

RESEARCH ARTICLE

Effects of different substrates on the sprint performance of lizards

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SUMMARY

The variation in substrate structure is one of the most important determinants of the locomotor abilities of lizards. Lizards are found across a range of habitats, from large rocks to loose sand, each of them with conflicting mechanical demands on locomotion. We examined the relationships among sprint speed, morphology and different types of substrate surfaces in species of lizards that exploit different structural habitats (arboreal, saxicolous, terrestrial and arenicolous) in a phylogenetic context. Our main goals were to assess which processes drive variability in morphology (i.e. phylogeny or adaptation to habitat) in order to understand how substrate structure affects sprint speed in species occupying different habitats and to determine the relationship between morphology and performance. Liolaemini lizards show that most morphological traits are constrained by phylogeny, particularly toe3, the femur and foot. All ecological groups showed significant differences on rocky surfaces. Surprisingly, no ecological group performed better on the surface resembling its own habitat. Moreover, all groups exhibited significant differences in sprint speed among the three different types of experimental substrates and showed the best performance on sand, with the exception of the arboreal group. Despite the fact that species use different types of habitats, the highly conservative morphology of Liolaemini species and the similar levels of performance on different types of substrates suggest that they confer to the 'jack of all trades and master of none' principle.

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Key words: substrate structure, performance, limb morphology, speed, lizard.

INTRODUCTION

The habitats and more specifically the substrates involved in lizard locomotion might be crucial determinants of the morphology of species, populations and individuals (Losos, 1990a; Losos, 1990b; Losos et al., 1998; Van Damme et al., 1998; Goodman et al., 2008; Bergmann et al., 2009; Bergmann and Irschick, 2010; Vanhooydonck et al., 2005; Vanhooydonck et al., 2011). For example, living in relatively open areas might be selective for high-speed sprinting over long distances; conversely, inhabiting highly structured habitats might favor short bursts of locomotion (Fuller et al., 2011). A considerable body of literature has focused on relationships between morphology and ecology (Miles and Ricklefs, 1984; Pounds, 1988; Herrel et al., 2002; Herrel et al., 2008; Herrel et al., 2011; Bickel and Losos, 2002; Irschick, 2002; Goodman et al., 2007; Goodman et al., 2008; Essner, 2007; Kohlsdorf et al., 2001; Kohlsdorf et al., 2004; Kohlsdorf et al., 2008; Marshall et al., 2008; McElroy et al., 2008; Collar et al., 2010; Grizante et al., 2010; Vanhooydonck et al., 2011) or between habitat use and performance (Losos, 1990a; Losos, 1990b; Irschick and Losos, 1999; Melville and Swain, 2000; Vanhooydonck and Van Damme, 2003; Vanhooydonck et al., 2005; Mattingly and Jayne, 2004; Autumm et al., 2006; Goodman et al., 2008; Johnson et al., 2010; Bonino et al., 2011; Fuller et al., 2011). However, there are relatively few studies about how habitat structure might influence the relationships between morphology and ecology (e.g. Fuller et al., 2011).

Many authors have stressed that the locomotor capabilities of organisms provide an excellent opportunity for determining whether

morphology, performance and kinematics have coevolved (e.g. Irschick and Jayne, 1998; Jayne and Irschick, 1999; Garland and Losos, 1994; Vanhooydonck and Van Damme, 1999; Vanhooydonck et al., 2002; Vanhooydonck et al., 2005; Goodman et al., 2008). In fact, morphological differences might account for the diversity in locomotor behavior exhibited by many species because living in different habitats might result in morphological differentiation (Arnold, 1983; Rewcastle, 1983; Lauder and Reilly, 1991; Blob, 2001). Several examples of the relationship between morphology and habitat use were provided by studies across different taxa, such as primates (Cartmill, 1974), bats (Norberg, 1990; Norberg, 1994; Reilly and Wainwright, 1994), squirrels (Essner, 2007) and lizards (Vanhooydonck et al., 2005), among others. However, some authors found that morphology and habitat type are not always tightly correlated (Jaksic et al., 1980; Schulte et al., 2004; Tulli et al., 2009; Tulli et al., 2011b).

One key aspect of the locomotor performance related to habitat use is the type of substrate over which animals run (Goodman et al., 2007; Higham and Russell, 2010; Tulli et al., 2011a). In fact, it was shown that acceleration and maximum climbing speed are higher on smooth surfaces, such as smooth bark or leaves, and substantially lower on rough substrates, such as tree bark or rocks in pad-bearing lizards (Vanhooydonck et al., 2005). Some authors found that maximum speed is influenced by substrate firmness (Claussen et al., 2002; Herreid and Full, 1986; Kerdok et al., 2002), whereas substrate roughness and texture affect clinging (Stork, 1980; Dai et al., 2002; Zani, 2000; Tulli et al., 2011a). However, little is

known about how substrate structure affects speed in species that use different microhabitats, such as climbing and terrestrial lizards (Irschick et al., 1997; Zani, 2000; Higham and Russell, 2010; Tulli et al., 2011a).

The focal subjects of our study are Liolaemini lizards, which are members of one of the most diverse and species-rich lizard clades of the world (Abdala and Quinteros, 2008; Quinteros et al., 2008; Lobo et al., 2010; Breitman et al., 2011). Liolaemini lizards occur in South America, from central Perú to Tierra del Fuego and from the Pacific to Atlantic coasts, across mostly deserts and high-elevation habitats (Cei, 1986). The line of this clade dates from 12.6 to 18 million years ago (Schulte et al., 2000; Albino, 2011). Some species show specialized morphology, for example the sand-dweller species of the *Liolaemus wiegmannii* group (Etheridge, 2000), whereas some others exhibit signs of isolation after the last glacial period (Breitman et al., 2011). Thus, these species show a diversity in habitat usage, including generalized terrestrial as well as habitat specialists living on arboreal substrates, rock boulders (using the crevices or slipping underneath them) or sand (Halloy et al., 1998; Schulte et al., 2004; Tulli et al., 2009; Tulli et al., 2011a). Only two studies of *Liolaemus* species have considered information on running performance from a mechanistic point of view for *Liolaemus* (Fernandez et al., 2011; Bonino et al., 2011), but none so far has investigated the effect of surface or habitat structure on performance within an evolutionary context. Thus, we selected *Liolaemus* as our primary study group, and other Liolaemini and Leiosaurine species served as outgroups. The ecological variability of these lizards and the well-resolved phylogenetic relationships among them make this group a very interesting model to explore the proximate relationships between morphology and locomotor function in a broad sense.

In this work, we investigate study sprint speed on different types of substrates, and limb morphology in 36 species of lizards with different habitat use (arboreal, saxicolous, terrestrial generalists and arenicolous). We gathered both performance and morphological data, considering also the ecological context (habitat use), and analyzed them using phylogenetically informed analyses. Consideration of an historical perspective allows us to test the expected evolutionary relationship between form and function as predicted by the evolutionary paradigm (Darwin, 1859).

Our main aims were, first, to explore which processes might drive variability in morphology (i.e. phylogeny or adaptation); second, to understand the relationship between substrate structure and sprint speed in species with different habitat usage; and, finally, to understand the relationship between morphology and performance. Additionally, we explored whether there is a trade-off between clinging ability and speed in these Liolaemini lizards using equivalent types of substrates. Considering the many previous results that relate morphology and ecological traits in the same lizard group (Jaksic et al., 1980; Schulte et al., 2004; Fernandez et al., 2011; Tulli et al., 2009; Tulli et al., 2011b; Bonino et al., 2011), we predicted that the morphological traits would be better explained by phylogeny. By contrast, because habitat structure might influence locomotor performance, it was reasonable to expect that lizard species would show better performance on a racetrack that mimics their own habitat structure. For instance, we expected that an arenicolous lizard would perform better when running on a sandy substrate than in a rocky or bark-mimicking substrate. Finally, considering that fast-running animals benefit from having long limbs (Biewener, 2003), we predicted that faster lizards would have longer limb segments to increase sprint speed.

MATERIALS AND METHODS

Study system

Lizards were collected during the spring and summer months (November–February) of 2007–2009 at different sites in western and southwestern Argentina. Twenty seven species of *Liolaemus*, seven species of *Phymaturus*, *Diplolaemus sexcinctus* and *Leiosaurus belli* (see supplementary material Table S1 for a list of species) were captured during normal activity periods either by hand or by noose. Only adult specimens of both sexes for all the species were measured and used in the experimental trials, and pregnant females were excluded. After capture, lizards were placed in cloth bags and transported to the laboratory in Bariloche, Argentina. Upon arrival in the laboratory, lizards were housed in glass terraria (120×60×40 cm), divided in five 0.12 m lanes by opaque walls. The specimens were kept in captivity for two to five days before the performance trials. Animals were acclimated in a climate-controlled room. We set up a thermal gradient to give the lizards the opportunity to choose their preferred temperature. For the thermal gradient, we set 150 W infrared (IR) lamps on one end of the terrarium at a height of 0.45 m, and 100 W incandescent lamps were set in the first third of the terraria length (0.4 m from the end where the IR lamps were placed at the same height). Through this arrangement, and with an ambient room temperature of 22±1.4°C, we created a gradient from approximately 19 to 45°C (for details, see Cruz et al., 2009). Lizards were fed *ad libitum* with live crickets or flower buds (depending on their diet type) and provided water twice a day. Lizards were fed two days before the experimental trials were performed. Voucher specimens of the species studied were deposited at the Herpetology Collection of the Fundación Miguel Lillo, Tucumán, Argentina (supplementary material Table S1). Species and sample sizes (together with traits and speed values) are listed in supplementary material Table S2.

Experimental protocol

Sprint speeds were measured on three different race tracks consisting of a base plate and two side-boards, placed horizontally. The track was 120 cm long and 10 cm wide, and the side boards were 10 cm high. Three different race tracks were covered with different substrates – loose sand, rock and cork substrates. For the ‘rock’ surface, we glued sand on the track surface, mimicking sandstone. To mimic tree bark, we used cork. These substrates resemble the natural habitats for sand-dwelling, saxicolous and arboreal lizards. Each lizard ran at least five times on each one of the three substrate surfaces. All races were held at a horizontal level. Sprint trials were held one day on each surface for each individual. Individual lizards were set randomly on each surface. Thus, trials for each individual were performed on different days, with trials on the different substrates alternated among the experimental days.

A Panasonic SV200 camcorder set at 30 frames s⁻¹ was mounted 61 cm above the surface in all cases, and a segment of length 20 cm was filmed, which related to a track distance of 0.45 to 0.65 m. Previous studies on the speed performance of 10 species of *Liolaemus* showed that maximum speed was obtained at a distance between 0.45 and 0.60 m from the starting point (Bonino et al., 2011). Additionally, the speed values obtained here are similar to those obtained by Bonino and colleagues, who used a racetrack with light-emitting diode sensors and an electronic timer. To obtain speed measurements, the lizards were filmed running across the tracks in dorsal view. The best of all races, based on the highest achieved speed per individual for each surface, was selected for further analysis (supplementary material Table S2).

Running trials

Prior to conducting performance trials and between trials, we placed the animals for at least 2 h in an incubator (Semedic I-290PF, Semedic, Buenos Aires, Argentina) to allow them to acclimate to their experimental environment. Lizards were positioned in a resting, motionless posture at the beginning of the racetrack with the entire body in the field of view of the camera. Lizards were induced to run across the track by tapping them slightly on the base of their tail and continuously chasing them across the track. After filming, each run was scored as 'good' or 'bad'. A 'good' sequence was classified as a sequence in which the lizard started from a stand-still and ran non-stop over the distance of the racetrack. As an estimate of the maximum speed capacity of an individual on each substrate, we computed the mean value recorded for each individual along the above-discussed 20 cm segment of racetrack for the fastest and best run of each individual. Each individual was induced to run three to four times along the raceway. For further analysis, we used only the best trial from each individual, which was defined as either the only trial in which that individual met our criteria (i.e. 'good' score) or the trial with the highest instantaneous speed while observed under the camera (i.e. the first 0.4 m of the 1.20 m racetrack).

Image analysis

Videos were uploaded using VideoMach (version 5.8.4, <http://gromada.com/videomach.html>), and each AVI-sequence was first down-sampled to obtain approximately 20 frames and subsequently saved as a JPEG sequence. Video from the dorsal view was used to estimate the position of the animal for each frame. We used the program DIDGE (version 2.3: <http://biology.creighton.edu/faculty/cullum/Didge/index.html>) to manually digitize a marker at the tip of the snout to obtain its position. We started our digitization at the frame when the first movement was observed and stopped after all frames included in the 0.2 m had been considered (Vanhooydonck et al., 2005). Speed during each trial was quantified by digitizing the displacement of the tip of the snout on each frame. For digitization, all the two- and three-dimensional coordinates were calculated from the digitized coordinates using macros for Microsoft Excel version 7.0 (written by G. Updegraff and B. Jayne). The *x* axis was the horizontal dimension parallel to the forward direction of travel of the lizards and the motion of the tread surface. The *y* axis was perpendicular to the tread surface, and the *z* axis was perpendicular to the *x*-*y* plane (Irschick and Jayne, 1999). Then, the coordinates were calculated and smoothed using a fourth-order zero phase shift Butterworth low-pass filter (see Winter, 1990; Robertson and Dowling, 2003). Velocity was calculated as the first derivative of the displacement data (from the digitized *x* coordinate of the snout).

Morphological traits

Before preservation, each lizard was weighed on an ZSW2 electronic balance (Ohaus Scout Pro SP202, Pine Brook, NJ, USA; accuracy ± 0.01 g), and the body dimensions from each specimen that ran were measured using digital callipers (Mitutoyo CD-15B; ± 0.01 mm). The following morphological traits were measured: snout-vent length (SVL); maximum body width (BW); body length (BL) measured from the base of the neck to the vent; and inter-limb length (ILL), which is the distance between the fore and hind limbs; forelimbs: humerus length (HL); radius length (RL); dorsum of the hand length (DHL: measured from the wrist to the base of the digits); dorsum of the hand width (DHW); length of all digits not including the claws; hind limbs: femur length (FL), tibia length (TL), sole foot length (SFL: measured from the ankle to the base of the toes) and

longest toe length (d3, d4 and d5), not including the claws. Additionally, and following the protocol described by Tulli and colleagues (Tulli et al., 2009), we calculated claw height (CH), claw length (CL) and claw curvature (CC) corresponding to digits III and IV of the hand, and 3, 4 and 5 of the feet. The selected digits and toes were used because they are the longest and, presumably, functionally the most important ones (Teixeira-Filho et al., 2001; Vrcibradic and Rocha, 1996).

Ecological data

Each lizard species was classified as generalized terrestrial, arenicolous (sand-dweller), saxicolous or arboreal, according to our own field observations and those of Tulli and colleagues (Tulli et al., 2011a). These data are summarized in Table 1.

Phylogeny and phylogenetic signal

Because species share part of their evolutionary history, they cannot be treated as independent data-points (Felsenstein, 1985; Harvey and Pagel, 1991). Thus, we ran independent contrasts analyses when possible. For this purpose, we constructed a composite tree from the available topologies of Liolaemini species where the species studied here were included. Our tree is based on several morphological and molecular studies, such as those of Lobo, Quinteros, Avila, Abdala and Frost (Lobo, 2001; Lobo, 2005; Lobo and Quinteros, 2005; Avila et al., 2006; Abdala, 2007; Lobo et al., 2010; Frost et al., 2001), for the Leiosaurine, our outgroup species. We built a resulting tree topology from the combination of the above-mentioned studies because a complete phylogenetic tree for all the species studied here is not available (Fig. 1). Branch lengths were arbitrarily set to unit length because the divergence times between the species included in the analysis were unclear owing to the diverse nature of the original phylogenetic analyses.

We calculated the K-statistic as an estimate of the phylogenetic signal relative to Brownian motion evolution, considering the topology and branch lengths (Blomberg et al., 2003). A K value greater than 1 (one) suggests a strong phylogenetic signal, whereas a value lower than 1 indicates that a trait is less similar among close relatives, and therefore has less phylogenetic signal than expected. We tested for phylogenetic signal in all traits by a randomization test (PHYSIG) (Blomberg et al., 2003). We considered constant branch lengths and branch length transformations under evolution model Ornstein-Uhlenbeck (OU) with d-values to 0.2 (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). Snout-vent length, claw curvature and performance variables were introduced in PHYSIG as \log_{10} -transformed variables. Other morphological traits (i.e. claw length, claw height, forelimb and hind-limb length as well as its segments) were size-corrected by following the method suggested by Blomberg and colleagues (Blomberg et al., 2003).

Statistical analysis

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) (supplementary material Table S2). For independent contrasts analyses, each morphological trait was \log_{10} transformed. Then, we obtained independent contrasts (Felsenstein, 1985) for each transformed variable, and next we regressed the morphological variables on the independent contrast of SVL to obtain the residuals. The calculated residuals were used in subsequent analyses as size-corrected morphological measures.

Table 1. Habitat use of the species examined in this study based on literature data and ecological habits

Species	Author	Function	Habits
<i>Diplolaemus sexcinctus</i>	Cei et al., 2003	Ground-dwelling	Terrestrial
<i>Liolaemus baguali</i>	Cei & Scolaro, 1996	Clinging ability	Saxicolous
<i>Liolaemus bibroni</i>	Schulte et al., 2000	Ground-dwelling	Terrestrial
<i>Liolaemus canqueli</i>	Etheridge, 2000	Sand-burying	Arenicolous
<i>Liolaemus ceii</i>	Cei, 1986	Clinging ability	Saxicolous
<i>Liolaemus coeruleus</i>	Pincheira-Donoso et al., 2007		
<i>Liolaemus crepuscularis</i>	Abdala and Diaz Gomez, 2006	Ground-dwelling	Terrestrial
<i>Liolaemus dorbignyi</i>	Abdala and Quinteros, 2008	Clinging ability	Saxicolous
<i>Liolaemus elongatus</i>	Cei, 1986		
<i>Liolaemus escarchadosi</i>	Scolaro and Cei, 1997	Ground-dwelling	Terrestrial
<i>Liolaemus fitzingeri</i>	Etheridge, 2000	Sand-burying	Arenicolous
<i>Liolaemus goestchi</i>			
<i>Liolaemus irregularis</i>	Abdala, 2007	Ground-dwelling	Terrestrial
<i>Liolaemus kingi</i>	Avila et al., 2006	Clinging ability	Saxicolous
<i>Liolaemus kolengh</i>	Abdala and Lobo, 2006		
<i>Liolaemus koslowskyi</i>	Etheridge, 2000		
<i>Liolaemus melanops</i>	Cei and Scolaro, 1983	Sand-burying	Arenicolous
<i>Liolaemus multimaculatus</i>	Halloy et al., 1998		
<i>Liolaemus olongasta</i>	Etheridge, 2000		
<i>Liolaemus ornatus</i>	Abdala, 2007	Ground-dwelling	Terrestrial
<i>Liolaemus petrophilus</i>	Avila et al., 2004		Saxicolous
<i>Liolaemus pictus</i>	Medel et al., 1988	Clinging ability	Arboreal
<i>Liolaemus poecilochromus</i>	C. Abdala, personal communication		Saxicolous
<i>Liolaemus riojanus</i>	Halloy et al., 1998	Sand-burying	Arenicolous
<i>Liolaemus rothi</i>	Etheridge, 2000	Clinging ability	Saxicolous
<i>Liolaemus sarmientoi</i>	Cei and Scolaro, 1996	Clinging ability	Saxicolous
<i>Liolaemus scapularis</i>	Halloy et al., 1998	Sand-burying	Arenicolous
<i>Liolaemus tenuis</i>	Medel et al., 1988	Clinging ability	Arboreal
<i>Liolaemus zullyi</i>	Cei and Scolaro, 1996	Ground-dwelling	Terrestrial
<i>Leiosaurus belli</i>	Laspiur et al., 2007		
<i>Phymaturus antofagastensis</i>	Pereyra, 1985		
<i>Phymaturus dorsimaculatus</i>			
<i>Phymaturus excelsus</i>			
<i>Phymaturus spectabilis</i>	Lobo and Quinteros, 2005	Clinging ability	Saxicolous
<i>Phymaturus spurcus</i>			
<i>Phymaturus tenebrosus</i>			

For comparing performances among different substrates, we used a RM-ANOVA. This analysis was under conventional statistics, thus the size correction for morphological data was based on the residuals from raw data. For this analysis, repeated measures of performance of each specimen on the three surfaces used (loose sand, cork and rock) were taken.

We ran multiple regressions to test the relationship between morphological variables and performance. For this, we used independent contrasts (IC) (Felsenstein, 1985; Felsenstein, 1988) of \log_{10} -transformed morphological variables and SVL as independent variables and performance variables as the dependent variable [forced through the origin (see Garland et al., 1992)]. We used the topology shown in Figure 3 in Mesquite v.2.72 (<http://mesquiteproject.org>) for calculating independent contrasts. Then, multiple regressions were run under a backward model, and significant partial correlations were retained. Multiple regressions were held for performance (maximum speed) and for each surface (loose sand, rock and cork).

For testing for differences in performance among ecological groups (terrestrial, saxicolous, arenicolous and arboreal), we used a phylogenetically informed univariate analysis of variance (PDANOVA); we generated an empirical null distribution of F-statistics, taking into account the phylogeny by using PDSIMUL and analyzed the outputs with PDANOVA (Garland et al., 1993). For each variable, we ran 1000 simulations using a speciation model of evolution, which sets all branch lengths to unit in

PDSIMUL (Martins and Garland, 1991). The means and variances of the simulations were set to the means and variances of the original data.

Because we wanted to establish the existence of a clear the relationship between sprint and clinging ability performances on similar and comparable substrates, we tested for trade-offs between the independent contrasts of sprint speeds and clinging ability of Liolaemini lizards by using moment-product relationships from a dataset of 36 species [the ones studied here and the corresponding ones published previously (Tulli et al., 2011a)].

RESULTS

Phylogenetic signal

K-values were significant for most of the morphological traits studied (Table 2) – particularly gross morphology and claw height showed K-values higher than 1. However, many of these values were intermediate – for example, SVL, body mass, femur length, etc. – and precluded us from making strong statements. K-values for the performance variables, by contrast, were lower than 1, suggesting that the variation in performance was a consequence of adaptation to ecological differences or measurement error (Table 2).

Performance–morphology relationship

Sprint-speed performance

Speed showed significant relationships with morphology. The three (one for each surface) backward multiple regressions were

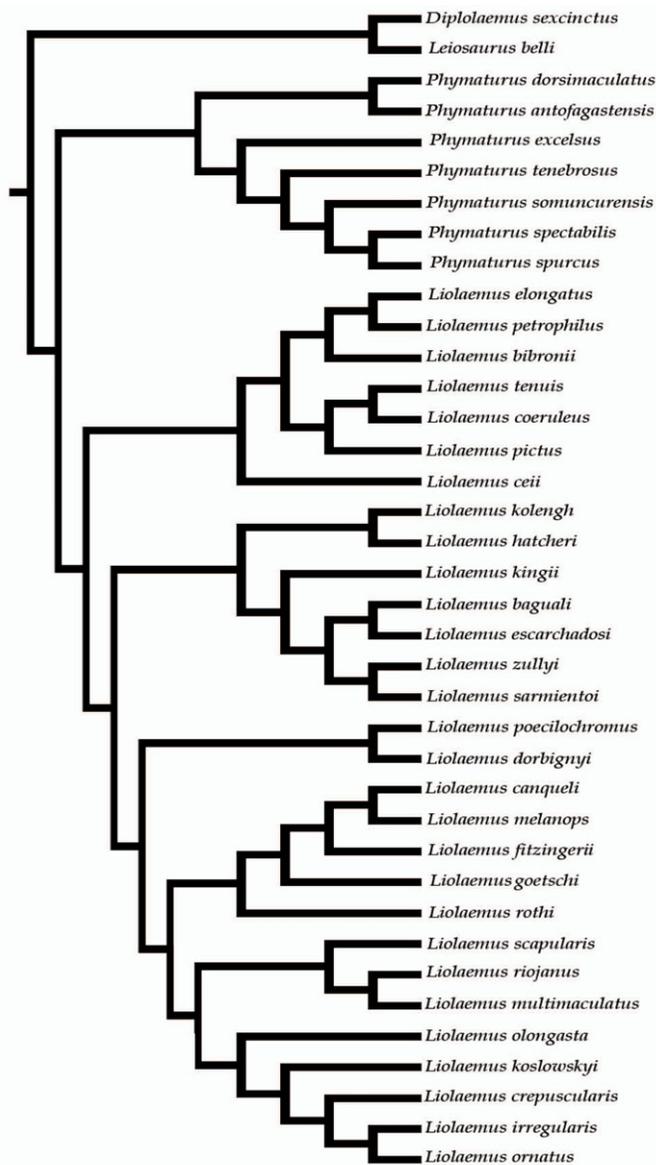


Fig. 1. Tree topology based on a combination of morphological and mitochondrial DNA analyses from studies by Lobo (Lobo, 2001; Lobo, 2005), Lobo and Quinteros (Lobo and Quinteros, 2005), Abdala (Abdala, 2007), Lobo and colleagues (Lobo et al., 2010) and Frost and colleagues (Frost et al., 2001). Branch lengths were arbitrarily set to unit (see text).

statistically significant after phylogenetically informed analyses (Table 3). Only three variables were informative across the three experimental trials – d3, femur length and foot length. Toe 3 (d3) and femur length showed a positive partial correlation with speed on cork and rock surfaces, but negative on sand; foot length showed a negative partial correlation on the three experimental surfaces. Digit III (DIII) length output was negatively correlated to speed on both firm surfaces (cork and rock; Table 3). Claws gave significant partial correlations on the three experimental trials; however, no clear pattern was observed.

Substrate structure and morphology

Results of multiple regressions show that, on a cork surface, several morphological variables contributed to the main effect of the model, among them femur and humerus length contributed more strongly

and positively, whereas DIII and DFL had opposite correlations. On a rock surface, the digits were the most important features contributing to the main significant effect of the corresponding model (speed on rock surface; Table 3), DIV positively and DIII negatively. Finally, on a loose-sand surface, the claw curvature of toe 3 was the feature that partially contributed the highest positive value to the main effect for the model, whereas the humerus length was the lowest negative partial correlation value (Table 3).

Ecological groups and performance

When comparing the performance of the four ecological groups (arboreal, saxicolous, arenicolous and terrestrial generalists), we found significant differences on rocky surface trials only (Table 4). Surprisingly, arboreal species showed the higher values for speed on the rock surface, whereas saxicolous species were not different from the other ecological groups. None of the values observed for each ecological group was better on the surface resembling its own habitat (e.g. saxicolous on rock, arenicolous on sand; Fig. 2), although it should be taken into consideration that the incline was not taken into account here. The RM-ANOVA showed that all groups exhibited significant differences in sprint speed among the three different types of substrates, except the arboreal group (Table 5). Interestingly, all ecological groups, except for the arboreal ones, showed the best performance on sand (Fig. 3).

After performing moment–product relationships of independent contrasts of speed and clinging force from the 36 species of lizards (the ones studied here and the corresponding species published previously (Tulli et al., 2011a), we found no indication of trade-offs between these performances, even when we used equivalent surfaces (Table 6).

DISCUSSION

K-statistics for morphological traits indicated some degree of phylogenetic clustering or at least a conservative gross morphology, supporting our first prediction. For example, K-values of the forelimbs are suggestive of an effect of phylogeny. These results are in accordance with previous studies on the relationship of morphology and habitat use in Liolaemini lizards (Schulte et al., 2004; Tulli et al., 2009; Tulli et al., 2011b) that show a similar strong phylogenetic signal in the morphological traits considered (but see Tulli et al., 2011a).

Surprisingly, we found that sprint speed on the typical substrate of each species was not higher – for example, arenicolous lizards did not exhibit significantly better performance on sand when compared with the other ecological groups. However, when running performance on the different substrates is compared within each group, the running performance of arenicolous lizards is higher on sand compared with their performance on other substrates (Fig. 3A). Remarkably and surprisingly, saxicolous lizards were the slowest of all the ecological groups on the rock surface. This might be a consequence of having heavier and stocky bodies – such as *Phymaturus* species (Tables 3 and 4). Thus, *Phymaturus* can show similar performances to those of horned lizards (*Phrynosoma*), the slower species among phrynosomatid lizards in a study by Bonine and Garland (Bonine and Garland, 1999). It has to be noted that these three genera resemble one another in body shape and limb proportions, influencing speed performance, as previously observed by those authors (Bonine and Garland, 1999). Furthermore, the comparison of performance of the saxicolous species across all substrates revealed that these lizards ran slightly faster on a sandy substrate (Fig. 3B). Most of the saxicolous Liolaemini lizard species occur on rock slopes, outcrops or boulders, where there are no long

Table 2. Summary of analyses calculating phylogenetic signal and using constant branch lengths (BL) and Ornstein–Uhlenbeck (OU)-transformed branch lengths

	BL=1		OU=0.2		OU=0.8	
	K	P	K	P	K	P
SVL	0.832	0.002	1.086	0.019	1.355	0.00
DIII	0.723	0.000	1.196	0.000	1.338	0.00
CH DIII	1.101	0.001	1.161	0.001	1.723	0.00
CC DIII	0.416	0.003	0.995	0.236	0.645	0.04
CL DIII	0.452	0.002	1.133	0.00	0.821	0.001
DIV	0.715	0.00	1.205	0.00	1.337	0.00
CH DIV	1.003	0.001	1.137	0.00	1.561	0.00
CC DIV	0.463	0.002	1.089	0.001	0.823	0.00
CL DIV	0.52	0.00	1.125	0.00	0.895	0.00
d3	0.619	0.006	1.103	0.009	1.106	0.001
CH d3	1.021	0.00	1.168	0.00	1.569	0.00
CC d3	1.028	0.00	1.227	0.001	1.429	0.00
CL d3	0.498	0.002	1.138	0.001	0.857	0.00
d4	0.307	0.151	1.017	0.065	0.603	0.081
CH d4	0.893	0.00	1.153	0.00	1.413	0.00
CC d4	0.431	0.011	1.106	0.001	0.768	0.007
CL d4	0.466	0.003	1.199	0.00	0.894	0.00
d5	0.414	0.003	1.126	0.00	0.796	0.00
CH d5	0.998	0.00	1.206	0.00	1.582	0.00
CC d5	0.687	0.02	1.079	0.315	1.068	0.078
CL d5	0.327	0.089	1.018	0.038	0.634	0.039
RL	2.032	0.00	1.219	0.001	2.876	0.00
HL	1.873	0.00	1.238	0.00	2.708	0.00
BL	0.276	0.371	0.821	0.942	0.458	0.808
BW	1.415	0.00	1.209	0.00	0.217	0.00
IIL	0.447	0.007	1.050	0.063	0.789	0.029
DML	1.401	0.00	1.157	0.00	1.999	0.000
DMW	2.153	0.00	1.198	0.001	2.815	0.000
FL	0.663	0.004	1.104	0.009	1.114	0.004
TL	1.356	0.00	1.213	0.069	2.013	0.001
SFL	0.226	0.913	1.012	0.057	0.549	0.237
Max speed: cork	0.341	0.187	1.027	0.054	0.694	0.048
Max speed: rock	0.409	0.189	0.962	0.435	0.719	0.218
Max speed: sand	0.317	0.488	0.898	0.885	0.535	0.778

Significant values ($P < 0.05$) and phylogenetic signal ($K > 1$) are indicated by bold values.

surfaces to run on, and these lizards actually crawl to the nearest crevice once they are chased (F. B. Cruz, personal observation). After examining the performance of terrestrial generalized Liolaemini lizards, it can be seen that the substrate type was not relevant for explaining their sprint performance (Fig. 3C). Terrestrial lizards perform equally well on all the substrates considered, supporting the categorization of these lizards as generalists. With regard to the arboreal lizards, the situation is very similar to the generalists (Fig. 3D). It is possible that the inclination of the substrate has an influence on the performance of arboreal and saxicolous lizards more than substrate *per se*. Thus, almost all the species examined here showed a clear relationship between a three-dimensional space (such as rock boulders and trees) and clinging ability compared with those species exploiting a two-dimensional microhabitat (Tulli et al., 2011a). It is expected that species exploring vertical surfaces run faster on an inclined surface than those species that use horizontal microhabitats, as shown for geckos (Higham and Russell, 2010). Apparently, differential energetic demands between climbers and runners produce different ways to perform on vertical or horizontal microhabitats (Higham et al., 2011).

It has been observed that Liolaemini species of Northern Neuquén province (Argentina) occupying sandy and less-dense vegetated zones run faster than species from complex and rocky habitats (Petriek et al., 2009), in agreement with what was suggested for

Tropidurus species (Kohlsdorf et al., 2004), varanids (Clemente et al., 2009) and scincid species (Goodman et al., 2008). It is likely that rocky habitats (rock boulders, promontories or rock aggregations) are not well suited for running efficiently when evading predators or capturing prey. Rocky substrates possess many crevices, and the extension of rock outcrops is not large; thus, running fast across long distances is not demanded and might not be as efficient as running through flat open habitats, as observed by Petriek and colleagues (Petriek et al., 2009). Liolaemini species are mostly sit-and-wait foragers or herbivores; thus, it is not surprising that speed is not the primary determinant for feeding in the way that acceleration might be. Then, for escaping predators, Liolaemini lizards might gain more benefit from crypsis (Schulte et al., 2004), short refuge distance and sand burrowing or diving (Halloy et al., 1998). Our data allow us to infer that the evolutionary processes seem to be focused on particular features. Combining the results obtained in the present study and those of an earlier study (Tulli et al., 2011a) on clinging performance on 38 Liolaemini species, we have found that variation in digits III and IV of the hands and feet is common in both analyses. Thus, speed is positively correlated to claw curvature of DIV, along with the length of toe 3. These results are in accordance with our observations. Multiple regression analyses of the residual independent contrast of morphological features and performance show that some traits such

Table 3. Multiple regression results for independent contrast (IC) of speed (dependent variables) against 31 morphological variables (IC of log of SVL, claw curvature and a further 25 residuals) as independent variables on each of the surfaces used in the trials (cork, rock and sand)

Dependent	d.f.	F	P	Independent	Partial correlation
Residual IC speed: cork	19, 16	9.14	0.000	DIII	-0.852
				CHDIII	0.739
				CHDIV	-0.632
				D3	0.777
				CHD3	0.564
				CLD3	0.670
				CHD4	-0.686
				CLD4	-0.786
				D5	0.716
				CLD5	0.578
				LF	0.849
				LH	0.837
				LR	-0.798
				DHL	-0.580
				SFL	-0.781
				CCDIII	0.600
				CCD5	-0.809
Residual IC speed: rock	25, 19	4.22	0.002	DIII	-0.716
				DIV	0.691
				CLDIV	-0.456
				D3	0.432
				D4	0.530
				LF	0.632
				SFL	-0.687
				CCDIV	0.552
				SVL	-0.919
				CHDIII	0.776
CLDIII	-0.866				
CHDIV	-0.887				
CLDIV	0.697				
D3	-0.842				
CLD3	0.891				
D5	0.780				
CHD5	0.887				
CLD5	0.699				
LF	-0.527				
LH	-0.947				
LR	0.924				
SFL	-0.894				
CCDIII	0.889				
CCDIV	-0.918				
CCD3	0.951				
CCD4	-0.884				
CCD5	-0.855				

A backward model was used, and all regressions were set to the origin. All traits were log-transformed, and an effect of SVL was removed prior to analysis. Bold values indicated the results on significant models, and significant independent variables and their partial correlations are given.

as DIII and d3 exhibit differences in their relationship with the residuals of sprint speed when different substrates are considered. The length of digit III of the hand is negatively correlated with higher speed on cork and rock. Digit IV of the hand is used as the main support when lizards are sprinting, and the role of its claw seems to be fundamental in achieving high sprint velocity. Previous reports (Texeira-Filho et al., 2001; Tulli et al., 2009; Tulli et al., 2011a) also show the importance of digit III and IV in locomotion. Digit IV is mainly used as support, and digit III seems to be the one driving clinging (Tulli et al., 2011a). It has previously been found that the claw morphology of digit III and IV is positively correlated with clinging performance on rough surfaces (such as tree bark or rocks)

because lizards use their hand claws to exert an interlocking grasp (Tulli et al., 2011a). Additionally, our videos also show that toe 3 acts to propel the animal forward, which is in accordance with the results of Melville and Swain (Melville and Swain, 2000).

The length of limb segments or of hind-limbs has been shown to be directly related to speed (Losos, 1990a; Losos, 1990b; Sinervo et al., 1991; Sinervo and Losos, 1991; Bauwens et al., 1995; Bonine and Garland, 1999; Melville and Swain, 2000; Melville and Swain, 2003; Vanhooydonck and Van Damme, 2001; Gifford et al., 2008). The correlation between speed and hind-limb length holds across a wide diversity of lizard taxa (Losos, 1990b; Miles, 1994; Bauwens et al., 1995; Bonine and Garland, 1999). From a biomechanical point

Table 4. Phylogenetically informed analysis of variance (PDANOVA) simulation results of the speed achieved by four ecological groups (arboreal, saxicolous, arenicolous and terrestrial generalist) using habitat types as the factor

Surface	F	P
Cork	8.151	0.214
Rock	8.416	0.026
Sand	8.669	0.517

Significant values ($P < 0.05$) are indicated by bold values.

of view, limb length would allow predicting speed performance and seems to be an important component of maximum sprint capacity (Garland, 1985; Losos, 1990a; Losos, 1990b; Garland and Losos, 1994; Bauwens et al., 1995). In a general sense, fast-running animals benefit from having long limbs (Cartmill, 1985; Losos and Sinervo, 1989; Losos, 1990a; Losos, 1990b; Sinervo and Losos, 1991; Macrini and Irschick, 1998; Bonine and Garland, 1999; Biewener, 2003), although this relationship between limb length and sprint speed has not always been deduced (van Berkum, 1986). We found positive relationships between limb-segment lengths and sprint speed on the three types of surfaces, demonstrating that the relationship between longer limbs and faster speed is common in lizards (but see Fernandez et al., 2011).

Compared with the rest of the limb morphology, the foot morphology in relation to performance has received little attention in Squamate reptiles (Autumn et al., 2000; Melville and Swain, 2000; Zani, 2000; Elstrott and Irschick, 2004; Grizante et al., 2010). According to our K-values, the morphology of the forelimbs is

Table 5. Repeated measurements ANOVA results of the speed achieved by four ecological groups (arboreal, saxicolous, generalists and arenicolous), comparing performances among different substrates (sand, cork and rock)

Ecological group	F	d.f.	P
Arboreal	0.825	2	0.491
Saxicolous	27.15	32	<0.000
Arenicolous	187.66	16	<0.000
Terrestrial	190.31	14	<0.000

constrained by phylogeny, and foot-related traits might be more evolutionarily flexible (Table 2). We found that sole foot length is negatively correlated with sprint speed on all substrates (Table 3). Shorter feet should be no problem for Liolaemini lizards because their relatively shorter distal segment can attain a higher stride frequency that counterbalances their length (McBrayer and Wylie, 2009). Saxicolous *Niveoscincus* lizards have long feet, which were suggested to be associated with high sprint speeds and the increase of propulsive forces for running and jumping (Melville and Swain, 2000). Kohlsdorf and colleagues (Kohlsdorf et al., 2004) and Grizante et al. (Grizante et al., 2010) found that sand lizards tend to have longer feet. The contrasting results of Melville and Swain (Melville and Swain, 2000), Kohlsdorf et al. (Kohlsdorf et al., 2004), Grizante et al. (Grizante et al., 2010) and ourselves might indicate that the evolution of morphological traits in relation to performance should be investigated considering that behavior might play an important role in compensating for low levels of performance (Toro et al., 2004). Our results allow us to put forward an adaptive interpretation of the variations of foot length in Liolaemini lizards, although a more comprehensive interpretation of the patterns of the variation is still needed.

Goodman and colleagues (Goodman et al., 2007) stressed that performance trade-offs might occur when morphological traits that enhance the performance of one task negatively affect another. However, whether morphology constrains performance, causing trade-offs in different habitats, remains a relatively open question (Losos and Sinervo, 1989; Sinervo and Losos, 1991; Vanhooydonck and Van Damme, 2001; Vanhooydonck et al., 2011). Interestingly, we were able to identify opposing relationships between morphological traits and running performance on firm-structured substrates *versus* running performance on loose sand. For example, toe length is positively correlated with speed on cork and rock, but negatively with speed on sand. Likewise, a lizard with a longer toe 3 can run faster than one with a shorter toe on cork and rock, but it is slower running in sand (Table 3). Conversely, lizards having a lesser degree of claw curvature for digit IV are faster runners on sand but slower on rock (Table 3). Possibly, what we detected are extreme points of a continuous gradient with, at one extreme, species

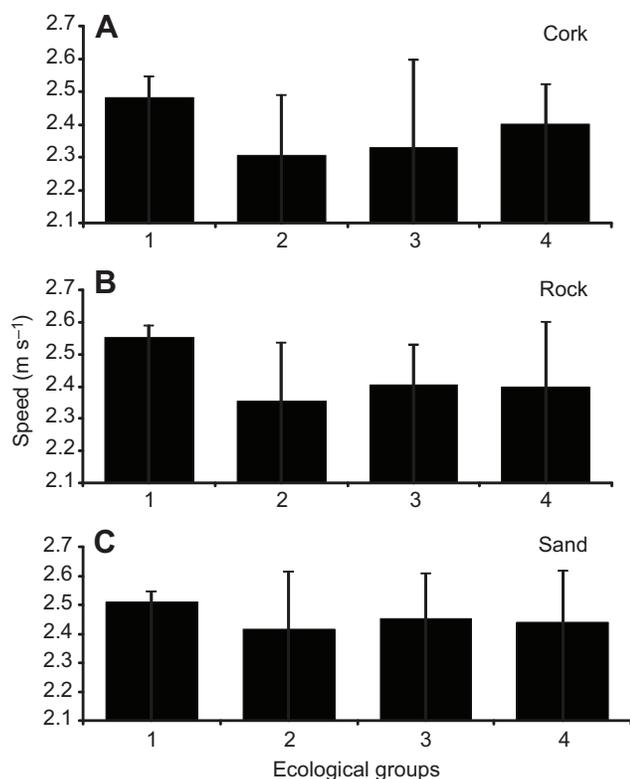


Fig. 2. Mean speed (m s^{-1}) measurements (bars, +s.e.m.) per ecological group divided by habitat use [1: arboreal ($N=2$), 2: saxicolous ($N=15$), 3: arenicolous ($N=8$), 4: terrestrial generalist ($N=11$)] on different surfaces where speed trials were conducted.

Table 6. Moment-product relationships passing through the origin between IC of speed on different surfaces (sand, cork and rock) and IC of residual clinging force on different surfaces (smooth rock, rough rock and bark)

Speed vs clinging	r	N	P
Sand-smooth-rock	-0.262	35	0.129
Smooth-rock-rough-rock	0.205	35	0.238
Cork-bark	-0.077	35	0.660

Significant values ($P < 0.05$). The type of surfaces confronted show progressive grip, from sand-smooth-rock to cork-bark.

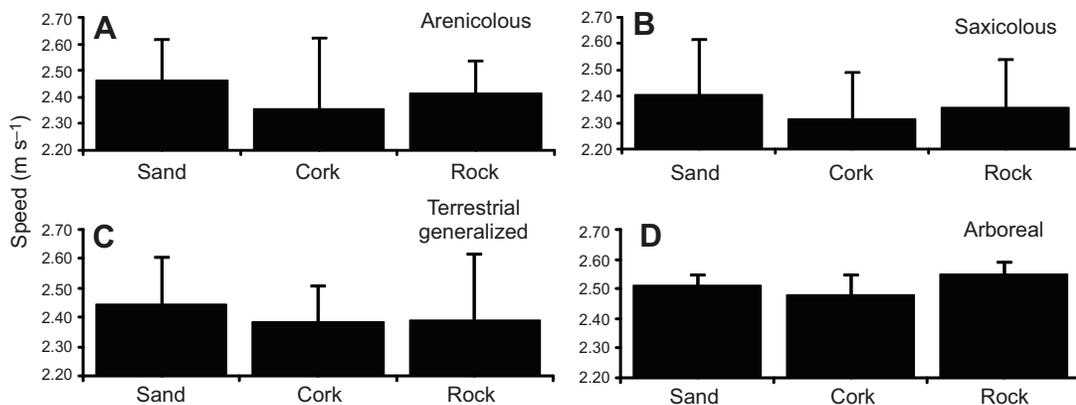


Fig. 3. Mean speed measurements (bars, +s.e.m.) per habitat (sand, cork and rock) for ecological groups: (A) arenicolous ($N=18$), (B) saxicolous ($N=15$), (C) terrestrial generalized ($N=11$) and (D) arboreal ($N=2$).

that can run relatively faster in sand substrates and species that can run relatively faster on rock or cork substrates at the other end (Vanhooydonck and Van Damme, 2001).

Clinging performance of Liolaemini species (Tulli et al., 2011a) and sprint-speed performance (this work) in Liolaemini lizards show different trends. However, those traits promoting clinging performance in a particular habitat apparently do not reduce sprinting performance in other habitats (Table 6). This suggests that this group of lizards converged on a functionally intermediate morphology (Arnold, 1998) having the ability to perform relatively well (or similarly badly) at several tasks and hence can be considered as 'jack of all trades and master of none'. Liolaemini are similar to lacertid lizards in that both have retained the same general body shape (Arnold, 1998; Vanhooydonck and Van Damme, 1999; Vanhooydonck et al., 2002) to face a wide range of microhabitats. Data from Liolaemini and lacertids contrast with those obtained for *Anolis* (e.g. Toro et al., 2004) and acontine lizards (Vanhooydonck et al., 2011). In these clades, trade-offs that prevent them from simultaneously optimizing different aspects of performance are present. It seems also evident that trade-offs tend to appear among those species highly modified to perform particular tasks, such as jumping *Anolis* (Toro et al., 2004) or burrowing skinks (Vanhooydonck et al., 2011), making it very difficult to identify these tendencies among lizards with a more generalized morphology (Vanhooydonck et al., 2002) (this work).

As mentioned above, some morphological traits, such as humerus and radius length, hand length and width, exhibit a significant phylogenetic signal and appear to be constrained by phylogeny. Liolaemini species as a group conform to the 'jack of all trades and master of none' principle with respect to sprinting; despite having a highly conservative morphology, they achieve similar performance on several types of substrates. Nevertheless, Liolaemini show a great variability in their ecological habits and distribution (Tulli et al., 2009; Tulli et al., 2011a; Tulli et al., 2011b; Lobo et al., 2010). However, despite the highly conservative morphology, other studies have showed that some performance characteristics can be exceptionally variable and ecologically relevant, such as the relationship between forelimb length and habitat exploitation on vertical surfaces (Arnold, 1998; Tulli et al., 2011a). Further studies of the effect of inclination on sprint speed and acceleration performance are needed to gain a better perspective on the evolution of locomotor morphology in the group.

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