MHNG 1034.14–19, Foulassi and surrounding, Cameroon, 1960–1961, coll. Perret; MNHN 1959.0025–0026, Cameroun, coll. Perret; MRAC B.103114–103116, Foulassi, 1960, coll. Perret; Congo: LIV 1991.11.208 Goumina, Congo Brazzaville, 27 November 1990; LIV 1991.11.206–207 (tadpoles), Béna, Congo Brazzaville, 22 November 1990, coll. Largen.; Democratic Republic of Congo (Zaire): ZSM 44/1984, Prov. Kivu, Irangi at river Luoho, 850 m, Zaire, 4.-7. March 1984, coll. Fuchs; MRAC B.112549 Bunyakiri, territory of Kalehe, Kivu, Congo Belge, 5.-7. June 1949, coll. Laurent.

Acanthixalus sonjae sp. nov.—type series.

Ecomorphological Differences in Toepad Characteristics between Mainland and Island Anoles

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ABSTRACT.—Anoles (*Anolis, Chamaeleolis, Chamaelinorops, Phenacosaurus*) differ greatly in size and shape of their subdigital toepads. We sampled 79 anole species to address two issues. First, is toepad size significantly related to habitat use? Second, do anoles from mainland Central and South America differ from Caribbean anoles in either the size of their toepads or in the relationship between toepad shape and habitat use? Among all anoles, toepad size increases with both perch height and diameter, although when the effects of body size are removed, these relationships are weakened. Morphological differences exist between toepads of anoles from the two regions. Caribbean anoles have larger toepads relative to snout–vent length and wider pads at larger body sizes compared to mainland species. Relationships between toepad morphology and habitat use characteristics do not differ significantly between the two groups of anoles. However, with effects of size removed, Caribbean anoles have larger and wider toepads relative to both perch height and diameter. These findings suggest that anoles in island habitats may require larger toepads than mainland anoles to use their arboreal habitats. The potential functional consequences of these differences in toepad morphology provide a promising avenue for future studies.

A fundamental issue in evolutionary biology concerns factors that influence shape of adaptive radiations. One means of addressing this issue is to compare morphological and ecological characteristics of closely related groups of species in different environments. An obvious comparison is between mainland and island faunas, which often display a remarkable array of differences in life history, morphology, and behavior (e.g., Nussbaum and Wu, 1995; Case and Schwaner, 1993; Petren and Case, 1997). Yet, with a few exceptions, most of these studies have focused only on one or two species and have not quantitatively compared groups of species in mainland and island habitats.

Caribbean and mainland (Central and South American) anoline lizards provide an excellent point of comparison for understanding how environmental differences shape the pathways of adaptive radiations. In both the Caribbean and the mainland, anoles have diversified tremendously (> 140 species in each region) under different selective pressures, producing species that vary in morphology, habitat use, behavior, and function (Williams, 1972, 1983; Fitch, 1975, 1976; Andrews, 1979; Pounds, 1988; Losos, 1995). In a comparison of 16 mainland and 33 Caribbean anole species, Irschick et al. (1997) showed that ecomorphological relationships differed dramatically in the two regions. An extension of that analysis, presented here, focuses on differences among regions in a key morphological characteristic, the subdigital toepad.

Lizard toepads provide an excellent opportunity to study patterns of adaptation and macroevolution (Bauer and Good, 1986; Irschick et al., 1996). Previous work has shown that toepads with clinging capabilities evolved independently in three different groups of arboreal lizards:

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geckos, anoles, and some skinks (Ruibal and Ernst, 1965; Williams and Peterson, 1982). In each case, the expanded subdigital pad is divided into a number of transverse scales, termed lamellae. Each lamella is covered with tens of thousands of microscopic, hairlike keratinous structures called setae, with each containing hundreds of projections that terminate in spatula-shaped structures (Maderson, 1964; Ruibal and Ernst, 1965; Bauer and Good, 1986). These spatulae play a prominent role in the ability of these lizards to cling to smooth surfaces (Hiller, 1968; Cartmill, 1985; Irschick et al., 1996; Autumn et al., 2000). A recent study that measured the adhesive force of setae of the Tokay gecko (*Gekko gecko*) supports the hypothesis that Van der Waal's forces may be responsible for adhesion (Autumn et al., 2000).

Repeated evolution of toepads in arboreal lizards and the obvious functional advantage they confer leaves little doubt that these structures evolved as adaptations for climbing. Some authors suggest that toepads are key innovations that facilitated occupation of a new adaptive zone and subsequent evolutionary diversification (e.g., Russell, 1979; Larson and Losos, 1996). However, surprisingly little research has directly examined the relationship between toepad characteristics and habitat use, even though such information is necessary to fully test hypotheses about the role of toepads in adaptive diversification.

Anolis lizards differ greatly in the size and structure of their toepads and also in their degree of arboreality. Researchers have noted that species with more lamellae perch higher off the ground than species with fewer lamellae (Collette, 1961; Williams, 1983; Glossip and Losos, 1997). However, other aspects of the toepad have received less attention. In particular, all else equal, one would expect relatively larger toepads to have more setae and thus provide greater clinging ability than relatively smaller toepads (Peterson, 1983; Bauer and Good, 1986) and, indeed, among a sample of anoles, geckos, and skinks, a correlation exists between relative toepad size and clinging ability (Irschick et al., 1996). As a result, one might expect more arboreal species to have relatively larger toepads than more terrestrial species.

Here, we addressed the above issues by focusing on the following questions: (1) How is toepad size related to habitat use? (2) Do mainland and Caribbean anoles differ in toepad shape and in the relationships between toepad size and habitat use? To answer these questions, we measured the toepad characteristics of 79 species of anoles and compared these data to previously collected data on habitat use.

MATERIALS AND METHODS

Morphological Data.—Five hundred fifty-six preserved specimens of 79 species of anoles were examined (63 from the Caribbean, 16 from Central or South America; list of species and means of morphological measurements available upon request). Included in this sample were species of *Chamaeleolis, Chamaelinorops*, and *Phenacosaurus*, all of which have arisen from within *Anolis* (Jackman et al., 1999).

Five morphological measurements were taken, all on adult males: snout–vent length (SVL), and width and area of the toepad on the fourth toe of the fore- and hind foot. The fourth toe was chosen because it is usually the largest among anoles. Toepad area was measured by digitizing the circumference of the subdigital toepad (not including the claw and the rest of the digit) using a video imaging system (Morphosys; Meacham and Duncan, 1990) connected to a personal computer. Toepad width was measured to 0.1 mm with calipers across the widest part of the pad. Each of the measurements was taken from the ventral aspect on the right side of the lizard.

Habitat Use Data.—Two measures of habitat use shown to be important for segregating anole species (Rand, 1964; Schoener, 1968; Losos, 1990b; Losos and Irschick, 1996) were employed here: mean perch height (PH) and mean perch diameter (PD; data from Losos, 1990b; Irschick and Losos, 1996; Losos and Irschick, 1996; Losos and de Queiroz, 1997). Both habitat features have the potential to influence toepad size and shape. For instance, lizard species that perch higher than other species might benefit from having relatively larger toepads (thus allowing more sure-footedness) because the cost of falling to the ground is greater. Also, relatively larger toepads may be useful for grasping narrow branches by providing greater flexibility and thus permitting the pads to better wrap around the surface. Consequently, one might expect a negative relationship among species between preferred perch diameter and toepad size.

Statistical Analyses.—Mean values for each variable for each species were used in all analyses. These means were natural log-transformed prior to analysis. Ecological data were not available for all species; therefore, sample sizes for morphology-ecology comparisons were smaller than for morphology-morphology comparisons.

Most quantitative and ecological variables increase with body size both within and among species of anoles (Losos, 1990b; Macrini and Irschick, 1998). Because toepads are important for clinging to vertical surfaces, mass is an obvious index of body size, but the use of mass is prob-

TABLE 1. Results from analyses of covariance relating toepad size to body size between mainland and Caribbean anole species. Abbreviations: ff = forefoot, hf = hind foot, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Relationship	Test of heterogeneity of slopes	Test of heterogeneity of intercepts
Toepad width (ff) vs. SVL	$F_{1,75} = 4.09$*	—
Toepad width (hf) vs. SVL	$F_{1,75} = 6.78$*	—
Toepad area (ff) vs. SVL	$F_{1,75} = 4.04$*	—
Toepad area (hf) vs. SVL	$F_{1,75} = 0.05$	$F_{1,76} = 16.62$***
Toepad area (ff) vs. toepad width	$F_{1,75} = 9.81$**	—
Toepad area (hf) vs. toepad width	$F_{1,75} = 0.51$	$F_{1,76} = 1.70$

lematic because it can fluctuate as environmental conditions change. In addition, mass measurements from preserved specimens are often inaccurate. Consequently, analyses were conducted using SVL, rather than mass, as a measure of body size. In any case, mass and SVL are highly correlated among anole species (Stamps et al., 1997).

Two variables might be correlated because both are related to body size. To examine whether two variables are correlated once the effect of size is statistically removed, we used residuals from regressions of each variable against SVL. Analysis of covariance (ANCOVA) was used to determine differences in ecomorphological relationships between Caribbean and mainland forms. Because of the preponderance of significant results in our analyses, we consider corrections for multiple tests to be overly conservative (increased Type II error outweighing the advantage of decreased Type I error). However, adjusted values can be calculated by the statistical information provided in the tables and in the text.

All regressions and correlations were conducted using standard statistical methods rather than phylogenetic comparative methods. This course was chosen for two reasons. First, Irschick et al. (1997) demonstrated for a very similar set of anole species that no phylogenetic effect exists for ecological and morphological variables (many of the same species included in this study). Closely related species are not necessarily similar ecologically or morphologically, and thus phylogenetic comparative methods are not necessary (Björklund, 1997; Ackerly and Donoghue, 1998; Losos, 1999). Furthermore, our understanding of anole relationships, particularly those in Central and South America, is still incomplete, rendering the use of phylogenetic comparative methods difficult. Nonetheless, it is clear that neither mainland nor Caribbean anoles are monophyletic with respect to one another (Jackman et al., 1999). The Caribbean was invaded at least twice by anoles, and the mainland was reinvaded at least once by Caribbean taxa. Hence, when comparing mainland and Caribbean taxa, the comparison is between groups that are not composed of species all more closely related to each other than they are to species in the other group. Nonetheless, this study should be considered preliminary; when a more robust phylogeny for mainland anoles becomes available, reexamination of these data will be desirable.

RESULTS

Toepad Proportions.—At small body sizes, pad width was similar for mainland and Caribbean anoles, but width increased with SVL at a higher rate for Caribbean anoles (Table 1). In addition, mainland anoles had smaller toepad area relative to SVL than Caribbean anoles (Table 1). At narrow forefoot toepad widths, the toepads of Caribbean anoles were greater in area than mainland anoles, but this difference was reversed at wider toepad widths (Fig. 1, Table 1). By contrast, the relationship between hind-foot area and width did not differ significantly between the groups (Table 1).

Ecological Associations

Non–Size-Removed.—Among all anoles, pad area was positively related to perch height (Fig.
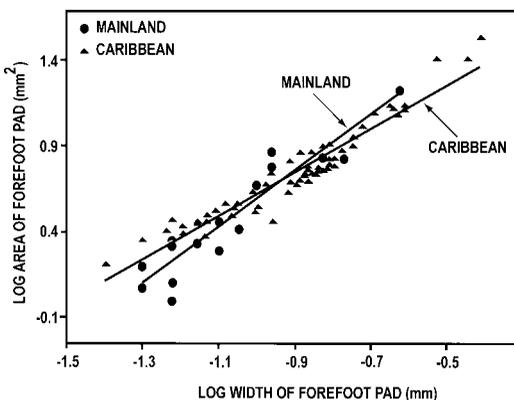

FIG. 1. Differences in shape of the forefoot toepad between Caribbean and mainland anoles. Lines on the plot represent linear regressions for the two groups of anoles.
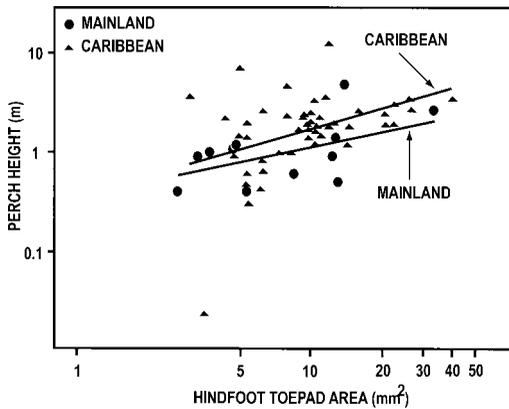
FIG. 2. The relationship between hind-foot toepad area and perch height for Caribbean and mainland anoles. Lines on the plot represent linear regressions for the two groups of anoles.

TABLE 2. Results from non–size removed analyses of covariance comparing relationships of habitat use to toepad morphology between mainland and Caribbean anoles. Perch diameter data were not available for two species: *Chamaelinorops barbouri* and *Anolis strahmi,* found only on flat surfaces (the ground and rock walls, respectively). Abbreviations are the same as in Table 1.

Relationship	Test of heterogeneity of slopes	Test of heterogeneity of intercepts
Toepad area (ff) vs. PH	$F_{1,57} = 0.55$	$F_{1,58} = 0.71$
Toepad area (hf) vs. PH	$F_{1,57} = 0.12$	$F_{1,58} = 1.74$
Toepad width (ff) vs. PH	$F_{1,57} = 0.13$	$F_{1,58} = 0.33$
Toepad width (hf) vs. PH	$F_{1,57} = 0.01$	$F_{1,58} = 0.32$
Toepad area (ff) vs. PD	$F_{1,55} = 3.47$	$F_{1,56} = 0.74$
Toepad area (hf) vs. PD	$F_{1,55} = 3.33$	$F_{1,56} = 0.33$
Toepad width (ff) vs. PD	$F_{1,55} = 1.26$	$F_{1,56} = 1.09$
Toepad width (hf) vs. PD	$F_{1,55} = 0.66$	$F_{1,56} = 1.37$

2; forefoot: $r^2 = 0.23$, $F_{1,59} = 19.16$, $P < 0.001$; hind foot: $r^2 = 0.19$, $F_{1,59} = 15.45$, $P < 0.001$), but Caribbean and mainland anoles did not differ in the relationship between pad area and perch height (Table 2). Similarly, perch height was positively related to toepad width (forefoot: $r^2 = 0.39$, $F_{1,59} = 39.74$, $P < 0.001$; hind foot: $r^2 = 0.40$, $F_{1,59} = 40.22$, $P < 0.001$), but the two groups did not differ significantly in this relationship (Table 2).

Pad area was also positively related to perch diameter among anoles (forefoot: $r^2 = 0.08$, $F_{1,59} = 5.92$, $P = 0.018$; hind foot: $r^2 = 0.08$, $F_{1,59} = 5.93$, $P = 0.018$), but the groups did not differ in this relationship (Table 2), although in both cases the slopes were nearly significantly different ($P < 0.075$). The results for toepad width were similar to those for toepad area. Perch diameter was positively related to both fore- ($r^2 = 0.11$, $F_{1,57} = 8.41$, $P = 0.005$) and hind-foot width ($r^2 = 0.15$, $F_{1,57} = 10.82$, $P = 0.002$), but the groups did not differ (Table 2).

All ecological and toepad characteristics were significantly related to body size among anoles examined (Table 3). However, the relationship between perch diameter and body size did not differ significantly between Caribbean and mainland anoles (differences in slopes, $F_{1,55} = 3.50$, $P = 0.07$, differences in intercepts, $F_{1,56} = 0.09$, $P = 0.76$). Our analyses indicate that Caribbean and mainland anoles did not differ in perch heights relative to body size, although the null hypothesis of homogeneity of intercepts was barely nonsignificant (differences in slopes, $F_{1,57} = 0.77$, $P = 0.38$, differences in intercepts, $F_{1,58} = 3.15$, $P = 0.08$).

Size-Removed Analyses.—Relative perch height (i.e., the residual value of the regression of perch height on SVL) was positively related to relative pad width (forefoot, $r^2 = 0.27$, $F_{1,59} = 23.07$, $P < 0.001$; hind foot, $r^2 = 0.25$, $F_{1,59} = 20.76$, $P < 0.001$). Analysis of covariance revealed that for anoles that perch relatively low to the ground, the relative width of the toepads of mainland anoles was less than that of Caribbean anoles (Fig. 3, Table 4). By contrast, mainland species had smaller relative hind-foot toepad areas at all relative perch heights (Table 4).

Relative perch diameter was positively related to relative pad width (forefoot, $r^2 = 0.08$, $F_{1,57} = 6.17$, $P = 0.016$; hind foot, $r^2 = 0.14$, $F_{1,57} = 10.30$, $P = 0.002$), but the relationship between relative pad area and relative perch diameter was marginally nonsignificant (forefoot, $r^2 = 0.03$, $F_{1,57} = 2.52$, $P = 0.12$; hind foot, $r^2 = 0.04$, $F_{1,57} = 3.61$, $P = 0.06$). Nonetheless, as in the analyses with relative perch height, Caribbean species had larger and wider toepads relative to perch diameter (Fig. 4, Table 4).

TABLE 3. Results from linear regressions between all ecological and toepad characteristics and body size among all anoles examined. Abbreviations: (+) = positive relationship, (−) = negative relationship; all other abbreviations are the same as in Table 1.

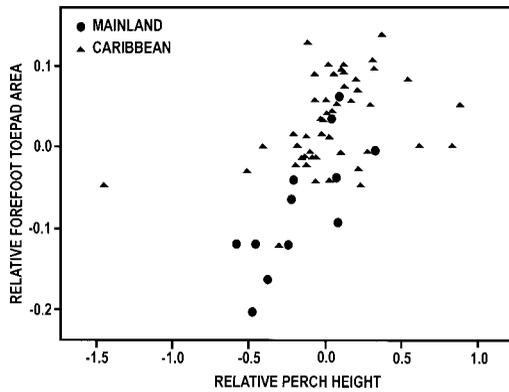| Characteristic vs. body size	Coefficient of determination	F ratio
Toepad width (ff)	$r^2 = 0.88$ (+)	$F_{1,77} = 570.52$***
Toepad width (hf)	$r^2 = 0.84$ (+)	$F_{1,77} = 424.48$***
Toepad area (ff)	$r^2 = 0.92$ (+)	$F_{1,77} = 847.87$***
Toepad area (hf)	$r^2 = 0.94$ (+)	$F_{1,77} = 1177.84$***
Perch height	$r^2 = 0.23$ (+)	$F_{1,59} = 19.20$***
Perch diameter	$r^2 = 0.05$ (−)	$F_{1,57} = 4.14$*

FIG. 3. The relationship between relative perch height and relative forefoot toepad area for Caribbean and mainland anoles. Both variables are residuals from regressions against body size, as represented by SVL.
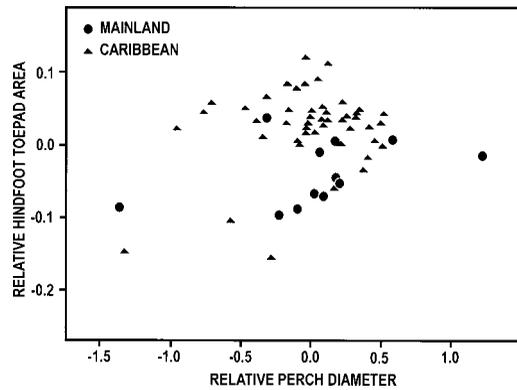
FIG. 4. The relationship between relative perch diameter and relative hind-foot toepad area for Caribbean and mainland anoles. Both variables are residuals from regressions against body size, as represented by SVL.

DISCUSSION

Ecological Correlates of Toepad Size.—Toepad size shows clear associations with habitat use. Species with larger toepads perch on higher and broader perches compared to species with smaller toepads (Fig. 2). When the effects of body size are statistically removed, these relationships are weakened but are still apparent. Also, the toepads of Caribbean and mainland anoles differ in shape (i.e., width vs. area). Finally, for a number of variables, mainland and Caribbean anoles differed in their relationships between toepad shape and habitat use.

The underlying factors that result in lizards with large toepads perching on high and broad perches are unclear, but several possibilities exist. First, relatively larger toepads may have more setae and thus greater adhesive ability compared to relatively smaller toepads. Species that perch higher may need greater adhesive ability, either because they more frequently use smooth surfaces (e.g., such as leaves) that require greater adhesive ability or because the consequences of falling may be greater. The pos-

itive relationship between perch diameter and pad area and width is contrary to our predictions. Perhaps because mechanical grip is not possible on broad surfaces, greater adhesive force—and hence larger pads—are necessary. Higher setal density might be an alternative means of increasing adhesive force without requiring relatively larger pads, but setal density appears to be relatively constant among anoles (Peterson, 1983; on gecko setal density, see also Bauer and Good, 1986).

Differences between Caribbean and Mainland Anoles.—Our results bolster a previous finding that Caribbean and mainland anoles exhibit fundamentally different relationships between morphology and habitat use. Irschick et al. (1997) showed among mainland anoles that toepad size is positively correlated with perch height, but tail length is negatively related to perch diameter. By contrast for Caribbean anoles, forelimb length and body mass are positively associated with perch diameter, and tail length and hind-limb length are negatively related to perch diameter.

TABLE 4. Results from size-removed analyses of covariance comparing relationships of habitat use to toepad morphology between mainland and Caribbean anoles. Abbreviations are the same as in Table 1.

Relationship	Test of heterogeneity of slopes	Test of heterogeneity of intercepts
Toepad width (ff) vs. PH	$F_{1,57} = 6.75*$	—
Toepad width (hf) vs. PH	$F_{1,57} = 14.61***$	—
Toepad area (ff) vs. PH	$F_{1,57} = 0.74$	$F_{1,58} = 61.10***$
Toepad area (hf) vs. PH	$F_{1,57} = 2.55$	$F_{1,58} = 20.20***$
Toepad width (ff) vs. PD	$F_{1,55} = 1.59$	$F_{1,56} = 35.19***$
Toepad width (hf) vs. PD	$F_{1,55} = 2.18$	$F_{1,56} = 31.05***$
Toepad area (ff) vs. PD	$F_{1,55} = 0.04$	$F_{1,56} = 69.28***$
Toepad area (hf) vs. PD	$F_{1,55} = 0.02$	$F_{1,56} = 16.49***$

The newly documented differences between anoles in the two regions reported here are interesting in several ways. First, the relatively larger toepads of Caribbean anoles suggest that they may have greater clinging capabilities than mainland anoles and thus may be able to use habitats requiring greater clinging capabilities. However, if this were the case, then for a given body size, Caribbean and mainland anoles should differ in their habitat use, but no such differences were found (although several were close to statistical significance).

Alternatively, Caribbean anoles may need larger toepads than mainland anoles to use the same habitat. If this were the case, with the effect of body size removed, a relationship should exist among all anoles between relative toepad size and relative habitat use, but that relationship should differ between mainland and Caribbean anoles. This prediction is strongly supported in these analyses (Figs. 3–4) and also by Irschick et al. (1997), who found that Caribbean anoles have relatively more subdigital lamellae than mainland anoles with comparable relative perch heights.

Morphological differences between the two geographic groups in setal density or distribution on the toepad seem unlikely, as toepad and setal structure are fairly conserved across anoles (Peterson, 1983). Perhaps other structures such as claws, which show correlation with clinging performance in other groups of lizards (Zani, 2000), differ significantly between the two groups of anoles. Indeed, the structural orientation of claws in species of arboreal geckos is known to vary (Russell and Bauer, 1989). However, no work so far has compared claw morphology or significance in clinging performance in anoles.

Behavioral differences between Caribbean and mainland anoles may also be a factor. Caribbean anoles generally have higher population densities (Schoener and Schoener, 1980, and references therein) and move more frequently than mainland anoles (Irschick et al., 1997), and thus territorial interactions are common (Losos, 1990a, 1990b). In addition, many Caribbean species rely on speed to escape predators and conspecifics (Irschick and Losos, 1998) and therefore may need clinging ability in a variety of contexts. By contrast, mainland anoles are generally less active and may rely more on crypsis to evade predators (see Irschick et al., 1997, and references therein) and consequently clinging ability may be less important. Clearly, more detailed studies on the relationships between pad morphology and clinging ability and between clinging ability and habitat use are needed to investigate the causes of differences we have found between mainland and Caribbean anole species.

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