Morphological evolution in Tropidurinae squamates: an integrated view along a continuum of ecological settings

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Abstract

Variation in squamate foot morphology is likely relevant during evolutionary processes of habitat colonization because distinct surfaces differ in energetic and functional demands for locomotion. We combined new foot morphological data with published information of limb and tail lengths to investigate evolutionary changes possibly associated with the differential usage of ecological settings by Tropidurinae species. Several traits exhibited significant phylogenetic signal, and we performed conventional and phylogenetic regressions of PC scores (retained from Principal Components Analyses of morphometric traits) on continuous ecological indices. Tropidurines from sandy habitats exhibit larger foot soles, opposite to the evolution of narrow feet in species that use branches and rocks. Also, species that usually move along trunks present longer femora. This study provides evidence for morphological adaptations associated with substrate usage in Tropidurinae, and suggests that opposite morphological profiles might evolve associated with the use of surfaces energetically and functionally contrasting, possibly leading to trade-offs.

Introduction

Changes in body size and limb or tail proportions are claimed to be associated with the evolution of locomotor performance in different ecological settings in several clades of squamates (e.g. Losos & Sinervo, 1989; Losos 1990a,b; Bonine & Garland, 1999; Van Damme & Vanhooydonck, 2002; Herrel et al., 2002; Goodman et al., 2008). Comparative studies investigating eco-morphological relationships suggest three main morphological characters that may explain differences in squamate locomotor performance, in context-specific ecological settings: body size (e.g. Losos, 1990a,b), relative limb proportions (e.g. Losos & Sinervo, 1989; Losos, 1990a,b; Bonine & Garland, 1999; Melville & Swain, 2000; Herrel et al., 2002), and foot morphology (e.g. Carothers, 1986; Glossip & Losos, 1997; Melville & Swain, 2000; Zani,

2000; Macrini et al., 2003; Elstrott & Irschick, 2004; Irschick et al., 2005). Evolutionary changes in these traits are associated with the concept of morphological specialization following the colonization of novel habitats, a process that has been studied most extensively in anoline species. Along the Greater Antilles islands, *Anolis* species with similar ecologies exhibit comparable behaviour and morphology (ecomorphs) independently of their evolutionary relationships, a pattern suggesting convergent evolution (Losos, 1990a; Losos, 1992; Losos et al., 1998; Beutell & Losos, 1999). A similar trend has been observed in *Anolis* from the Bahamas (Losos et al., 1994) and, to a lesser degree, in continental *Anolis* from Costa Rica (Pounds, 1988; Pinto et al., 2008). Interestingly, inter-annual changes in ecological and environmental factors seem to be directly related to morphological variation in body size and limb length among different years in anoline species (Calsbeek, 2009; Calsbeek et al., 2009), which reinforces the evidence for a clear association between ecology and morphology in the group.

Aside from *Anolis*, the ecological correlates of body size and limb proportions are less apparent in studies of other

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genera of squamates, including *Sceloporus, Acanthodactylus, Adolfus, Lacerta, Podarcis, Petrosaurus, Uta, Tropidurus,* and *Liolaemus* (Miles, 1994; Vanhooydonck & Van Damme, 1999; Warheit *et al.*, 1999; Kohlsdorf *et al.*, 2001; Schulte *et al.*, 2004). In addition, the evolution of foot morphology associated with habitat usage has received comparatively less attention in squamates, although foot morphology exhibits clear performance correlates in some cases (e.g. Carothers, 1986; Autumn *et al.*, 2000; Zani, 2000; Elstrott & Irschick, 2004), and some studies suggest that foot length (Melville & Swain, 2000) or specific traits of foot morphology, such as claws and toepads (e.g. Glossip & Losos, 1997; Zani, 2000; Macrini *et al.*, 2003; Elstrott & Irschick, 2004), may have evolved in association with habitat usage. Surprisingly, foot morphology and relative foot size have usually been studied separately, although these two traits would be expected to evolve in association.

Locomotion in squamates may be affected by subtle evolutionary changes in foot morphology that improve performance on specific substrate types. For example, locomotion on sand involves low friction and force restitution coefficients (and therefore increased energetic demands for movement; Lejeune *et al.*, 1998), as sand is a noncompact substrate that is displaced when a force is exerted on the surface. Evolutionary adjustments such as increased foot area might be important for species that run and walk on loose sand dunes, given that total area in contact with the surface may change friction coefficients. The sand specialist *Uma scoparia*, for example, exhibits many morphological modifications associated with locomotion on sand, including fringed toes, smooth skin, and short tail and hind limbs, characteristics that may favour quick running and burrowing in the sand (Carothers, 1986; Irschick & Garland, 2001). *Niveoscincus* species that run on sand exhibit relatively long feet, which presumably increase the propulsive force in both running and jumping on a loose substrate (Melville & Swain, 2000).

The diameter of cylindrical substrates, from tree trunks to twigs, also affects mechanical demands for locomotion, and such demands differ from those of flat surfaces. Perch diameter influences locomotor performance in *Anolis* species, particularly in those with long legs (Losos & Sinervo, 1989). Arboreal habitats involve locomotion on trunks or branches with variable angles and diameters. This complex three-dimensional environment imposes several functional challenges (Higham *et al.*, 2001; Irschick & Garland, 2001; Spezzano & Jayne, 2004), and favours the evolution of morphological adaptations that improve body stability and manoeuvreability (Van Damme & Vanhooydonck, 2002). For example, squamate clinging ability may be enhanced by increased nail lengths (Zani, 2000).

Tropidurinae (Iguania: Tropiduridae; Frost, 1992) is a suitable model for investigating eco-morphological relationships because it is diverse in habitat and substrate usage. Tropidurinae species can be found in forested and nonforested habitats (Kohlsdorf *et al.*, 2001), the latter including Caatingas (Brazilian habitat characterized by sandy soil and scattered shrubs, for a description see Rocha, 1998) and Cerrados (Brazilian habitat similar to a savannah, characterized by scattered trees and bushes and exposed rocks, for a description see Van Sluys, 1991). Some Tropidurinae species are arboreal (e.g. Vitt, 1991a; Vitt *et al.*, 1997; Ellinger *et al.*, 2001, Kohlsdorf *et al.*, 2008) and frequently experience vertical climbing, where nails may play a relevant role in clinging performance, whereas other species are strictly ground-dwelling and, specifically when moving over sand dunes, do not have to attach to the substrate but must deal with the low friction and force restitution coefficients associated with locomotion over loose surfaces. In the present study, we investigate evolutionary changes in foot morphology, body size, and limb and tail proportions associated with the use of different substrates by Tropidurinae species. Specifically, we test the hypothesis that both 'gross morphology' (body size and limb proportions) and finer-scale aspects of foot morphology are associated with the use of different Brazilian habitats by tropical tropidurines.

Methods

Animals, measurements, and ecological data

Six morphometric traits of the right feet (length, width and height of the fourth toe, nail length, foot sole width and length) were measured on adult males of 23 species from Tropidurinae (Table 1) available in the collection of the Museum of Zoology from the University of São Paulo (MZUSP), SP, Brazil. The number of individuals from each species ranged from four to 20 according to availability. Because of limitations of the collection, data from two populations were pooled for *Uracentron flaviceps, Tropidurus cocorobensis, T. hygomi, Plica plica,* and *P. umbra.* For the other species, only individuals from the best-represented population were considered. All measures were made by MBG, using digital calipers to the nearest 0.01 mm.

Since the publication of a previous paper on related topics (Kohlsdorf *et al.*, 2001), a more recent phylogenetic hypothesis has become available for the Tropidurinae sub-family (Frost *et al.*, 2001). Consequently, data presented in that paper were also re-analysed here together with the new information available. The morphometric traits re-analysed were: SVL, tail, femur, tibia, humerus, and hand+radius lengths. All species included in the phylogeny proposed by Frost *et al.*, (2001) and available in the Museum of Zoology of University of São Paulo (MZUSP) were included. Thus, in the present study we analyse in an integrated approach the previous data on limb and tail proportions from Kohlsdorf *et al.* (2001), including new species available at the MZUSP, and the

Table 1 Means and standard errors of foot morphological traits for each Tropidurinae species.

Species	Tip Order	n	SVL	Foot length	Toe length	Toe width	Toe height	Foot sole length	Foot sole width	Nail length
U. superciliosum*	1	20	113.16 ± 2.22	40.27 ± 0.66	24.29 ± 0.40	1.15 ± 0.03	1.25 ± 0.03	15.98 ± 0.29	5.88 ± 0.16	2.93 ± 0.09
E. divaricatus†	2	20	77.12 ± 2.15	23.15 ± 0.52	13.28 ± 0.32	0.73 ± 0.03	0.83 ± 0.03	9.86 ± 0.22	3.70 ± 0.14	2.27 ± 0.06
E. amathites†	3	20	63.77 ± 1.33	22.82 ± 0.31	12.63 ± 0.17	0.64 ± 0.02	0.77 ± 0.02	10.19 ± 0.19	3.05 ± 0.07	1.83 ± 0.07
E. nanuzae†	4	20	48.29 ± 0.97	14.33 ± 0.27	7.68 ± 0.16	0.43 ± 0.01	0.52 ± 0.02	6.65 ± 0.15	2.31 ± 0.05	1.14 ± 0.04
S. torquatus‡	5	15	89.64 ± 1.69	26.08 ± 0.44	15.56 ± 0.28	0.77 ± 0.03	0.92 ± 0.03	10.51 ± 0.18	4.12 ± 0.10	2.09 ± 0.07
U. azureus§	6	4	74.07 ± 1.99	21.08 ± 0.42	11.86 ± 0.38	0.74 ± 0.02	0.96 ± 0.04	9.21 ± 0.12	3.69 ± 0.05	1.55 ± 0.04
U. flaviceps§	7	10	79.29 ± 5.90	21.19 ± 1.23	12.13 ± 0.67	0.69 ± 0.04	0.85 ± 0.05	9.06 ± 0.57	3.53 ± 0.23	1.58 ± 0.14
P. umbra¶	8	20	80.39 ± 1.31	26.60 ± 0.36	15.34 ± 0.23	0.67 ± 0.02	0.77 ± 0.02	11.25 ± 0.17	3.39 ± 0.07	1.64 ± 0.04
P. plica¶	9	20	140.88 ± 4.43	47.34 ± 1.06	27.96 ± 0.67	1.12 ± 0.03	1.45 ± 0.05	19.38 ± 0.46	6.27 ± 0.20	2.81 ± 0.10
T. spinulosus**	10	20	94.51 ± 3.45	27.41 ± 0.85	15.94 ± 0.49	0.87 ± 0.04	1.06 ± 0.05	11.47 ± 0.37	4.59 ± 0.18	2.10 ± 0.11
T. semitaeniatus**	11	20	85.95 ± 0.85	25.75 ± 0.29	13.54 ± 0.22	0.92 ± 0.01	1.06 ± 0.02	12.21 ± 0.12	3.98 ± 0.07	1.62 ± 0.04
T. hygomi**	12	20	65.60 ± 0.96	25.68 ± 0.25	14.39 ± 0.17	0.81 ± 0.01	0.92 ± 0.02	11.29 ± 0.10	3.68 ± 0.07	1.66 ± 0.04
T. itambere**	13	20	73.79 ± 2.17	20.79 ± 0.46	10.67 ± 0.24	0.70 ± 0.03	0.84 ± 0.03	10.11 ± 0.23	3.57 ± 0.12	1.75 ± 0.07
T. psammonastes**	14	15	88.42 ± 2.12	31.01 ± 0.47	17.06 ± 0.26	1.07 ± 0.03	1.07 ± 0.04	13.95 ± 0.24	4.94 ± 0.16	2.37 ± 0.10
T. cocorobensis**	15	17	66.31 ± 1.58	22.63 ± 0.34	12.57 ± 0.20	0.63 ± 0.02	0.75 ± 0.02	10.06 ± 0.18	3.32 ± 0.08	1.80 ± 0.06
T. etheridgei**	16	20	82.11 ± 1.18	22.32 ± 0.33	11.74 ± 0.22	0.75 ± 0.02	0.88 ± 0.02	10.58 ± 0.14	4.02 ± 0.06	1.93 ± 0.05
T. montanus**	17	20	90.49 ± 1.64	25.82 ± 0.48	13.70 ± 0.27	0.85 ± 0.02	0.98 ± 0.03	12.12 ± 0.22	4.32 ± 0.13	1.82 ± 0.06
T. erythrocephalus**	18	20	76.95 ± 1.40	23.06 ± 0.38	12.11 ± 0.24	0.68 ± 0.01	0.79 ± 0.02	10.95 ± 0.16	3.62 ± 0.07	1.56 ± 0.04
T. mucujensis**	19	4	66.67 ± 2.42	20.70 ± 0.38	11.18 ± 0.33	0.53 ± 0.01	0.65 ± 0.02	9.51 ± 0.20	3.10 ± 0.09	1.72 ± 0.10
T. insulanus**	20	20	77.50 ± 1.44	21.20 ± 0.29	10.78 ± 0.18	0.80 ± 0.02	0.94 ± 0.03	10.42 ± 0.15	3.62 ± 0.06	1.49 ± 0.04
T. oreadicus**	21	20	97.23 ± 1.29	28.59 ± 0.40	15.37 ± 0.28	0.88 ± 0.02	1.03 ± 0.02	13.21 ± 0.17	4.68 ± 0.06	2.40 ± 0.05
T. hispidus**	22	20	85.40 ± 2.25	26.31 ± 0.62	13.88 ± 0.34	0.95 ± 0.03	1.11 ± 0.06	12.43 ± 0.31	4.62 ± 0.15	1.76 ± 0.06
T. torquatus**	23	20	102.00 ± 2.05	32.11 ± 0.52	17.53 ± 0.30	1.00 ± 0.03	1.15 ± 0.03	14.58 ± 0.26	5.44 ± 0.14	2.38 ± 0.08

Measurements are given in millimeters; number of individuals measured for each species (*n*) is shown.

Names follow Frost *et al.* (2001), being:

*Uranoscodon sp.

†*Eurolophosaurus* sp.

‡*Strobilurus* sp.

§*Uracentron* sp.

¶*Plica* sp.

**Tropidurus sp.

refined morphometric data for the feet of Brazilian tropidurines that are still unpublished.

Five categories of substrates used by Tropidurinae were identified as sand, rocks, branches, tree trunks and ground, and the use of these ecological settings was treated as a continuum (i.e. inside each category the proportion of substrate usage could gradually range from zero to one), as many species can be found in more than one habitat type, therefore using more than one kind of substrate. Thus, ecological indices were built as an attempt to estimate the proportion of substrate usage by individuals in a population (Table 2). This estimation was based on published information (Table 2) of how many individuals were captured in a given substrate, resulting in a value ranging from zero (none of the individuals sampled using that substrate type) to one (all individuals sampled using that substrate type) for each of the five substrate categories adopted (branches, trunks, sand, rocks and ground). For example, for a given population that is strictly ground-dwelling in sand dunes, the indices for branches, trunks and rocks would be equal to zero, whereas the index for sand would be equal to

one. Alternatively, a more generalist population from an arboreal species could present indices equal to 0.5 for trunks and branches (in this case, half of the individuals would be found on trunks and half on branches), and the indices for ground, sand and rocks would be equal to zero. This ecological information was confirmed by the field experience of TK, MBG and CAN with many Tropidurinae species from nonarboreal habitats (e.g. *T. itambere, T. oreadicus, T. hispidus, T. torquatus, T. hygomi, T. psammonastes, T. semitaeniatus, T. cocorobensis, T. erythrocephalus, E. divaricatus, E. amathites*). It is important to point out that although these indices are based on ratios of microhabitat selection by individuals in a species, they might be biased by differences among populations. However, we have tried, whenever it was possible, to measure a population of each species included in the present study for which we had published data on habitat usage available or that we knew had a similar ecological profile to the ones described in the literature. About 44% of the populations measured corresponded to the same population for which published information was available, and additional 30% of the populations measured

Table 2 Ecological indices estimated for the use of five substrates by Tropidurinae species.

Species	Sand	Rocks	Trunk	Branches	Ground	Literature source
Uranoscodon superciliosum	0.00	0.06	0.66	0.00	0.28	Howland *et al.*, 1990
Eurolophosaurus divaricatus	1.00	0.00	0.00	0.00	0.00	Rodrigues, 1986
Eurolophosaurus amathites	1.00	0.00	0.00	0.00	0.00	Rodrigues, 1984, 1996
Eurolophosaurus nanuzae	0.00	1.00	0.00	0.00	0.00	Rodrigues, 1981
Strobilurus torquatus	0.00	0.00	0.66	0.26	0.08	Rodrigues *et al.*, 1989
Uracentron azureus	0.00	0.00	0.00	1.00	0.00	Ellinger *et al.*, 2001
Uracentron flaviceps	0.00	0.00	0.00	0.97	0.03	Vitt & Zani, 1996
Plica umbra	0.00	0.00	0.87	0.08	0.05	Vitt *et al.*, 1997
Plica plica	0.00	0.00	1.00	0.00	0.00	Vitt, 1991a
Tropidurus spinulosus	0.00	0.00	0.97	0.00	0.03	Colli *et al.*, 1992; Vitt, 1991b
Tropidurus semitaeniatus	0.00	1.00	0.00	0.00	0.00	Vitt, 1993, 1995; Rodrigues, 1996
Tropidurus hygomi	0.90	0.00	0.00	0.10	0.00	Vanzolini & Gomes, 1979
Tropidurus itambere	0.00	1.00	0.00	0.00	0.00	Van Sluys, 1993, 1998
Tropidurus psammonastes	1.00	0.00	0.00	0.00	0.00	Rodrigues, 1988, 1996
Tropidurus cocorobensis	1.00	0.00	0.00	0.00	0.00	Rodrigues *et al.*, 1989; Rodrigues, 1996
Tropidurus etheridgei	1.00	0.00	0.00	0.00	0.00	Vitt, 1991b
Tropidurus montanus	0.00	0.82	0.00	0.00	0.18	Rodrigues, 1988; Van Sluys *et al.*, 2004
Tropidurus erythrocephalus	0.00	1.00	0.00	0.00	0.00	Rodrigues, 1988, 1996
Tropidurus mucujensis	0.00	1.00	0.00	0.00	0.00	Rodrigues, 1988
Tropidurus insulanus	0.00	1.00	0.00	0.00	0.00	Rodrigues, 1987
Tropidurus oreadicus	0.00	0.35	0.35	0.00	0.30	Colli *et al.*, 1992; Vitt & Caldwell, 1993
Tropidurus hispidus	0.95	0.03	0.00	0.00	0.02	Rodrigues, 1988; Vitt, 1995; Vitt *et al.*, 1996; Van Sluys *et al.*, 2004
Tropidurus torquatus	0.45	0.50	0.00	0.05	0.00	Rodrigues 1981, 1988; Araújo, 1991; Bergallo & Rocha, 1993; Rocha & Bergallo, 1997

Values indicate the proportion of individuals usually found using each ecological category, based both on personal observations/communications and the literature available, listed in the column in the right.

were at least from the same Brazilian State (but not exactly the same locality); from the remaining 26% species measured (for which information was published for populations from different Brazilian States), half of the cases (three species) belong to species claimed as relatively conservative regarding substrate usage (*Uracentron flaviceps* and *U. azureus*, and *Plica umbra*), while two other species are considered as generalists in relation to substrate usage (*Tropidurus oreadicus* and *T. torquatus*), and therefore had their ecological indices calculated from compiled information from multiple studies. Despite the possible limitation and subjectivity of this approach, the inferred ecological indices might reflect in an unambiguous manner the ordinal intraspecific differences in substrate usage by Tropidurinae species.
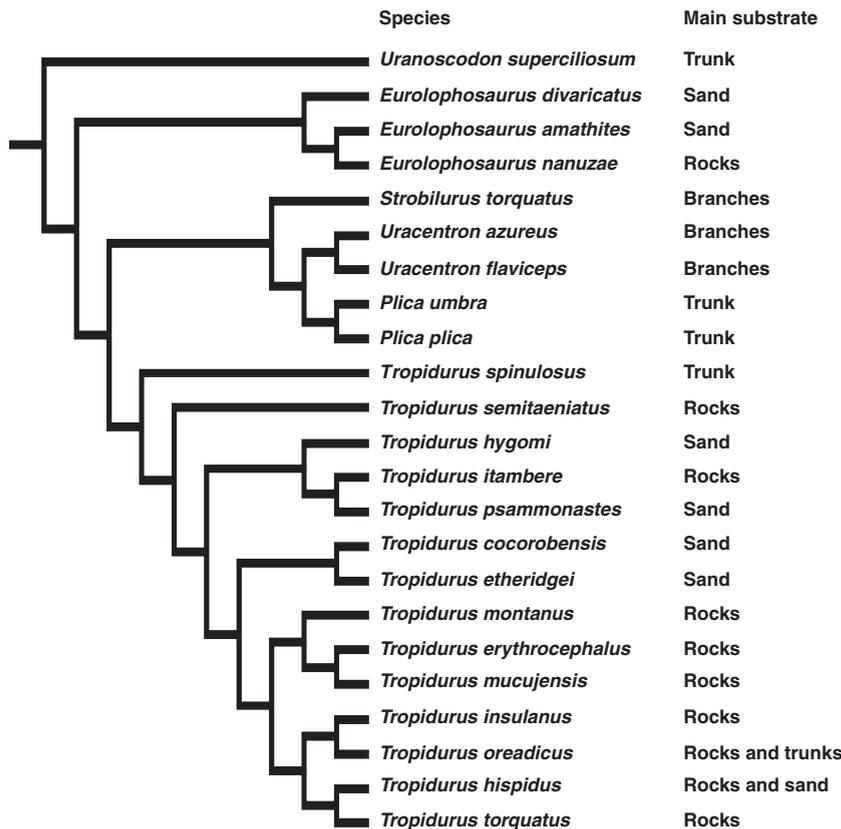
Statistical analysis

Mean values of all measured traits (shown in Table 1) were log_{10} transformed prior to statistical analysis. To remove the effects of body size differences among species, all log-transformed traits (except SVL) were regressed on snout-vent length and residuals were calculated.

In general, whether conventional or phylogenetic statistical analysis should be more reliable for a given empirical data set depends on whether a trait shows phylogenetic signal (*sensu* Blomberg *et al.*, 2003; see also Freckleton *et al.*, 2002; Lavin *et al.*, 2008; Ives & Garland,

2009). Therefore, we used the randomization test described in Blomberg *et al.* (2003) to test for phylogenetic signal and also computed their K statistic to indicate the amount of signal. In addition, we report the Mean Squared Error (MSE) and the ln likelihood for both a star and the hierarchical phylogenies for each trait analysed. A lower MSE or a higher likelihood indicates a better fit to the tip data. Thus, if a star phylogeny better fits a set of tip data (i.e. has a lower MSE and higher likelihood), then the randomization test for phylogenetic signal usually will be nonsignificant, although exceptions occur because the two approaches test somewhat different null hypotheses (see Blomberg *et al.*, 2003). The foregoing tests and statistics were computed with PHYSIG_LL.M (available by request to TG) in MATLAB version 6.1.0 for Windows PCs.

We based our analyses on the topology proposed by Frost *et al.* (2001), which is the most comprehensive current phylogenetic hypothesis for the Tropidurinae group (Fig. 1). This topology adds molecular information to the morphological characters used by Frost (1992) and Harvey & Gutberlet (2000), incorporates a few additional species to the sub-family Tropidurinae (particularly from sandy habitats), and does not present polytomies (Fig. 1). Phylogenetically based statistical methods generally require branch lengths in units proportional to the expected variance of character evolution for each character analysed (reviewed in Rezende & Garland, 2003;

Species	Main substrate
Uranoscodon superciliosum	Trunk
Eurolophosaurus divaricatus	Sand
Eurolophosaurus amathites	Sand
Eurolophosaurus nanuzae	Rocks
Strobilurus torquatus	Branches
Uracentron azureus	Branches
Uracentron flaviceps	Branches
Plica umbra	Trunk
Plica plica	Trunk
Tropidurus spinulosus	Trunk
Tropidurus semitaeniatus	Rocks
Tropidurus hygomi	Sand
Tropidurus itambere	Rocks
Tropidurus psammonastes	Sand
Tropidurus cocorobensis	Sand
Tropidurus etheridgei	Sand
Tropidurus montanus	Rocks
Tropidurus erythrocephalus	Rocks
Tropidurus mucujensis	Rocks
Tropidurus insulanus	Rocks
Tropidurus oreadicus	Rocks and trunks
Tropidurus hispidus	Rocks and sand
Tropidurus torquatus	Rocks

Fig. 1 Phylogenetic tree used for comparative statistical analysis in the present study, with the main substrate used by each species, inferred from data presented in Table 2. The topology follows fig. 6 of Frost *et al.* (2001); branch lengths are arbitrary and follow Pagel (1992).

Garland *et al.*, 2005). Although the clade Iguania might have originated between 150 (Wiens *et al.*, 2006) and 180 Mya (Vidal & Hedges, 2005), Tropiduridae likely originated only in the Miocene (< 24 Mya; Conrad *et al.*, 2007). However, precise estimates of phylogenetic branch lengths in units of divergence times or genetic distances are unavailable for the Tropidurinae topology used. Therefore, we tried four different types of arbitrary branch lengths, including all = 1 (Constant), Grafen (1989), Pagel (1992), and Nee (cited in Purvis, 1995, p. 416). Constant and Nee arbitrary branch lengths provided the best standardization of phylogenetically independent contrasts, as indicated by the absence of statistically significant trends in diagnostic plots for most traits (Garland *et al.*, 1992). Therefore, we used both of these arbitrary branch lengths. The MS-DOS computer program PDTREE (Garland *et al.*, 1993, 1999; Garland & Ives, 2000) was used to enter trees and to examine diagnostic plots of independent contrasts. We acknowledge that our analyses would probably be more powerful if branch lengths in units of divergence time were used (e.g. Díaz-Uriarte & Garland, 1998; Garland & Díaz-Uriarte, 1999), but molecular information is not available for all Tropidurinae species used in the present study (see Frost *et al.*, 2001). If in the future a newer phylogenetic study attempts to estimate branch lengths

from molecular data, based for example on paleontological information (e.g. Marjanovic & Laurin, 2007; Laurin *et al.*, 2009), then it would be appropriate to reanalyse our data.

We performed both conventional and phylogenetic statistics based on Principal Component Analysis (PCA) of the morphometric data (e.g. see Clobert *et al.*, 1998), followed by regressions of the PC scores on the five ecological indices. First, a PCA was performed, using SPSS v.12.0 for PC, for the twelve morphometric traits studied (SVL and residuals of tail, nail, tibia, femur, humerus, hand+radius lengths and digit length, height and width, and foot sole length and width). Principal components with eigenvalues >1 were retained for further analysis. The PC scores were also saved and then used as input for regression models with the ecological indices entered as independent variables. We used the REGRESSIONV.2.M MATLAB (version 6.1.0 for PC) program of Lavin *et al.* (2008) to implement phylogenetic generalized least-squares (PGLS) analysis (this program is available on request from TG). The MS-DOS computer program PDDIST (Garland & Ives, 2000) was used to generate the necessary phylogenetic variance-covariance matrix used in the analysis (Garland *et al.*, 2005; Lavin *et al.*, 2008). The REGRESSIONV.2.M program also computes ordinary least-squares (OLS) regressions, which are equivalent to

assuming that the phylogeny is a star (single hard polytomy) with contemporaneous tips (Purvis & Garland, 1993). Note that the PGLS results from REGRESSIONV.2.M are the same as what can be obtained by use of phylogenetically independent contrasts.

Whether a conventional or phylogenetic regression analysis is more reliable can be judged by comparison of the likelihoods of the two models (e.g. see Lavin et al., 2008), with a higher likelihood indicating a better fit to the tip data. When two regression models have the same number of parameters, then, as a rule of thumb, if twice the difference in ln likelihoods exceeds 3.841 (the critical value for a χ^2 distribution with 1 d.f. and $\alpha = 0.05$), then one model can be considered 'significantly' better than then other (e.g. see Felsenstein, 2004, p. 309). Beyond this, a regression model can be fitted while simultaneously allowing the branch lengths to vary such that a continuum of trees between a star and the hierarchical tree is considered (Grafen, 1989; Freckleton et al., 2002; Duncan et al., 2007; Spoor et al., 2007; Lavin et al., 2008; Gartner et al., 2010). These models contain one additional parameter (for transformation of the branch lengths to maximize the likelihood of the model), and so their fit can be compared with that for the models using a star or the original tree by use of a log likelihood ratio test with 1 degree of freedom. However, we did not use these transformation models in the present study due to the relatively small sample size of 23 species. It is also possible to use regression models that account for within-species variation (Ives et al., 2007), but we did not have estimates of the standard errors for the ecological indices.

To control for the multiple comparisons presented in Table 5, we carried out a False Discovery Rate (FDR) analysis using the QVALUE software package (Storey, 2002) for R (version 2.4.0; R Development Core Team, 2007). The total number of hypotheses under test in Table 5 is 60. Given the relatively low number of P-values, we used the 'bootstrap' option of QVALUE in estimating the proportion of true null hypotheses. Results of the FDR analysis indicated that a more conservative level of $\alpha = 0.0218$ (corresponding to a positive false discovery rate of 5%; Storey, 2002) is appropriate given the number of hypotheses tested and the distribution of P-values we obtained. In Table 5, we present nominal P-values for two-tailed tests, but indicate in bold those that have P-values ≤ 0.0218.

Results

Means and standard errors of traits measured in this study for all species considered are presented in Table 1. Data reported previously in Kohlsdorf et al. (2001) were analysed together with the new data for foot morphology generated for the present study. The phylogeny proposed by Frost et al. (2001) includes four additional sand species scattered across the topology (Fig. 1), thus enhancing statistical power (see Garland, 2001 and references

therein) in comparison with our previous study (Kohlsdorf et al., 2001).

As shown in Table 3, none of the body-size corrected traits related to foot morphology exhibited statistically significant phylogenetic signal, based on the randomization test of Blomberg et al. (2003; $P > 0.05$) using both Constant and Nee arbitrary branch lengths), nor did the measurement of body size (SVL, Table 3). However, tail length and one of the traits related to the front limb (hand+radius length) did exhibit significant phylogenetic signal (see Table 3, $P < 0.05$). The lack of phylogenetic signal based on the randomization test is corroborated by the comparison of likelihoods, which are higher for the star than the hierarchal tree, except for tail length (Table 3). The discrepancy to this pattern for hand+radius length reflects the fact that the randomization test and comparison of likelihoods are not testing exactly the same null hypothesis (see Blomberg et al., 2003; Ives & Garland, 2009).

The Principal Component Analysis based on SVL and residuals of eleven morphometric traits resulted in four components with eigenvalues >1 (Table 4). Component one explained 31.5% of the variance and was related to foot sole shape (foot sole width and length); the second component explained 27.0% of the variance and was mostly related to femur length; the third component explained 13.3% of the variance and enclosed variables associated with the toe shape (toe width and height and nail length) and to humerus length; finally, component four explained 9.1% of the variance and was related to body size (SVL) and to toe, tail, tibia and radius+hand lengths. The tropidurine species with larger foot soles were clearly associated with the use of sandy substrates, as indicated by the regression for the scores of the first PC and the ecological indices (result confirmed both by conventional and phylogenetic analyses), while species with narrower foot soles were associated with a frequent use of rocks and branches (Fig. 2, Table 5). Also, species that often move along trunks exhibit longer femora, a result confirmed both by conventional and the phylogenetic analyses performed using Nee branch lengths (Table 5).

As discussed in the methods, likelihoods can be used to judge if a conventional or a phylogenetic analysis is more reliable. In this context, the result relating foot sole shape (PC1) with use of branches was only supported by the conventional statistics, but the difference in likelihoods was larger than two (so twice the difference in ln likelihoods exceeded 3.841, see Table 5) and this model is preferred over the phylogenetic ones. The significant regression between the second principal component (related to femur length) and the ecological indices for 'branches' was restricted to the phylogenetic analysis, but, due to its higher likelihood (Table 5), the result from the phylogenetic statistics should be preferred. It is important to point out, however, that the difference in ln likelihoods in this analysis was less than two, so we

Table 3 Indicators of phylogenetic signal for morphometric traits.

Trait	Branches	MSEtree	MSEStar	K	P phylogenetic signal	ln Likelihood tree	ln Likelihood star
SVL	Nee	0.0110	0.0089	0.5680	0.204	19.78	22.21
	Constant	0.0105		0.5732	0.103	20.22	
Toe length	Nee	0.0179	0.0137	0.5586	0.279	14.12	17.23
	Constant	0.0173		0.8134	0.172	14.56	
Toe width	Nee	0.0129	0.0104	0.5668	0.186	17.87	20.40
	Constant	0.0124		0.6110	0.140	18.34	
Toe height	Nee	0.0119	0.0092	0.5419	0.264	18.88	21.84
	Constant	0.0112		0.5058	0.166	19.50	
Foot sole length	Nee	0.0119	0.0089	0.5193	0.348	18.83	22.17
	Constant	0.0115		0.5186	0.236	19.26	
Foot sole width	Nee	0.0126	0.0097	0.5396	0.260	18.18	21.21
	Constant	0.0122		0.6128	0.172	18.59	
Nail length	Nee	0.0155	0.0092	0.4321	0.764	15.77	21.82
	Constant	0.0145		0.6856	0.689	16.55	
Tail length	Nee	0.0333	0.0349	0.7502	0.022*	7.00	6.45
	Constant	0.0327		0.9334	0.010*	7.20	
Tibia length	Nee	0.0165	0.0116	0.4846	0.445	15.11	19.16
	Constant	0.0151		0.3724	0.246	16.13	
Femur length	Nee	0.0169	0.0144	0.5963	0.190	14.80	16.64
	Constant	0.0160		0.5510	0.051	15.45	
Humerus length	Nee	0.0161	0.0131	0.5676	0.211	15.32	17.72
	Constant	0.0148		0.4461	0.074	16.30	
Radius+hand length	Nee	0.0130	0.0112	0.6001	0.134	17.85	19.55
	Constant	0.0120		0.5076	0.028*	18.76	

Significant values indicated by an asterisk. All traits were log-transformed, and effects of SVL were removed prior to analysis as described in Blomberg *et al.* (2003).

cannot conclude that one model is 'significantly' better than the other.

Discussion

The present study is one of the first to investigate the evolution of several morphometric traits (body size, limb and tail proportions, and refined aspects of foot shape and size) using the integrative approach of identifying principal components that associate specific traits and correlating those with habitat usage, treated as a set of continuous-valued indices. Although substrate type was divided into five distinct categories, the percentage of substrate usage within each category might vary from zero to one, which reflects the gradual ecological variation that exists among some tropidurines as well

Table 4 Component scores resulting from a Principal Component Analysis (PCA) performed on the morphometric traits.

	PC 1	PC 2	PC 3	PC 4
Eigenvalue/%variation explained	3.78/31.46	3.24/27.00	1.60/13.30	1.09/9.06
SVL	0.011	0.015	−0.041	**−0.523**
Toe Length	0.179	0.071	−0.098	**0.476**
Toe Width	0. 182	−0.164	**0.268**	−0.070
Toe Height	0.146	−0.140	**0.414**	−0.019
Foot Sole Length	**0.245**	0.064	0.005	−0.038
Foot Sole Width	**0.190**	−0.169	0.093	0.038
Nail	0.123	−0.073	**−0.393**	0.378
Tail	0.170	0.135	−0.227	**−0.277**
Tibia	0.158	0.200	−0.061	**−0.206**
Femur	0.083	**0.266**	0.110	−0.127
Humerus	−0.078	0.183	**0.291**	0.239
Radius-Hand	0.001	0.237	0.239	**0.277**

All traits were log-transformed, and effects of body size were removed prior to analysis by computing residuals from regressions on SVL (except for SVL itself). Traits contributing most to each component are indicated in bold. The total amount of variance in the data explained by these first four principal components is 80.8%.
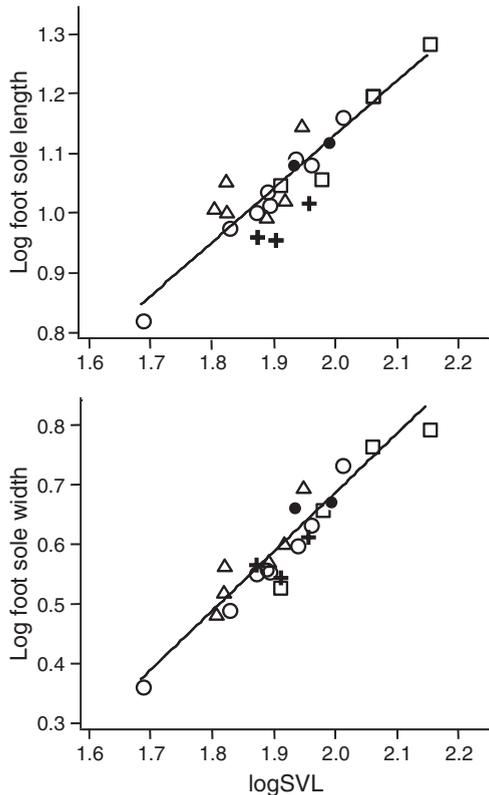
Fig. 2 Scatterplots relating $\log_{10}$ of SVL with $\log_{10}$ of measured foot traits. The symbols indicate microhabitat usage: triangle corresponds to species from sandy habitats, square indicates trunk species, cross indicates branch species, open circle indicates rock species, and filled circles indicate species that use equally more than one substrate type.

as the multiple uses of different ecological settings by others. This innovative approach enabled the identification of morphological changes in foot sole shape (foot sole length and width, captured in PC1: Table 4) associated to the frequent use of sandy environments by some Tropidurinae and the use of rocks or branches by other species (Table 5). Specifically, Tropidurinae species that locomote mostly on sand exhibit larger foot soles (longer and wider), a morphological profile that probably counters the energetic and mechanical limitations associated with the low friction and force restitution coefficients implied by locomotion on sand (Lejeune *et al.*, 1998). In contrast, species that often move on rocks and branches exhibit narrower foot soles, which may directly affect the clinging ability of these squamates. Morphological variation in limb proportions is also associated with the use of forested habitats, as arboreal tropidurines that move more often in trunks exhibit longer femora. Together, these findings strongly suggest that adaptive changes in the overall morphology integrating foot shape and hind limb size played a role in the

colonization of several habitats (which actually represent continua of ecological settings) by Tropidurinae lineages. Considering recent estimates for the origin of Tropiduridae (in the Miocene, less than 24 Mya; Conrad *et al.*, 2007), it is possible to assume that these adaptive changes may have occurred in a relatively narrow window of evolutionary time.

The evolution of foot sole shape in Tropidurinae is particularly interesting in the ecological context of differential habitat use, as it provides evidence that the shape of a given morphological trait might evolve in opposite directions according to the mechanical and energetic demands imposed by locomotion in contrasting surfaces. In the present study, the ancestral morphological and ecological states for the Tropidurinae sub-family were not formally reconstructed, but given that the species using mostly sand, rocks or branches likely evolved from a single ancestor originated in forested habitats (Howland *et al.*, 1990), the large foot soles exhibited by sand species and the narrow feet of species that use mostly rocks and branches may represent extremes of a continuum not only in habitat use but also in morphological change. At this point, it is not possible to state that these differences in foot morphology have occurred in the same way (for a broad discussion about homology, see Wagner, 1989a,b), as the genetic and developmental mechanisms underlying foot sole reduction and broadening in Tropidurinae are unknown, and the specific osteological and muscular structures that changed during the evolutionary processes of foot sole differentiation cannot be inferred solely from the two linear measurements obtained. Even so, the morphological specialization observed in the foot soles of Tropidurinae suggests that a shape that probably maximizes performance of these squamates in sand is opposite to the shape that probably enhances locomotion on rocks or branches, corroborating the idea that evolution of some morphological traits often occurs in close association with the ecological setting used by a given species and that this may lead to trade-offs (Garland & Losos, 1994; Clobert *et al.*, 2000; but see Goodman *et al.*, 2007).

Adaptations in foot morphology associated with the use of sandy habitats by Tropidurinae likely lead to differences in locomotor performance between species that often locomote on sand and other tropidurines that are rarely (or never) found in open sand dunes. Considering the increased risk of predation and overheating in sandy environments (Lima & Dill, 1990), high-speed locomotion between refuges might be favoured by natural selection in this habitat. In fact, the sand species *T. psammonastes* runs faster than congenerics from rocky habitats, particularly when running on sand (Kohlsdorf *et al.*, 2004), and in general Tropidurinae species that live in the Caatingas perform more horizontal jumps during obstacle-crossing than tropidurines from the rocky Cerrados (Kohlsdorf & Navas, 2007). The main evidence for the influence of morphology on running performance,

Table 5 Results of regressions of the scores of the four principal components obtained from morphometric data (Table 4) on the five ecological indices (Table 2), using both conventional and phylogenetic [with Nee and Constant (All=1) branch lengths] analyses.

			PC1	PC2	PC3	PC4
SAND	Conventional	t/P	**3.069/0.0058**	0.425/0.6752	0.727/0.4753	1.304/0.2063
		ln Likelihood	−27.86	−30.02	−31.83	−30.88
		Partial Regression Coefficient	1.217	0.222	−0.343	0.590
	Phylogenetic(Nee)	t/P	**3.503/0.0021**	2.248/0.0354	0.339/0.7380	1.049/0.3061
		ln Likelihood	−27.67	−31.37	−33.42	−32.39
		Partial Regression Coefficient	1.314	−0.990	−0.192	0.483
	Phylogenetic(All = 1)	t/P	**2.814/0.0104**	2.168/0.0418	0.625/0.5387	1.304/0.2063
		ln Likelihood	−27.86	−30.61	−33.72	−30.88
		Partial Regression Coefficient	1.217	−0.919	−0.303	0.624
ROCKS	Conventional	t/P	0.772/0.4487	1.071/0.2963	0.270/0.7898	1.857/0.0774
		ln Likelihood	−31.80	−31.51	−32.08	−30.02
		Partial Regression Coefficient	−0.370	0.507	0.133	−0.824
	Phylogenetic(Nee)	t/P	**2.935/0.0079**	1.648/0.1142	0.881/0.3883	1.225/0.2341
		ln Likelihood	−29.00	−32.45	−32.71	−32.18
		Partial Regression Coefficient	−1.134	0.739	0.578	−0.543
	Phylogenetic(All =1)	t/P	**2.478/0.0218**	1.895/0.0719	1.394/0.1779	1.357/0.1892
		ln Likelihood	−31.80	−31.12	−32.92	−31.69
		Partial Regression Coefficient	−1.014	0.507	0.639	−0.590
TRUNKS	Conventional	t/P	0.455/0.6538	**2.567/0.0180**	0.625/0.5387	0.491/0.6285
		ln Likelihood	−32.01	−28.98	−31.92	−31.64
		Partial Regression Coefficient	−0.027	1.368	−0.379	−0.294
	Phylogenetic(Nee)	t/P	0. 551/0.5874	**2.496/0.0210**	1.421/0.1700	0.650/0.5227
		ln Likelihood	−32.79	−30.86	−32.45	−31.64
		Partial Regression Coefficient	0.431	1.797	−1.096	−0.508
	Phylogenetic(All = 1)	t/P	0.373/0.7129	1.669/0.1100	1.596/0.1254	0.809/0.4276
		ln Likelihood	−33.188	−31.50	−32.62	−32.30
		Partial Regression Coefficient	0.272	1.133	1.137	−0.568
BRANCHES	Conventional	t/P	**2.857/0.0094**	1.550/0.1361	2.118/0.0463	1.811/0.0845
		ln Likelihood	−28.34	−30.87	−29.89	−29.98
		Partial Regression Coefficient	−1.868	−1.132	1.481	1.27
	Phylogenetic(Nee)	t/P	1.381/0.1818	**2.560/0.0182**	1.450/0.1618	1.354/0.1901
		ln Likelihood	−31.96	−30.72	−32.41	−32.01
		Partial Regression Coefficient	−1.381	−2.422	1.476	1.355
	Phylogenetic(All = 1)	t/P	1.210/0.2397	**2.537/0.0192**	1.308/0.2050	1.811/.0845
		ln Likelihood	−32.48	−29.86	−33.03	−30.11
		Partial Regression Coefficient	−1.316	−2.42	1.457	1.278
GROUND	Conventional	t/P	0.272/0.7883	0.013/0.9898	1.399/0.1764	1.211/0.2393
		ln Likelihood	−32.08	−32.12	−31.10	−31.00
		Partial Regression Coefficient	0.672	0.074	−3.312	−2.856
	Phylogenetic(Nee)	t/P	0.151/0.8814	0.589/0.5621	1.541/0.1383	0.033/0.9740
		ln Likelihood	−32.95	−33.66	−32.27	−32.97
		Partial Regression Coefficient	0.340	1.365	−3.362	−0.075
	Phylogenetic(All = 1)	t/P	0.393/0.6983	0.430/0.6716	1.471/0.1561	1.413/0.1723
		ln Likelihood	−33.17	−32.84	−32.81	−31.61
		Partial Regression Coefficient	0.84	0.944	−3.220	1.480

Values of significance (two-tailed) are presented, and the ones lower than 0.0218 (based on a False Discovery rate analysis – see text) are indicated in bold. Likelihood values and partial regression coefficients are also presented.

associated with differentiated habitat usage, comes from studies focusing on limb proportions and body size. In *Anolis* squamates, species that are morphologically similar exhibit comparable locomotor performance (Losos, 1990a), and an increase in body size and relative hind limb length improves sprint speed (Losos, 1990b). Among phrynosomatid squamates, the subclade termed 'sand lizards' also has higher sprint speeds associated with

longer hind limbs, in comparison with other species from the same family (Bonine & Garland, 1999; Bonine *et al.*, 2001, 2005). Regarding foot morphology, removal of the toe fringes of the strictly sand-dwelling phrynosomatid *Uma scoparia* reduces maximal sprint speed and acceleration on sand, but not on rubber surfaces (Carothers, 1986). Melville & Swain (2000) suggested that the long feet of saxicolous *Niveoscincus* squamates are associated

with high sprint speeds and presumably increased propulsive forces for running and jumping. Also, scincid squamates living at sand dunes in Egypt exhibit differences in limb and foot morphology that seem associated with habitat partitioning and may be related to predator escape (Attum *et al.*, 2007). Future kinematic and biomechanical studies on Tropidurinae species from different habitats running over sandy and hard surfaces would elucidate whether the morphological profile of squamates with increased foot sole areas in contact with substrate actually improves performance on surfaces that hinder propulsion, such as sand.

Forested environments also likely impose several functional challenges for small, arboreal vertebrates, such as different-diameter perches, obstacle-filled pathways, and the risk of falling (Cartmill, 1985; Higham *et al.*, 2001; Elstrott & Irschick, 2004; Spezzano & Jayne, 2004). Changes in perch diameter affect locomotor performance (Losos & Sinervo, 1989) and hind limb kinematics (Spezzano & Jayne, 2004) in *Anolis* species, while turning angles influence escape behaviour and performance in arboreal species (Higham *et al.*, 2001). The relationship between performance, habitat, and morphology seems evident in these squamates; for example, the performance of long-legged species seems to be more affected by perch diameter than that of short-legged species (Losos & Sinervo, 1989). In contrast, our previous study of morphological changes in limb and tail sizes in Tropidurinae species (Kohlsdorf *et al.*, 2001) had already suggested that this sub-family exhibits modest differentiation in body proportions, which are mostly associated with the colonization of forested environments. In that study, arboreal species were either classified as 'trunk species' or 'branch species', and shorter tails and hind limbs were associated with species that use branches and large evolutionary rates were detected between two sister species that move vertically over large trunks in the Amazonian forest (Kohlsdorf *et al.*, 2001). In the present study, the Tropidurinae species were scored according to an increased use of trunks or branches. Even when the use of these arboreal surfaces was considered as a continuum, a dichotomy is evident in forested environments: some species move almost exclusively on trunks (like *Plica plica*) and others spend more than 90% of their time on branches. This ecological dichotomy seems coupled to the evolution of two different morphological profiles: species that very often use branches exhibit narrow foot soles, while the three species that spend more than 85% of their time on trunks are the ones that exhibit the longest relative hind limbs, specifically longer femora.

The disparity between arboreal species using different microhabitats (trunks or branches) in the Brazilian forests is likely related to the contrasting biomechanical demands involved in each type of locomotion. In one case, narrow foot soles may influence gripping ability and decrease the risk of falling from thin branches. Also,

shorter tendons (given by short foot soles) might increase the ability to control length changes resulting from tendon compression (Rack & Ross, 1984; Ker *et al.*, 1988), which may improve control when dealing with the frequent shifts in substrate incline and diameter imposed by structurally complex forested habitats. Several additional morphological adaptations that may improve arboreal locomotion have been described in squamates. For example, increased digital lamellae (Glossip & Losos, 1997) and larger toepads (Irschick *et al.*, 1996; Elstrott & Irschick, 2004; Irschick *et al.*, 2005) seem to improve climbing performance in anoles, and toe-clipping reduces clinging performance in *Anolis carolinensis* (Bloch & Irschick, 2005). Moreover, the size and shape of the tips of geckos' foot hair are directly related to their stickiness capacity (Autumn *et al.*, 2000). In contrast, Tropidurinae species that grip on vertical surfaces with large diameters, such as trunks, may have their performance improved by longer limbs. Arboreal squamates moving up inclined or vertical surfaces tend to maintain their trunk close and parallel to the substrate by flexing the forearms in a very spread posture (Jayne & Irschick, 1999; Zaaf *et al.*, 1999), and some species, including geckos (Zaaf *et al.*, 2001) and lacertids (Russell & Bels, 2001), exhibit a brief swing phase during climbing and other speed-modulation strategies during vertical climbing to ensure accuracy of fore and hind limb positioning (Zaaf *et al.*, 2001).

In addition to changes in limb and foot morphology observed in association with an increased use of sandy, rocky or forested environments, it is also possible that species in this sub-family evolved physiological, behavioural or kinematic adaptations that improve locomotor performance along the continuum of ecological settings colonized by Tropidurinae lineages. For example, in phrynosomatid species, high sprint speeds of the sand lizard clade can be explained, in part, by variation in muscle fiber-type composition (Bonine *et al.*, 2001, 2005). It has also been observed that humans adjust their leg stiffness when changing from sand to hard surfaces, in order to minimize oscillation of the centre of mass, with considerable energetic economy (Ferris *et al.*, 1999). Squamates are distinct from other vertebrates in relation to trunk lateral bending and support of centre of mass by legs (Avery *et al.*, 1987; Ritter, 1992, 1995), but it is also known that some species exhibit kinematic adjustments to increase sprint speed (Irschick & Jayne, 1998; Jayne & Irschick, 1999; Vanhooydonck *et al.*, 2002), improve jumping capacity (Toro *et al.*, 2003), and to cope with differences in the complexity of their structural habitats (Kohlsdorf & Biewener, 2006). It is also known that squamate species from different habitats exhibit behavioural differences, related to the propensity of performing specific locomotor activities (Bulova, 1994; Irschick & Jayne, 1998; Jayne & Irschick, 2000), which has been described even in specific species of tropidurines (Kohlsdorf *et al.*, 2004; Kohlsdorf & Navas, 2007). Future

investigations of adaptive changes during the colonization of different ecological settings by Tropidurinae species might include integrating new data on physiology and behaviour with the morphological study described in the present work, in order to investigate how multiple traits, which likely affect performance in a given environment, evolve in a correlated fashion (Garland & Losos, 1994; Irschick & Garland, 2001).

Acknowledgments

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