Head shape evolution in Tropidurinae lizards: does locomotion constrain diet?

T. KOHLSDORF,* M. B. GRIZANTE,* C. A. NAVAS† & A. HERREL‡

*Department of Biology, FFCLRP – University of São Paulo, Ribeirão Preto, SP, Brazil
†Department of Physiology, IB-University of São Paulo, São Paulo, SP, Brazil
‡Department of Biology, University of Antwerp, Antwerpen, Belgium

Abstract

Different components of complex integrated systems may be specialized for different functions, and thus the selective pressures acting on the system as a whole may be conflicting and can ultimately constrain organismal performance and evolution. The vertebrate cranial system is one of the most striking examples of a complex system with several possible functions, being associated to activities as different as locomotion, prey capture, display and defensive behaviours. Therefore, selective pressures on the cranial system as a whole are possibly complex and may be conflicting. The present study focuses on the influence of potentially conflicting selective pressures (diet vs. locomotion) on the evolution of head shape in Tropidurinae lizards. For example, the expected adaptations leading to flat heads and bodies in species living on vertical structures may conflict with the need for improved bite performance associated with the inclusion of hard or tough prey into the diet, a common phenomenon in Tropidurinae lizards. Body size and six variables describing head shape were quantified in preserved specimens of 23 species, and information on diet and substrate usage was obtained from the literature. No phylogenetic signal was observed in the morphological data at any branch length tested, suggesting adaptive evolution of head shape in Tropidurinae. This pattern was confirmed by both factor analysis and independent contrast analysis, which suggested adaptive co-variation between the head shape and the inclusion of hard prey into the diet. In contrast to our expectations, habitat use did not constrain or drive head shape evolution in the group.

Introduction

Complex integrated systems, such as those involved in vertebrate feeding or locomotion, are more than the sum of their components. The different components (e.g. muscles, bones and sensory organs) must interact to result in an appropriate behavioural or motor program (Wagner & Schwenk, 2000; Herrel *et al.*, 2001a). However, the different components of the system may be specialized for different functions, leading to both phenotypic trade-offs and evolutionary

Correspondence: Tiana Kohlsdorf, Department of Biology, FFCLRP, University of São Paulo, Avenida Bandeirantes, 3900, Bairro Monte Alegre, Ribeirão Preto, SP 14040-901, Brazil.
Tel.: +55 16 3602 4964; fax: +55 16 3602 4886;
e-mail: tiana@usp.br

constraints (Roth & Wake, 1989). For example, the specialized chemoreceptive tongue of snakes and varanid lizards is nonfunctional for prey transport (Schwenk, 2000). Also, the axial system in lizards has an important role during both locomotion and breathing, and the interplay between these two functions may constrain endurance capacity (Carrier, 1991; but see Owerkowicz *et al.*, 1999). The field of athletic performance illustrates that simultaneous specialization for activities requiring contrasting abilities such as power and stamina is not possible, neither in the context of individual training (Van Damme *et al.*, 2002), nor by means of artificial selection (Pasi & Carrier, 2003). Consequently, selective pressures on the different functions that need to be carried out by such complex systems may be conflicting, and ultimately may put

limits on the extent and direction of the evolution of morphology and performance (Arnold, 1992; Schwenk, 1995).

The vertebrate cranial system is one of the most striking examples of a complex system with a plethora of possible functions, including feeding, breathing, drinking, protection of the brain and sensory systems, defensive behaviours, display and sensory perception (Cooper & Vitt, 1993; Bels *et al.*, 1994; Schwenk, 2000; Herrel *et al.*, 2001a; Lappin & Husak, 2005). Selective pressures on the cranial system as a whole are possibly complex and may be conflicting. For example, to effectively crush large and hard prey, animals need large, tall and wide heads that can accommodate large jaw muscles leading to an improved bite performance (Herrel *et al.*, 1999, 2001a; b). Additionally, animals can improve bite performance by adjusting the proportions of the jaw lever system, for example by increasing the length of the jaw closing in-lever. This may trade-off, however, with the precision and speed for capturing elusive prey, which requires longer snouts and jaw out-levers as well as a longer in-lever for jaw opening. The contrast between alligators and gharials illustrates an extreme case, but more subtle examples exist among lizards, even within a genus as demonstrated by *Anolis* lizards. In this taxon the evolution towards short and broad heads contrasts with the evolution of long and narrow heads (Harmon *et al.*, 2005).

Changes in cranial morphology may also constrain locomotor performance because big and tall heads may shift the animal's centre of mass away from the substrate, thus conflicting with its ability to climb vertical structures (Vanhooydonck & Van Damme, 1999; Herrel *et al.*, 2001a, 2002a; Zaaf & Van Damme, 2001; b). Conversely, the flat heads and bodies of climbing lizards probably improve balance and ability to hide in cracks and crevices, important refuges in open vertical habitats (Arnold, 1998; Vitt *et al.*, 1997a). Even so, some lizards appear to circumvent these constraints by morphological, behavioural or ecological specializations (Herrel *et al.*, 2001b; Lappin *et al.*, 2006).

In the present study, we focus on the potential influence of trade-offs between diet and locomotion on the evolution of head shape in tropidurine lizards. The sub-family Tropidurinae is an ideal group to test eco-morphological hypotheses because several rock- and tree-dwelling species evolved independently within the group (see Kohlsdorf *et al.*, 2001 and references therein). The expected adaptations leading to flat heads and bodies in species experiencing the strong constraints of living on vertical structures (Arnold, 1998; Vanhooydonck & Van Damme, 1999; Zaaf & Van Damme, 2001; Herrel *et al.*, 2001b) may conflict with the need for improved bite performance associated with the inclusion of hard or tough prey into the diet, a common phenomenon in tropidurine lizards (Table 1). We first test for the presence of phylogenetic signal in our morphological data to explore which components of head shape may have evolved adaptively. Absence of phylogenetic signal in the data set suggests that the trait distribution has little or no phylogenetic structure and may thus be the result of adaptive evolution. Next, we explore which components of head shape have evolved most strongly in the Tropidurinae family and, finally, we test for associations among head shape, diet and habitat use. Based on previously published data on head shape (Vanhooydonck & Van Damme, 1999; Herrel *et al.*, 2001c, 2002a; Zaaf & Van Damme, 2001), and biomechanical models of climbing (Vanhooydonck & Van Damme, 1999) and biting (Herrel *et al.*, 1998a,b) in lizards, we predict that (i) lizards that usually crush hard prey as part of their feeding habits will have wider and taller heads and a greater jaw closing in-lever, (ii) species that tend to capture more elusive prey will have a greater jaw opening in-lever and longer snouts and (iii) animals that inhabit vertical structures such as rocks or trees, where crevices are essential refuges and climbing is the major mode of locomotion, will have shallower but broader heads than ground-dwelling lizard species, independent of their preferred prey type.

Materials and methods

Specimens

Morphological measurements were performed in preserved specimens of 23 species of Tropidurinae from the collection at the Museum of Zoology of the University of São Paulo (MZUSP), SP, Brazil. To improve consistency, we did not include data on juveniles or females. The number of individuals per species varied with availability and ranged from 3 to 20 (Table 1). For each species, we tried to measure lizards from a single population, choosing that which had the greater number of individuals available at MZUSP. However, because of restrictions in the quantity of material available, we pooled the data of two populations for *Uracentron flaviceps*, *Tropidurus cocorobensis*, *T. hygomi*, *Plica plica*, and *P. umbra*. Measurements were carried out by the same person using digital calipers to the nearest 0.01 mm.

Morphology

Body size (given by snout-vent length, SVL) and six variables of head morphology were measured in specimens of 23 Tropidurinae species. Morphological data measured (see Fig. 1) included head length (measured from the back of the parietal bone to the tip of the snout), head width (measured as the widest point of the head), head depth (measured at the tallest part of the head), lower jaw length (measured from the back of the retro-articular process to the tip of the lower jaw), and snout length (measured from the back of the jugal bone to the tip of the upper jaw). Additionally, the distance from the

Table 1 Body size, head dimensions and diet of the Tropidurinae species considered in the present study.

Species	N	SVL (mm)	Head length (mm)	Head width (mm)	Head height (mm)	Lower jaw length (mm)	Out-lever (mm)	Snout length (mm)	Open in-lever (mm)	Close in-lever (mm)	% Hard prey	% Elusive prey
U. superciliosum[1]	7	111.19 ± 4.79	20.24 ± 1.42	17.78 ± 1.75	16.22 ± 1.42	25.55 ± 2.05	22.07 ± 1.46	18.05 ± 1.55	3.48	4.02	8	44
E. nanuzae	20	48.90 ± 3.10	12.14 ± 0.81	9.99 ± 0.70	7.36 ± 0.59	14.02 ± 0.86	12.66 ± 0.84	9.56 ± 0.56	1.36	3.10		
T. cocorobensis	9	68.84 ± 4.88	15.30 ± 0.64	13.36 ± 0.75	9.20 ± 0.62	19.35 ± 1.03	17.42 ± 0.98	12.86 ± 0.46	1.92	4.56		
T. hygomy	20	67.19 ± 2.95	15.52 ± 0.61	13.49 ± 0.58	10.14 ± 0.54	19.36 ± 0.69	17.54 ± 0.68	13.15 ± 0.50	1.82	4.39		
T. erythrocephalus[2]	20	79.31 ± 4.87	17.29 ± 0.75	16.23 ± 1.00	11.37 ± 0.83	22.39 ± 1.39	20.05 ± 0.91	16.77 ± 0.93	2.34	3.29		
T. itambere	20	81.68 ± 6.19	17.78 ± 1.10	17.32 ± 1.26	12.07 ± 1.08	23.98 ± 1.79	21.01 ± 1.60	15.23 ± 1.12	2.97	5.78	15.12	10.84
T. insulanus	13	79.58 ± 5.17	17.10 ± 0.82	16.04 ± 0.88	11.21 ± 0.55	22.60 ± 1.39	19.91 ± 1.01	14.72 ± 0.97	2.69	5.19		
T. oreadicus[3]	20	98.27 ± 4.89	20.53 ± 0.96	20.96 ± 1.66	15.02 ± 1.15	27.41 ± 2.67	24.90 ± 1.40	19.00 ± 1.27	2.50	5.90	18.37	18.77
T. hispidus[4]	20	87.82 ± 6.71	18.88 ± 1.13	18.67 ± 1.61	13.54 ± 1.25	23.78 ± 1.60	22.50 ± 2.43	18.28 ± 1.23	1.28	4.22	21.7	21.4
T. montanus[4]	18	85.22 ± 6.97	18.40 ± 1.30	17.06 ± 1.75	11.20 ± 1.58	23.75 ± 2.23	21.06 ± 1.88	15.42 ± 1.36	2.69	5.64	10	11.9
T. mucujensis	3	66.38 ± 5.79	15.07 ± 1.05	13.40 ± 1.43	8.77 ± 0.84	18.96 ± 1.98	16.81 ± 1.54	12.26 ± 1.17	2.15	4.55		
T. torquatus[5]	20	95.09 ± 5.65	20.17 ± 1.15	19.24 ± 1.36	14.11 ± 1.20	27.02 ± 1.63	23.18 ± 4.48	17.80 ± 0.89	3.83	5.38	5.98	10.3
T. semitaeniatus	17	83.54 ± 5.44	16.33 ± 0.89	14.61 ± 1.23	8.10 ± 0.85	21.21 ± 1.36	18.95 ± 1.18	13.57 ± 0.74	2.26	5.38		
T. spinulosus[3]	8	95.47 ± 9.26	19.24 ± 1.79	19.24 ± 2.09	13.37 ± 1.42	23.63 ± 3.11	22.11 ± 2.47	16.41 ± 1.59	1.51	5.71	38.1	36
P. plica[6]	11	147.06 ± 17.06	29.08 ± 3.21	31.68 ± 4.00	20.52 ± 2.71	39.77 ± 5.47	35.22 ± 4.53	25.91 ± 2.73	4.55	9.31	31.3	18.21
P. umbra[7]	20	79.39 ± 3.93	17.46 ± 1.02	14.67 ± 0.93	12.07 ± 0.80	20.97 ± 1.42	18.13 ± 1.26	14.90 ± 1.01	2.84	3.22	1.49	1.08
S. torquatus	14	90.00 ± 6.41	19.65 ± 1.48	20.10 ± 1.95	15.09 ± 2.04	26.91 ± 2.11	23.74 ± 1.88	16.75 ± 1.17	3.17	6.99		
U. azureus[8]	6	73.23 ± 7.30	16.41 ± 1.49	13.59 ± 1.51	10.59 ± 0.92	20.75 ± 2.34	18.39 ± 2.03	14.85 ± 1.48	2.36	3.54	4.2	4.2
U. flaviceps[9]	8	92.70 ± 10.22	18.80 ± 2.36	19.04 ± 4.11	13.51 ± 2.75	24.80 ± 3.77	21.87 ± 3.14	17.60 ± 2.31	2.94	4.27	12.1	8.26
E. divaricatus[10]	18	79.23 ± 7.94	15.72 ± 1.35	12.77 ± 1.64	10.30 ± 1.70	19.22 ± 2.24	17.47 ± 1.97	14.22 ± 1.29	1.76	3.24	20.4	15.6
T. psamonastes[10]	20	90.37 ± 5.09	19.15 ± 0.74	18.62 ± 2.22	13.81 ± 0.73	25.71 ± 1.05	22.97 ± 1.00	16.58 ± 0.84	2.75	6.38	46.3	41.4
T. etheridgei	16	81.45 ± 6.30	17.44 ± 0.99	17.15 ± 1.38	12.56 ± 1.17	23.11 ± 1.64	20.41 ± 1.32	15.06 ± 1.14	2.70	5.36		
E. amathites	20	66.83 ± 4.03	14.45 ± 0.62	12.04 ± 0.56	9.42 ± 0.63	17.41 ± 0.84	15.77 ± 0.85	11.58 ± 0.84	1.63	4.20		

Table entries are means ± standard deviations.

1, Gasnier et al. (1994); 2, Van Sluys (1993); 3, Colli et al. (1992); 4, Van Sluys et al. (2004); 5, Fialho et al. (2000); 6, Vitt (1991); 7, Vitt et al. (1997b); 8, Ellinger et al. (2001); 9, Vitt & Zani (1996); 10, Rocha (1998).
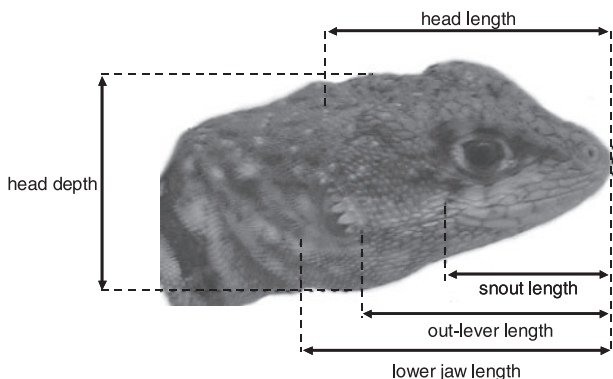
Fig. 1 Lateral view of the head of *Tropidurus torquatus* illustrating the morphological measurements taken.

back of the quadrate to the tip of the lower jaw was measured and used as an estimate of the jaw out-lever length. Based on these measurements, two additional values were calculated: the in-lever for jaw opening, being the lower jaw length minus the jaw out-lever length; and the in-lever for jaw closing, being the jaw out-lever length minus the snout length.

Ecological data

Ecological data on habitat usage were pruned from the extensive literature on tropidurine lizards (see summary in Kohlsdorf *et al.*, 2001). Species were classified as either climbing or ground-dwelling based on data presented in figure 1 of Kohlsdorf *et al.* (2001) (see Fig. 2). Dietary data were recovered from the literature for 13 species
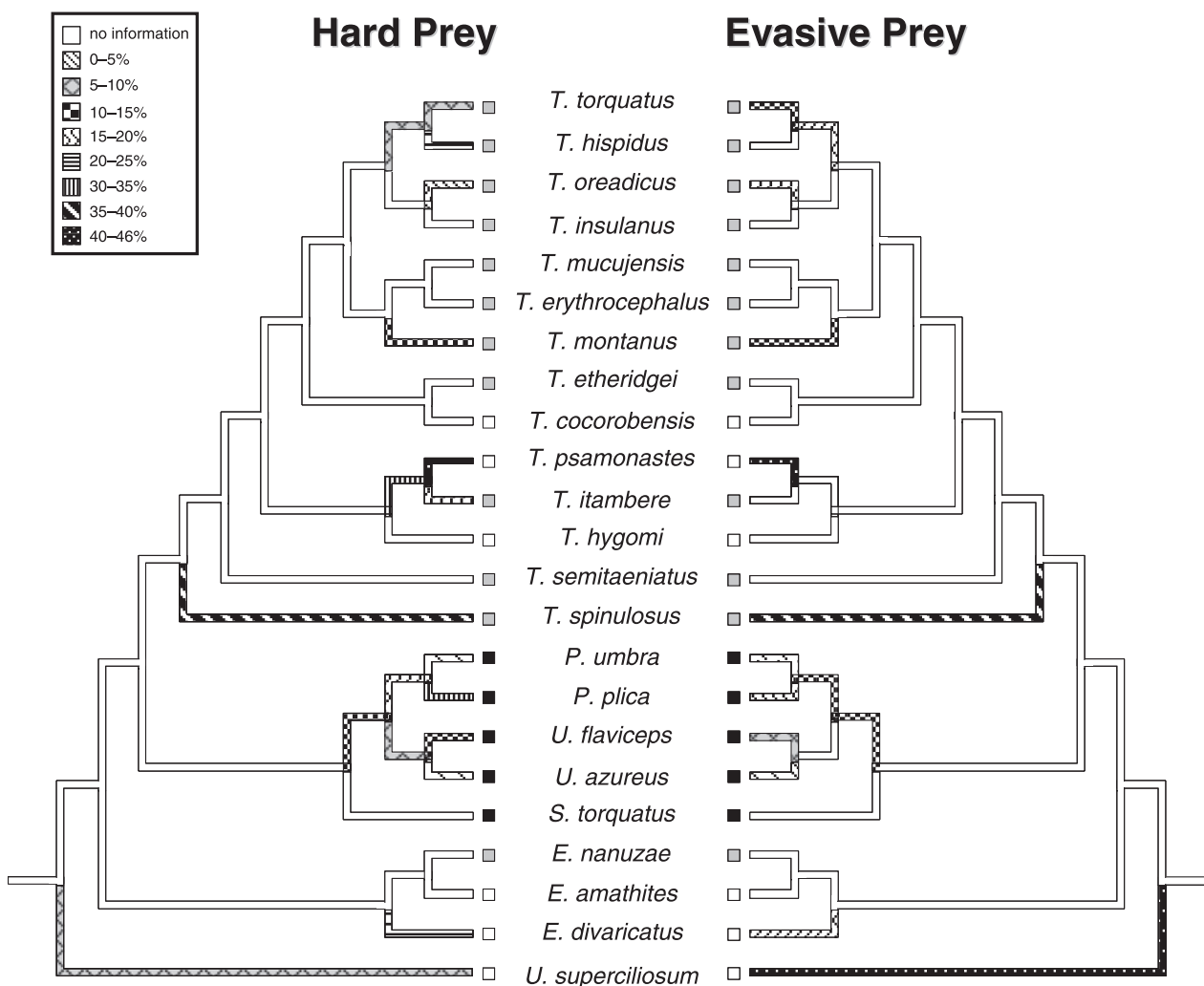

Fig. 2 Topology for Tropidurinae (based on Frost *et al.*, 2001) used to calculate the phylogenetic signal; branch lengths follow Pagel (1992). The squares close to each species' name indicate substrate usage as follows: black square = arboreal, white square = exclusively ground-dweller, gray square = rock climber. Ancestral reconstructions for the use of hard prey (left panel) and elusive prey (right panel) were performed in the program Mesquite (Maddison & Maddison 2004, http://www.mesquiteproject.org) using parsimony, and are shown along the tree branches.

(Table 1). When available, volumetric data were used to establish the proportion of hard and elusive prey in the diet of Tropidurinae lizards (Table 1). Prey types were classified in functional groups according to Vanhooydonck *et al.* (2007): Coleoptera, Gastropoda, Homoptera, Hymenoptera, Solifugae, vegetable matter, and vertebrate prey were considered hard food items; Blattaria, Diptera, flying Hymenoptera, adult Lepidoptera, Odonata, Orthoptera, adult Trichoptera, and Vertebrate prey were considered evasive prey.

Analyses

All morphological variables were log10 transformed before further analyses; proportions of hard and evasive prey were arcsine transformed. The adequacy of using conventional or phylogenetic statistical analyses for a given empirical data set depends on whether a trait shows phylogenetic signal (Blomberg *et al.*, 2003; see also Freckleton *et al.*, 2002). Therefore, we applied the randomization test described in Blomberg *et al.* (2003) to test for phylogenetic signal and computed the *K* statistic (an index of phylogenetic signal) for the variables under analysis. This analysis was implemented with Matlab version 6.1.0 for PC, using the module 'PHYSIG' (available by request to Dr. T. Garland, University of California at Riverside). We used a topology based on the phylogenetic hypothesis proposed by Frost *et al.* (2001), as shown in Fig. 2. This is the most comprehensive current phylogenetic hypothesis for the Tropidurinae group: it 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. Because estimates of phylogenetic branch lengths in units of divergence times or genetic distances are unavailable for the topology used, we tested four different types of arbitrary branch lengths, including all = 1 (constant), Grafen (1989), Pagel (1992) and Nee (cited in Purvis, 1995).

To remove the effects of body size differences between species from our data set, all cranial variables were regressed against snout-vent length and residuals were calculated. To explore head shape variation in the group, factor analyses coupled to a varimax rotation were performed on residual head measures. Factors with eigenvalues greater than 1 were retained for further analyses and factor scores were saved. Factor scores on the first three factors were then used to test whether species living and moving on vertical substrates have differently shaped heads than ground-dwelling species. Additionally, factor scores were used as input for regression models with the proportion of hard and elusive prey as independent variables.

As our inability to detect phylogenetic signal does not necessarily imply the absence of phylogenetic signal *per se*, phylogenetically informed analyses were performed as well. First, we calculated contrasts of all morphological traits and the proportion of evasive and hard prey in the diet using the tree depicted in Fig. 2 and with all branch lengths constant (= 1). Next, contrasts were standardized by dividing them by the square root of the sum of the branch lengths. Residuals of morphological and ecological traits were calculated by regression of each trait against snout-vent length (regression through the origin). Finally, regression models were constructed using the contrasts of the proportions of hard and evasive prey as independents and the raw or residual contrasts of the morphological traits as dependent variables.

To test for differences in head shape among species living in different habitats, phylogenetic analyses of co-variance were conducted. To do so, we used the phylogeny described above with all branches constant. Simulation analyses were performed using the PDSIMUL and PDANOVA programs (Garland *et al.*, 1993). In the PDSIMUL program, we used Brownian motion as our model for evolutionary change and ran 1000 unbounded simulations to create an empirical null-distribution against which the *F*-value from the original data could be compared. In the PDANOVA program, habitat use was entered as a factor, head dimensions were used as independent variables and snout-vent length was used as a covariate. We considered differences among categories significant if the original *F*-value was higher than the *F*95-value derived from the empirical distribution.

All conventional analyses were performed in SPPS V. 13.0; phylogenetically informed analyses were performed using the PDAP package (Garland *et al.*, 1999).

Results

Head shape

The tests for phylogenetic signal as described in Blomberg *et al.* (2003) suggested that none of the traits related to head morphology exhibit significant phylogenetic signal (Table 2; all *P*-values larger than 0.05 when using Constant, Nee, Pagel and Graffen arbitrary branch lengths). Surprisingly, SVL also did not exhibit significant phylogenetic signal (Table 2), which differs from results of studies with other taxonomic groups such as birds, lizards, and some mammals (Blomberg *et al.*, 2003).

A factor analysis coupled to a varimax rotation retained three factors that together explained 90% of the variation in the residual morphological data. The first factor was positively and strongly correlated with the residuals of the jaw closing in-lever, head width, the jaw out-lever and overall lower jaw length. The second factor was positively and strongly correlated with the residuals of snout length and head depth. The third factor was positively correlated with the residuals of the jaw opening in-lever (Table 3, Fig. 3).

Table 2 Values of significance (*P*) and amount of signal (*K*) from the tests for phylogenetic signal (Blomberg *et al.*, 2003) on body size and head morphology in Tropidurinae.

	Branch length							
	Constant		Nee		Pagel		Graffen	
	P	*K*	*P*	*K*	*P*	*K*	*P*	*K*
SVL	0.185	0.504	0.337	0.259	0.324	0.303	0.404	0.144
Head length	0.104	0.370	0.214	0.556	0.271	0.304	0.285	0.148
Head height	0.157	0.497	0.097	0.610	0.118	0.353	0.159	0.177
Head width	0.213	0.297	0.316	0.520	0.378	0.280	0.417	0.135
Lower jaw length	0.120	0.329	0.246	0.541	0.321	0.294	0.363	0.141
Jaw out-lever length	0.211	0.305	0.308	0.512	0.398	0.276	0.400	0.132
Snout length	0.089	0.372	0.204	0.554	0.236	0.304	0.309	0.146

Tests were performed for four types of arbitrary branch lengths using the topology proposed by Frost *et al.* (2001).

Table 3 Results of a factor analysis with varimax rotation performed on the head shape variables.

	Factor 1	Factor 2	Factor 3
Eigenvalue/% variation explained	4.76/59.44	1.46/18.20	1.02/12.78
Residual snout length (mm)	0.170	**0.920**	−0.097
Residual head depth (mm)	0.101	**0.798**	0.126
Residual lower jaw length (mm)	**0.788**	0.469	0.360
Residual out-lever (mm)	**0.852**	0.492	0.002
Residual open in-lever (mm)	0.101	0.029	**0.990**
Residual close in-lever (mm)	**0.927**	−0.297	0.092
Residual head length (mm)	0.652	0.647	0.181
Residual head width (mm)	**0.824**	0.493	−0.017

Variables contributing most to each factor are indicated in bold.

Ecological correlates

Head shape did not differ among species occupying vertical vs. horizontal habitats (factor scores as input for a MANOVA; Wilk's Lambda: $F_{6,32} = 1.07$; $P = 0.40$), suggesting that habitat use has not shaped the evolution of cranial morphology in Tropidurinae lizards. Even analyses contrasting rock dwellers to all other species (Wilk's Lambda $F_{3,17} = 1.11$; $P = 0.37$), or testing for differences among the three groups (Wilk's Lambda $F_{6,32} = 1.07$; $P = 0.40$) did not show significant differences in head shape. Similarly, phylogenetic analyses of co-variance detected no difference in head shape among the three groups (all $F_{phyl} > 10.02$; all $F_{trad} < 2.64$; all $P > 0.05$) suggesting that the occupation of vertical habitats was not associated with the evolution of head shape in this group.

The proportion of hard prey in the diet was correlated with cranial morphology (regression model using the factor scores on the first three factors as input; $r = 0.77$; $P = 0.04$). Although the first factor was positively corre-lated with the proportion of hard prey in the diet (Fig. 4; Beta = 0.47), the second and third factors were negatively associated (Beta = −0.39 & −0.49 respectively). Thus, the factor analysis indicated that animals which include more hard prey into their diet exhibit greater jaw closing in-levers, greater head width and a greater jaw out-lever and lower jaw length, but exhibit relatively short snouts and short jaw opening in-levers.

A stepwise multiple regression model using the standardized contrasts of head shape variables as dependents and the contrast of the proportion of hard prey in the diet as independent variable retained a significant model with the contrasts of the jaw closing and the jaw opening in-levers as only variables ($r = 0.83$; $P = 0.003$). Although the contrast of the jaw closing in-lever was positively correlated (Beta = 0.93), the contrast of the jaw opening in-lever was negatively correlated (Beta =-0.70) with the proportion of hard prey in the diet. A stepwise regression model with the residual contrast of the proportion of hard prey in the diet as independent and the residual contrasts of the morphological variables as dependent variables retained a significant model with the residual contrast of the jaw opening in-lever as only predictor ($r = −0.68$; $P = 0.01$).

No significant model was retained when correlating the proportion of elusive prey in the diet with cranial morphology. Similarly, regression models based on the raw or residual contrasts did not retain a significant model when correlating cranial morphology to diet.

Discussion

Surprisingly, no phylogenetic signal was observed in the morphological data at any branch length tested. This is very unusual for a morphological data set containing more than 20 species (Blomberg *et al.*, 2003; Garland *et al.*, 2005), and suggests remarkable evolutionary liability of head shape in Tropidurinae lizards. Previous studies suggest that rapid evolutionary changes in external morphology (Kohlsdorf *et al.*, 2001), muscle physiology (Kohlsdorf *et al.*, 2004) and jumping performance (Kohlsdorf & Navas, 2007) may occur in tropidurines. The absence of phylogenetic signal in the data set analysed in the present study provides evidence that an evolutionarily labile morphology characterizes the skull as well. Head shape evolution in Tropidurinae species seems strongly associated with changes in biomechanically relevant traits of the jaw system, such as the in-levers for jaw closing and jaw opening. The pool of traits expected to be related to rapid jaw opening are associated with different factors than those likely associated with the generation of high bite force (e.g. jaw closing in-lever, head width). This finding suggests that different pathways in the evolution of head shape in Tropidurinae relate to different functional demands on the cranial system. However, climbing and ground-dwelling species exhibit comparable head shapes. Previous research on
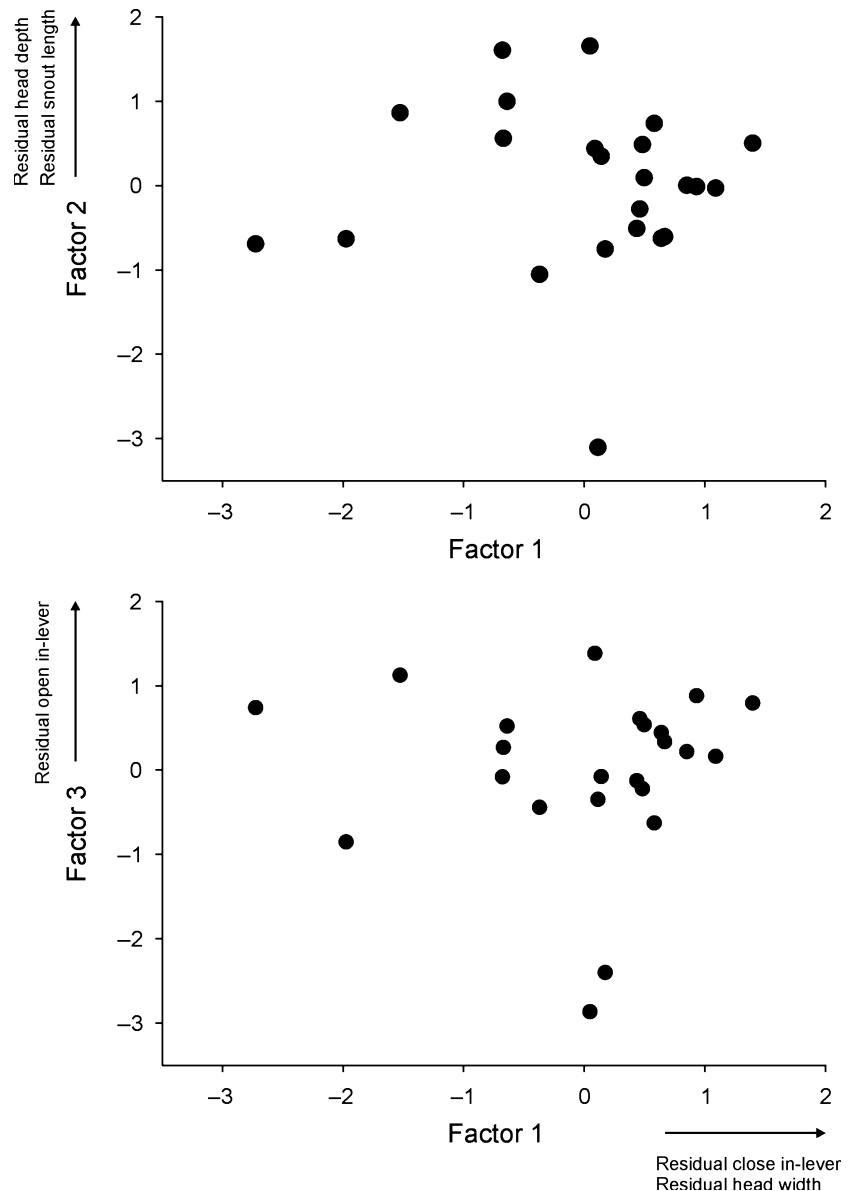
Fig. 3 Graphs illustrating the distribution of tropidurine lizards in morphological space. Major axes of divergence include traits associated with the ability to bite hard (axes 1 and 2) or to open the jaws rapidly.

the lizard *Tropidurus hispidus*, for example, suggests that the occupation of rocky habitats by some populations is associated with the evolution of a more dorso-ventrally compressed body (Vitt *et al.*, 1997a). Although the mechanics of climbing in trees and branches with rough textures may be different from climbing on smooth substrates such as rocks, our results suggest that rock dwellers have similar head shapes to other Tropidurinae species.

Overall, our analysis suggests a lack of association between head shape and climbing habits in tropidurine lizards, and suggests differences in the climbing style of Tropidurinae and lacertids (Vanhooydonck & Van Damme, 1999), phrynosomatids (Herrel *et al.*, 2001a) and

geckos (Zaaf & Van Damme, 2001). We should point out, however, that we pooled all arboreal *Tropidurine* species, although they differ regarding the use of inclined vs. truly vertical substrates. For example, two Amazonian species, *Plica plica* (Vitt, 1991) and *P. umbra* (Vitt *et al.*, 1997b), move vertically along tree trunks, whereas three other arboreal species, *Uracentron flaviceps* (Vitt & Zani, 1996), *U. azureus* (MTU Rodrigues, personal communication), and *Strobilurus torquatus* (Rodrigues *et al.*, 1989), locomote along tree branches of various diameters and inclinations. Moreover, Tropidurinae lizards may also rely on their claws to generate friction on rough substrates (Zani, 2000) and thus prevent back toppling while climbing. Clearly, more information on the
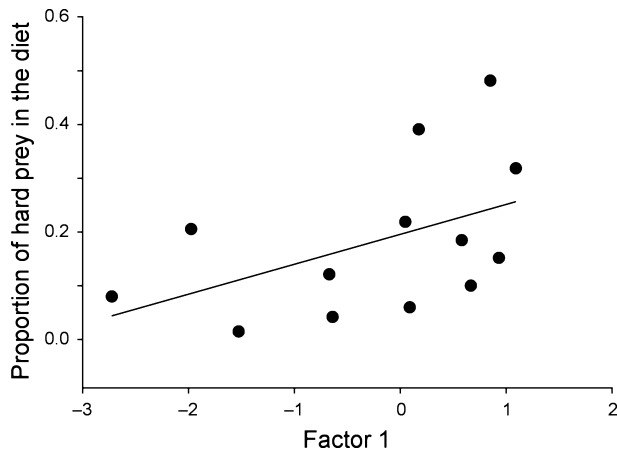
Fig. 4 Graph illustrating the correlation between head shape and functional components of diet in lizards of the subfamily Tropidurinae.

mechanics of climbing and clambering in Tropidurinae lizards is needed to elucidate the apparent dissociation between head morphology and vertical locomotion in the group.

In contrast to the lack of differences observed for species with different habitat usage, a clear correlation between head shape and diet could be detected. The proportion of hard prey in the diet was associated with the first factor, explaining roughly 60% of the variation in head shape among species. Morphological traits loading highly on this first factor are also those predicted to be associated with high bite force capacities. Animals with wider heads can pack more muscle into their heads, which may result in a greater bite force, allowing animals to consume harder prey more efficiently (see Herrel *et al.*, 1999, 2001a,b; Verwaijen *et al.*, 2002). Interestingly, the proportion of hard prey in the diet was negatively associated with the second and third factors, suggesting that animals with long snouts (second factor) and longer opening in-levers (third factor) bite less hard.

These results are corroborated by our independent contrast analyses suggesting that the evolution of the jaw opening (negatively) and jaw closing (positively) in-levers have gone hand-in-hand with the inclusion of the hard prey in the diet. The strong negative correlation of the in-lever for jaw opening with the proportion of hard prey in the diet points towards a potential force–velocity trade-off (Westneat, 1994; Paul & Gronenberg, 1999; Levinton & Allen, 2005) in the jaw system of these lizards: species are either geared towards the generation of bite force or high jaw velocity, but not both. There are no empirical demonstrations of such trade-off in the vertebrate head, although biomechanical evidence suggests that it should be relevant in fishes (Westneat, 1994), birds (Podos, 2000) and turtles (Herrel *et al.*, 2002b).

Head morphology in tropidurine lizards is not associated with the proportion of elusive prey in the diet. Although this finding could be an artefact of our arbitrary assignment of prey into functional groups, a very similar categorization led to clear correlations between prey traits and locomotor endurance in lacertid lizards (Vanhooydonck *et al.*, 2007). It is possible that the role of the tongue during prey capture obscures the expected relationship, as the use of adhesive tongues to capture elusive prey may compensate for lack of changes in cranial mechanics. Although no kinematic data are available for prey capture in tropidurine lizards, other closely related iguanians such as phrynosomatids and iguanids use their tongue to capture prey (Meyers & Nishikawa, 2000; Schwenk, 2000), and field personal observations suggest that the tongue may also be involved in prey capture in Tropidurinae (T.K. personal communication). Thus, tongue movement speed or adhesiveness may be more important in determining the ability of lizards to capture elusive prey. Alternatively, locomotor burst performance capacity may drive the ability of lizards to capture elusive prey. Data on kinematics of prey capture in tropidurine lizards are needed to evaluate these hypotheses.

In conclusion, our data suggest strong adaptive evolution of head shape in tropidurine lizards associated with the inclusion of hard prey into the diet. In contrast to our expectations, however, habitat use did not constrain head shape evolution in the group. Further studies focusing on the mechanics of climbing in Tropidurinae species are needed to explore the apparent dissociation between head shape and locomotor performance in the family. In addition, information on the kinematics of prey capture in these lizards may generate interesting insights into understanding the patterns of head shape evolution in the group.

Acknowledgments

References

Arnold, E.N. 1998. Cranial kinesis in lizards – Variations, uses, and origins. *Evol. Biol.* **30**: 323–357.

Arnold, S.J. 1992. Constraints on phenotypic evolution. *Am. Natl.* **140**: S85–S107.

Bels, V.L., Chardon, M. & Kardong, K.V. 1994. Biomechanics of the hyolingual system in squamata. In: *Biomechanics of Feeding*

in Vertebrates (V. L. Bels, M. Chardon & P. Vandewalle, eds), pp. 197–240. Springer Verlag, Berlin.

Blomberg, S.P., Garland, T. & Ives, A.R. Jr 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.

Carrier, D.R. 1991. Conflict in the hypaxial musculo-skeletal system: documenting an evolutionary constraint. *Am. Zool.* **31**: 644–656.

Colli, G.R., Araujo, A.F.B., Silveira, R. & Roma, F. 1992. Niche partitioning and morphology of two syntopic *Tropidurus* (Sauria: Tropiduridae) in Mato Grosso, Brazil. *J. Herpetol.* **26**: 66–69.

Cooper, W.E. & Vitt, L.J. 1993. Female mate choice of large male broad-headed skinks. *Anim. Behav.* **45**: 683–693.

Ellinger, N., Schlatte, G., Jerome, N. & Hodl, W. 2001. Habitat use and activity patterns of the neotropical arboreal lizard *Tropidurus* (= *Uracentron*) *azureus werneri* (Tropiduridae). *J. Herpetol.* **35**: 395–402.

Fialho, R.F., Rocha, C.F.D. & Vrcibradic, D. 2000. Feeding ecology of *Tropidurus torquatus*: ontogenetic shift in plant consumption and seasonal trends in diet. *J. Herpetol.* **34**: 325–330.

Freckleton, R.P., Harvey, P.H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Natl.* **160**: 712–726.

Frost, D. 1992. Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). *Am. Mus.* **3033**: 68.

Frost, D.R., Rodrigues, M.T. & Grant, T. 2001. Phylogenetics of the lizard genus *Tropidurus* (Squamata: Tropiduridae: Tropidurinae): direct optimization, descriptive efficiency, and sensitivity analysis of congruence between molecular data and morphology. *Mol. Phyl. Evol.* **21**: 352–371.

Garland, T. Jr, Dickerman, A.W., Janis, C.M. & Jones, J.A. 1993. Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* **42**: 265–92.

Garland, T. Jr, Midford, P.E. & Ives, A.R. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral states. *Am. Zool.* **39**: 374–88.

Garland, T. Jr, Bennet, A.F. & Rezende, E.L. 2005. Phylogenetic approaches in comparative physiology. *J. Exp. Biol.* **208**: 3015–3035.

Gasnier, T.R., Magnusson, W.E. & Lima, A.P. 1994. Foraging activity and diet of four sympatric lizard species in a tropical rainforest. *J. Herpetol.* **28**: 187–192.

Grafen, A 1989. The phylogenetic regression. *Phil. Trans. Royal Soc. London B* **326**: 119–157.

Harmon, L.J., Kolbe, J.J., Cheverud, J.M. & Losos, J.B. 2005. Convergence and the multi dimensional niche. *Evolution* **59**: 409–421.

Harvey, M.B. & Gutberlet, R.L. Jr 2000. A phylogenetic analysis of the tropidurine lizards (Squamata: Tropiduridae), including new characters of squamation and epidermal microstructure. *Zool. J. Linn. Soc.* **128**: 189–233.

Herrel, A., Aerts, P. & DeVree, F. 1998a. Ecomorphology of the lizard feeding apparatus: a modeling approach. *Neth. J. Zool.* **48**: 1–25.

Herrel, A., Aerts, P. & DeVree, F. 1998b. Static biting in lizards: functional morphology of the temporal ligaments. *J. Zool.* **244**: 135–143.

Herrel, A., Spithoven, L., Van Damme, R. & De Vree, F. 1999. Sexual dimorphism of head size in Gallotia galloti: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* **13**: 289–297.

Herrel, A., Meyers, J.J. & Vanhooydonck, B. 2001a. Relations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. *Biol. J. Linn. Soc.* **74**: 305–314.

Herrel, A., Van Damme, R., Vanhooydonck, B. & De Vree, F. 2001b. The implications of bite performance for diet in two species of lacertid lizards. *Can. J. Zool.* **79**: 662–670.

Herrel, A., De Grauw, E. & Lemos-Espinal, J.A. 2001c. Head shape and bite performance in xenosaurid lizards. *J. Exp. Zool.* **290**: 101–107.

Herrel, A., Meyers, J.J. & Vanhooydonck, B. 2002a. Relations between microhabitat use and limb shape in phrynosomatid lizards. *Biol. J. Linn. Soc.* **77**: 149–163.

Herrel, A., O'Reilly, J.C. & Richmond, A.M. 2002b. Evolution of bite performance in turtles. *J. Evol. Biol.* **15**: 1083–1094.

Kohlsdorf, T. & Navas, C.A. 2007. Evolution of jumping capacity in Tropidurinae lizards: does habitat complexity influence obstacle-crossing ability? *Biol. J. Linn. Soc.* **91**: 393–402.

Kohlsdorf, T., Garland, T. Jr & Navas, C.A. 2001. Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *J. Morphol.* **248**: 151–164.

Kohlsdorf, T., James, R.S., Carvalho, J.E., Wilson, R.S., Pae-Silva, M.D. & Navas, C.A. 2004. Locomotor performance of closely related *Tropidurus* species: relationships with physiological parameters and ecological divergence. *J. Exp. Biol.* **207**: 1183–1192.

Lappin, A.K. & Husak, J.F. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *Am. Nat.* **166**: 426–436.

Lappin, A.K., Hamilton, P.S. & Sullivan, B.K. 2006. Bite-force performance and head shape in a sexually dimorphic crevice-dwelling lizard, the common chckwalla [*Sauromalus ater* (=*obesus*)]. *Biol. J. Linn. Soc.* **88**: 215–222.

Levinton, J.S. & Allen, B.J. 2005. The paradox of the weakening combatant: trade-off between closing force and gripping speed in a sexually selected combat structure. *Func. Ecol.* **19**: 159–165.

Meyers, J.J. & Nishikawa, K.C. 2000. Comparative study of tongue protrusion in three iguanian lizards, *Sceloporus undulates*, *Pseudotrapilus sinaitus* and *Chamaeleo Jacksonii*. *J. Exp. Biol.* **203**: 2833–2849.

Owerkowicz, T., Farmer, C., Hicks, J.W. & Brainerd, E.L. 1999. Contribution of gular pumping to lung ventilation in monitor lizards. *Science* **284**: 1661–1663.

Pagel, M.D. 1992. A method for the analysis of comparative data. *J. Theor. Biol.* **156**: 431–442.

Pasi, B.M. & Carrier, D.R. 2003. Functional trade-offs in the limb muscles of dogs selected for running *versus* fighting. *J. Evol. Biol.* **16**: 324–332.

Paul, J. & Gronenberg, W. 1999. Optimizing force and velocity: mandible muscle fibre attachments in ants. *J. Exp. Biol.* **202**: 797–808.

Podos, J. 2000. Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* **409**: 185–188.

Purvis, A. 1995. A composite estimate of primate phylogeny. *Phil. Trans. Royal Soc. London B* **348**: 405–421.

Rocha, P.L.B.1998. *Uso e Partição de Recursos pelas espécies de Lagartos das Dunas do Rio São Francisco, Bahia (Squamata)*.

Doctoral Thesis. Department of Zoology, Biosciences Institute, University of São Paulo, Brazil.

Rodrigues, M.T., Yionenaga-Yassuda, Y. & Kasahara, S. 1989. Notes on the ecology and karyotypic description of *Strobilurus torquatus* (Sauria, Iguanidae). *Rev. Bras. Gen.* **12**: 747–759.

Roth, G. & Wake, D. B. 1989. Conservation and innovation in the evolution of feeding in vertebrates. In: *Complex Organismal Functions: Integration and Evolution in Vertebrates* (D. B. Wake & G. Roth, eds), pp. 7–21. Wiley & Sons, New York.

Schwenk, K. 1995. A utilitarian approach to evolutionary constraint. *Zoology* **98**: 251–262.

Schwenk, K. 2000. Extrinsic *vs.* intrinsic lingual muscles: the amniote tongue as a functional unit. *Am. Zool.* **40**: 1203–1204.

Van Damme, R., Wilson, R.S., Vanhooydonck, B. & Aerts, P. 2002. Performance constraints in decathletes. *Nature* **415**: 755–756.

Van Sluys, M. 1993. Food habits of the lizard *Tropidurus itambere* (Tropiduridae) in Southeastern Brazil. *J. Herpetol.* **27**: 347–351.

Van Sluys, M., Rocha, C.F.D., Vrcibradic, D., Aleksander, C., Galdino, B. & Fontes, A.F. 2004. Diet, activity, and microhabitat use of two syntopic *Tropidurus* species (Lacertilia: Tropiduridae) in Minas Gerais, Brazil. *J. Herpetol.* **38**: 606–611.

Vanhooydonck, B. & Van Damme, R. 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evol. Ecol. Res.* **1**: 785–805.

Vanhooydonck, B., Herrel, A. & Van Damme, R. 2007. Interactions between habitat use, behaviour and the trophic niche of lacertid lizards. In: *Evolutionary Consequences of Foraging Mode in Lizards* (S. M. Reilly, L. D. McBrayer & D. B. Miles, eds), pp. 427–449. Cambridge University Press, Cambridge.

Verwaijen, P., Van Damme, R. & Herrel, A. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Func. Ecol.* **16**: 842–850.

Vitt, L.J. 1991a. Ecology and life history of the scansorial arboreal lizard *Plica plica* (Iguanidae) in Amazonian Brazil. *Can. J. Zool.* **69**: 504–511.

Vitt, L.J. & Zani, P.A. 1996. Ecology of the elusive tropical lizard *Tropidurus* [=*Uracentron*] *flaviceps* (Tropiduridae) in lowland rain forest of Ecuador. *Herpetologica* **52**: 121–132.

Vitt, L.J., Caldwell, J.P., Zani, P.A. & Titus, T.A. 1997a. The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. *P.N.A.S.* **94**: 3828–3832.

Vitt, L.J., Zani, P.A. & Avila-Pires, T.C.S. 1997b. Ecology of the arboreal tropidurid lizard *Tropidurus* (= *Plica*) *umbra* in the Amazon region. *Can. J. Zool.* **75**: 1876–1882.

Wagner, G.P. & Schwenk, K. 2000. Evolutionary Stable Configurations: functional integration and the evolution of phenotypic stability. *Evol. Biol.* **31**: 155–217.

Westneat, M.W. 1994. Transmission forces and velocity in the feeding mechanisms of labrid fishes (Teleostei, Perciformes). *Zoomorphology* **114**: 103–118.

Zaaf, A. & Van Damme, R. 2001. Limb proportions in climbing and ground-dwelling geckoes: a phylogenetically informed analysis. *Zoomorphology* **121**: 45–53.

Zani, P.A. 2000. The comparative evolution of lizard claw and toe morphology and clinging performance. *J. Evol. Biol.* **13**: 316–325.