic transformation (e.g. Felsenstein contrasts) to the final analyses (e.g. Losos, 1990a) in an effort, perhaps, to clarify the evolutionary interpretation of the results. Doing so runs the risk of computing PCAs, correlations and the like on nonindependent, heteroscedastic data. Although the strength of Felsenstein contrasts is in the evolutionary interpretation, it is also possible to consider the method as a purely statistical way of 'correcting for phylogeny'. To determine if the results from my analyses are sensitive to the order in which body size and phylogeny are taken into account, I conducted two additional statistical analyses in which this order was varied. For the correlations described above, I conducted Felsenstein contrasts first, followed by the body-size correction, and then a PCA to create composite morphology and performance variables for use in correlation analyses. For the first alternate set of analyses, I corrected for body size first, then created Felsenstein contrasts, followed by PCAs on morphology and performance for use in correlation analyses. For the second set of alternate analyses, I corrected for body size first, then conducted PCAs on size-free morphology and performance, and finally conducted Felsenstein contrasts for use in correlation analyses.

Results

Correlations

Principal-component analyses (PCAs) of claw and toe morphology and clinging performance were performed on size-free Felsenstein (1985) contrasts using a speciation model of branch lengths (Table 2). The traits corresponding to lizard claw and toe morphology reduced to three main components explaining 73.0% of the total variation. Claw PC1 was an axis based on increased claw curvature, toe width and adhesive lamella number. Claw PC2 was an axis describing claw height and the inverse of toe length, while PC3 consisted of claw length. The three clinging-performance measures reduced to two main components explaining 84.8% of the total variation. Performance PC1 was an axis describing clinging on rough substrates (rock and wood clinging), while PC2 was based on Plexiglas clinging.

Correlations of component scores between morphology and performance indicated that two measures of

Table 3 Phylogenetic correlations between morphology and performance contrasts from 85 lizard taxa. Branch lengths used to correct for phylogeny are: all equal 1 (speciational), branches at tree base 100× longer than at tips (nonindependent), or branches at tree tips 100× longer than at base (independent). Results on raw data (no phylogenetic correction) are also given (raw). Traits are based on PCA factor scores (Table 2).

	Branch lengths	Claw PC1	Claw PC2	Claw PC3
Performance PC1	Speciational	-0.030	0.431†	-0.197
	Nonindependent	-0.079	0.283*	-0.342*
	Independent	-0.141	0.542†	-0.316*
	Raw	-0.098	0.606†	-0.308*
Performance PC2	Speciational	0.631†	-0.069	-0.097
	Nonindependent	0.583†	-0.080	-0.142
	Independent	0.579†	-0.032	-0.080
	Raw	0.656†	-0.011	-0.082

* $P < 0.01$. † $P < 0.001$.

claw and toe morphology were related to lizard clinging ability (Table 3; speciational). Performance PC2 (Plexiglas clinging) was highly positively correlated with claw PC1 (claw curvature, hind-toe width, adhesive lamella number; $r = 0.645$; $P < 0.001$; Fig. 3A). In addition, performance PC1 (rough-surface clinging) was highly positively correlated with claw PC2 (claw height, inverse toe length; $r = 0.417$; $P < 0.001$; Fig. 3B).

Sensitivity analyses

Branch lengths

In addition to the above analyses, I conducted several sets of alternative analyses to test for sensitivity to statistical conditions. First, I compared correlation analyses in which extreme branch lengths were used to standardize the data. When the correlations were computed using a phylogeny in which the basal branch lengths were elongated 100× that of speciation (nonindependent), claw PC1 remained highly correlated to performance PC2 ($r = 0.583$; Table 3). However, the correlation between claw PC2 and performance PC1 was only significant to the $P < 0.01$ level ($r = 0.283$). In addition, one correlation that was previously insignificant was now statistically significant: claw PC3 (claw length) was now negatively correlated with performance PC1 ($r = -0.342$; Table 3). When correlations were computed using a phylogeny in which the branches at the tips of the phylogenetic hypothesis were elongated 100× that of speciation (independent), the resulting correlations indicate that claw PC1 remained correlated to performance PC2 ($r = 0.579$; Table 3), that claw PC2 was correlated to performance PC1 ($r = 0.542$) and that claw PC3 was negatively correlated to performance PC1 ($r = -0.316$). When I computed correlations using no phylogenetic correction (correlation analyses conducted on raw data), claw PC1 was correlated to performance PC2 ($r = 0.656$; Table 3), claw PC2 was correlated to

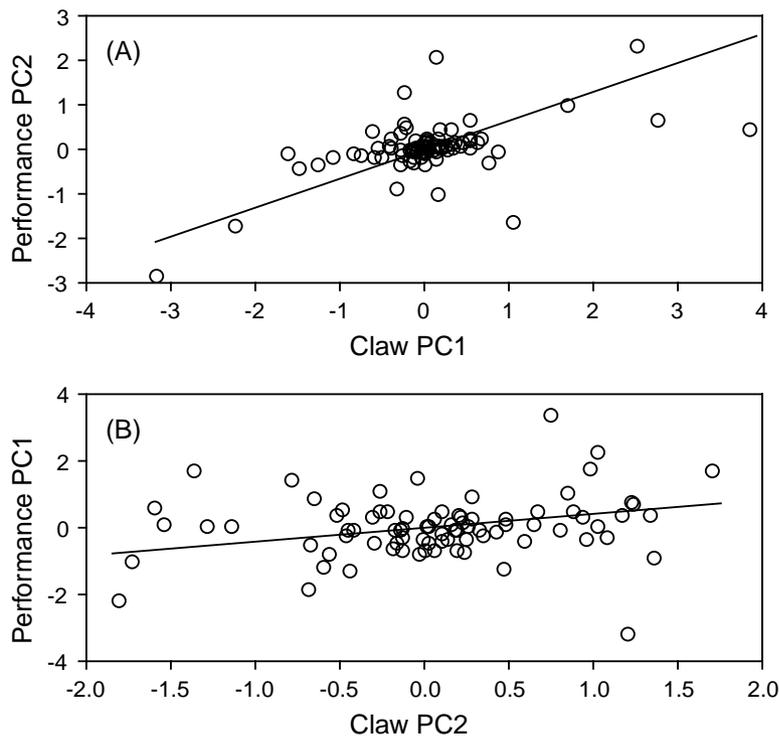


Fig. 3 Comparisons between size-free independent contrasts representing morphology and performance. Axes are principal components conducted on size-free data (residuals using body size PC1) in which phylogenetic relationships were first taken into account (Felsenstein contrasts). (A) Claw PC1 (claw curvature, hind-toe width, adhesive lamella number) vs. performance PC2 (smooth-surface clinging; $r = 0.631$; $P < 0.001$). (B) Claw PC2 (claw height, inverse toe length) vs. performance PC1 (rough-surface clinging; $r = 0.431$; $P < 0.001$).

performance PC1 ($r=0.0606$; Table 3) and claw PC3 was negatively correlated to performance PC1 ($r=-0.308$; Table 3).

Statistical order

In the second set of sensitivity analyses, I varied the procedural order in which size- and phylogeny-corrections were computed for use in correlational analyses. In the original analyses, Felsenstein contrasts were computed on raw data (using speciation branch lengths), followed by body-size correction and PCAs. For the first alternative, body size was taken into account prior to conducting Felsenstein contrasts, followed by PCAs on these data. Correlation analyses indicate that both previously significant results (claw PC1 vs. performance PC2; claw PC2 vs. performance PC1) remained statistically significant ($r=0.658$ and 0.395 , respectively). All other correlations remained insignificant. For the second alternative, the correction for body size followed by PCAs on these size-free variables were both conducted prior to Felsenstein contrasts. Once again, the resulting correlations indicate that claw PC1 remained correlated to performance PC2 ($r=0.624$), that claw PC2 was correlated to performance PC1 ($r=0.373$), and that no other correlations were significant. Since it does not appear that conducting Felsenstein contrasts before or after body size corrections alters the results in this case, I will primarily discuss the results from the original analyses: phylogenetic correction (contrasts) on raw data followed by body size correction and PCAs for use in correlation analyses.

Discussion

Based on the results from this study, there appears to be a positive relationship between toe morphology and clinging performance such that lizards with wider toes and more adhesive lamella are better able to cling to smooth substrates (Fig. 3A). These results are consistent with previous studies of toe pads in frogs (Emerson & Diehl, 1980; Emerson, 1991) and lizards (Losos, 1990a; Irschick *et al.*, 1996). While these results suggest that this mechanism of clinging has allowed certain lizard taxa to increase their clinging ability, it should be noted that toe pads appear to be specialized for clinging to smooth surfaces (Mahendra, 1941). Indeed, in the present study the relationship between the toe-pad characteristics (claw PC1) and clinging to rough surfaces (performance PC1) was not significant (Table 3). Thus, the evolution of adhesive toe pads may have allowed lizards to expand their niche space to include smooth substrates, such as leaves, while not greatly enhancing performance ability on rough substrates.

In addition to the above trend, lizards with higher claws (i.e. measure D , Fig. 1) and shorter toes are significantly better able to cling to rough substrates (Fig. 3B). These results are consistent with theoretical

predictions of claw strength based on beam theory (Alexander, 1968, 1971; see also Zani, 1999). However, other attributes of the claw (increased claw curvature and decreased claw length) were predicted to be correlated to performance as well (Zani, 1999). The results of this study do not indicate that a significant correlation exists between these other variables, even though the trends are in the expected direction (Table 3). Thus, I cannot disprove the null hypothesis that evolutionary changes in these traits have not occurred in concordance with functional predictions. Further examination of the functional relationships between claw morphology and claw performance may shed light on this issue.

The strength of the functional relationship between lizard claw morphology and performance is apparent when one considers results from sensitivity analyses. With one exception, I found no qualitative differences among comparisons regardless of the length of branches used to correct for phylogeny (Table 3), or the procedural order in which size- and phylogenetic-correction occurred. The exception to this result came in the comparison between claw length (claw PC3) and rough-surface clinging (performance PC1). In this case, a relationship that was insignificant when speciation branches were used was significant using all three alternative branch lengths (nonindependent, independent, raw data). Thus, detection of the relationship between claw length and rough-surface clinging appears dependent on the evolutionary model used for phylogenetic correction. In spite of this result, the general agreement of my remaining comparisons indicates that the functional evolutionary link between lizard claw and toe morphology and clinging performance tends to be robust to changes in statistical conditions.

The results of this study demonstrate that the evolution of lizard claw and toe morphology is correlated to the evolution of clinging-performance ability. Sensitivity analyses indicate that these results are for the most part insensitive to changes in either branch lengths or the order of statistical procedures used to correct for body size and phylogeny. One aspect of these ecomorphological relationships that was not included here is the ecological variation associated with lizard claws. Detailed examination of the functional relationships linking morphology and performance to the ecology of clinging ability is needed to answer questions concerning the types of performance required by animals. Such studies should aid in our understanding of the evolutionary ecology of animal claws and clinging.

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