The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*

(Amazon/ecomorphology/microevolution)

Laurie J. Vitt,*† Janalee P. Caldwell,* Peter A. Zani*‡, and Tom A. Titus§

*Oklahoma Museum of Natural History and Zoology Department, University of Oklahoma, Norman, OK 73019, and §Department of Biology, University of Oregon, Eugene, OR 97403

ABSTRACT We compared morphology of two geographically close populations of the tropical lizard *Tropidurus hispidus* to test the hypothesis that habitat structure influences the evolution of morphology and ecology at the population level. *T. hispidus* isolated on a rock outcrop surrounded by tropical forest use rock crevices for refuge and appear dorsoventrally compressed compared with those in open savanna. A principal components analysis revealed that the populations were differentially distributed along an axis representing primarily three components of shape: body width, body height, and hind-leg length. Morphological divergence was supported by a principal components analysis of size-free morphological variables. Mitochondrial DNA sequences of ATPase 6 indicate that these populations are closely related relative to other *T. hispidus*, the rock outcrop morphology and ecology are derived within *T. hispidus*, and morphological and ecological divergence has occurred more rapidly than genetic divergence. This suggests that natural selection can rapidly adjust morphology and ecology in response to a recent history of exposure to habitats differing in structure, a result heretofore implied from comparative studies among lizard species.

There has been a recent upsurge of interest in innovative techniques to account for evolutionary relationships in comparative analyses (1–4). Phylogenetic analyses provide the opportunity to polarize the direction of character change and to estimate the time over which divergence has occurred. With respect to lizards, numerous techniques have been used to compare ecology and morphology among closely related species (5, 6). These studies and others (7–13) suggest that morphology can be adjusted by adaptation to differing structural characteristics of habitats. However, there have been few ecomorphological studies comparing populations within species (14, 15) and none directly integrating morphological change at the population level with recent change in structural habitat in lizards.

One underlying assumption of the ecomorphology paradigm (16) is that morphology differs among species as a result of competition (17, 18) or habitat shift (6). We demonstrate that morphological evolution has occurred at the population level as an adaptation to rock dwelling in South American lizards in the genus *Tropidurus* (19, 20), a clade that is much less speciose than Caribbean and Central American *Anolis* lizards in which most ecomorphology studies have been done (7–9, 21).

Species of *Tropidurus* occur in savanna, cerrado, caatinga, and lowland forest habitats of South America (20). All are insectivores (22–26) with a tendency toward ant specialization in arboreal species (23, 25). A recent study (26) found that species that

inhabited isolated rock outcrops in the southern Amazon region and used narrow crevices for escape were more compressed dorsoventrally than a widespread species (*Tropidurus hispidus*) that used a diversity of habitats and microhabitats. However, because a phylogeny for those populations did not exist (they comprise at least two undescribed taxa; ref. 27), it was not possible to polarize the direction of character change.

T. hispidus, which is widespread north and south of the Amazon River in South America, is the only "open formation" species (see ref. 23 for discussion of *Tropidurus* taxonomy) occurring north of the Amazon. During a field expedition to the Brazilian state of Roraima in 1993, we discovered a population of *T. hispidus* isolated on a granitic rock outcrop within approximately 40 km of a large savanna area known locally as lavrado (28). *T. hispidus* is widespread in the savanna and uses a variety of microhabitats (29, 30). It does not occur in terra firme tropical forest habitats except on isolated granitic outcrops. Populations on outcrops within tropical forest are isolated from savanna populations and from other rock outcrop populations.

The structure of savanna and rock outcrop habitats is very different, and the occurrence of populations in each habitat offered a unique opportunity to directly test the hypothesis that adaptation to rock outcrops causes morphological change in lizards over relatively short time periods. Based on the observation that other rock outcrop *Tropidurus* appear dorsoventrally compressed in morphology (23), we predicted that the rock outcrop population of *T. hispidus* would be relatively more compressed in morphology than the savanna population. Because the rock surfaces provide a much more open microhabitat for lizards than the grassy savanna, we predicted that the rock outcrop population would have relatively longer hind limbs as shown in other lizards (31, 32). Because the isolated rock outcrop in which we studied *Tropidurus* was part of a continuous savanna habitat until recently (33–39), we also predicted that the rock outcrop population was derived from the savanna population and that divergence had been a relatively recent event. We used morphological comparisons to demonstrate morphological divergence and molecular data to polarize the direction of change and examine the degree of genetic divergence.

MATERIALS AND METHODS

Populations of *T. hispidus* were studied during 1991 (May through July) in savanna near Boa Vista (2° 50′ N latitude by 60° 40′ W longitude) and 1993 (June through Aug) on a rock outcrop in terra firme forest near Caracaraí (2° 0′ N latitude by 62° 50′ W longitude), both in the Brazilian state of Roraima.
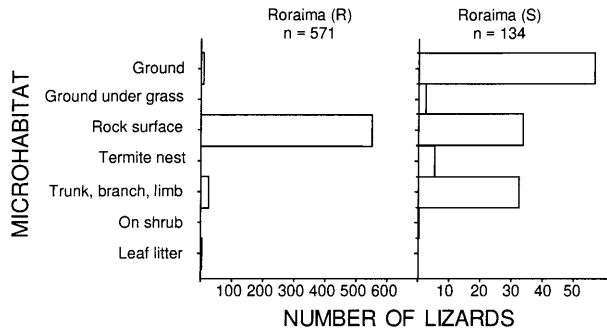

FIG. 1. Patterns of microhabitat use by two populations of *T. hispidus*. The number of observations is indicated by *n*.

Savanna in Roraima consists of open grasslands with a low density (if any) of low trees and small shrubs, most of which comprise a subset of vegetation found in the cerrados of central Brazil (28, 29, 40, 41). Terra firme forest to the northwest of Caracaraí has a continuous canopy approximately 30 m in height. Aside from areas deforested by humans, the only patches within the forest that receive direct sun exposure are small granitic rock outcrops.

We collected microhabitat data on individual lizards in both populations by walking haphazard transects and recording microhabitat associations of individual lizards (29, 30). Lizards occurred on the following microhabitats: (*i*) ground in open; (*ii*) ground under grass; (*iii*) rock; (*iv*) termite nest; (*v*) leaf or grass litter on ground; (*vi*) trunk, branch, or limb of tree; (*vii*) canopy of tree; (*viii*) on grass off ground; (*ix*) on shrub; and (*x*) in tangle of vegetation. Because we were also studying lizards in terra firme forest in the area, we were able to establish that *T. hispidus* does not occur within the forest. Microhabitat niche breadths were calculated with the reciprocal of Simpson's (42) formula (31, 43). Niche breadth values vary from 1 to *n* with low values indicating primary use of one or a few categories and values approaching *n* indicating even use of all categories.

For morphological comparison of lizards between populations, we recorded the following variables: (*i*) snout-vent length (SVL); (*ii*) total body mass; (*iii*) head width; (*iv*) head length; (*v*) head height; (*vi*) body width; (*vii*) body height, and (*vii*) hind-leg length (26, 30).

We first compared body size of *Tropidurus* between populations. Because ontogenetic and sexual size variation existed within populations, we restricted our size comparisons between populations to the same sex. Other morphological analyses were based on regressions of morphological traits on size. Consequently, all individuals (adults and immatures) were included. For these, we transformed all morphological variables to $\log_{10}$ and used a principal components analysis (PCA) to detect sources of variation in morphology in our samples.

We also calculated residuals of the regressions of logs of all morphological variables versus log SVL and applied a second PCA to the residuals to examine morphological variation on size-adjusted variables (6). The advantage of this analysis over a series of pairwise comparisons of individual variables is that by examining variation in all variables simultaneously, morphological change can be assessed.

Values appear as means ± 1 standard error. Voucher specimens have been deposited in the herpetology collections of the Museu Paraense Emílio Goeldi in Belém, the Museu de Zoologia da Universidade de São Paulo, and the Oklahoma Museum of Natural History. Representative frozen tissue samples are deposited in the Genetic Resource Collection of the Museum of Science, Louisiana State University.

DNA Amplification and Sequencing. Mitochondrial DNA sequences were obtained for 10 *T. hispidus* individuals representing four populations; six from the Roraima rock outcrop population (designated Roraima R) (LJV 4294-4296, 4298, 4300, 4303), two from the Roraima savanna population (designated Roraima S) (LJV 4443, 4458), one from northeastern Brazil (Ibiraba, Bahia, MTR 886994, from M. T. Rodrigues), and one from Venezuela (Bolivar, Cerro Guaiquinima, 450 km NW Boa Vista; AMNH 136170). *Tropidurus montanus* (Serra do Cipó, Minas Gerais, Brazil, MTR 887609, from M. T. Rodrigues, University of São Paulo) served as an outgroup for phylogenetic analyses. Morphological evidence indicates that *T. montanus* is within a clade that is the sister group to other populations of *T. hispidus* (19).

Genomic DNA was extracted from frozen muscle tissue (44). A 714-bp fragment of the mitochondrial gene encoding ATPase subunit 6 was amplified using PCR. Primers were as follows: L9252(5′-AACCTGACCATGAACCTAAGCT-3′) and H9923(5′-TAGGAGTGTGCTTGGTGTGCCAT-3′). Numbers correspond to the most 3′ base in the chicken sequence (45). The amplification program was 30 cycles of 92°C for 45 s, 55°C for 60 s, and 72°C for 90 s. Initial amplifications from genomic DNA were gel purified (46) and reamplified under identical conditions in a volume of 25 μl. This second reaction was electrophoresed in 0.7% agarose, excised, and purified with Geneclean (Bio 101). Approximately 100 ng of template DNA was sequenced in a thermal cycler (Perkin–Elmer/Cetus model 480) using the fmol Sequencing System (Promega) with primer end-labeling. Reaction conditions for cycle sequencing were 95°C for 2 min, followed by 30 cycles of 95°C for 30 s, 55°C for 30 s, and 72°C for 60 s.

Reactions were denatured at 73°C for 3 min and electrophoresed on 8% Longranger (AT Biochem, Malvern, PA) gels.

DNA Sequence Analysis. DNA sequences were aligned manually. Estimates of sequence divergence were computed using MEGA (47). Evolutionary relationships among haplotypes were inferred under the optimality criterion of parsimony

Table 1. Factor scores (unrotated) for PCA on log-transformed morphological variables and the same variables adjusted for the effect of body size (SVL) for *T. hispidus* from Brazil

|	Log-transformed		Size-adjusted		
	PC I	PC II	PC I	PC II	PC III
Snout-vent length	0.989	−0.057			
Mass	0.995	−0.020	0.778	−0.066	0.439
Head width	0.985	−0.110	0.738	0.484	−0.235
Head length	0.989	−0.001	0.813	−0.066	−0.317
Head height	0.980	−0.082	0.785	0.336	−0.164
Body width	0.945	0.219	0.447	−0.578	0.499
Body height	0.940	0.286	0.552	−0.653	−0.128
Hind-leg length	0.963	−0.217	0.133	0.775	0.493
Eigen values	7.580	1.990	2.950	1.716	0.883
% of variance	94.7	2.5	42.1	24.5	12.6

PC, principal component.
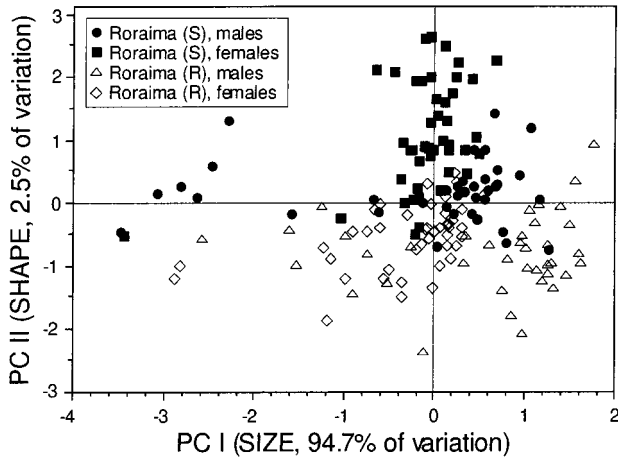
FIG. 2.　Bivariate plot of PCA on morphological characteristics of two *T. hispidus* populations occupying structurally different habitats showing the first two principal components (PC) of log-transformed morphological variables. R and S designate Roraima rock outcrop and savanna populations, respectively.

as implemented in PAUP 3.1 (48) using the exhaustive search option and equal weighting of all substitutions.

RESULTS

Ecological and Morphological Variation. *Tropidurus* used a greater diversity of microhabitats in savanna than in the rock outcrop (Fig. 1; refs. 29 and 30). Correspondingly, microhabitat niche breadths were greater in the savanna (3.213) than in the rock outcrop population (1.096). Virtually every individual observed in the rock outcrop population ultimately retreated to either rock crevices or under rocks situated on the outcrops.

No individuals retreated to the forest which acted as a complete barrier to dispersal. Surveys of lizards in nearby forest revealed a complete absence of *Tropidurus* even though 16 species in seven lizard families were found (30).

There was no significant difference between populations in body size of sexually mature females (Kolmogorov–Smirnov test, $\chi^2 = 27.1$, $P = 0.1069$; rock population, $\bar{\chi} = 74.9 \pm 1.60$ mm, $n = 40$; savanna population, $\bar{\chi} = 74.8 \pm 0.89$ mm, $n = 44$), but there was a significant difference in male size (Kolmogorov–Smirnov test, $\chi^2 = 5.9$, $P < 0.0001$; rock population, $\bar{\chi} = 106.0 \pm 1.83$ mm, $n = 29$; savanna population, $\bar{\chi} = 87.6 \pm 1.55$ mm, $n = 32$).

A PCA of logs of morphological variables (Table 1) revealed a size axis accounting for nearly 95% of the variation (PC I; Fig. 2) with a shape axis (PC II) accounting for another 2.5% of the variation (PC II, Fig. 2). It is evident in the bivariate plot that both size and shape differ among populations. The size differences are primarily due to differences in male size. The PCA on size-adjusted morphological variables revealed three axes accounting for 79.2% of the variation in shape (Table 1). Factor I describes a variation gradient based primarily on relative head size (head width, length, and height); factor II describes a gradient based primarily on relative hind-leg length and body height; and factor III describes a gradient based on relative body width and body mass. Lizards on the rock outcrop are relatively more flattened dorsoventrally and have longer hind limbs when compared with those in the savanna ($F_{1,161} = 52.5$, $P < 0.0001$). They also weigh relatively less and have relatively narrower bodies ($F_{1,161} = 13.7$, $P = 0.0003$).

Genetic Variation. Six hundred thirty-eight bases of ATPase 6 sequence were obtained for all individuals (Fig. 3). Of these, 115 positions were variable. All localities were characterized by unique haplotypes, and no mitochondrial polymorphisms were observed for the six individuals sampled from the rock outcrop population from Roraima. Among the *T. hispidus* haplotypes, the smallest distance (1.4%) was between the two Roraima haplo-

FIG. 3.　Aligned ATPase 6 sequences for *T. montanus* and four *T. hispidus* haplotypes. R and S designate Roraima rock outcrop and savanna populations, respectively. Sequences are deposited in the GenBank database (accession nos. U83494–U83498).

Table 2. Uncorrected (below the diagonal) and Kimura (above the diagonal) genetic distances among *T. hispidus* (2–5) and *T. montanus* (1) haplotypes

Haplotype	1	2	3	4	5
1. *T. montanus*	—	0.172	0.183	0.175	0.172
2. Venezuela	0.151	—	0.039	0.046	0.048
3. Ibiraba	0.159	0.038	—	0.026	0.021
4. Roraima (S)	0.153	0.044	0.025	—	0.014
5. Roraima (R)	0.151	0.046	0.020	0.014	—

S, savanna population; R, rock outcrop population.

types, and the largest distance (4.8%) was between the Brazilian Ibiraba haplotype and the Roraima rock outcrop haplotype (Table 2). Distances were considerably larger between *T. montanus* and the four *T. hispidus* haplotypes (17.2–18.3%) than among *T. hispidus* haplotypes. Phylogenetic analysis of the four *T. hispidus* haplotypes using *T. montanus* as the outgroup produced a single most parsimonious tree in which the Ibiraba haplotype is the sister to a lineage containing the Venezuelan and Roraima haplotypes, within which the two Roraima haplotypes are most closely related to one another (Fig. 4).

DISCUSSION

One of the primary objectives of studies on ecomorphology is to link morphological differences among species to potential causes of those differences (12, 49–54). Application of standard statistical tests for comparison has been criticized because it does not account for the influence of nonindependent evolutionary history. More explicitly, statistical tests assume that data points are independent (3, 18, 55). This has led to an explosion in the development of techniques generally referred to as modern comparative methods (1, 2, 5, 56–65). Standard statistical techniques can be used to compare evolutionary units (populations or species) when the units are sister taxa (but see ref. 66). These techniques have been used to examine the coevolution of morphology, ecology, and performance among species (7, 45, 65, 67–69).

We have shown that even between geographically close populations of a widespread lizard, *T. hispidus*, morphology and ecology can vary in response to changing habitat characteristics. Lizards occurring on rock surface habitats are morphologically compressed compared with savanna populations and have relatively longer hind limbs. The morphological compression is
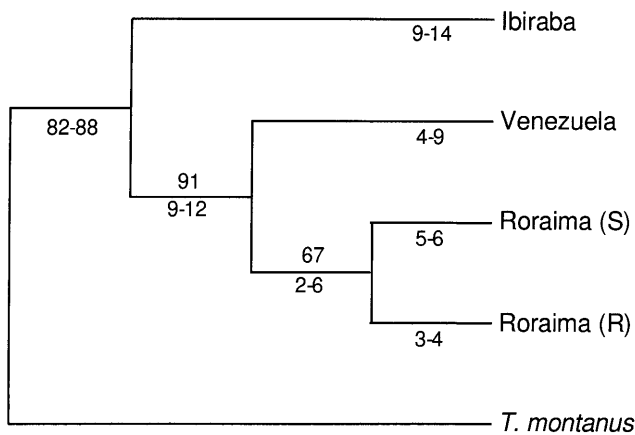

FIG. 4. Most parsimonious relationships among *T. montanus* and *T. hispidus* haplotypes (total number of mutational steps, 127; consistency index for characters informative under parsimony, 0.704). Numbers above internal branches are the proportion of times the branch appeared in 1,000 bootstrap replicates. Numbers below each branch are the minimum and maximum number of mutations occurring along each branch under all possible optimizations. R and S designate Roraima rock outcrop and savanna populations, respectively.

similar to that reported in other populations and species of *Tropidurus* occurring on rock surfaces in South America (26, 70). Relatively longer hind legs on lizards from the rock surfaces is consistent with the observation that lizards using open microhabitats tend to have longer hind legs than those using relatively less open microhabitats (21, 31, 32, 43, 71–73). Presumably, longer hind legs provide a performance advantage in open habitats, where running speed is important for predator escape or prey capture. However, performance consequences of morphological divergence remain to be determined for these *Tropidurus* populations. Microevolutionary change in morphology (limb length) has been observed in Caribbean anoles that were transplanted to different islands, but the extent to which the morphological change was due to habitat differences remains unclear (18). Our results differ from those of Losos (18) suggesting phenotypic response in morphology to habitat change in that we suggest adaptive genetic change in morphology in a manner predicted by habitat change.

The low genetic distance between the Roraima rock outcrop haplotype and that in the nearest savanna population relative to other *T. hispidus* haplotypes indicates that these populations are closely related, recently diverged, and have not had a long history of genetic isolation. Morphological stasis can occur despite extensive molecular divergence among populations and species [e.g., plethodontid salamanders (74)], or morphological evolution may be quite rapid and accompanied by little divergence at the molecular level [e.g., cichlid fishes (75) and echinoids (76)]. Morphological differentiation in the rock outcrop *T. hispidus* appears to have been quite rapid relative to molecular evolution.

Evaluating the causal basis of character evolution requires integration of ecological and phylogenetic data (19, 54, 63, 77, 78) to test hypotheses of the origin and maintenance of adaptation (79). Phylogenetic analysis indicates that the Roraima rock outcrop haplotype is nested within other *T. hispidus* haplotypes. If the mitochondrial gene tree is representative of the history of *T. hispidus* populations, then morphological divergence in the rock outcrop population is a derived feature within *T. hispidus*. Likewise, the rock outcrop habitat represents a derived selective regime within *T. hispidus*. Morphological changes exhibited by the rock outcrop population may provide a performance advantage to individuals, in particular the ability to use narrow crevices for escape (26, 70) and potentially greater sprint speed associated with increased hind-leg length (8). This change in selective regime coupled with phenotypic evolution is consistent with an hypothesis of adaptive morphological evolution in these lizards. Moreover, genetic and paleoclimatological data indicate that adaptive evolution has occurred rapidly in the rock outcrop population, possibly resulting from the combined effects of a small effective population size, cessation of gene flow from the neighboring savanna populations following isolation, and selection.

An alternative hypothesis is that differences in morphology between populations reflect opposite extremes of a distribution of morphological phenotypes (54). The differences in morphology between populations are (*i*) consistent with predictions based on other studies, (*ii*) in the direction predicted (i.e., they are derived), and (*iii*) involve at least some skeletal features (hind-limb bones). Taken together, the morphological

variation is not consistent with an explanation based *entirely* on differential expression of morphological phenotypes (i.e., phenotypic plasticity). Moreover, the morphological variation between these populations of *T. hispidus* is greater than morphological variation within any of 11 *Tropidurus* species we have examined (L.J.V., unpublished data).

1. Felsenstein, J. (1985) *Am. Nat.* **125,** 1–15.
2. Harvey, P. H. & Pagel, M. D. (1991) *The Comparative Method in Evolutionary Biology* (Oxford Univ. Press, Oxford).
3. Miles, D. B. & Dunham, A. E. (1993) *Annu. Rev. Ecol. Syst.* **24,** 587–619.
4. Losos, J. B. & Miles, D. B. (1994) in *Ecological Morphology: Integrative Organismal Biology*, eds. Wainwright, P. C. & Reilly, S. M. (Univ. of Chicago Press, Chicago), pp. 240–302.
5. Losos, J. B. (1990) *Evolution* **44,** 558–569.
6. Miles, D. B. (1994) in *Lizard Ecology: Historical and Experimental Perspectives*, eds. Vitt, L. J. & Pianka, E. R. (Princeton Univ. Press, Princeton), pp. 207–235.
7. Losos, J. B. (1990) *Ecol. Monogr.* **60,** 369–388.
8. Losos, J. B. (1990) *Evolution* **44,** 1189–1203.
9. Losos, J. B. (1992) *Syst. Biol.* **41,** 403–420.
10. Miles, D. B. & Ricklefs, R. E. (1984) *Ecology* **65,** 1629–1640.
11. Miles, D. B., Ricklefs, R. E. & Travis, J. (1987) *Am. Nat.* **129,** 347–364.
12. Ricklefs, R. E. & Miles, D. B. (1994) in *Ecological Morphology: Integrative Organismal Biology*, eds. P. C. Wainwright & Reilly, S. M. (Univ. of Chicago Press, Chicago), pp. 13–41.
13. Ricklefs, R. E., Cochran, D. & Pianka, E. R. (1981) *Ecology* **62,** 1474–1483.
14. Mulvihill, R. S. & Chander, C. R. (1991) *Condor* **93,** 172–175.
15. Carascall, L. M., Moreno, E. & Valido, A. (1994) *Evol. Ecol.* **8,** 25–35.
16. Arnold, S. J. (1983) *Am. Zool.* **23,** 347–361.
17. Losos, J. B. (1995) *Philos. Trans. R. Soc. London B* **349,** 69–75.
18. Losos, J. B. (1994) *Annu. Rev. Ecol. Syst.* **25,** 467–493.
19. Frost, D. R. (1992) *Am. Mus. Novit.* **3033,** 1–68.
20. Rodrigues, M. T. (1987) *Arq. Zool.* **31,** 105–230.
21. Williams, E. E. (1983) in *Lizard Ecology: Studies of a Model Organism*, eds. Huey, R. B., Pianka, E. R. & Schoener, T. W. (Harvard Univ. Press, Cambridge), pp. 326–370.
22. Vitt, L. J. (1991) *J. Herpetol.* **25,** 79–90.
23. Vitt, L. J. (1991) *Can. J. Zool.* **69,** 504–511.
24. Vitt, L. J. (1995) *Occas. Pap. Oklah. Mus. Nat. Hist.* **1,** 1–29.
25. Vitt, L. J. & Zani, P. A. (1996) *Herpetologica* **52,** 121–132.
26. Vitt, L. J. (1993) *Can. J. Zool.* **71,** 2370–2390.
27. Vanzolini, P. E. (1986) *Relatorio de Pesquisa* (Brasilia) No. 1, 50 pp.
28. Vanzolini, P. E. & Carvalho, C. M. (1991) *Pap. Avulsos Zool.* **37,** 173–226.
29. Vitt, L. J. & Carvalho, C. M. (1995) *Copeia* **1995,** 305–329.
30. Vitt, L. J., Zani, P. A. & Caldwell, J. P. (1996) *J. Trop. Ecol.* **12,** 81–101.
31. Pianka, E. R. (1986) *Ecology and Natural History of Desert Lizards* (Princeton Univ. Press, Princeton).
32. Pianka, E. R. (1969) *Ecology* **50,** 1012–1030.
33. Ab'Saber, A. N. (1982) in *Biological Diversification in the Tropics*, ed. Prance, G. T. (Columbia Univ. Press, New York), pp. 41–59.
34. Absy, M. L. & van der Hammen, T. (1976) *Acta Amazonica* **6,** 293–299.
35. Huber, O. (1982) in *Biological Diversification in the Tropics*, ed. Prance, G. T. (Columbia Univ. Press, New York), pp. 221–244.
36. Vuilleumier, B. S. (1971) *Science* **173,** 771–780.
37. Haffer, J. (1987) in *Biogeography and Quaternary History in Tropical America*, eds. Whitmore, T. C. & Prance, G. T. (Oxford Univ. Press, Oxford), pp. 1–18.
38. Prance, G. T. (1978) *Interciencia* **3,** 297–322.
39. Prance, G. T. (1987) in *Biogeography and Quaternary History in Tropical America*, eds. Whitmore, T. C. & Prance, G. T. (Oxford Univ. Press, Oxford), pp. 28–45.
40. Eiten, G. (1978) *Vegetatio* **36,** 169–178.
41. Ab'Saber, A. N. (1977) *Geomorfologia* **52,** 1–21.
42. Simpson, E. H. (1949) *Nature (London)* **163,** 688.
43. Pianka, E. R. (1973) *Annu. Rev. Ecol. Syst.* **4,** 53–74.
44. Hillis, D. M., Larson, A., Davis, S. K. & Zimmer, E. A. (1990) in *Molecular Systematics*, eds. Hillis, D. M. & Moritz, C. (Sinauer, Sunderland, MA), pp. 318–370.
45. Desjardins, P. & Morais, R. (1990) *J. Mol. Biol.* **212,** 599–634.
46. Titus, T. A. & Larson, A. (1995) *Syst. Biol.* **44,** 125–151.
47. Kumar, S., Tamura, K. & Nei, M. (1993) MEGA: Molecular Evolutionary Genetics Analysis (Pennsylvania State Univ., University Park), Version 1.0.
48. Swofford, D. L. (1993) PAUP: Phylogenetic Analysis Using Parsimony (Illinois Biological Survey, Urbana), Version 3.1.1.
49. Malhotra, A. & Thorpe, R. S. (1991) *Nature (London)* **353,** 347–348.
50. Emlet, R. B. (1991) *Am. Zool.* **31,** 707–725.
51. Emlet, R. B. (1994) *Am. Zool.* **34,** 570–585.
52. Goldschmid, A. & Kotrschal, K. (1989) in *Ecomorphology: Development and Concepts*, eds. Splechtna, H. & Hilgers, H. (Gustac Fischer, Stutgart, Germany), pp. 501–512.
53. Mullaney, M. D. & Gale, L. D. (1996) *Copeia* **1996,** 167–180.
54. Wainwright, P. C. & Reilly, S. M., eds. (1994) *Ecological Morphology: Integrative Organismal Biology* (Univ. of Chicago Press, Chicago).
55. Martins, E. P. & Hansen, T. F. (1996) in *Phylogenies and the Comparative Method in Animal Behavior*, ed. Martins, E. P. (Oxford Univ. Press, Oxford), pp. 22–75.
56. Martins, E. P. (1996) *Evolution* **50,** 12–22.
57. Martins, E. P. (1996) *Evolution* **50,** 1750–1765.
58. Lauder, G. V. (1982) *J. Theor. Biol.* **97,** 57–67.
59. Lauder, G. V. (1990) *Annu. Rev. Ecol. Syst.* **20,** 317–340.
60. Lauder, G. V. (1991) in *Biomechanics in Evolution*, eds. Rayner, J. M. V. & Wooton, R. J. (Cambridge Univ. Press, Cambridge), pp. 1–19.
61. Brooks, D. R. (1985) *Ann. Mo. Bot. Gard.* **72,** 660–680.
62. Lauder, G. V. & Liem, K. F. (1989) in *Complex Organismal Functions: Integration and Evolution in Vertebrates*, eds. Wake, D. B. & Roth, G. (Wiley, Chichester, U.K.), pp. 63–78.
63. Brooks, D. R. & McLennan, D. A. (1991) *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology* (Univ. of Chicago Press, Chicago), pp. 60–98.
64. Lauder, G. V., Armand, M. L. & Rose, M. R. (1993) *Trends Ecol. Evol.* **8,** 294–297.
65. Losos, J. B. (1994) in *Lizard Ecology: Historical and Experimental Perspectives*, eds. Vitt, L. J. & Pianka, E. R. (Princeton Univ. Press, Princeton), pp. 319–333.
66. Garland, T., Jr., & Adolf, S. C. (1994) *Physiol. Zool.* **67,** 797–828.
67. Huey, R. B. (1982) *Koedoe* **25,** 43–48.
68. Garland, T., Jr. (1994) in *Lizard Ecology: Historical and Experimental Perspectives*, eds. Vitt, L. J. & Pianka, E. R. (Princeton Univ. Press, Princeton), pp. 237–259.
69. Garland, T., Jr., & Losos, J. B. (1994) in *Ecological Morphology: Integrative Organismal Biology*, eds. Wainwright, P. C. & Reilly, S. M. (Univ. of Chicago Press, Chicago), pp. 240–302.
70. Vitt, L. J. (1981) *Am. Nat.* **117,** 506–514.
71. Lundelius, E. L., Jr. (1957) *Evolution* **11,** 65–83.
72. Collette, B. B. (1961) *Bull. Mus. Comp. Zool.* **125,** 137–162.
73. Pounds, J. A. (1988) *Ecol. Monogr.* **58,** 299–320.
74. Larson, A. (1989) in *Speciation and its Consequences*, eds. Otte, D. & Endler, J. A. (Sinauer, Sundland, MA), pp. 579–598.
75. Meyer, A., Kocher, T. D., Basasibwaki, P. & Wilson, A. C. (1990) *Nature* (*London*) **347,** 550–553.
76. Smith, A. B., Littlewood, D. T. J. & Wray, G. A. (1995) *Philos. Trans. R. Soc. London B* **349,** 11–18.
77. Mayden, R. L. (1987) in *Community and Evolutionary Ecology of North American Stream Fishes*, eds. Matthews, W. J. & Heins, D. C. (Univ. of Oklahoma Press, Norman), pp. 210–222.
78. Gorman, O. T. (1992) in *Systematics, Historical Ecology, and North American Freshwater Fishes*, ed. Mayden, R. L. (Stanford Univ. Press, Stanford), pp. 659–688.
79. Baum, D. A. & Larson, A. (1991) *Syst. Zool.* **40,** 1–18.