

Anatomy of the Crus and Pes of Neotropical Iguanian Lizards in Relation to Habitat use and Digitally Based Grasping Capabilities

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ABSTRACT

Ecomorphological studies of lizards have explored the role of various morphological traits and how these may be associated with, among other things, habitat use. We present an analysis of selected traits of internal morphology of the hind limbs of Neotropical iguanian lizards and their relationship to habitat use. Considering that one of the most widely-held hypotheses relating to the origin of grasping is associated with the exploitation of the narrow-branch arboreal habitat, we include subdivisions of this designation as two of our ecologically defined categories of habitat exploitation for analysis, and compare lizards assigned to these categories to the features displayed by terrestrial lizards. The influence of phylogeny in shaping the morphology of lizards was assessed by using the comparative method. *K* values were significant for several osteological traits. Most of the *K* values for the variables based upon muscle and tendon morphometric characters (13 out of 21), by contrast, had values <1, suggesting that their variation cannot be explained by phylogeny alone. Results of our phylogenetic and conventional ANCOVA analyses reveal that the characters highlighted through the application of the comparative method are not absolutely related to habitat in terms of the categories considered here. It appears that the bauplan of the lizard pes incorporates a morphological configuration that is sufficiently versatile to enable exploitation of almost all of the available habitats. As unexpected as conservation of internal gross morphology appears, it represents a means of accommodating to environmental challenges by apparently permitting adequacy for all situations examined. *Anat Rec*, 00:000–000, 2014. © 2014 Wiley Periodicals, Inc.

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Lizards exhibit a diverse array of lifestyles and exploit a variety of environments (Pincheira-Donoso et al., 2013), ranging from rainforest to sandy deserts, and may occur in rivers and marine littoral habitats. Such ecological diversity is reflected, among other things, in variation in body size, body shape, and limb proportions (Vitt and Pianka, 1994; Pianka and Vitt, 2003; Losos, 2009; Tulli et al., 2009). Ecomorphological studies of lizards have explored the roles of various morphological traits and how these may be associated with, among other aspects, habitat use (Odendall, 1979; Peterson, 1984; Losos 1990a,b, Losos, 2009; Losos et al., 1998, 2002; Huey et al., 2003, Vanhooydonck et al., 2006, 2009, 2010; Herrel et al., 2008; Schulte et al., 2003, 2004; Russell and Higham, 2009; Grizante et al., 2010; Tulli et al., 2011, 2012a,b).

Following the tenets of ecomorphology that hold that different ecological demands lead to different organismal “designs,” it is reasonable to expect that morphological differences in muscles, tendons, and bones of the hind limb of lizards will reflect their ecological specializations (Wainwright and Reilly, 1994). The structurally complex arboreal environment presents one of most challenging microhabitats exploited by tetrapods, and becomes increasingly demanding with decreasing width of branches. Prehensile, or grasping, capabilities have played a major role in the evolutionary history of tetrapods, and seem to have originated at the very root of the tetrapod tree (Iwaniuk and Wishaw, 2000). It has been suggested that prehensile or grasping capabilities have arisen as a means of accommodating to the mechanical demands of locomotion on narrow branches (Feduccia, 1999; Youlatus, 2008; Abdala et al., 2009).

The evident manual grasping capabilities of primates are well-documented, but more recently there has been a burgeoning of interest in this phenomenon in other taxa (Manzano et al., 2008; Abdala et al., 2009; Sustaita et al., 2013). However, pedal grasping is also exhibited among a wide array of tetrapods (e.g., frogs, reptiles, birds, and mammals; Sustaita et al., 2013), but has received considerably less attention for these groups. Because of this, the origins and anatomical and functional characteristics of pedal grasping are much less well understood.

Grasping by the manus of lizards is achieved by using the digits collectively as one jaw of a clamp, with the palm forming the opposing jaw (Sustaita et al., 2013). Pedal grasping, however, is accomplished by forming the pes into a clamp in which the first and fifth digits are arranged in opposition to each other and are curled around the perch, with the sole of the pes being arranged as a longitudinal arch that cups the perch (Robinson, 1975; Brinkman, 1980; Abdala and Tulli, unpublished data).

Here we conduct an ecomorphologically based analysis of selected internal morphological traits of the hindlimbs of pleurodont Neotropical iguanian lizards and assess

them in the context of their relationship to habitat use and grasping capacity. Considering that the most widely held hypotheses relating to the origin of lizard grasping relates to the exploitation of the narrow-branch arboreal habitat (Abdala et al., 2009; Sustaita et al., 2013), we include this designation among our ecologically-defined categories of habitat exploitation (as represented by trunk-crown and grass-bush species) for analysis and comparison with results for homologous features displayed by terrestrial, saxicolous, trunk-ground, and crown-giant taxa.

Ours is the first attempt to explore pedal grasping in lizards from an ecomorphological perspective, and such an approach is yet to be undertaken for manual grasping. Taking into consideration the idea that fore and hind limbs are generally considered to be serially homologous structures (Owen, 1849, 1876; Humphry, 1872; Quain et al., 1894; Abassi, 2011), it would be anticipated that the modifications of the manus that are related to grasping are repeated as similar modifications of the pes. Thus, based upon modifications of the manus that reflect grasping capabilities, we predict that lizards that move on narrow branches will exhibit the following general morphological characteristics when compared to lizards that do not move on such perches: (1) some specialized traits are best explained by adaptation rather than strictly as a result of phylogeny; (2) the metatarsals and phalanges will be relatively longer than they are in nongrasping forms, and this will be associated with the presence of slender elements that permit some degree of cupping around branches; (3) there will be more strongly developed, longer tendons and relatively longer and wider aponeuroses than will be the case for nongrasping lizards, these tendinous systems likely playing a role in facilitating a secure grip on perches through digital flexion (Vanhooydonck and Van Damme 2001; Tulli et al., 2012a); (4) there will be a relative reduction in the dimensions of the muscles associated with rotation of the metatarsus (the gastrocnemius, peroneus longus and brevis) in direct relation to the relative enlargement of the tendinous components put forth in our third prediction. However, we note that Diogo et al. (2013) have questioned the concept of serial homology as applied to limbs of vertebrates, and thus we may, if that interpretation is correct, expect that the manus and pes display quite different patterns, even when possessed by lizards occupying particular habitats.

Our analyses of pedal grasping in Neotropical iguanian lizards focus on the morphometrics of the muscles that provide the forces for associated movements, and we thus examine the morphology and morphometry of the tendinous structures that transmit the motor input that brings about grasping, and the relative proportions of the skeletal elements involved (femur, tibia, phalanges, metatarsals, and tarsals). These initial observations and comparisons lay the groundwork for future,

more detailed, osteological, arthrological, and kinematic considerations.

Our current goals are to test whether the internal morphology of the lizard hind limb, as assessed through the analysis of 55 characters, differs among taxa that occupy different habitats, and whether such patterns can be accounted solely by the phylogenetic affinities of the 23 species examined (Fig. 1), or by another underlying factor.

MATERIALS AND METHODS

In this study, we dissected the crus and pes of 92 adult specimens of both sexes, representing 23 species of Neotropical iguanian lizards (Appendix 1), and investigated the morphology of muscles, tendons, and bones of these regions. Specimens were selected to represent a range of species and families that display a wide range of habitat use.

Morphology

The muscles and tendons of the right hind limb and foot were dissected under a binocular microscope (Nikon SMZ645). The number of adult specimens dissected per species varied according to availability (range, 1–10). Snout-vent length, (SVL) and traits related to the hind limb and internal foot morphology (described below) were measured with digital calipers (Mitutoyo CD-15B; ± 0.01 mm, Japan). Species means, standard deviations and the number of individuals per species are available from the corresponding author upon request.

To explore digital dimensions and the contributions of the autopodial elements we measured the length of each metatarsal, and the length of each phalanx of each digit. To quantify the contributions of the stylopodial and zeugopodial elements, we measured femur and tibia length.

To investigate the variability between muscle and tendon dimensions of the structures directly implicated in pedal rotation, plantar flexion and stabilization of the ankle joint, we measured the following structures: lengths and widths of the femorotibial aponeurosis (Russell, 1993); femorotibial gastrocnemius; femoral gastrocnemius superficialis; and flexor digitorum longus muscles (Brinkman, 1980; Russell and Bauer, 2008); and the length and width of the aponeurosis of the flexor digitorum longus (Russell, 1993) (Fig. 2). All of the muscles that we investigated exhibit a parallel-fibered arrangement. In addition to lengths, maximum widths of the muscles were also recorded to obtain an estimate of the morphometric variation of each muscle as a whole, and to permit correlation with aponeurosis and tendon dimensions that are associated with these muscles, for which we report width and length.

Because the peroneus complex plays a major role in movements of the fifth metatarsal, which is used by lizards to achieve opposition of the fifth digit to the first (Robinson, 1975; Brinkman, 1980), we also measured the lengths and widths of the peroneus longus and brevis muscle bellies, and the visible lengths, from the myotendinous junction to insertion point, of the tendons of both peroneus muscles. Flexor tendon length of each pedal digit (Fig. 2) was measured from its base, where it proceeds from the plantar aponeurosis of the flexor digitorum longus, to its insertion on the distalmost phalanx (Fig. 2).

Habitat Use

Lizard species were grouped in six ecomorphological categories according to their habitat occupancy (Table 1): terrestrial, saxicolous, arboreal narrow-branch trunk-crown, arboreal narrow-branch, grass-bush, trunk-ground, crown giant. Live specimens of *Iguana iguana* (Iguanidae),

TABLE 1. Habitat use of the species examined in this study, based on literature data (see text)

Species	Author	Habitat	Grasping capabilities	Author
<i>Anolis cuvieri</i>	Losos (2009)	Crown-giant	Present	Daza J*
<i>Anolis evermanni</i>	Losos (2009)	Trunk-crown	Present	Daza J*
<i>Anolis stratulus</i>	Losos (2009)	Trunk-crown	Present	This work
<i>Anolis gundlachi</i>	Losos (2009)	Trunk-ground	Present	Daza J*
<i>Anolis krugi</i>	Losos (2009)	Grass-bush	Present	Daza J*
<i>Diplolaemus sexcinctus</i>	Cei et al. (2003)	Terrestrial	Absent	Abdala V*
<i>Enyalius catenatus</i>	Frost et al. (2001)	Trunk-crown	Present	Quatman W*
<i>Enyalius iheringi</i>	Frost et al. (2001)	Trunk-ground	Present	Quatman W*
<i>Iguana iguana</i>	Hirth (1963)	Trunk-ground	Absent	This work
<i>Liolaemus albiceps</i>	Abdala (2007)	Terrestrial	Absent	Abdala C*
<i>Liolaemus elongatus</i>	Cei (1986)	Saxicolous	Absent	Cruz, Tulli*
<i>Liolaemus escarchadosi</i>	Scolaro and Cei (1997)	Terrestrial	Absent	Cruz, Tulli*
<i>Liolaemus fitzingerii</i>	Etheridge (2000)	Terrestrial	Absent	Cruz, Tulli*
<i>Liolaemus irregularis</i>	Abdala (2007)	Terrestrial	Absent	Abdala C*
<i>Liolaemus kriegi</i>	Espinoza et al. (2000)	Saxicolous	Absent	Cruz, Tulli*
<i>Liolaemus petrophilus</i>	Avila et al. (2004)	Saxicolous	Absent	Cruz, Tulli*
<i>Liolaemus pictus</i>	Medel et al. (1988)	Trunk-ground	Absent	This work
<i>Leiosaurus belli</i>	Laspiur et al. (2007)	Terrestrial	Absent	Abdala V*
<i>Leiosaurus catamarcensis</i>	Laspiur et al. (2007)	Terrestrial	Absent	Abdala V*
<i>Phymaturus ceii</i>	Lobo and Quinteros (2005)	Saxicolous	Absent	Cruz, Tulli*
<i>Phymaturus spectabilis</i>	Lobo and Quinteros (2005)	Saxicolous	Absent	Cruz, Tulli*
<i>Polychrus acutirostris</i>	Frost et al. (2001)	Trunk-crown	Present	This work
<i>Tropidurus etheridgei</i>	Frost (1992)	Terrestrial	Absent	Cruz F*

Asterisk corresponds to field observations and photographs.

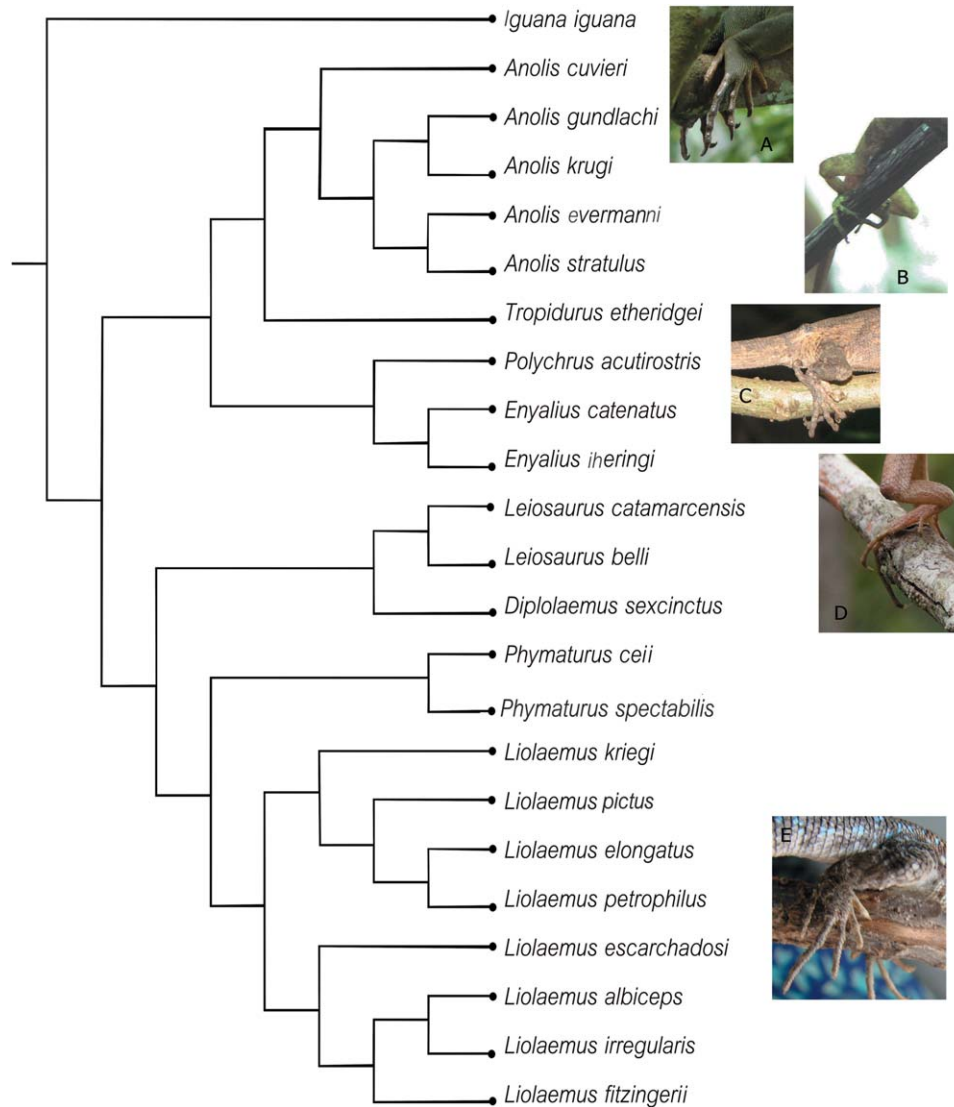


Fig. 1. Tree topology based on a combination of morphological and mitochondrial DNA analyses based on Lobo (2001, 2005); Lobo and Quinteros (2005); Avila et al. (2006); Abdala (2007); Lobo et al. (2010); Frost et al. (2001), and Nicholson et al. (2012). Photograph beside the nodes illustrate the grasping capacities of (A) *Iguana iguana*; (B) *Anolis* sp.; (C) *Polychrus acutirostris*; (D) *Enyalius* sp.; (E) *Liolaemus* sp. Photos A, B and E by M.J. Tulli; C by Victor Zaracho, and D by William E. Quatman.

Polychrus acutirostris (Polychrotidae), *Liolaemus* sp. (Liolaemidae), *L. pictus* (Liolaemidae), and *Anolis stratulus* (Dactyloidae) were observed to examine their pedal grasping capabilities [see Napier, 1956 (hominids); Robinson, 1975 (*Anolis equestris*); Gray et al., 1997 (anurans); Iwaniuk and Wishau, 2000 (tetrapods); Mendick and Horn, 2011 (*Varanus beccari*) for similar approaches]. We investigated whether each one of these species is able to oppose the fifth and the first digit, and if they are able to arrange digits one to four in a clasping grip around a branch (Robinson, 1975). The animals were photographed in lateral view at different points in the step cycle while moving across dowels of different diameters (3.9 and 20 mm, and 20 cm) (Fig. 1). Additionally, similar data on *Anolis equestris* were obtained from Abdala et al. (2009), and on the rest of the taxa surveyed from field observations. These

data, and the assignment of all lizard species examined to either the pedal grasping or nongrasping category, are summarized in Table 1.

Phylogenetic Signal

Because species share portions of their evolutionary histories, they cannot be treated as independent sources of data (Felsenstein, 1985; Harvey and Pagel, 1991). Accordingly, we ran analyses of independent contrasts where appropriate. Here, we consider the application of this method to three fundamental questions: (1) Does a trait exhibit differences beyond what the phylogenetic relationships may account for?; (2) are related taxa more similar to one another than would be expected by random chance?; and (3) are two or more characters

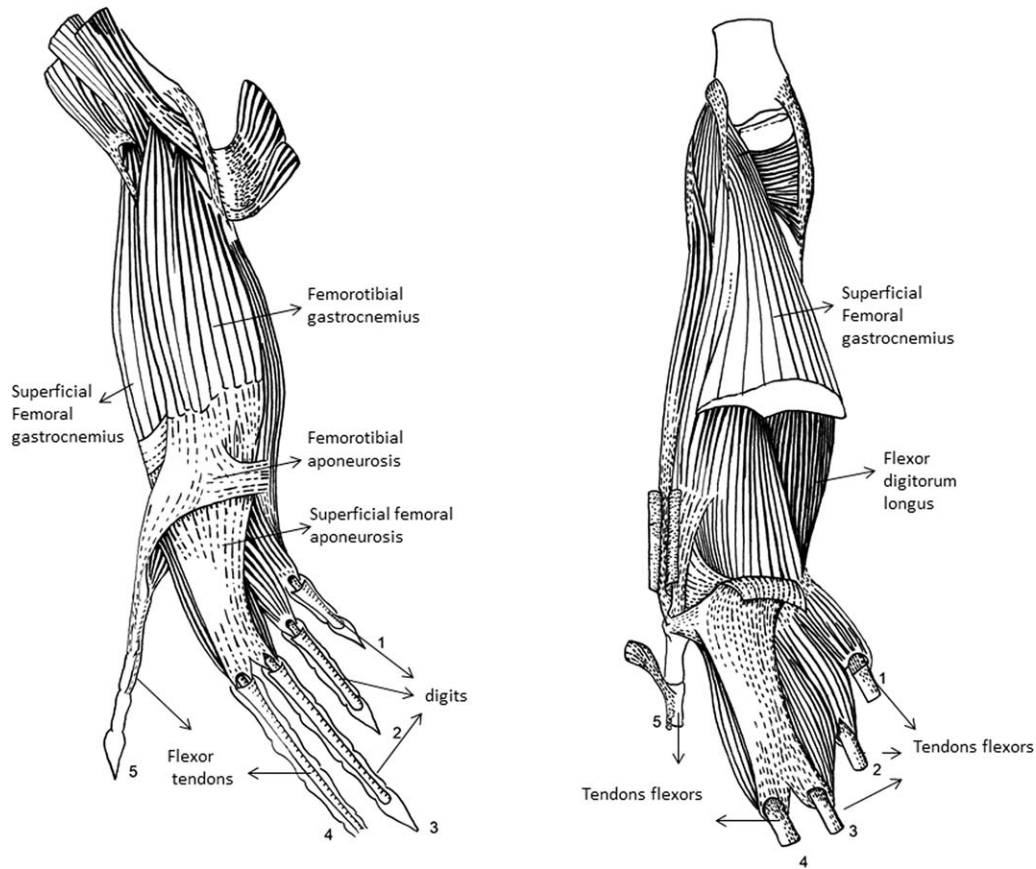


Fig. 2. General scheme of some of the muscles and tendons examined for morphometric traits (redrawn from Russell and Bauer, 2008).

correlated after controlling for phylogenetic relatedness? Questions two and three were formulated according to criteria set out by Blomberg and Garland (2002). To investigate this, we constructed a metatree from the available topologies that depict the pattern of relationships of the species studied. That tree (Fig. 1) is based on the results of several morphological and molecular studies (Frost et al., 2001; Lobo 2001, 2005; Lobo and Quinteros, 2005; Avila et al., 2006; Abdala, 2007; Lobo et al., 2010; Nicholson et al., 2012).

We calculated the K -statistic to allow us to estimate the level of phylogenetic signal under a Brownian motion model of evolution considering the tree topology and branch lengths. A K -statistic lower than one implies that relatives resemble each other less than would be expected under Brownian motion evolution (Blomberg et al., 2003). Thus, $K=0$ indicates that there is an absence of phylogenetic signal; $K=1$ or higher indicates the presence of non-trivial phylogenetic signal (Blomberg et al., 2003). To test whether topology or branch length affects the results, we carried out branch length manipulations as follows: we used untransformed branch lengths and two different branch length transformations in an Ornstein–Uhlenbeck model of evolution (Blomberg et al., 2003). Each of these transformations represents the relative strength of stabilizing selection, in which a low value of the OU transformation index ($d=0.2$) represents a more “adaptive” scenario associated with a

more star-like topology, whereas an OU transformation closer to unity ($d=0.8$) represents a greater role played by Brownian motion (Blomberg et al., 2003), resulting in a more hierarchical topology.

We tested for phylogenetic signal for each character by a randomization test (PHYSIG) (Blomberg et al., 2003). Mean values of all morphometric traits corresponding to each species were \log_{10} transformed prior to analyses to meet the requirements of normality and homoscedasticity (Zar, 1999) and were employed in this form in PHYSIG. Additionally, because traits are affected by body size, we computed size-corrected values of all characters, except for SVL, as follows: First, we log transformed the trait as well as the measure of size (mass or snout-vent length). Second, we computed standardized phylogenetically independent contrasts for both traits. Third, we computed a least-squares linear regression through the origin for the contrasts and noted the slope, b (allometric exponent). Finally, we computed size corrected values for the original trait (not contrasts) using the following formula: $\log[\text{trait}/(\text{size}^b)]$. **Results of these analyses are summarized in tables 2 and 3.**

Statistical Analyses

To reduce the dimensionality of the habitat and size-corrected morphological data sets, we used principal component (PC) analyses based on the correlation

matrix (calculated through the origin) of independent contrasts of each trait as input data. Previous work has demonstrated that the procedural order of this approach does not affect the results (Zani, 2000; Goodman et al., 2008). The number of PC axes used in subsequent analyses was determined from a scree plot of the eigenvalues (Jackson, 1993). Then, using those informative traits (Tables 4 and 5 in boldface) we tested for differences among six ecological categories. To test for trait differences among ecological groups, we ran traditional and phylogenetically informed analyses of covariance (ANCOVA and PDANCOVA, respectively). For the PDANCOVA, we generated an empirical null distribution of F statistics, taking into account phylogeny, by using PDSIMUL (Garland et al., 1993). For each variable, we ran 1,000 simulations using a speciation model of evolution (Martins and Garland, 1991). The means and variances of the simulations were set to the means and variances of the original data. Because PDANCOVA does not perform post hoc tests, to elucidate whether grasping species show differences in comparison to nongrasping species, we ran a PDANCOVA comparing the grasping species as a group against all other species pooled into another (nongrasping) group (see Table 1).

We also took into account the influence of untransformed measurements, because what matters to an animal in its environment is its absolute performance rather than relative dimensions. For this reason we conducted ANOVA and PDANOVA analyses on nonsized corrected traits.

RESULTS

Grasping Capabilities

Three of the lizard species examined perching on dowels were unable to close their pedal digits around any of the perches: *Iguana iguana* (Fig. 1A), *Liolaemus* sp. (Fig. 1E), and *Liolaemus pictus* (Fig. 3B). In contrast, *Polychrus acutirostris* (Figs. 1C and 3A) and *Anolis stratulus* (Fig. 1B) were able to curl their digits around the narrow perches (20 mm). We also employed images of similar situations obtained by another investigator (W. Quatman), for *Enyalius* sp. (Fig. 1D).

Phylogenetic Signal

K values were higher than one and statistically significant for several of the morphological traits studied (Tables 2 and 3)—particularly those relating to osteological traits. However, other values were intermediate on the K value scale ($K < 1$ and $P < 0.05$; e.g., tibia length, femur length) and so do not permit us to draw absolutely categorical conclusions. Most of the K values for the variables based upon muscle and tendon morphometric characters (13 of 21), by contrast, were less than 1, or not statistically significant after the randomization test, suggesting that their variability is a consequence of adaptation or the result of measurement error (*sensu* Blomberg et al., 2003) (Table 3).

Interestingly, following branch length manipulation, we observed that as OU transformation “ d ” values decrease, from untransformed, through $d = 1$, to $d = 0.8$, and then to $d = 0.2$, the phylogenetic signal trends to greater than unity for several traits (tibia length, femur length, superficial femorotibial aponeurosis length, and

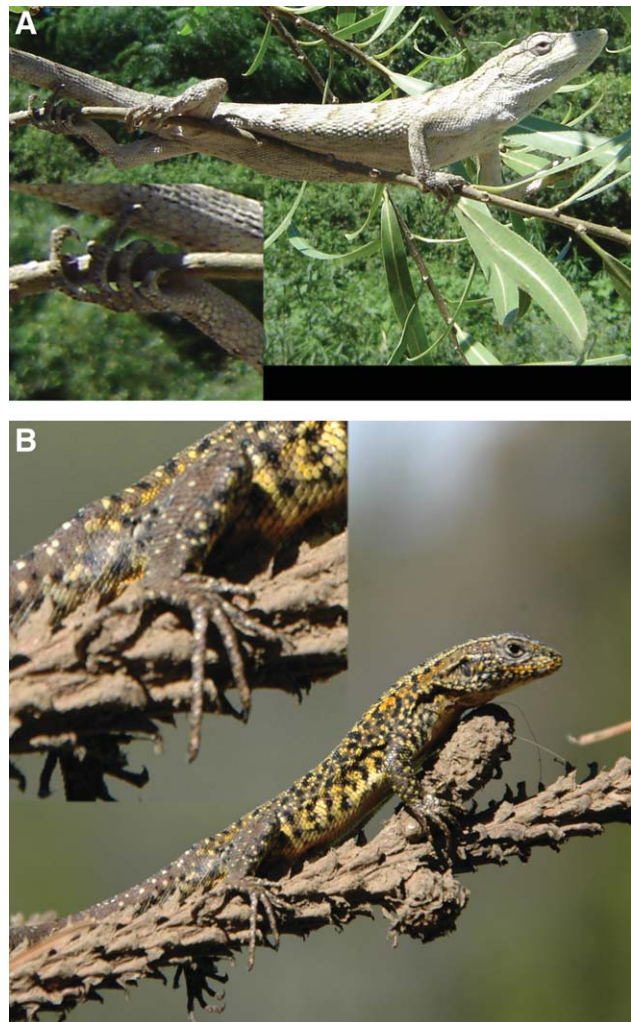


Fig. 3. (A) *Polychrus acutirostris* with its pedal digits curled around a narrow branch. Photo by Victor Zaracho. (B) *Liolaemus pictus* employing the fifth metatarsal and the proximal phalanx of the fifth digit to achieve opposition of the fifth digit to the first. The remainder of the digits is rigid. Photo by Cristian Abdala.

femoral gastrocnemius superficialis length—Tables 2 and 3).

Habitat Use and the Role of Grasping

ANCOVA and PDANCOVA analyses reveal that most of the traits determined to be informative in the PCA did not differ among lizards assigned to different types of habitat use (see Tables 4 and 5). For the size-corrected data, however, tibia length shows differences among these groups using a conventional ANCOVA, but not using the PDANCOVA (Table 7). When the absolute differences are considered using a conventional ANOVA, three traits are recovered: femoral gastrocnemius superficialis width, tibia length, and the length of the fourth phalanx of digit 3 (Table 6). No trait was recovered with the PDANOVA.

Conventional analysis of covariance indicates that grasping species display a relatively longer tibia than do non-grasping species, as well as a wider femoral gastrocnemius superficialis (Table 8). Such differences

TABLE 2. Summary of analyses calculating phylogenetic signal using constant branch lengths (BL) and Orstein-Uhlenbeck (OU) transformed branch lengths (osteological morphometric traits)

Traits	BL = 1		OU d = 0.8		OU d = 0.2	
	<i>K</i>	<i>P</i>	<i>K</i>	<i>P</i>	<i>K</i>	<i>P</i>
Femur length	0.664	0.003	0.015	0.943	1.024	0.882
Tibia length	0.524	0.045	0.013	0.023	1.072	0.903
Metatarsal I	2.052	0.010	0.190	0.998	0.828	2.201
Ph1 digit 1	1.032	0.009	0.030	0.816	0.986	1.392
Ph 2 digit 1	1.060	0.051	0.152	0.902	0.905	1.388
Metatarsal II	1.068	0.011	0.190	0.869	0.920	1.282
Ph 1 digit 2	1.863	0.002	0.034	0.914	0.889	2.166
Ph 2 digit 2	2.006	< 0.00	0.002	0.907	0.911	2.106
Ph 3 digit 2	<i>0.871</i>	<i>0.094</i>	0.106	0.815	0.937	1.230
Metatarsal III	1.108	0.044	0.357	0.932	0.901	1.366
Ph 1 digit 3	2.826	< 0.00	0.013	0.965	0.860	2.693
Ph 2 digit 3	2.398	0.012	0.392	0.992	0.830	2.428
Ph 3 digit 3	2.225	< 0.00	0.002	0.908	0.910	2.345
Ph 4 digit 3	0.799	0.023	0.044	0.536	0.85	1.099
Metatarsal IV	1.287	0.052	0.410	0.953	0.871	1.528
Ph 1 digit 4	1.362	0.071	0.607	0.992	0.869	1.576
Ph 2 digit 4	1.299	0.008	0.156	0.981	0.902	1.502
Ph 3 digit 4	1.632	0.036	0.426	0.995	0.854	1.805
Ph 4 digit 4	1.802	0.003	0.009	0.918	0.909	1.975
Ph 5 digit 4	<i>0.365</i>	<i>0.267</i>	<i>0.792</i>	<i>0.673</i>	<i>0.946</i>	<i>0.538</i>
Metatarsal V	1.279	0.003	0.030	0.840	0.933	1.538
Ph 1 digit 5	1.680	0.084	0.723	0.998	0.813	1.858
Ph 2 digit 5	1.778	0.105	0.839	0.998	0.828	1.949
Ph 3 digit 5	1.611	0.001	0.042	0.911	0.901	1.664
Ph 4 digit 5	1.045	0.070	0.237	0.892	0.896	1.322

K values > 1 and *P* values < 0.05, in bold, indicate the presence of phylogenetic signal. Absence of phylogenetic signal is indicated in italic by *K* < 1 and *P* values > 0.05.

TABLE 3. Summary of analyses calculating phylogenetic signal using constant branch lengths (BL) and Orstein-Uhlenbeck (OU) transformed branch lengths (muscle and tendon morphometric characters)

Traits	BL = 1		OU d = 0.8		OU d = 0.2	
	<i>K</i>	<i>P</i>	<i>K</i>	<i>P</i>	<i>K</i>	<i>P</i>
SVL	1.339	0.002	1.564	0.038	0.908	0.923
Peroneus longus length	<i>0.940</i>	<i>0.147</i>	1.111	0.872	0.842	0.998
Peroneus longus width	1.186	0.001	1.509	0.000	1.065	0.080
Peroneus longus tendon length	<i>0.916</i>	<i>0.066</i>	1.416	0.031	0.948	0.777
Peroneus brevis length	<i>0.844</i>	<i>0.080</i>	<i>1.063</i>	0.498	0.879	0.918
Peroneus brevis width	1.164	0.007	1.611	0.003	0.993	0.604
Peroneus brevis tendon length	<i>0.819</i>	<i>0.618</i>	1.555	0.180	0.956	0.845
Superficial femorotibial aponeurosis length	0.619	0.002	0.878	0.006	1.060	0.028
Superficial femorotibial aponeurosis width	1.399	< 0.00	1.753	0.003	1.001	0.397
Femoral gastrocnemius sup length	<i>0.502</i>	<i>0.190</i>	0.941	0.109	1.004	0.464
Femoral gastrocnemius sup width	1.031	< 0.00	1.410	< 0.00	1.140	0.001
Femorotibial gastrocnemius length	<i>0.585</i>	<i>0.072</i>	0.978	0.163	0.979	0.568
Femorotibial gastrocnemius width	<i>0.852</i>	<i>0.229</i>	1.270	0.260	0.913	0.882
Flexor digitorum longus length	<i>0.467</i>	<i>0.126</i>	0.627	0.883	0.864	0.942
Flexor digitorum longus width	1.307	0.003	1.767	< 0.00	1.005	0.644
Flexor digitorum longus aponeurosis length	0.701	0.009	1.029	0.009	0.997	0.341
Flexor digitorum longus aponeurosis width	1.231	0.040	1.423	0.016	0.941	0.850
Digital flexor tendon digit 1	0.709	0.019	0.913	0.156	0.931	0.748
Digital flexor tendon digit 2	1.225	0.037	1.464	0.238	0.868	0.967
Digital flexor tendon digit 3	1.523	0.041	1.705	0.424	0.833	1.000
Digital flexor tendon digit 4	1.223	0.099	1.383	0.778	0.827	1.000
Digital flexor tendon digit 5	1.097	0.144	1.316	0.804	0.845	0.996

K values > 1 and *P* values < 0.05, in bold, indicate the presence of phylogenetic signal. Absence of phylogenetic signal is indicated in italic by *K* < 1 and *P* values > 0.05.

disappear, however, upon taking into account phylogenetic relationships (Tables 8 and 9). When absolute sizes are considered using a conventional ANOVA, two traits

are recovered: femoral gastrocnemius superficialis width and femorotibial gastrocnemius width (Table 9). No trait is recovered with the PDANOVA (Table 9).

TABLE 4. Component scores resulting from a principal component analysis (PCA) performed on the morphological traits (osteological morphometric traits)

Traits	AX1	AX2	AX3
Metatarsal I	-1.1516	-0.8194	0.1884
Ph1 digit 1	-0.9143	1.1015	0.7377
Ph2 digit 1	-0.4427	2.3738	-1.5763
Metatarsal II	-1.0535	-0.581	-0.2913
Ph1 digit 2	-1.0651	0.3443	-0.9324
Ph 2 digit 2	-0.9056	0.7934	1.2336
Ph 3 digit 2	-0.5542	1.0592	-1.0177
Metatarsal III	-1.1116	-0.9424	-0.3033
Ph 1 digit 3	-0.9955	0.0131	0.5366
Ph 2 digit 3	-0.9609	-0.51	-0.7668
Ph 3 digit 3	-0.8327	0.759	1.2517
Ph 4 digit 3	-0.6477	1.6415	-0.443
Metatarsal IV	-1.257	-0.6036	0.322
Ph 1 digit 4	-1.3242	-0.743	-0.4439
Ph 2 digit 4	-1.3124	-0.4004	-0.6637
Ph 3 digit 4	-1.2542	-0.9683	-0.7394
Ph 4 digit 4	-0.8595	0.156	0.9856
Ph 5 digit 4	-0.6432	2.2728	1.3974
Metatarsal V	-1.1365	-0.178	1.1623
Ph 1 digit 5	-1.2154	-0.2458	-0.0106
Ph 2 digit 5	-1.1314	-0.3067	-1.5074
Ph 3 digit 5	-0.9853	-0.1575	1.7534
Ph 4 digit 5	-0.4539	1.1994	-1.6683
Eigenvalues	0.3578	0.1011	0.036
Cumulative variance	59.9	76.9	82.9

All traits were log-transformed, and the effects of body size were removed. Traits contributing most to each component are indicated in bold. The total amount of variance in the data explained by these first three principal components is 82.9%.

Extracted axes from the Principal Component Analysis (PCA) accounting for 82.9 % of the total variation considered.

DISCUSSION

Our proposed hypotheses were based on the concept of serial homology (Diogo et al., 2013). Our data, however, tend to support the conclusions of for example, Diogo et al. (2013), entailing falsification of the serial-homology theory by studying the comparative myology of tetrapods. Thus, our analysis of morphological traits indicates a high degree of conservatism of gross morphology (Tables 2 and 3), and contrary to what was found in the forelimb studies (Manzano et al., 2008; Abdala et al., 2009), there are no defining differences, anatomically, between grasping and nongrasping lizards, or between habitat types. Hence, only the first of our proposed hypotheses was supported by our data: some specialized traits cannot be explained strictly as a result of phylogeny, although these traits cannot be related to the ecological or functional aspects addressed in this work.

Our results, however, agree with previous conclusions concerning the relationship between morphology and habitat use for certain iguanian lizards, such as the Liolaemidae (Schulte et al., 2004; Tulli et al., 2012a,b), which exhibit a similarly strong phylogenetic signal for the morphological traits considered (but see Tulli et al., 2011). The prevalence of phylogeny in shaping internal morphological traits correlated with external ones (e.g., femur and tibia length) is striking when contrasted with

the observation that, in general, changes in body size and limb and tail proportions have been demonstrated to be associated with the evolution of locomotor performance in different ecological settings for several clades of squamates (e.g., Losos and Sinervo, 1989; Losos 1990a,b; Bonine and Garland, 1999; Vanhooydonck and Van Damme, 1999, 2001; Higham et al., 2001; Herrel et al., 2002; Goodman et al., 2008). Indeed, many traits of the species examined here exhibited a trend towards an increase in their K value as a result of the OU analysis: tibia length, femur length, superficial femorotibial aponeurosis length, and femoral gastrocnemius superficialis length, (Tables 2 and 3). The overwhelming effect of phylogeny in shaping morphology has been repeatedly obtained in studies of various taxa, although the features studied have been quite different (e.g., external morphology of lacertids: Vanhooydonck and Van Damme, 1999; external morphology of skinks: Goodman et al., 2008; external morphology of liolaemids: Schulte et al., 2004 and Tulli et al., 2009; thermal biology of liolaemids: Cruz et al., 2009; internal morphology of geckos and liolaemids: Zaaf et al., 1999 and Tulli et al., 2012, respectively). This probably indicates that stabilizing selection has acted upon these features (Harmon and Glor, 2010; Harmon et al., 2010; Cabrera et al., 2013). In contrast, Caribbean *Anolis* lizards exhibit morphologies that are clearly related to their habitat use on each of the islands colonized (Losos, 1990a,b). Herrel et al. (2008) also showed that differences in the morphology, muscle mass, and muscle mass distribution of the limbs of *Anolis valencienni* and *A. sagrei* were correlated with locomotor performance and locomotor style. It could be inferred that ecomorphological models based on *Anolis* are not reflective of the evolution of locomotor performance in other lizard taxa (see also Vanhooydonck and Van Damme, 1999, 2001). Interestingly, our data set includes features of five dactyloid species, and none was recovered as being evolutionarily labile. Because most of our data are from liolaemids, however, the possibility of sampling bias should be considered.

The majority of the osteological traits examined by us exhibit a high K -values, except for the lengths of distal phalanges of digits 2 and 4 (Table 2). These last elements are the only ones of digits 2 and 4 that display evolutionary flexibility. Tulli et al. (2009) showed that the heights the claws of pedal digits 3, 4 and 5 are adaptive, which suggests that the distal regions of the pes are evolutionarily more labile than are the more proximal ones. Interestingly, these distal parts are the last to appear during ontogeny of the autopodia, and are the first to be lost in phylogenetic limb reduction (Shubin and Alberch, 1983; Shapiro et al., 2007). Many other traits of digits 4 and 5 of the pes showed a positive morphological/functional response in previous studies (Tulli et al., 2009, 2011, 2012b). Differences observed in relation to these two pedal digits highlight the asymmetry present in the pes of the majority of lepidosaurs (Brinkman, 1980; Russell et al., 1997; Russell and Bauer, 2008). This asymmetry is mainly related to the morphology of the fifth metatarsal (Robinson, 1975; Russell and Bauer, 2008), and to differences in length of the first four metatarsals and their respective digits (Brinkman, 1980; Russell and Bauer, 2008). The special role of the fifth digit in the locomotion of squamates was considered by Robinson (1975), who found that the peculiar

TABLE 5. Component scores resulting from a principal component analysis (PCA) performed on the morphological traits (muscle and tendon morphometric characters)

Traits	Ax1	Ax2	Ax3
Peroneus longus length	-1.2414	0.6679	-0.2126
Peroneus longus width	-0.8908	0.0995	-0.0799
Peroneus longus tendon length	-0.8836	-0.9039	1.1345
Peroneus brevis length	-1.0971	0.7357	-0.294
Peroneus brevis width	-0.9961	-0.1513	-0.3551
Peroneus brevis tendon length	-0.5899	-1.9641	0.8638
Superficial femorotibial aponeurosis length	-0.9152	0.4464	0.7078
Superficial femorotibial aponeurosis width	-0.9351	0.3769	0.3582
Femoral gastrocnemius sup length	-1.107	-0.1691	-0.6659
Femoral gastrocnemius sup width	-0.9291	0.3217	2.1952
Femorotibial gastrocnemius length	-1.3713	0.025	0.1529
Femorotibial gastrocnemius width	-0.641	-2.0956	-1.415
Flexor digitorum longus length	-0.9927	-1.0072	-0.4624
Flexor digitorum longus width	-0.5921	-1.9622	-1.4808
Flexor digitorum longus aponeurosis length	-1.007	-1.6603	0.6364
Flexor digitorum longus aponeurosis width	-0.1426	1.0098	-2.9232
Digital flexor tendon digit 1	-1.1893	0.8652	-0.0908
Digital flexor tendon digit 2	-1.2312	0.9062	-0.1087
Digital flexor tendon digit 3	-1.2515	0.7761	-0.5146
Digital flexor tendon digit 4	-1.305	0.6391	-0.1213
Digital flexor tendon digit 5	-1.1796	0.3184	-0.0996
Eigen vector value	0.4042	0.1141	0.0628
Cumulative variance %	51.3	65.7	73.7

All traits were log-transformed, and the effects of body size were removed. Traits contributing most to each component are indicated in bold. The total amount of variance in the data explained by these first three principal components is 82.9%. Extracted axes from the principal component analysis (PCA) accounting for 73.7% of the total variation considered.

TABLE 6. Conventional analysis of covariance and PDANCOVA simulation results of the morphological variables for the six habitat types, (SVL as covariable) (terrestrial, saxicolous, crown-giant, trunk-crown, trunk-ground, grass-bush)

ANCOVA	Conventional		Phylogenetic	
	$F_{(5, 16)}$	P	$F_{(5, 16)}$	P
Peroneus brevis tendon length	0.413	0.833	6.932	0.938
Femorotibial gastrocnemius length	0.836	0.543	7.596	0.824
Femorotibial gastrocnemius width	1.806	0.168	6.481	0.539
Femoral gastrocnemius sup width	1.669	0.199	7.634	0.582
Digital flexor tendon digit 2	1.090	0.403	6.928	0.747
Tibia length	3.096	0.038	6.594	0.291
Ph 2 digit 1	0.411	0.834	6.929	0.941
Ph 4 digit 3	0.924	0.491	7.652	0.819
Ph 5 digit 4	0.986	0.456	7.449	0.782

The analyses show significant differences among the six groups. F and P values are for conventional and phylogenetic ANCOVA with SVL as the covariate and habitat type as factor.

character of the fifth metatarsal is consistent with the functioning of the fifth digit in a different manner from that of the other four pedal digits (Robinson, 1975; p 468; see also Brinkman, 1980). It is interesting that our analyses indicate a high K value for the only character considered in relation to the fifth metatarsal, its length (Table 2). We posit that the crucial role played by this element in locomotion precludes its flexibility in size. The same holds for the phalanges of the fifth digit, all of which exhibit high K values (Table 2).

K statistics for muscle and tendon morphometric characters revealed that most (13 of 21) of the characters considered exhibit little phylogenetic signal, whereas the remainder display high K values (Table 3). Interestingly, muscle length and width dimensions are decoupled, with muscle width being phylogenetically constrained whereas

muscle length is variable and evolutionarily labile, at least for the muscles of the zeugopodium (Table 3). Most of the tendinous sheets and ligaments emanating from the distal end of the crural flexors are shifted to the fibular side of the tarsal region, and this lateral shift of many of the muscles and ligamentous anchorages to the bones is closely associated with the hooked fifth metatarsal (Robinson, 1975). According to our data, the lengths of the bellies of the crural muscles are evolutionarily labile (Table 3). Our data also indicate that the general morphology of the femorotibial gastrocnemius does not vary with phylogeny (Table 3) and, because of that future studies may reveal a linkage between this muscle and as yet unknown ecological/functional aspects.

It is noteworthy that *Polychrus* and *Anolis* are able to accomplish active grasping through use of the pedal

TABLE 7. Results for the same data for nonsize corrected traits

ANOVA	Conventional		Phylogenetic	
	$F_{(5, 22)}$	P	$F_{(5, 22)}$	P
Traits				
Peroneus brevis tendon length	0.531	0.750	6.488	0.914
Femorotibial gastrocnemius length	0.277	0.920	6.754	0.979
Femorotibial gastrocnemius width	1.786	0.170	6.496	0.491
Femoral gastrocnemius sup width	3.123	0.035	6.247	0.261
Digital flexor tendon digit 2	1.985	0.133	6.630	0.448
Tibia length	4.712	0.007	6.663	0.118
Ph 2 digit 1	1.822	0.162	6.532	0.489
Ph 4 digit 3	2.883	0.046	5.786	0.228
Ph 5 digit 4	0.931	0.486	6.807	0.777

The analyses show significant differences among the six groups. F and P values are for conventional and phylogenetic ANOVA.

TABLE 8. Conventional analysis of covariance and phylogenetic ANCOVA simulation results after determining the most variable characters revealed by their PC score for grasping and nongrasping lizards

ANCOVA	Conventional		Phylogenetic	
	$F_{(1, 21)}$	P	$F_{(1, 21)}$	P
Traits				
Peroneus brevis tendon length	0.612	0.443	25.368	0.975
Femorotibial gastrocnemius length	0.049	0.828	28.222	0.933
Femorotibial gastrocnemius width	3.083	0.094	24.269	0.516
Femoral gastrocnemius sup width	6.603	0.018	24.621	0.365
Digital flexor tendon digit 2	0.022	0.883	25.673	0.952
Tibia length	9.464	0.006	26.152	0.258
Ph 2 digit 1	0.001	0.976	25.406	0.987
Ph 4 digit 3	0.676	0.421	26.615	0.789
Ph 5 digit 4	0.491	0.492	26.305	0.786

The analysis shows significant differences among the four groups. F and P values are for conventional nonphylogenetic ANCOVA and phylogenetic ANCOVA with SVL as the covariate.

digits, and can curl them around narrow branches (Figs. 1 and 3A). However, we were unable to identify a particular set of morphological attributes associated with this ability. The remainder of the taxa examined appears to be incapable of actively wrapping their digits around narrow branches by longitudinal flexion combined with adductive and abductive movements. It is possible that more detailed studies of the interphalangeal joints and the anatomical configuration of the metatarsals and distal tarsals may reveal more information pertinent to an understanding of these issues. Previous studies (Abdala et al., 2009; Sustaita et al., 2013) reveal that only a limited group of lizards possess digitally-based manual grasping capabilities (the same taxa that possess this capability in the foot) but, unlike the situation for pedal anatomy, these taxa show differences in the tendinous pattern of the manus (Abdala et al., 2009; Tulli et al., 2012a). Most of the taxa investigated here are unable to exercise any degree of manual or pedal digitally-based grasping (Fig. 1, Table 1). With respect to skeletal features, it is evident that the kinematic patterns of the fore and hind limbs are quite different. This will influence how grasping is accomplished. Whereas the metacarpals largely radiate from their proximal extremities, and their proximal heads abut but do not imbricate (Russell et al., 1997; Russell and Bauer, 2008), the metatarsals overlap proximally and display much greater discrepancies in the lengths of the individual rays (Russell et al., 1997; Russell and Bauer, 2008). Moreover, the forelegs bear some of the burden of supporting body

weight during level running (Autumn et al., 2006), but also provide propulsive forces that pull the body toward the surface during climbing (Cartmill, 1985). The hind legs support more of the body weight and transmit most of the propulsive force during level running (Autumn et al., 2006). The force needed for efficient propulsion of the lizard can probably be best accomplished if the surface area of the plantar aspect of the pes that contacts the substratum is maximized, as well as the time of contact with the substrate that allows an animal to accelerate longer and thus to generate higher terminal velocities. The divergent disposition of digits 1 and 5 probably relates to selective forces that led to the maximization of pedal plantar surface area. The opposition of these digits, permitting grasping capabilities, may be interpreted as a corollary of this. This arrangement could have been exaptive in arboreal habitats because the plantar surface of the pes may have enhanced grasping capabilities, resulting in a decrease in the risk of falling from narrow branches.

The results of our phylogenetic and conventional analyses reveal that the characters detected as being informative through the application of the comparative method are not absolutely related to habitat in terms of the ecological categories considered here (Tables 6 and 7) (see also Wainwright et al., 2005 and Alfaro et al., 2005). Apparently, the exploitation of different habitats is not associable with particular morphologies of the lizard pes. It appears that the *bauplan* of the lizard pes incorporates a morphological configuration that is sufficiently

TABLE 9. Results for the same data for non-size corrected traits

ANOVA	Conventional		Phylogenetic	
	$F_{(1, 22)}$	P	$F_{(1, 22)}$	P
Traits				
Peroneus brevis tendon length	1.765	0.198	23.021	0.588
Femorotibial gastrocnemius length	0.218	0.645	23.187	0.858
Femorotibial gastrocnemius width	4.435	0.047	22.393	0.372
Femoral gastrocnemius sup width	8.271	0.009	22.951	0.243
Digital flexor tendon digit 2	0.535	0.473	24.617	0.762
Tibia length	2.981	0.099	24.449	0.509
Ph 2 digit 1	0.878	0.359	21.743	0.698
Ph 4 digit 3	2.126	0.160	18.336	0.520
Ph 5 digit 4	0.220	0.644	22.961	0.861

The analysis shows significant differences among the four groups. F and P values are for conventional and phylogenetic ANOVA.

versatile to enable exploitation of almost all of the available habitats. It is also apparent that selection related to function may result in alternative anatomical solutions to achieve the same functional ends. This may have prevented us from being able to detect anatomical differences that are related to our questions and hypotheses. Thus, the forelimb turned out not to be a good predictor of what is present in the hindlimb of the same taxa. It should be noted, however, that no ecomorphological studies of manual grasping are available for comparison. The only study to consider the tendinous patterns of the manus found that most of the variability was explicable as a result of phylogeny (Tulli et al., 2012a). The hindlimb should be investigated in other ways to determine what may be correlated with grasping capabilities. For example, neurological differences may permit some taxa to configure their digits in ways not demonstrated by others. It is known that the relationship between structure and realized functional output may be regulated by the ways that movements are programmed and orchestrated by patterns of motor output (Lauder, 1996), without obvious morphological differences being evident.

The relationship between morphology and function in the system that we investigated remains unclear, because even in the cases in which phylogenetic signal is suggestive of evolutionary flexibility (or measurement error), when testing for differences between our predetermined ecological and functional groups (use of habitat, digitally based graspers vs. nongraspers), the results revealed only two differences, those relating to relative tibia length (Tables 6–8) and relative femoral gastrocnemius superficialis width (Tables 7–9), although these differences are no longer sustained after the phylogenetic analyses. It is noteworthy, also, that the muscles of the crus are evolutionarily labile, which may indicate that variation is differentially expressed between the various segments of the limbs.

Our results reveal an overwhelming influence of phylogeny as the explanation for observed morphological variation in the hindlimb of iguanian lizards. As surprising as the conservation of internal gross morphology may seem, it may represent a mechanism that is able to accommodate to a wide array of environmental challenges by permitting adequacy in all such circumstances (Gans, 1993). Broader and deeper taxon sampling may help to better elucidate the ecological/functional factors that are related to morphology in these lizards.

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APPENDIX 1

Codes for collections where voucher specimens of the species studied are deposited. FBC, Félix Benjamín Cruz, field series; GS, Gustavo Scrocchi, field series; MZUSP, Museu de Zoologia da Universidade de São Paulo; PT, Proyecto Tupinambis; PR, Puerto Rico; RT, Richard Thomas, field series; UNNEC, Universidad Nacional del Nordeste Corrientes. Specimens belonging to PT, FBC, GS, and RT housed at Fundación Miguel Lillo, Argentina.

Anolis cuvieri **PR** 005694 (1 specimen); *Anolis gundlachi* **RT** 14476-77, 14480-81, 14487a-b (6 specimens); *Anolis evermani* **RT** 14483-86, 14488, 14491 (6 specimens); *Anolis stratulus* **RT** 14492 (1 specimen); *Anolis krugi* **RT** 14489-90 (2 specimens); *Diplolaemus sexcinctus* **PT** 4833, **FBC** 055, **FBC** 0053-54, **PT** 4832, **PT** 3715, **PT** 4999 (8 specimens); *Enyalius cattenatus* **MZUSP** 66153, *Enyalius hieringii* **MZUSP** 74901; *Iguana iguana* **W/D** (1 specimen); *Liolaemus albiceps* **FBC** 1165, **FBC** 1169, **FBC** 1170, **FBC** 1173-75 (6 specimens); *Liolaemus elongatus* **GS** 3211-13; **GS** 3163, **GS** 3165 (6 specimens); *Liolaemus escarchadosi* **GS** 3199, **GS** 3203 (2 specimens); *Liolaemus fitzingerii* **FBC** 1310, **FBC** 1319, **FBC** 1328,, **FBC** 1366-70, **FBC** 1378, **FBC** 1381-83 (12 specimens); *Liolaemus irregularis* **FBC** 1160-63 (4 specimens); *Liolaemus kriegi* **FBC** 1231, **PT** 4850, **PT** 4848, **GS** 3305-06, **GS** 3295-96, **FBC** 1315, **FBC** 1309, **FBC** 1234, **FBC** 1282 (11 specimens); *Liolaemus petrophilus* **FBC** 1289 (4), **FBC** 1290 (5), **FBC** 1219, **FBC** 1290, **GS** 3276; *Liolaemus tenuis* **FBC** 1186, **FBC** 1211 (2 specimen); *Leiosaurus belli* **PT** 4782 (1 specimen); *Leiosaurus catamarcensis* **FBC** 0105, **FBC** 0104, **FBC** 0145 (3 specimens); *Phymaturus ceii* **W/D** (1 specimen); *Phymaturus spectabilis* **GS** 3131, **GS** 3132, **GS** 3172, **GS** 3173 (4 specimens); *Polychrus acutirostris* **UNNEC** 8606, **UNNEC** 8610, **UNNEC** 48154, **UNNEC** 48166 (4 specimens); *Tropidurus etheridgei* **FBC** 301, **FBC** 308, **FBC** 310, **PT** 3391 (4 specimens).