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ECOLOGICAL CORRELATES OF NUMBER OF SUBDIGITAL LAMELLAE IN ANOLES

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ABSTRACT: We investigated whether a relationship exists between the number of lamellae and the height and diameter of perches utilized by a diverse set of anoline lizards. Although the number of lamellae on both the fore- and hindfoot is related to both ecological variables, these results are confounded by body size. When the effect of size is removed, the number of lamellae is related to perch height, but not perch diameter. When the data are analyzed in a phylogenetic framework, results are similar, but only the number of lamellae on the forefoot is related to perch height. Consequently, although inter- and intraspecific correlations exist among the number of lamellae on different toes of the fore- and hindfeet, examining the number of lamellae on a single toe may be insufficient for ecomorphological analyses.

Key words: Anolis; Habitat use; Lamellae; Toe-pad

SUBDIGITAL toe-pads composed of expanded scales, termed lamellae, have evolved independently in three lineages of arboreal lizards: anoles, geckos, and praesinohaemid skinks (Ruibal and Ernst, 1965; Williams and Peterson, 1982). In theory, pads could provide increased functional capabilities in two ways. First, in most species, pads are covered with millions of microscopic setae (Ruibal and Ernst, 1965; Williams and Peterson, 1982) which are thought to enhance adhesive ability on smooth surfaces by forming intermolecular bonds with free electrons on the surface of the substrate (Cartmill, 1975; Hiller, 1968, 1975). In support of this hypothesis, a recent study of anoles, geckos, and skinks indicated that species with relatively larger pads, and presumably greater numbers of setae, have greater ability to cling to a smooth surface (Irschick et al., 1996). Second, lamellae may enhance the flexibility of the toe so that pads can be molded to narrow or irregular surfaces such as twigs (Cartmill, 1985). Consequently, species that use particularly narrow or irregular surfaces might be expected to have high numbers of lamellae because of the enhanced pad flexibility that they would provide. However, this second hypothesis has never been tested.

Although toe-pads clearly arose as adaptations to arboreality (Larson and Losos, 1996), little research has been directed to understanding the manner in which variation in pad structure among species represents adaptation to different environmental conditions. Nonetheless, a number of studies have reported a correlation between perch height and pad size or lamellae number in geckos (Collette, 1962; Dixon and Huey, 1970; Huey and Dixon, 1970; Pianka, 1986; Pianka and Pianka, 1976) and anoles (Collette, 1961; Lister, 1976). However, most of these studies have included relatively few species. In addition, these studies were conducted prior to the realization that comparative analyses that ignore phylogenetic information may be statistically invalid (Felsenstein, 1985); incorporation of such information may reveal that support for a relationship is weaker than previously believed. To circumvent these difficulties, we present an analysis of the relationship between lamellae number and substrate characteristics for 53 species of anoline lizards. Although the phylogeny of anoles is not completely resolved, enough information is available to permit this analysis to be conducted in a phylogenetic framework.

In addition to investigating whether number of lamellae correlates with the height or diameter of perchs, the evolu-

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tionary radiation of Caribbean *Anolis* provides an additional means of examining the adaptive importance of lamellae number. On each island of the Greater Antilles, species have diversified into a series of ecomorphs, which differ in morphology, habitat use, and behavior (Williams, 1972, 1983). Comparison among the anole faunas of the Greater Antilles indicates that the same set of six ecomorph classes has evolved independently on each island, with the exception that the "trunk" ecomorph is absent on Puerto Rico and Jamaica and the "grass-bush" ecomorph is absent on Jamaica (Hass et al., 1993; Losos, 1992; Williams, 1983). Members of the same ecomorph class are similar not only in their use of habitats, but also in the manner in which they move through the environment; for example, "trunk-ground" anoles tend to jump frequently whereas "twig" anoles move predominantly by crawling (Losos, 1990*a*; Moermond, 1979). To the extent that differences in habitat use and locomotor patterns favor differences in toe-pad structure, we would expect that the ecomorph types should vary in number of lamellae.

MATERIALS AND METHODS

We examined 545 adult male individuals of 62 species of Caribbean anoles and *Phenacosaurus heterodermus* ($\bar{x}$ = 8.7 individuals/species; range 1–34). The number of lamellae on the second and third toes of the forelimb and the third and fourth toes of the hindlimb were counted by the first author using a dissecting microscope. On the fourth hindlimb toe, we counted all lamellae underlying the third and fourth phalanges of pedal digit IV. On the other toes, all expanded and undivided scales were counted. Snout–vent length (SVL) of each specimen was measured as part of a larger morphometric study (K. Beuttel and J. Losos, unpublished data). The mean of each variable was calculated for each species.

Data for adult males were available on mean perch height for 53 species and mean perch diameter for 50 species (Irschick and Losos, 1996; Losos, 1990*b*, 1992, unpublished); three species (*Anolis longitibialis*,

A. strahmi, and *Chamaelinorops barbouri*) primarily use habitats (rock walls or ground) upon which perch diameter cannot be meaningfully recorded. All morphological and ecological variables were ln-transformed for statistical analyses. To remove the effects of body size, each variable was regressed against SVL and the species means of the resulting residual values were used in subsequent analyses.

Comparative analyses using species values may be invalid because the values for species may not be independent (Felsenstein, 1985). To circumvent this problem, we used Felsenstein's (1985) independent contrast method utilizing a phylogenetic hypothesis (Fig. 1), which is a composite drawn from previous works (Burnell and Hedges, 1990; Hass et al., 1993; Hedges and Burnell, 1990; Losos, 1992; Roughgarden and Pacala, 1989). Purvis and Garland (1993) have provided a method for analyzing data using a phylogeny containing polytomies (see also Stamps et al., 1997, for discussion of this method). This method involves arbitrarily resolving all polytomies into a tree composed entirely of bifurcating branches, but with the branches between members of a polytomy set to a length of zero. Results of an independent contrasts analysis are then evaluated with both the normal number of degrees of freedom and with the usual number minus the number of lineages involved within polytomies. These two interpretations, then, represent the maximally liberal and conservative interpretation of statistical results given the polytomies (Purvis and Garland, 1993).

This procedure was used in the analyses of number of lamellae versus perch height and diameter. Residuals were calculated by regressing contrasts of each variable against contrasts in SVL. Because data for branch lengths were not available for this phylogeny, all branches, except those involved in polytomies, were set to a length of one, thus implying a speciational model of character evolution (Garland et al., 1992). All correlations and regressions involving contrasts were conducted through the origin (Garland et al., 1992). For significant results, we report the most con-

roquet
extremus
aeneus
trinitatis
richardi
griseus
luciae
occultus, twig, Puerto Rico
Phenacosaurus heterodermus
Chamaelinorops barbouri
sheplani, twig, Hispaniola
fowleri
equestris, crown-giant, Cuba
darlingtoni, twig, Hispaniola
porcatus, trunk-crown, Cuba
carolinensis
longiceps
maynardi
angusticeps, twig, Cuba
evermanni, trunk-crown, Puerto Rico
stratulus, trunk-crown, Puerto Rico
acutus
cristatellus, trunk-ground, Puerto Rico
cooki, trunk-ground, Puerto Rico
monensis
gundlachi, trunk-ground, Puerto Rico
poncensis, grass-bush, Puerto Rico
pulchellus, grass-bush, Puerto Rico
krugi, grass-bush, Puerto Rico
distichus, trunk, Hispaniola
brevirostris, trunk, Hispaniola
schwartzi
wattsi
pogus
leachi
gingivinus
bimaculatus
lividus
ferreus
sabanus
marmoratus
cuvieri, crown-giant, Puerto Rico
coelestinus, trunk-crown, Hispaniola
chlorocyanus, trunk-crown, Hispaniola
aliniger, trunk-crown, Hispaniola
semilineatus, grass-bush, Hispaniola
olssoni, grass-bush, Hispaniola
bahorucoensis, grass-bush, Hispaniola
etheridgei
christophei
strahmi, trunk-ground, Hispaniola
longitibialis, trunk-ground, Hispaniola
cybotes, trunk-ground, Hispaniola
marcanoi, trunk-ground, Hispaniola
insolitus, twig, Hispaniola
sagrei, trunk-ground, Cuba and Jamaica
valencienni, twig, Jamaica
reconditus
lineatopus, trunk-ground, Jamaica
garmani, crown-giant, Jamaica
opalinus, trunk-crown, Jamaica
conspersus
grahami, trunk-crown, Jamaica

FIG. 1.—Phylogenetic relationships of the taxa in this study based on a number of studies (see text). Island and ecomorph class indicated for all Greater Antillean species belonging to one of the ecomorph classes; some species do not belong in any of the classes.

servative probability value given the number of polytomies in the phylogenetic tree; for non-significant results, we report the most liberal P-value. In no case was there a qualitative difference between the most liberal and conservative interpretation.

We also used analysis of variance to examine whether the ecomorphs of *Anolis* differed in number of lamellae. To correct for possible phylogenetic effects, we chose only one member (the first one alphabetically) of each ecomorph class from each of the Greater Antillean islands. This procedure reduced the data set to 18 species: four species from Jamaica and Cuba, five from Hispaniola and Puerto Rico; four

trunk-ground, trunk-crown, and twig anoles, three crown-giants, two grass-bush anoles, and one trunk anole. Studies of anole phylogeny indicate that members of the same ecomorph on different islands are never closely related, with the possible exception of the crown-giants of Puerto Rico and Hispaniola (Burnell and Hedges, 1990; Cannatella and de Queiroz, 1989; Guyer and Savage, 1986; Hass et al., 1993); inspection of Fig. 1 indicates that in no case are members of the same ecomorph class included in this analysis closely related. Thus, phylogenetic artifacts should not confound this analysis.

We examined intraspecific variation for one species, *A. carolinensis*. Adult lizards were purchased from a dealer in Schrieber, Louisiana. Lamellae were counted on toes 2–5 on the fore- and hindfeet of 42 males and 24 females. The number of lamellae on a toe was counted by identifying the most proximal undivided scale at least twice as wide as surrounding plantar scales and then counting all scales distal to that scale. Size effects were not considered, because number of lamellae does not change ontogenetically (Collette, 1961).

RESULTS

Interspecific Comparisons

Number of lamellae on different toes was highly correlated among species ($r^2 >$ 0.86 for all pairwise comparisons; $n = 63$); the highest correlation was between lamellae on forefoot toe 2 and forefoot toe 3 ($r^2 = 0.96$). However, these correlations could arise incidentally if the number of lamellae on each toe is a function of body size. Indeed, number of lamellae on all toes correlates strongly with SVL ($r^2 > 0.62$; $P < 0.001$, $n = 63$). Nonetheless, number of lamellae on all toes is still highly correlated when the effect of size is removed through the use of residuals ($r^2 > 0.65$, $P < 0.0005$). Again, the highest correlation is between lamellae on the forefeet ($r^2 = 0.90$).

Due to the high correlations among toes in number of lamellae, we used only forefoot toe 3 and hindfoot toe 4 in analyses of the relationship between number of lamellae and use of microhabitats. Using least-squares regression, height and di-
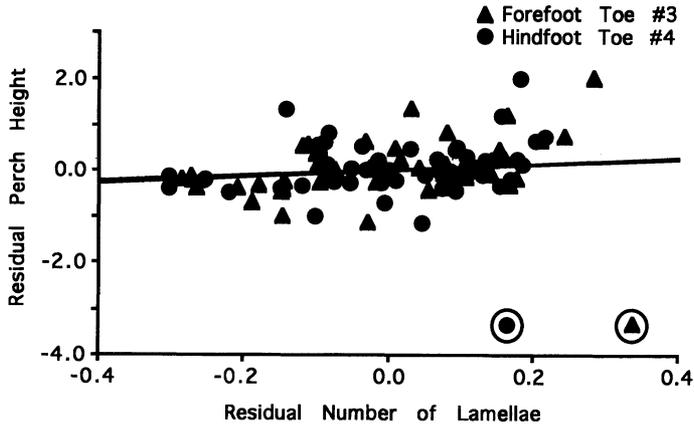
FIG. 2.—Relationship between residual perch height and residual number of lamellae. Residuals calculated from regressions against snout–vent length. Circled points are *Chamaelinorops barbouri.*

ameter of perches are related to number of lamellae on forefoot toe 3 (height: r^2 = 0.20, P < 0.001, n = 53; diameter: r^2 = 0.13, P < 0.01, n = 50) and hindfoot toe 4 (height: r^2 = 0.19, P < 0.001, n = 53; diameter: r^2 = 0.10, P < 0.01, n = 50). However, both height (r^2 = 0.25, P < 0.001, n = 53) and diameter (r^2 = 0.17, P < 0.002, n = 50) are related to SVL. With the effect of size removed from height, diameter, and number of lamellae using residuals, neither perch height (Fig. 2: forefoot toe 3: r^2 = 0.00, P > 0.30; hindfoot toe 4: r^2 = 0.00; P > 0.40) nor perch diameter (forefoot toe 3: r^2 = 0.00, P > 0.60; hindfoot toe 4: r^2 = 0.00, P > 0.95) is related to number of lamellae. However, in the analysis between number of lamellae and perch height, *Chamaelinorops barbouri* is a conspicuous outlier (Fig. 2). *Chamaelinorops barbouri* is a morphologically, ecologically, and behaviorally aberrant anoline lizard in many respects (Flores et al., 1994; Forsgaard, 1983; Jenssen and Feely, 1991); of relevance to this study are the observations that this species is almost exclusively terrestrial (Flores et al., 1994) and the fine structure of the subdigital setae differs from other anoles (Peterson, 1983). If *C. barbouri* is excluded from the analysis of perch height (note that no data are available for perch diameter because this species is rarely observed off the ground), a significant relationship exists between relative perch height and relative number of lamellae (forefoot toe 3: r^2 = 0.21, P <

0.001, n = 52; hindfoot toe 4: r^2 = 0.06, P < 0.05).

In the phylogenetic analyses, many of the results are qualitatively similar. Contrasts for lamellae number are highly correlated with each other (r^2 > 0.68 for all comparisons, n = 62, P < 0.001) and with contrasts for SVL (r^2 > 0.03, n = 62, P < 0.05). Even with the effect of SVL removed, numbers of lamellae are still correlated (r^2 > 0.68, n = 62, P < 0.001). Contrasts in number of lamellae are related to perch height (regression through the origin, n = 52, forefoot toe 3: r^2 = 0.08, P < 0.05; hindfoot toe 4: r^2 = 0.08, P < 0.05) and diameter (n = 49, forefoot toe 3: r^2 = 0.14, P < 0.01; hindfoot toe 4: r^2 = 0.15, P < 0.01). With the effect of SVL removed, no relationship exists between number of lamellae and height or diameter when all contrasts are considered (height: n = 52, forefoot toe 3, r^2 = 0.02, P < 0.35; hindfoot toe 4, r^2 = 0.03, P < 0.25; diameter: n = 49, forefoot toe 3, r^2 = 0.01, P < 0.50; hindfoot toe 4, r^2 = 0.01, P < 0.45). However, when the analysis is conducted excluding *Chamaelinorops*, a significant relationship exists between perch height and forefoot toe 3 (r^2 = 0.14; P < 0.01) but not hindfoot toe 4 (r^2 = 0.002, P < 0.80).

Variation among Ecomorphs

Variation exists in number of lamellae among the anole ecomorphs (Fig. 3; Analyses of Variance, $F_{5,33}$ > 12.59, P < 0.001
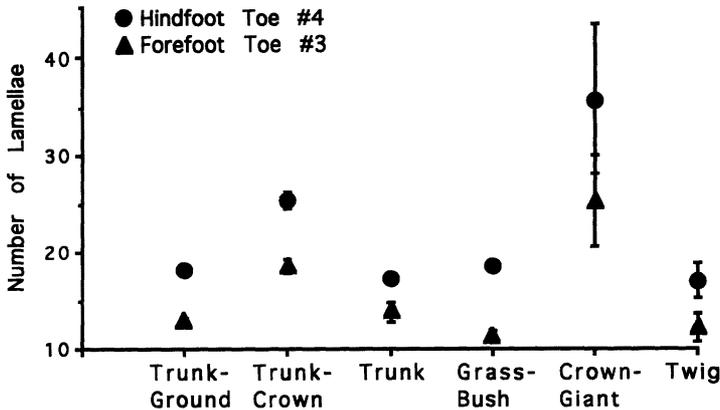
FIG. 3.—Mean ± 1 SE for number of lamellae for the ecomorph classes.

in all cases; patterns are almost identical for forefoot toes 2 and 3 and for hindfoot toes 3 and 4). Post-hoc comparisons using Tukey's test indicate that crown-giants have significantly more lamellae than other ecomorphs, except that trunk-crown and crown-giants are in some cases not statistically distinct. Similarly, trunk-crown anoles have more lamellae than all other anoles, except that trunk-crown and trunk anoles are not distinct for number of lamellae on forefeet toes 2 and 3. The other four ecomorphs are not statistically distinguishable. When the data set is reduced to one member of each ecomorph class per island (see Materials and Methods), significant variation is still discovered ($F_{5, 12} > 6.61$, $P < 0.005$; $n = 18$).

Variation also exists among ecomorphs when number of lamellae (forefoot toe 3 and hindfoot toe 4) is corrected for size (Fig. 4). In both cases, the analysis of variance was significant ($F_{5, 33} > 13.0$, $P < 0.001$). Post-hoc analyses indicate that, with the effect of size removed, trunk-crown anoles have more lamellae on toe 3 of the forefoot than do trunk-ground, grass-bush, and twig anoles (with the trunk-crown versus crown-giant and trunk versus trunk-ground comparisons nearly significant). With regard to hindfoot toe 4, trunk-crown, grass-bush, and crown-giant anoles have more lamellae than trunk-ground anoles, and trunk-crown and grass-bush anoles have more lamellae than twig anoles. In the smaller data set, size-corrected hind-

foot toe 4 is marginally non-significant ($F_{5, 12} = 2.77$, $P < 0.07$), but all analyses on other toes are significant ($F_{5, 12} > 4.63$, $P < 0.025$).

Intraspecific Comparison

Males of *A. carolinensis* have more lamellae on each toe than females of the species (mean difference = 1.2; t-test, $t > 2.74$, $P < 0.01$ in all cases). Among males, 25 of 28 pairwise correlations between number of lamellae on different toes are significant (the exceptions being hindfoot toe 2 versus hindfoot toe 4 and hindfoot toe 5 versus hindfeet toes 3 and 4). For females, 15 of 28 correlations are significant with no pattern of which comparisons are significant and which are not. In separate analyses of the toes of males and females, only two of 16 correlations with SVL are significant (male forefoot toe 2 and hindfoot toe 2).

DISCUSSION

In agreement with previous studies, we found that a significant relationship exists between number of lamellae and height and diameter of perches among a diverse set of anoles. However, both of these relationships are confounded by body size; larger species of anoles not only have more lamellae, but also perch higher and on broader supports than smaller species. Because of their greater mass, larger anoles presumably need better developed toe-pads (Collette, 1961). Larger lizards by
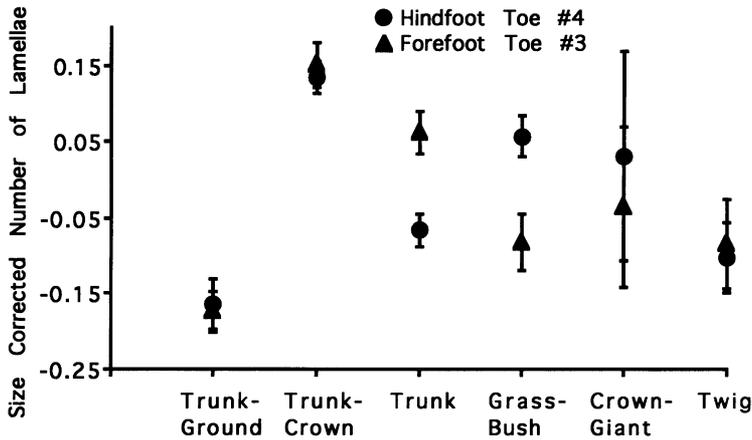
FIG. 4.—Mean ± 1 SE for residual number of lamellae for the ecomorph classes.

necessity must use larger diameter supports than smaller lizards. Consequently, the relationship between number of lamellae and perch diameter may be artifactual. Indeed, with the confounding effect of body size removed, no relationship exists between number of lamellae and perch diameter.

Similarly, larger lizards may perch higher for a variety of reasons related, for example, to foraging (Rummel and Roughgarden, 1985) or thermoregulation (O. J. Sexton, personal communication), in which case the relationship between number of lamellae and perch height might also be artifactual. With the effect of size removed, however, a relationship is still found between number of lamellae and perch height. When phylogenetic information is incorporated into this analysis, a relationship exists between number of lamellae on the forefoot and perch height, but no relationship occurs between perch height and number of lamellae on the hindfoot.

A relationship between number of lamellae and habitat use is also revealed by comparison of the number of lamellae of ecomorphs. The anole ecomorph classes, which have evolved independently on each island in the Greater Antilles, differ consistently in habitat use and locomotor patterns (references in Introduction). Our results indicate that variation exists among ecomorphs in number of lamellae. In par-

ticular, the trunk-crown anoles, which perch high, often use narrow supports, and often tend to move slowly and jump relatively infrequently (Irschick and Losos, 1996; Moermond, 1979), have the greatest number of lamellae.

These results beg the question of why species that perch higher have greater numbers of lamellae. On one hand, biomechanical studies still need to establish the functional consequences of lamellae number. Recent studies have established that lizards with relatively larger toe-pads have greater clinging ability on smooth surfaces (Irschick et al., 1996). However, these studies involve the size of the pad rather than the number of lamellae comprising it; the two measures are not necessarily correlated, because pads may be increased in size either by increasing the size or number of lamellae. Unless the number of lamellae is correlated with the size of the pad, the functional significance of lamellae number will require further investigation.

In addition, further research is required to understand why greater clinging capabilities are required by species that perch higher (Moermond, 1979). One possibility is that the structural habitat changes with perch height such that higher perches are more difficult to cling to and thus require greater capabilities. Alternatively, the cost of falling may be greater from higher points, either as a result of injury [unlikely

for most anoles, which are too small to be hurt by falling (e.g., Oliver, 1951)] or as a result of the cost of climbing back up the tree. A third possibility is that differences in perch height are correlated with differences in the way the environment is used in terms of activities such as foraging, locomotion, social interactions, and escape from predators. Differences in the demands made by such activities, then, may be responsible for the different functional requirements leading to differences in number of lamellae. The ecomorphs tend to differ in all of these activities (Hicks and Trivers, 1983; Irschick and Losos, 1996; Losos, 1990a; Moermond, 1979, 1981), which suggests that this possibility requires further investigation.

Our detailed investigation of one species, A. carolinensis, found that males have slightly more lamellae than females, a finding that has been noted for other species (e.g., Collette, 1961). Intersexual variation in habitat use and locomotion is common in anoles (e.g., Jenssen et al., 1995; Schoener, 1967, 1968). Investigation of whether an intersexual relationship exists between number of lamellae and habitat use and/or behavior would prove interesting.

Our results indicate that both within- and among-species, the number of lamellae on different toes is highly correlated. Nonetheless, the relationship between number of lamellae and habitat use varies among toes. For example, we found that number of lamellae on the forefoot, but not on the hindfoot, is related to perch height. Furthermore, trunk and grass–bush anoles have relatively many lamellae on their hindfeet, but not on their forefeet, relative to other ecomorphs (Fig. 4). An interesting area for future research would be investigation of the manner in which the relationship between number of lamellae and habitat differs among toes. In addition, these results indicate that future studies should examine the number of lamellae on more than just one toe.

LITERATURE CITED

BURNELL, K. L., AND S. B. HEDGES. 1990. Relationships of West Indian Anolis (Sauria: Iguanidae): An approach using slow-evolving protein loci. Carib. J. Science. 26:7–30.

CANNATELLA, D. C., AND K. DE QUEIROZ. 1989. Phylogenetic systematics of the anoles: Is a new taxonomy warranted? Syst. Zool. 38:57–68.

CARTMILL, M. 1985. Climbing. Pp. 73–88. In M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, (Eds.), Functional Vertebrate Morphology. Belknap Press, Cambridge, Massachusetts.

COLLETTE, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. Bull. Mus. Comp. Zool. 125:137–162.

———. 1962. Arboreality, lamellae, and body size in two species of Cuban geckos. Copeia 1962:644–645.

DIXON, J. R., AND R. B. HUEY. 1970. Systematics of the lizards of the gekkonid genus Phyllodactylus of mainland South America. Los Angeles County Mus. Contrib. Sci. 192:1–78.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. Am. Nat. 125:1–15.

FLORES, G., J. H. LENZYCKI, AND J. PALUMBO, JR. 1994. An ecological study of the endemic Hispaniolan anoline, Chamaelinorops barbouri (Lacertilia: Iguanidae). Breviora 499:1–23.

FORSGAARD, K. 1983. The axial skeleton of Chamaelinorops. Pp. 284–295. In A. G. J. Rhodin and K. Miyata, (Eds.), Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

GARLAND, T., Jr., P. H. HARVEY, AND A. R. IVES. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst. Biol. 41:18–32.

GUYER, C., AND J. M. SAVAGE. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). Syst. Zool. 35:509–531.

HASS, C. A., S. B. HEDGES, AND L. R. MAXSON. 1993. Molecular insights into the relationships and biogeography of West Indian anoline lizards. Biochem. Syst. Ecol. 21:97–114.

HEDGES, S. B., AND K. L. BURNELL. 1990. The Jamaican radiation of Anolis (Sauria: Iguanidae): An analysis of relationships and biogeography using sequential electrophoresis. Carib. J. Sci. 26:31–44.

HICKS, R. A., AND R. L. TRIVERS. 1983. The social behavior of Anolis valencienni. Pp. 570–595. In A. G. J. Rhodin and K. Miyata, (Eds.), Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

HILLER, U. 1968. Untersuchungen zum Feinbau und zur Funktion der Haftborsten von Reptilien. Z. Morphol. Tiere 62:307–362.

————. 1975. Comparative studies on the functional morphology of two gekkonid lizards. J. Bombay Nat. Hist. Soc. 73:278–282.

HUEY, R. B., AND J. R. DIXON. 1970. A new *Pseudogonatodes* from Peru with remarks on other species of the genus. Copeia 1970:538–542.

IRSCHICK, D. J., C. C. AUSTIN, K. PETREN, R. N. FISHER, J. B. LOSOS, AND O. ELLERS. 1996. A comparative analysis of clinging ability among pad-bearing lizards. Biol. J. Linn. Soc. 59:21–35.

IRSCHICK, D. J., AND J. B. LOSOS. 1996. Morphology, ecology, and behavior of the twig anole *Anolis angusticeps*. Pp. 291–301. *In* R. Powell and R. W. Henderson, (Eds.), Contributions to West Indian Herpetology: A Tribute to Albert Schwartz. Society for the Study of Amphibians and Reptiles: Ithaca, New York.

JENSSEN, T. A., AND P. C. FEELY. 1991. Social behavior of the male anoline lizard *Chamaelinorops barbouri*, with a comparison to *Anolis*. J. Herpetol. 25:454–462.

JENSSEN, T. A., N. GREENBERG, AND K. A. HOVDE. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. Herpetol. Monogr. 8:41–62.

LARSON, A., AND J. B. LOSOS. 1996. Phylogenetic systematics of adaptation. Pp. 187–220. *In* G. Lauder and M. Rose, (Eds.), Adaptation. Academic Press, New York, New York.

LISTER, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: Ecological consequences of reduced competition. Evolution 30:659–676.

LOSOS, J. B. 1990a. Concordant evolution of locomotor behaviour, display rate, and morphology in *Anolis* lizards. Anim. Behav. 39:879–890.

————. 1990b. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: An evolutionary analysis. Ecol. Monogr. 60:369–388.

————. 1992. The evolution of convergent structure in Caribbean *Anolis* communities. Syst. Biol. 41:403–420.

MOERMOND, T. C. 1979. The influence of habitat structure on *Anolis* foraging behavior. Behaviour 70:147–167.

————. 1981. Prey-attack behavior of *Anolis* lizards. Z. Tierpsychol. 56:128–136.

OLIVER, J. A. 1951. "Gliding" in amphibians and reptiles, with a remark on an arboreal adaptation in the lizard, *Anolis carolinensis carolinensis* Voigt. Am. Nat. 85:171–176.

PETERSON, J. A. 1983. The evolution of the subdigital pad in *Anolis*. I. Comparisons among the anoline genera. Pp. 245–283. *In* A. G. J. Rhodin and K. Miyata, (Eds.), Advances in Herpetology and Evolutionary Biology. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

PIANKA, E. R. 1986. Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure. Princeton University Press, Princeton, New Jersey.

PIANKA, E. R., AND H. D. PIANKA. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. Copeia 1976:125–142.

PURVIS, A., AND T. GARLAND, Jr. 1993. Polytomies in comparative analyses of continuous characters. Syst. Biol. 42:569–575.

ROUGHGARDEN, J., AND S. PACALA. 1989. Taxon cycle among *Anolis* lizard populations: Review of the evidence. Pp. 403–432. *In* D. Otte and J. Endler (Eds.), Speciation and Its Consequences. Sinauer, Sunderland, Massachusetts.

RUIBAL, R., AND V. ERNST. 1965. The structure of the digital setae of lizards. J. Morphol. 117:271–294.

RUMMEL, J. D., AND J. ROUGHGARDEN. 1985. Effects of reduced perch-height separation on competition between two *Anolis* lizards. Ecology 66:430–444.

SCHOENER, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. Science 155:474–477.

————. 1968. The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. Ecology 49:704–726.

STAMPS, J. A., J. B. LOSOS, AND R. M. ANDREWS. 1997. A comparative study of population density and sexual size dimorphism in lizards. Am. Nat. 149:64–90.

WILLIAMS, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. Evol. Biol. 6:47–89.

————. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge, Massachusetts.

WILLIAMS, E. E., AND J. A. PETERSON. 1982. Convergent and alternative designs in the digital adhesive pads of scincid lizards. Science 215:1509–1511.