Limb and Tail Lengths in Relation to Substrate Usage in *Tropidurus* Lizards

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ABSTRACT A close relationship between morphology and habitat is well documented for anoline lizards. To test the generality of this relationship in lizards, snout-vent, tail, and limb lengths of 18 species of *Tropidurus* (Tropiduridae) were measured and comparisons made between body proportions and substrate usage. Phylogenetic analysis of covariance by computer simulation suggests that the three species inhabiting sandy soils have relatively longer feet than do other species. Phylogenetic ANCOVA also demonstrates that the three species inhabiting tree canopies and locomoting on small branches have short tails and hind limbs. These three species constitute a single subclade within the overall *Tropidurus* phylogeny and analyses with independent contrasts indicate that divergence in relative tail and hind limb length has been rapid since they split from their sister clade. Being restricted to a single subclade, the difference in body proportions could logically be interpreted as either an adaptation to the clade's lifestyle or simply a nonadaptive synapomorphy for this lineage. Nevertheless, previous comparative studies of another clade of lizards (*Anolis*) as well as experimental studies of *Sceloporus* lizards sprinting on rods of different diameters support the adaptive interpretation. J. Morphol. 248:151–164, 2001.
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KEY WORDS: comparative phylogenetic method; morphology; habitat; leg; lizard; evolution; tail

Lizards exhibit a diverse suite of lifestyles and exploit a variety of habitats, ranging from rainforests to sandy deserts (Huey et al., 1983; Greer, 1989; Vitt and Pianka, 1994). This ecological diversity is associated with variation in body size, body shape, and limb proportions. In terms of body size, extant lizards range from geckos weighing approximately 0.1 g (MacLean, 1975) to the massive Komodo dragon, which may exceed 50 kg (Auffenberg, 1981). Lizards also vary greatly in locomotor modes. For example, basilisk lizards display water-running ability (Glasheen and McMahon, 1996), various species are capable of bipedal locomotion (Irschick and Jayne, 1999a,b), and agamids in the genus *Draco* are arboreal and able to glide (Mori and Hikida, 1993; McGuire, 1998).

Special attention has been given to the study of limb size and proportions, which may affect locomotor performance in context-specific ways (Losos, 1990a; Garland and Losos, 1994; Miles et al., 1995; Macrini and Irschick, 1998; Bonine and Garland, 1999). Locomotor performance, in turn, is believed to affect Darwinian fitness (Christian and Tracy, 1981; Jayne and Bennett, 1990; Bennett, 1991; Robson and Miles, 2000). Accordingly, lizard species should exhibit morphological specializations that improve behavioral performance in the microhabitats used (Melville and Swain, 2000), and should avoid microhabitats in which performance is submaximal (Irschick and Losos, 1999). Pianka (1969, 1986), for example, presented data suggesting that skinks in the genus *Ctenotus* that have longer legs prefer open spaces, whereas those with shorter legs occur more commonly in patches of denser vegetation. Similarly, a study of North American lizards showed that iguanians from open areas tend to be smaller, more slender, and to have shorter legs than species from more densely vegetated habitats (Scheibe, 1987). In contrast, Jaksic et al. (1980), using a more detailed ecological classification, did not find morphological differentiation among *Liolaemus* lizards in relation to microhabitat: they found that although the 12 species studied exhibit dramatic ecological differences, these lizards are remarkably similar in limb and tail proportions. Conclusions from the above studies, however, are weakened because inadequate attention has been given to the possible confounding influences of variation in body size and/or phylogenetic relationships (Garland and Losos, 1994).

The most convincing evidence of a relationship between lizard morphology and habitat comes from studies of *Anolis* in the Greater Antilles. Six "eco-

morphs" (crown-giant, grass-bush, trunk, trunk-crown, trunk-ground, and twig) have been described (Williams, 1972, 1983) that show similar morphological and behavioral traits across islands. As *Anolis* appear to have colonized different islands of the Greater Antilles in multiple evolutionary events, the similarities among ecomorphs suggest evolutionary convergence and thus adaptation to a certain type of microhabitat (Losos, 1992; Losos et al., 1998; Beutell and Losos, 1999). A similarly adaptive trend is evident in the *Anolis* lizards that colonized the Bahamas from Cuba (Losos et al., 1994) and in *Anolis* in mainland Costa Rica (Pounds, 1988). Morphological similarity among ecomorphs is evident in characters related to locomotion (but is not limited to these traits; e.g., see Beutell and Losos, 1999). Species with long legs occur more commonly on wide perches and are prone to jump, whereas species with short legs tend to crawl. The morphometric diversification (disparity) exhibited by *Anolis* is unparalleled by other lizard clades studied. For example, the genus *Sceloporus* shares several ecological attributes with *Anolis* and originated at approximately the same time in geological history, but exhibits substantially less disparity than *Anolis* (Warheit et al., 1999). Hence, *Anolis* may constitute a unique case of morphometric diversification among lizards because of its remarkable radiation along Caribbean islands (Irschick et al., 1997) and the evolution of expanded toe-pads, a putative key adaptation that improves climbing ability (Warheit et al., 1999).

Phylogenetically based studies in lizard taxa other than *Anolis* provide ambiguous evidence of an evolutionary relationship between habitat use and limb or tail morphology. Melville and Swain (2000) report a significant evolutionary relationship between habitat openness, sprint speed, and limb morphology in *Niveoscincus* lizards (Scincidae: Lygosominae). Miles (1994) questioned if phrynosomatid lizards that prefer similar substrates exhibit a convergent suite of morphological characters. He analyzed a series of morphometric traits, including mass-independent tail, femur, tibia, metatarsus, and toe length. He included species in the genera *Petrosaurus, Uta, Urosaurus, Sceloporus*, and *Cophosaurus*, which can be classified according to the most common substrate used (e.g., sand, rocks, tree trunks or soil). His study demonstrates mass-independent morphometric diversification among species, but does not support a clear-cut relationship between morphology and habitat use. Similarly, Vanhooydonck and Van Damme (1999) could not demonstrate a relationship between habitat use and body, head or limb proportions in a phylogenetic analysis that included 35 species of lacertid lizards. Nevertheless, it is possible that an evolutionary coupling between ecology and body shape actually exists in non-anoline lizards, but it is obscured by constraints imposed by the nature of the available data. For example, clustering of ecological variables

within particular clades or inaccurate ecological classification of species may be associated with low statistical power in phylogenetic tests involving ecomorphological hypotheses (Garland et al., 1993; Vanhooydonck and Van Damme, 1999).

A phylogenetic approach was used here to test the hypothesis that morphometric adaptation relates to habitat in the lizard genus *Tropidurus*. This iguanian genus is particularly interesting for ecomorphological studies because it occupies a wide variety of habitats and exhibits obvious morphological variation. In addition, well-corroborated hypotheses of phylogenetic relationships within the genus are available (Frost, 1992; Harvey and Gutberlet, 2000), good information on natural history and behavior has been published and specimens are available in museum collections.

MATERIALS AND METHODS
Background on the Genus

Tropidurus apparently originated from a divergence from the *Stenocercus* group, which is accepted as more derived than *Leiocephalus* (Estes and Pregill, 1988). As *Leiocephalus* seemingly originated in the Lower Pleistocene (Estes, 1983), *Tropidurus* may be roughly two million years old. Although the poor fossil record available does not allow for a definite conclusion, it seems likely that *Tropidurus* is more recent than some of the other well-studied lizard clades, such as *Anolis* or *Sceloporus*, which apparently originated in the lower Miocene (Warheit et al., 1999). *Tropidurus* is widely distributed in South America (see fig. 1 in Frost, 1992), except in the Andes, and is common in Brazilian habitats as diverse as the arid caatinga (see Fig. 1 and caption) and the rain forest. They are generally described as heliothermic sit-and-wait predators and appear to be highly territorial (Rodrigues, 1988; Vitt, 1991a; Bergallo and Rocha, 1993; Vitt et al., 1997a; Díaz-Uriarte, 1999).

Specimens and Measures

Seven morphometric traits relating to locomotion were measured in 18 species of *Tropidurus* (Fig. 1). The preserved specimens were 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 traits were snout–vent length, tail length, foot length, tibia length, femur length, humerus length, and end of longest finger-to-elbow length. Total hind limb length and front limb length could not be measured directly in preserved animals because the limbs could not be straightened. These values were calculated as the sums of the corresponding segment lengths. The number of individuals per species varied with availability and ranged from 3 to 20 (Table 1). All individuals measured had intact tails. For

Source

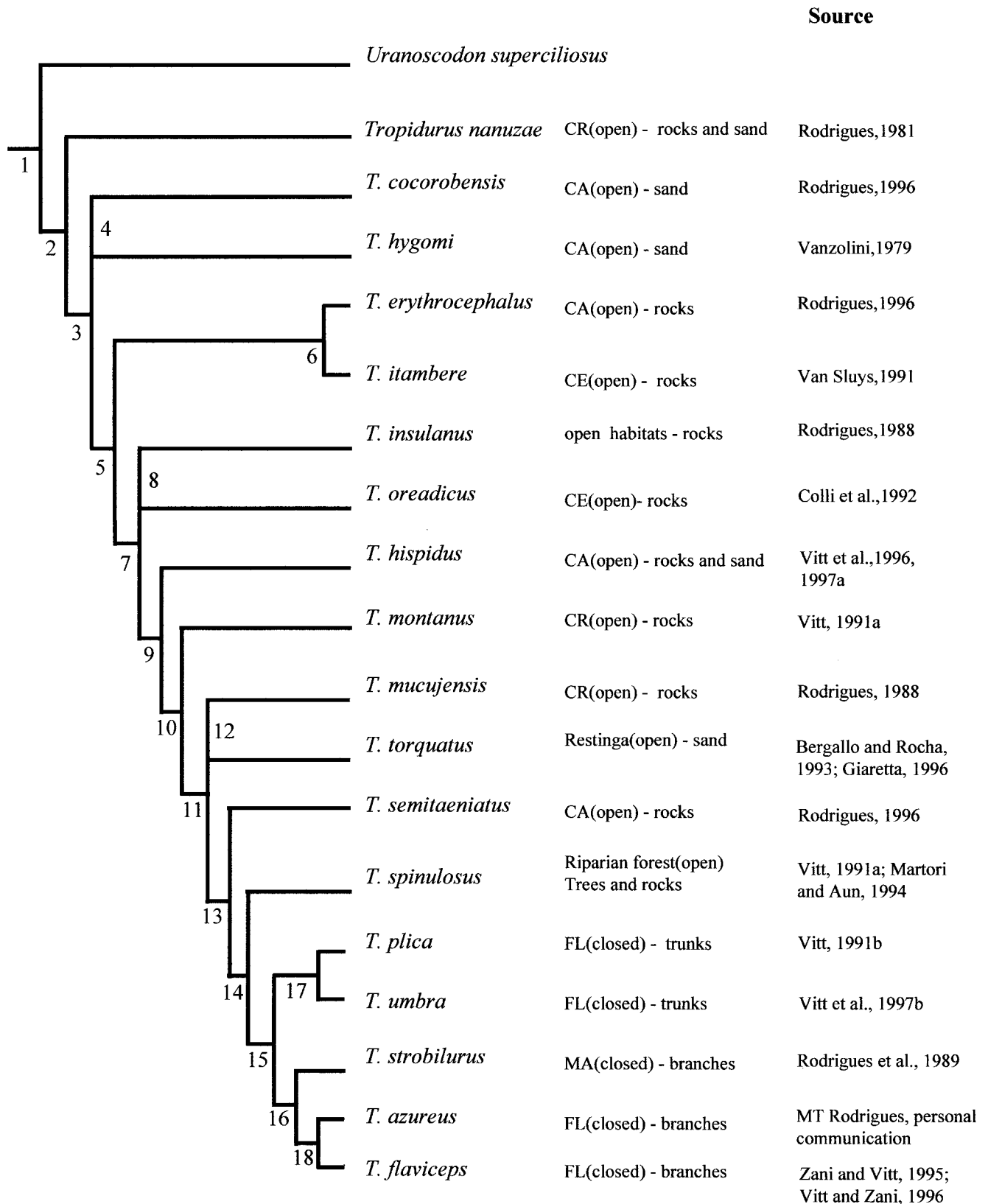|		
Uranoscodon superciliosus		
Tropidurus nanuzae	CR(open) - rocks and sand	Rodrigues,1981
T. cocorobensis	CA(open) - sand	Rodrigues,1996
T. hygomi	CA(open) - sand	Vanzolini,1979
T. erythrocephalus	CA(open) - rocks	Rodrigues,1996
T. itambere	CE(open) - rocks	Van Sluys,1991
T. insulanus	open habitats - rocks	Rodrigues,1988
T. oreadicus	CE(open)- rocks	Colli et al.,1992
T. hispidus	CA(open) - rocks and sand	Vitt et al.,1996, 1997a
T. montanus	CR(open) - rocks	Vitt, 1991a
T. mucujensis	CR(open) - rocks	Rodrigues, 1988
T. torquatus	Restinga(open) - sand	Bergallo and Rocha, 1993; Giaretta, 1996
T. semitaeniatus	CA(open) - rocks	Rodrigues, 1996
T. spinulosus	Riparian forest(open) Trees and rocks	Vitt, 1991a; Martori and Aun, 1994
T. plica	FL(closed) - trunks	Vitt, 1991b
T. umbra	FL(closed) - trunks	Vitt et al., 1997b
T. strobilurus	MA(closed) - branches	Rodrigues et al., 1989
T. azureus	FL(closed) - branches	MT Rodrigues, personal communication
T. flaviceps	FL(closed) - branches	Zani and Vitt, 1995; Vitt and Zani, 1996

Fig. 1. Phylogenetic tree used for comparative statistical analyses. Topology follows figure 33 of Frost (1992). Branch lengths are arbitrary and follow Pagel (1992). Nodes are marked with arbitrary numbers for reference. The column to the right of the species name indicates typical habitat: CR = campos rupestres, CA = caatinga, CE = cerrado (savanna), MA = Atlantic forest , FL = rain forest; habitat openness (open, closed), and substrate usage (branch, rock, sand, trunk). Caatinga is a dry, semiarid open habitat with scattered shrubs and a sandy-rocky soil. Campos rupestres are characterized by grassy-rocky soils and isolated trees and scrubs. The restinga is a seashore habitat in which the density of trees and scrubs increases with distance from the beach.

TABLE 1. *Means and standard errors for each species*

Species	Code	N	SVL Mean ± SE	Tail Mean ± SE	Foot Mean ± SE	Tibia Mean ± SE	Femur Mean ± SE	Humerus Mean ± SE	End of the longest finger-to-elbow Mean ± SE	Hindlimb Mean ± SE	Front limb Mean ± SE
Uranoscodon superciliosum		20	109.3 ± 2.32	246.6 ± 6.39	40.4 ± 0.50	26.5 ± 0.57	24.6 ± 0.67	16.6 ± 0.44	36.1 ± 0.66	91.5 ± 1.58	52.7 ± 1.06
Tropidurus nanuzae	TN	20	46.4 ± 1.15	54.2 ± 1.15	15.9 ± 0.31	12.1 ± 0.21	10.1 ± 0.32	7.5 ± 0.24	15.8 ± 0.26	38.0 ± 0.65	23.3 ± 0.39
T. cocorobensis	TC	12	68.7 ± 1.50	101.6 ± 4.37	23.8 ± 0.51	17.7 ± 0.57	13.8 ± 0.58	10.3 ± 0.41	22.9 ± 0.47	55.2 ± 1.45	33.2 ± 0.80
T. hygomi	TG	15	65.4 ± 1.32	105.4 ± 4.82	25.0 ± 0.45	18.1 ± 0.48	14.2 ± 0.38	9.8 ± 0.22	22.1 ± 0.37	57.3 ± 1.20	31.9 ± 0.54
T. erythrocephalus	TE	20	71.7 ± 1.52	98.5 ± 2.82	22.1 ± 0.50	18.3 ± 0.40	14.6 ± 0.44	11.1 ± 0.40	22.7 ± 0.47	55.0 ± 1.11	33.8 ± 0.83
T. itambere	TI	20	78.3 ± 1.86	101.1 ± 2.92	22.5 ± 0.32	18.8 ± 0.38	15.9 ± 0.37	12.3 ± 0.31	24.9 ± 0.51	57.2 ± 1.04	37.2 ± 0.79
T. insulanus	TY	13	75.2 ± 2.36	101.1 ± 5.56	21.6 ± 0.53	19.2 ± 0.45	15.0 ± 0.45	11.2 ± 0.41	23.9 ± 0.54	55.6 ± 1.19	35.1 ± 0.85
T. oreadicus	TO	20	92.7 ± 1.63	150.8 ± 3.37	28.5 ± 0.37	25.0 ± 0.40	21.2 ± 0.37	15.8 ± 0.42	31.3 ± 0.45	74.6 ± 1.07	47.0 ± 0.80
T. hispidus	TH	20	95.8 ± 2.43	144.5 ± 4.55	29.5 ± 0.49	25.9 ± 0.60	20.3 ± 0.49	15.8 ± 0.38	32.5 ± 0.69	75.8 ± 1.49	48.3 ± 1.02
T. montanus	TM	17	83.6 ± 1.36	124.4 ± 0.53	25.1 ± 0.34	20.5 ± 0.34	16.5 ± 0.71	11.8 ± 0.45	26.9 ± 0.39	62.1 ± 1.08	38.8 ± 0.66
T. mucujensis	TJ	3	66.0 ± 3.60	95.9 ± 11.01	21.2 ± 0.32	18.0 ± 0.98	13.4 ± 1.70	9.9 ± 0.52	22.3 ± 0.99	52.5 ± 2.96	32.3 ± 1.46
T. torquatus	TT	16	97.4 ± 2.62	139.3 ± 4.38	32.8 ± 0.81	25.2 ± 0.66	20.7 ± 0.68	15.3 ± 0.90	33.5 ± 0.73	78.7 ± 1.73	48.8 ± 1.25
T. semitaeniatus	TS	20	86.2 ± 1.06	140.0 ± 4.68	27.5 ± 0.45	22.7 ± 0.26	20.5 ± 0.26	16.0 ± 0.31	30.1 ± 0.32	70.7 ± 0.77	46.1 ± 0.51
T. spinulosus	TP	11	89.6 ± 4.64	129.5 ± 6.31	26.4 ± 0.75	21.3 ± 1.03	18.1 ± 1.06	14.8 ± 0.80	29.2 ± 1.73	65.8 ± 2.74	44.1 ± 2.42
T. plica	TL	12	149.2 ± 3.91	247.5 ± 7.14	45.7 ± 0.83	45.1 ± 1.06	41.2 ± 1.47	28.1 ± 0.94	57.3 ± 1.20	132.1 ± 3.05	85.3 ± 1.88
T. umbra	TU	20	80.1 ± 2.13	168.2 ± 6.77	27.5 ± 0.86	21.5 ± 0.67	19.1 ± 0.58	13.6 ± 0.41	29.8 ± 1.27	68.1 ± 1.96	43.4 ± 1.54
T. strobilurus	TR	10	89.8 ± 2.09	86.8 ± 1.38	26.4 ± 0.55	19.5 ± 0.31	16.4 ± 0.76	15.0 ± 0.60	30.7 ± 0.48	62.3 ± 1.21	45.8 ± 0.73
T. azureus	TA	5	73.7 ± 1.64	42.6 ± 2.37	20.8 ± 0.34	14.6 ± 0.52	13.8 ± 0.32	12.0 ± 0.52	25.6 ± 0.54	49.3 ± 0.97	37.6 ± 0.87
T. flaviceps	TF	7	90.4 ± 7.34	50.0 ± 3.97	26.8 ± 1.16	19.3 ± 1.79	16.7 ± 1.37	14.8 ± 1.11	30.3 ± 2.54	62.9 ± 4.17	45.1 ± 3.46

All measurement values are mm.

each species, we tried to measure lizards from a single population, choosing that which had the most individuals available at MZUSP. However, because of restrictions in the amount of material available, we pooled the data of two populations of *Tropidurus flaviceps, T. cocorobensis, T. hygomi, T. plica*, and *T. umbra*. Measures were made with digital calipers to the nearest 0.01 mm. All measurements were made by TK.

Each species was assigned to one of two general habitat categories. The general habitat category "open" includes the Brazilian habitats known as caatinga, cerrado, restinga, and campos rupestres (Fig. 1; see caption for habitat descriptions), and the category "closed" refers to forested environments (Rizzini, 1997). Within habitats, four substrates most commonly used by *Tropidurus* were identified. These substrates were sand, rocks, branches, and tree trunks. Each species was assigned to one of the four substrate categories based on the available information on that species' natural history (Fig. 1). Although several species locomote on more than one type of substrate (e.g., see Vitt, 1991a; Vitt et al., 1997a), the substrate category assigned was intended to represent the most commonly used by any given species in natural habitats. *Tropidurus spinulosus* was assigned to the "open" category based on published reports (Martori and Aun, 1994; Vitt, 1991a), although some populations occupy the interface between open areas and riparian forests (G. Colli, personal communication). Recently, the name *Tropidurus guarani* has been proposed for the Brazilian populations of this species, considering only chaco populations as *Tropidurus spinulosus* (Frost et al., 1998).

Statistical Analyses

Table 1 shows the mean measurement values for each species. These mean values were converted into $\log_{10}$ values prior to comparative analyses because allometric principles suggest that log-transformed morphometric traits should be linearly related, which simplifies fitting of statistical models. This was true for our data and log transformation also eliminated heteroscedasticity in bivariate relationships. Two different but complementary phylogenetically based statistical methods were used to compare limb and tail proportions of lizards that use different substrates, while controlling for associations with snout–vent length (reviews in Martins and Hansen, 1996; Garland et al., 1999): a computer-simulated phylogenetic analysis of covariance (ANCOVA) (Garland et al., 1993; Harris and Steudel, 1997), and a phylogenetically independent contrasts analysis (Felsenstein, 1985). Contrasts that are large in magnitude imply high rates of evolution (which may reflect adaptation, e.g., see fig. 4 in Garland and Adolph, 1994) in that particular bifurcation of the phylogenetic tree (Garland, 1992;

Garland and Adolph, 1994). Other applications of independent contrasts to morphometric data include Losos (1990b), Irschick et al. (1996), Harris and Steudel (1997), Beutell and Losos (1999), Bleiweiss (1999), and Bonine and Garland (1999).

We checked for standardized contrasts that were influential or statistical outliers and analyzed patterns in both bivariate plots of limb or tail length vs. snout-vent length and in diagnostic plots (Garland et al., 1992) of the absolute values of standardized contrasts vs. their standard deviations (square roots of sums of branch lengths). Ratios were avoided because 1) they have some undesirable statistical properties (e.g., see Atchley, 1978); 2) they are generally redundant with analyses of individual traits; and 3) they could lead to inflated Type I error rates because of data overanalysis. However, some ratios have traditionally been considered important functional indicators, such as metatarsal/femur ratio in mammals (e.g., Garland and Janis, 1993). Therefore, bivariate plots of tibia/femur ratios were examined and statistical analyses performed as these might discriminate between ecological categories.

The phylogenetic topology (Fig. 1) and taxonomy used for analyses follows Frost (1992). His tree represents a strict consensus and is one of the 36 equally parsimonious trees generated by analysis of 77 morphological characters, including aspects of dentition, pectoral girdle, limbs, axial skeleton, and hemipenes. This study includes species previously in the genera *Uracentron, Strobilurus, Plica*, and *Tapinurus,* which are now placed in the genus *Tropidurus* and does not consider species previously placed in *Tropidurus* which are now placed in *Microlophus* and *Plesiomicrolophus*. For the 18 species included herein, Frost's (1992) topology includes three soft polytomies (three-way splits), indicating that the characters analyzed are inadequate to allow hypotheses about what are presumed to have been bifurcating speciation events. Soft polytomies lead to uncertainty in analyses with phylogenetically based statistical methods. An efficient way to deal with soft polytomies when using computer-simulated null distributions of test statistics has not yet been developed (Garland et al., 1993).

With independent contrasts, degrees of freedom can be reduced to account for soft polytomies (Purvis and Garland, 1993). For simplicity, however, and because computer simulations have shown that a small number of soft polytomies often does not greatly affect analyses (estimates are unbiased and Type I error rates are not greatly inflated: Garland and Diaz-Uriarte, 1999), the three "soft" polytomies in this study are treated as "hard" polytomies. In the PDTREE program (see below), topologies are initially entered as bifurcating, then internode branch segments are changed to zero length (collapsed) to create a polytomy. The arbitrary order of entry within a polytomy thus created (e.g., [[A,B]C] vs. [A[B,C]]) does not affect estimates of slopes or cor-

relations for the overall dataset. However, this entry method does affect the values of the contrasts within a particular polytomy and would make inferences about those particular contrasts suspect. Therefore, inferences concerning contrasts within polytomies are not made here. In fact, this concern was irrelevant, as none of those contrasts appeared as influential points or as outliers.

The phylogenetically based statistical methods used here require that branch lengths be available in units proportional to expected variance of character evolution for each character analyzed. Estimates of phylogenetic branch lengths in units of divergence times, genetic distances, or some other common metric were unavailable. Therefore, arbitrary branch lengths were used, as shown in Figure 1 (following Pagel, 1992). These branch lengths, which yield contemporaneous tips, assume that the expected variance of character change is equal for the evolutionary history that leads from the root of the tree to each tip species. Preliminary analyses indicated that these arbitrary branch lengths provided adequate standardization of independent contrasts (see Garland et al., 1992; Díaz-Uriarte and Garland, 1996, 1998; Garland and Díaz-Uriarte, 1999), and so they were used for all analyses, including computer simulations.

The MS-DOS computer program PDTREE (Garland et al., 1993, 1999; Garland and Ives, 2000) was used to enter trees and to perform analyses with independent contrasts (Felsenstein, 1985). PDSIMUL was used to simulate bivariate character evolution under simple Brownian motion and PDANOVA was used to analyze the simulated data (Garland et al., 1993). Heterogeneity of slopes was tested in all phylogenetic ANCOVAs, but not one was statistically significant at $P = 0.05$, so results are not shown.

RESULTS

Considering each trait separately, the diagnostic plots shown in Figure 2 indicate that, although some individual contrasts are notably large in magnitude, no trends are evident. This lack of overall trends indicates that, in general, the arbitrary branch lengths used for analyses (as shown in Fig. 1) adequately standardized the contrasts (Garland et al., 1992). This result is important because simulation studies have demonstrated that errors in branch lengths (Díaz-Uriarte and Garland, 1998) or deviations from the assumed Brownian motion model of bivariate character evolution (Díaz-Uriarte and Garland, 1996) can cause inflated Type I error rates when testing for correlations between traits. As absolute values are plotted on the Y-axes shown in Figure 2, the distributions should also approximate half of a normal if the branch lengths are statistically adequate (see Garland, 1992).

Habitat is associated with phylogeny in *Tropidurus,* as the five closed-habitat species are members of a single clade (Fig. 1). Therefore, examination of the contrast (node 14 in Fig. 1) between those species and their sister in the dataset (*T. spinulosus*) can be used to indicate whether the shift in habitat has been associated with a significant shift in body proportions. Substrate usage is also associated with phylogeny, e.g., the three "branch" species are a single clade (*T. strobilurus, T. azureus, T. flaviceps*) that is defined by a synapomorphy involving shorter tails (metatarsus length but not hind limb length or substrate type are involved in Frost's study [1992]).

As Figure 3 shows, none of the relationships between limb or tail length and snout–vent length deviate strongly from the "null expectation" of a slope of 1.00, which is the expected scaling relationship for linear body dimensions in geometrically similar animals. Snout–vent length does not vary consistently in relation to either habitat or substrate usage. With snout–vent length as a covariate, however, phylogenetic ANCOVA indicates some relevant statistically significant differences among substrate categories (see below) for tail length, hindlimb length, and foot length, but not foreleg length (Table 2). Figure 3 indicates that the differences in tail and hind limb length are because the three "branch" species have short tails and hind limbs for their SVL. Differences in foot length appear to result from the three "sand" species which have relatively long feet (Fig. 3). Figure 4 suggests that species from closed habitats (clade 16 in Fig. 1) tend to be larger in snout–vent length and to have shorter tibias relative to their femur lengths than do species from open habitats. Conventional ANOVA indicates that $\log_{10}$ snout–vent length does not, in fact, vary significantly in relation to habitat (F = 2.75, d.f. = 1,16, $P > 0.10$), and P is even greater in phylogenetic ANOVA ($P = 0.344$). Conventional ANOVA indicates, however, that tibia/femur ratio does vary in relation to habitat (F = 11.14, d.f. = 1,16, $P < 0.005$), and conventional ANCOVA supports this result (F for habitat = 7.57, d.f. = 1,15, $P < 0.02$; F for $\log_{10}$ snout–vent length as the covariate = 0.58, d.f. = 1,15, $P > 0.35$). Phylogenetic ANOVA by computer simulation indicates a marginally significant effect of habitat ($P = 0.050$), but phylogenetic ANCOVA indicates a nonsignificant effect of both habitat ($P = 0.086$) and $\log_{10}$ snout–vent length ($P = 0.526$). Thus, there is limited statistical support for the tendency of closed-habitat species to have relatively low tibia/femur ratios.

In Figure 3 (conventional log-log plots), the dataset includes two potentially influential points, the small *Tropidurus nanuzae* and the large *T. plica*. The *T. plica* translates into a very large vertical standardized independent contrast when compared to its sister species (Fig. 2), which would have large influences on the regressions with independent contrasts (Fig. 5). The contrast between *T. plica* and *T. umbra* (node 17) is clearly unusually large for snout–vent length, hindleg length, and foreleg

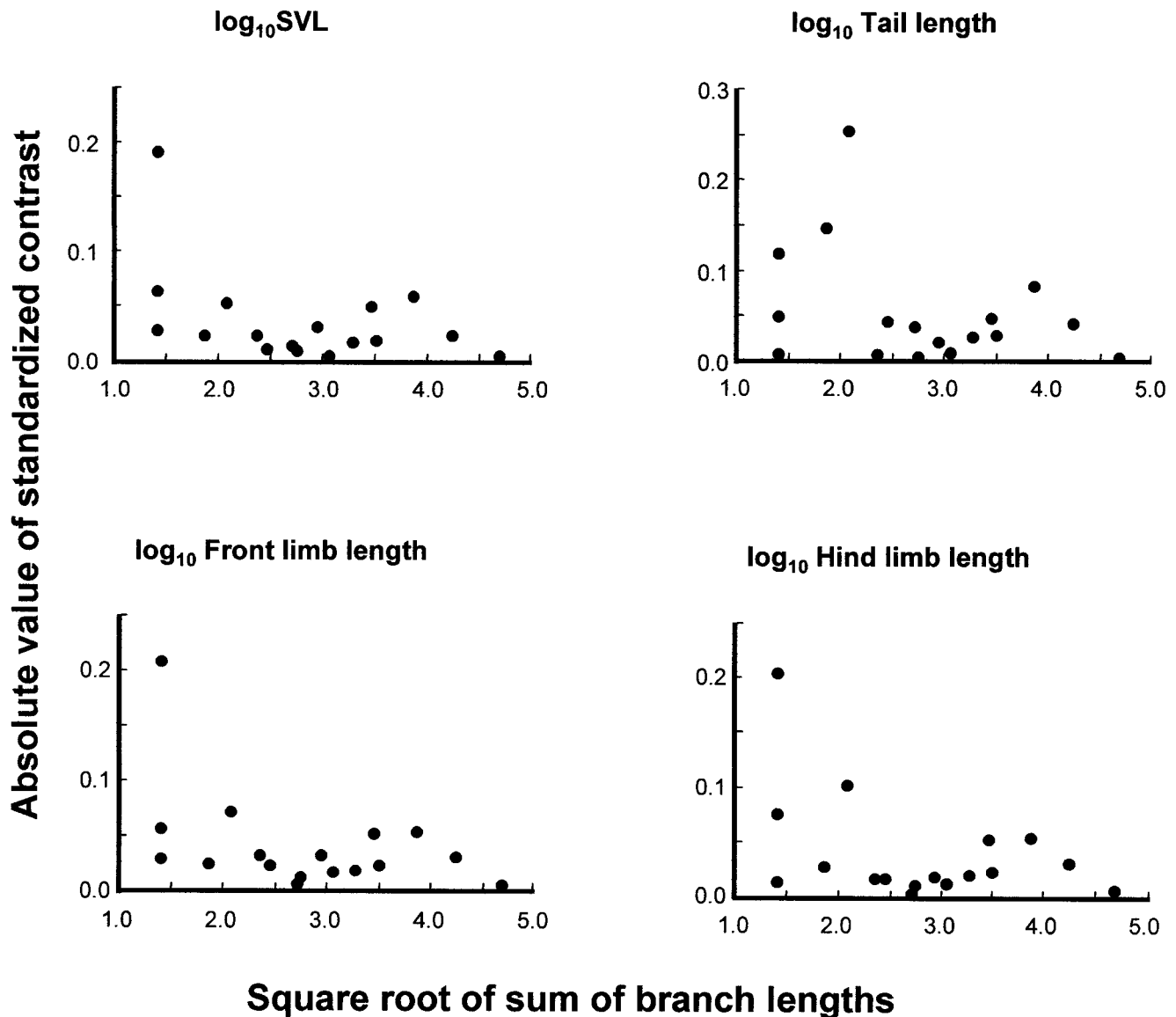**Square root of sum of branch lengths**

Fig. 2. Diagnostic plots (following Garland et al., 1992) for phylogenetically independent contrasts applied to the four $\log_{10}$ body dimensions. Statistical adequacy of the branch lengths (shown in Fig. 1) used for computing the contrasts is suggested by an absence of linear trends and by each distribution approximating one-half of a normal distribution (in the vertical direction). An extreme point in the vertical direction suggests that the rate of evolution has been unusually high since the time the two species diverged (see Garland, 1992; Garland and Adolph, 1994). Given this interpretation, *Tropidurus plica* and *T. umbra* have diverged rapidly in snout–vent length, hindlimb length, and foreleg length; similarly, rapid divergence in tail length occurred at node 16 in Figure 1.

length. Such a large contrast indicates that the differences in lengths have evolved rapidly since the two species separated. In addition, the contrast representing node 16 (see Fig. 1) is unusually large for tail length: this reflects the unusually short tails of the three "branch" species (Fig. 5).

Bivariate scatterplots of standardized independent contrasts (Fig. 5) also indicate that node 16 is unusual for tail length in relation to snout–vent length as it deviates from the 1:1 relationship expected if these lizards are geometrically similar. The bivariate plots also show that the contrast representing node 17 (*Tropidurus plica* vs. *Tropidurus*

umbra) is far from the origin for tail, hindlimb, and foreleg length, but not far from the 1:1 line.

DISCUSSION

This study suggests that some evolutionary changes in body proportions and body size are coupled with divergence in habitat and/or substrate usage among species in the lizard genus *Tropidurus*. Morphometric specialization was detected when considering typical substrates for locomotion, but not when broader ecological categories were used
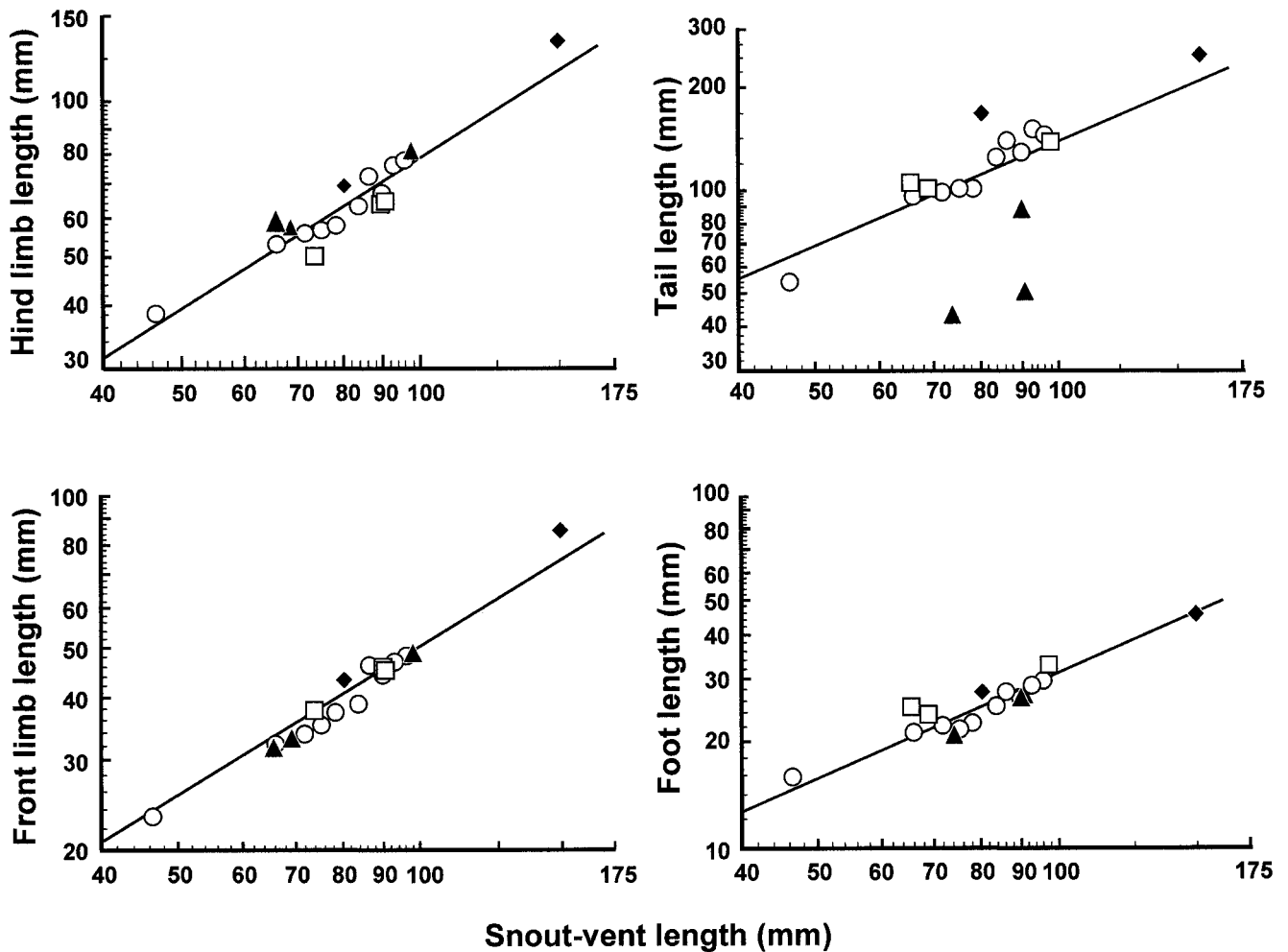
Fig. 3. Conventional allometric plots for tail, foot, and limb lengths in relation to snout–vent length for 18 species of *Tropidurus* lizards. Solid lines indicate slopes of 1.00 (isometry) and pass through the point indicating the means of the two traits. Symbol color indicates open (white) and closed (black) environments and symbol shape shows substrate type: diamonds, tree trunks; triangles, tree branches; squares, sand; circles, rocks.

(i.e., "closed" vs. "open" habitats). Evidently, as might be expected, relatively more detailed ecobehavioral data enhance resolution when testing ecomorphological hypotheses. For example, the use of a single category, such as "arboreal" for "trunk" as well as "branch" lizards, would have been inappropriate. Because of the association between ecology and phylogeny (see Results), the observed morphological differences may be interpreted as either adaptations to the behavior and ecology of species in the clade or as nonadaptive synapomorphies. Nevertheless, given that "branch" species are clearly different in body proportions from other *Tropidurus*, and that perch characteristics have been related to morphology and performance in some lizard taxa (see below), our results support an adaptive interpretation of the patterns found. Sand species may have longer feet in comparison with species that use other substrates. However, all three of these "sand" species are parts of polytomies (Fig. 1), so conclusions

about the statistical significance of relative foot length, as indicated by the phylogenetic ANCOVA (Table 2), should be accepted cautiously. In any case, this finding is consistent with what has been observed in *Niveoscincus* genus, in which longer feet are associated with higher sprint speeds in saxicolous species (Melville and Swain, 2000).

The presumed evolutionary transition of *Tropidurus*, from ancestral open habitats (D.R. Frost, personal communication; M.T. Rodrigues, personal communication) to derived forested environments, has involved diverse morphological tendencies. Conservative limb and tail proportions (but not necessarily body shape, see below) characterize the "trunk" species of *Tropidurus plica* and *T. umbra*, with *T. plica* being larger than other *Tropidurus*. The three "branch" species, on the other hand, have similar body size but short tails and limbs in comparison with most other congenerics (see fig. 1A in Vitt and Zani [1996], for a picture of the spiny tail of

TABLE 2. Analyses of covariance comparing log tail and log limb lengths among substrate categories, with log snout–vent length as a covariate

Trait and source of variation	Sum of squares	Mean df	Square	F	Conventional tabular		Phylogenetic simulation	
					Critical value	P	Critical value	P
Tail								
Substrate	0.308974	3	0.102991	20.90	3.41	<0.001	6.024	<0.001
$\log_{10}$ snout–vent	0.188711	1	0.188711	38.29	4.67	<0.001	7.257	<0.001
Error	0.064073	13	0.004929					
Total	0.618325	17	0.036372					
Hindlimb								
Substrate	0.012615	3	0.004205	7.14	3.41	<0.005	5.896	0.032
$\log_{10}$ snout–vent	0.140920	1	0.140920	239.33	4.67	<0.001	7.675	<0.001
Error	0.007655	13	0.000589					
Total	0.206650	17	0.012156					
Front limb								
Substrate	0.001616	3	0.000539	1.36	3.41	>0.25	6.374	0.495
$\log_{10}$ snout–vent	0.155033	1	0.155033	392.54	4.67	<0.001	6.724	<0.001
Error	0.005134	13	0.000395					
Total	0.228906	17	0.013465					
Foot								
Substrate	0.011359	3	0.003786	7.68	3.41	<0.005	6.527	0.034
$\log_{10}$ snout–vent	0.102634	1	0.102634	208.25	4.67	<0.001	7.665	<0.001
Error	0.006407	13	0.000493					
Total	0.154643	17						

Tropidurus flaviceps. The nonspiny tails of *T. hispidus* and *T. semitaeniatus* can be seen in plate 1F,G of Vitt [1995]).

The remarkable morphological differences between "branch" and "trunk" species should be robust to at least some of the existing phylogenetic uncertainty (see Fig. 1). Frost (1992, fig. 35), for example, presents an equally parsimonious alternative tree, which nevertheless retains the relationships of the five species involved in the most important contrasts used in our analysis. Additionally, since this article was first submitted, a new phylogenetic analysis of
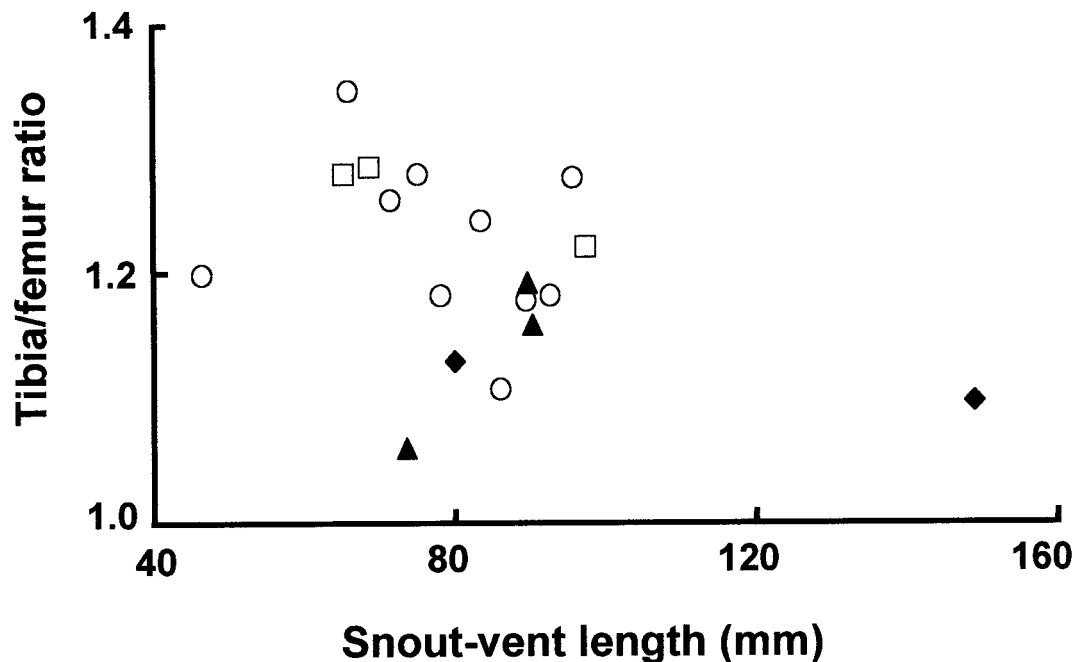

Fig. 4. Tibia/femur ratio in relation to snout–vent length. Phylogenetic ANOVA by computer simulation indicates that tibia/femur ratio shows a marginally significant difference between species from open and closed habitats ($P = 0.050$). Symbols as in Figure 3.
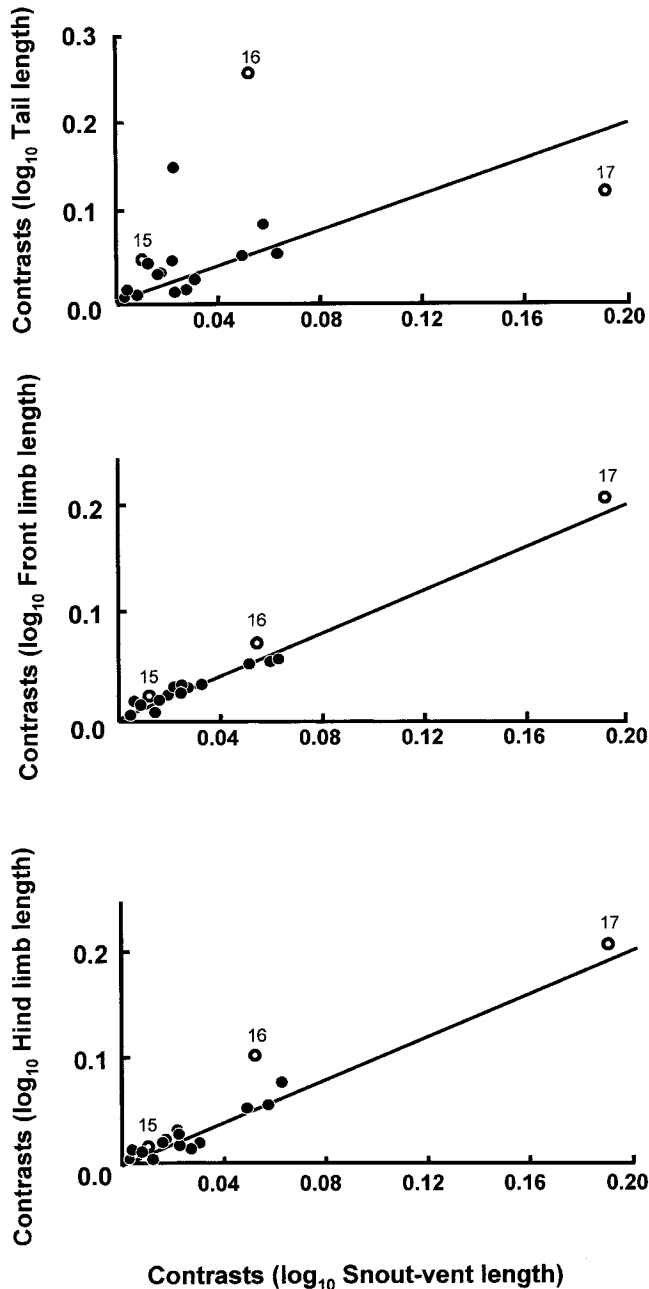
Fig. 5. Independent contrasts allometric plots for tail and limb lengths in relation to snout–vent length. Lines indicate slopes of 1.00 (isometry) and pass through the origin. Numbers adjacent to three highlighted points indicate contrasts at the corresponding nodes shown in Figure 1. See text for discussion of these points.

tropidurines, based on Frost's characters plus new characters derived from microscale structure, has appeared (Harvey and Gutberlet, 2000). One of the most relevant differences between their majority consensus tree (their fig. 13A) and the phylogeny we have used (Fig. 1) is the repositioning of *Uranodoscon* as sister species to *Tropidurus umbra*. This change is not germane to our discussion, because we

did not include *Uranodoscon* in the analyses. Additionally, *T. plica* and *T. umbra* remain as close species within a small clade, and soft polytomies remain. An important direction for future studies, however, will be to reanalyze data when more resolved phylogenetic information becomes available, to include *Uranodoscon* as an outgroup taxa, and to consider analyses with multiple phylogenetic trees (e.g., see Losos et al., 1994; Bauwens et al., 1995; Abouheif, 1999).

At present, field and laboratory data to fully interpret the morphological differentiation observed in "branch" *Tropidurus* are lacking. Morphological specialization in arboreal lizards varies with behavioral and ecological correlates. The distinction between these correlates, however, is not simple, because a behavior (e.g., a preferred type of locomotion) may be associated with the structural characteristics of a given microhabitat (e.g., habitat-matrix model, Pounds, 1988). For example, lizards on small perches tend to jump more often than to run, a behavioral shift that seems related to decreased sprint performance on thin surfaces (Losos and Irschick, 1996). Sprint speed is inversely proportional to perch diameter in *Anolis* (Losos and Sinervo, 1989), but the effects of reduced perch diameter are less dramatic in *A. valencianni*, a species with short legs, than in long-legged species (Losos and Irschick, 1996). Losos (1990b) also reports that, in a phylogenetic analysis with effects of body size controlled, an increase in hind limb length is correlated to an increase in both sprint and jumping performance. Conversely, both front limb and tail length show a negative evolutionary correlation with the two measures of locomotor performance. Finally, morphological specialization in relation to typical substrate slope is conceivable because substrate slope affects the kinematics of lizard locomotion (Irschick and Jayne, 1998; Jayne and Irschick, 1999).

It is possible that reduced limb size and a short, flat, and spiny tail aid "branch" *Tropidurus* in keeping the center of gravity close to the substrate, or in clinging to branches in a similar way that the tails of woodpeckers help birds to locomote on trees (Bock, 1999). Tails are unlikely to serve as a balancing organ in the same sense suggested for *Anolis* (Ballinger, 1973), although "branch" *Tropidurus* fall from trees less often than do "trunk" species (L.J. Vitt, personal communication). On the other hand, flat, dark, and spiny tails may increase heat gain (L.J. Vitt, personal communication, as suggested to him by M.L. Cody). Despite the occupation of a forested environment, "branch" *Tropidurus* appear to be similar to other conspecifics in that they are territorial and thermoregulate (M. Martins, L.J. Vitt, personal communication), in contrast with other forest lizards which are thermoconformers (Ballinger et al., 1995; Rummery et al., 1994; Tanaka, 1986). For example, mean body temperatures of active *T. fla-*

viceps, a "branch" species, are (mean ± SE) 31.2 ± 0.6°C (Vitt and Zani, 1996). However, the nonarboreal lizard *Hoplocercus spinosus* (Hoplocercidae: Iguaninae) exhibits a similar tail morphology and uses the tail to cover retreat entrances when threatened (G. Colli, personal communication). It is uncertain whether "branch" *Tropidurus* use their tails in a similar way.

Although short rear limbs and robust tails in "branch" *Tropidurus* may improve balance while moving in the trees, such traits may decrease jumping performance. Locomotor compromises have been reported for other lizards. Losos et al. (1993), for example, showed that the semiarboreal chameleon (*Chamaleo dilepis*) runs faster but has lower clinging ability than the more arboreal species *C. jacksonii*. Additionally, Sinervo and Losos (1991) reported that *Sceloporus occidentalis* from more arboreal populations are faster on thin rods but slower on thick rods than lizards from more terrestrial populations. Interestingly, arboreal lizards, although slower than their nonarboreal counterparts, are less prone to stumble, suggesting a trade-off between speed and sure-footedness. In contrast, Van Damme et al. (1997) did not find a trade-off between running and climbing performance in a study of mainland and island subspecies of the Mediterranean lizard *Podarcis hispanica*, despite population differences in typical substrates.

Rapid modifications of morphology have occurred since *Tropidurus plica* and *T. umbra* split, so that the two species have evolved striking differences in body size and shape. *Tropidurus plica* is larger than other *Tropidurus*, and has a flattened body in comparison with most congenerics (Vitt, 1991b). These differences may be coupled with ecological divergence. Both species move with the body close to the tree trunk and the legs spread wide apart (L.J. Vitt, personal communication); however, they do not share a similar microhabitat. *Tropidurus plica* clings to smooth vertical trunks of large forest trees and moves mainly along a vertical plane, whereas *T. umbra* is found usually in medium-sized trees and thus uses smaller perches than *T. plica* (Vitt, 1991b; Vitt et al., 1997b; L.J. Vitt, personal communication). Although it is not known which of these two species first invaded forested environments, it is worth noticing that presently they are sympatric along their geographic range, so size divergence could involve character displacement. This evolutionary process seems responsible for large differences in body size between pairs of *Anolis* species in the northern Lesser Antilles (Butler and Losos, 1997). It is also possible that the highly territorial nature of *T. plica* has contributed to divergence in microhabitat use between *T. plica* and *T. umbra*. Several researches have observed intense chases and other intraspecific aggressive interactions in *T. plica* (G. Colli, M. Martins, M.T. Rodrigues, personal

communications) and it would be conceivable that interspecific interactions also exist.

Instances of rapid morphometric adaptation may be common in lizards (see Sumner et al., 1999). For example, populations of *Anolis sagrei* were experimentally introduced to various islands in the Bahamas in 1977 and 1981 and studied in 1991. Individuals derived from these experimental populations show a correlation between hindlimb length (adjusted for body mass) and typical island perch diameter (Losos et al., 1997). Vitt et al. (1997a) showed morphological differentiation in male *Tropidurus hispidus* from populations inhabiting savanna and rocky outcrops. The populations typical of rock outcrops are considered derived in this species, and the exploitation of this novel habitat appears associated with the evolution of a more compressed body shape. Such population differences must be interpreted cautiously in the absence of data on common garden experiments (Garland and Adolph, 1991), but recently Losos (1999) has shown that *Anolis* lizards of the same species, when raised in different microhabitats (e.g., perch diameter), show minor but measurable differences in limb proportions.

The functional significance of morphometric variation in *Tropidurus* is still hypothetical and a full understanding of the ecomorphological interactions of the genus will require additional field and laboratory studies. Irschick and Losos (1998), for example, found that *Anolis* species, when disturbed in the field, sprint at or near the maximum capacity exhibited in laboratory tests. In contrast, jumping in the field is in all cases less than the maximum jumping ability observed in the laboratory. Saxicolous species of *Niveoscincus* exhibit shorter interlimb intervals and longer limbs than other ecomorph types, and are also able to achieve higher sprint speeds. Higher sprint speed may also be advantageous in open spaces where distance to retreat sites may be long (Melville and Swain, 2000). Field observation will allow monitoring of the frequency and intensity of locomotor modes exhibited in nature (e.g., Perry, 1999), while laboratory studies can indicate how maximum capacities for locomotor performance relate to behavior, morphology, and physiology. For example, combining behavioral and physiological information, Garland (1999) found that laboratory endurance capacities of lizards are positively correlated with both percentage of time moving and the daily distance traveled in nature. A similar approach would allow for a better understanding of the relationships that exist between morphology and performance in *Tropidurus*. Under an adaptive scenario, for example, *Tropidurus* species should locomote best on their typical substrates and locomotor modes, and differences in performance should be partially explained by morphometric variation among species. Informal observations, however, suggest that differences in the ability to jump of nonarboreal species of *Tropidurus* may relate to changes

in muscle physiology (see also Bonine et al., 2000) more than to modifications in body proportions.

In summary, the most important pattern suggested by this study is that the recent genus *Tropidurus* has undergone rapid morphometric differentiation, presumably adaptive, and mainly related to the transition from open to arboreal habitats. This finding contrasts with the results of two previous phylogenetic studies with non-anoline lizards (Miles, 1994; Vanhooydonck and Van Damme, 1999) and are consistent with the findings of Melville and Swain (2000). The traits involved in the *Tropidurus* transition include body size as well as limb and tail proportions, and apparently reflect specialization in behavior and habitat, possibly perch size and incline. Subtle morphological differences in other characters related to locomotion (e.g., see Glossip and Losos, 1997) may exist among terrestrial species. However, it seems evident that species that use nonarboreal microhabitats ("sand" and "rock") exhibit a less conspicuous pattern of morphometric differentiation. Therefore, a generalized morphology may allow adequate locomotor performance and may even be selected for in terrestrial habitats.

ACKNOWLEDGMENTS

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