First Record of the Genus *Acanthixalus* Laurent, 1944 from the Upper Guinean Rain Forest, West Africa, with the Description of a New Species

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ABSTRACT.—We describe a new species of *Acanthixalus* from southwestern Ivory Coast. *Acanthixalus sonjae* sp. nov. differs from the Central African *Acanthixalus spinosus* genetically by 4.6 % in the investigated 16S rRNA. Morphologically adult frogs are very similar to *A. spinosus*. Male *A. sonjae* have wider heads and probably smaller gular glands than *A. spinosus*. Tadpoles of *A. sonjae* differ by much longer tails. *Acanthixalus sonjae* males are apparently mute. The new species is semiaquatic and lives in large water-filled cavities of trees in secondary and primary rain forest. Tadpoles complete metamorphosis in three months. They are at least partly carnivorous.

The name *Acanthixalus* was introduced in 1944 by Laurent as a subgenus for the species *Hyperolius spinosus* Buchholz and Peters, 1875. This species was previously placed either in *Hyperolius* or *Megalixalus*. In 1950, Laurent and Combaz raised *Acanthixalus* to genus level. According to Drewes (1984), *Acanthixalus* is the sister group to *Callixalus pictus* Laurent, 1950. Channing (1989), following Drewes (1984) and Liem (1970), placed *Acanthixalus spinosus* within the Hyperoliinae. Its tadpoles were first described by Lamotte et al. (1959). The most detailed information on the biology of *A. spinosus*, namely habitat selection, tadpole biology, and death feigning of frogs, were published by Perret (1961) and Largen and Dowsett-Lemaire (1991). Affa'a and Amiet (Affa'a, 1979; Amiet and Affa'a, 1985; Affa'a and Amiet, 1994) published several papers on endo-commensal ciliates of different anurans including *A. spinosus* tadpoles and adults. All these authors considered *Acanthixalus* to be monotypic. The range of *A. spinosus* was reported to stretch from southeastern Nigeria, to northeast of the Democratic Republic of Congo, and from Cameroon south to the extreme western Democratic Republic of Congo and the island of Bioko (Reid et al., 1990; Duellman, 1993; Poynton, 1999).

In September 2000, we discovered *Acanthixalus* frogs nearly 2000 km further west, in Taï National Park (TNP), southwestern Ivory Coast. Although morphologically very similar to Central African members of the genus, our specimens differ genetically. Therefore, we describe them herein as a new species *Acanthixalus sonjae*

sp. nov. We also describe the tadpole and aspects of the biology of the new species.

Materials and Methods

Study Area.—TNP is the largest protected area of rain forest in West Africa. Yearly precipitation reaches 2200 mm in the southwest and 1700 in the northeast of the park. Most precipitation occurs from April to July and from September to November. The first dry period lasts from December to February; normally a second one occurs in August. Temperatures vary between 20 and 33°C, with daily temperature differences of up to 10°C. Mean annual temperature is about 25°C. Humidity fluctuates from 85% (day) to 90–100% (night). During the dry season, humidity may drop below 60% even in closed forest. Our main investigation area was located 23 km southeast of the small town of Taï and comprised about 30 km² of primary and secondary rain forest around the ''Station de Recherche en Ecologie Tropicale'' (SRET, 5°50'N, 7°20'W, formerly CRE and IET). Between 1991–1999 mean annual precipitation at the SRET station was 1854 mm (SD ± 249; range 1424–2194 mm; R. Noë, pers. comm.). The area is situated within the equatorial climate (Riezebos et al., 1994; Parren and de Graaf, 1995), floristically it belongs to the Guinea-Congo-Region (Guillaumet, 1967).

Origin of Specimens.—We investigated museum specimens of *A. spinosus* from the entire known range (Fig. 1). Museum specimens under investigation originated from and are deposited in the following collections: Liverpool Museum (LIV); the Muséum d'Histoire Naturelle, Genève (MHNG); the Muséum National d'Histoire Naturelle, Paris (MNHN); the Musée Royal de l'Afrique Centrale, Tervuren (MRAC); the Port

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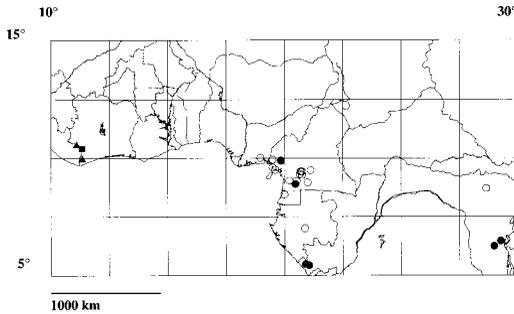
FIG. 1. Known distribution of *Acanthixalus sonjae* sp. nov. (triangles; square for type locality) and *Acanthixalus spinosus* (circles). Closed symbols represent localities of checked specimens, open symbols represent unchecked literature records; sources: Buchholz and Peters, 1875; Werner, 1898; Boulenger, 1903; Nieden, 1908, 1910; Lampe, 1911; Noble, 1924; Laurent, 1941; Lamotte et al., 1959; Perret, 1961, 1966; Schiøtz, 1963, 1967, 1999; Amiet and Perret, 1969; Affa'a, 1979; Amiet, 1986; Largen and Dowsett-Lemaire, 1991; Schmitz et al., 1999; Frétey and Blanc, 2000. We haven't found exact localities for Gabon, and Bioko.

FIG. 2. Adult male *Acanthixalus sonjae* sp. nov. from Taï National Park, Ivory Coast.

Elisabeth Museum (PEM); the Staatliches Museum für Naturkunde, Stuttgart (SMNS), the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK); Museum für Naturkunde, Humboldt Universität Berlin (ZMB); and the Zoologische Staatssammlung des bayerischen Staates, München (ZSM).

Morphological Data.—Frogs were sacrificed in a chlorbutole solution and preserved in 4% formaldehyde and subsequently to ethanol or 70% ethanol. Larvae of different stages preserved in 4% formaldehyde and transferred to 70% ethanol after two months. Most specimens of the new species are still alive and in the possession of the Department of Animal Ecology and Tropical Biology, Würzburg University. Measurements were taken with a dial caliper (± 0.1 mm) or a measuring ocular in a dissecting microscope (± 0.1 mm, Zeiss Stemi SV 6). All measurements are given in millimeters and were taken by one person (M-OR). We measured snout–vent length (SVL), head width (HW), femur length (F), length of the tibula fibula (TF), length of foot including longest toe, distance from eye to snout tip, and length and width of gular glands in males. We counted dark bars on femur and tibia and number of spines on tarsus. Webbing formula is in accordance with Rödel (2000). Staging of tadpoles was according to Gosner (1960). Tadpole description is based on specimens of Gosner stage 25–27. Measurements taken on tadpoles were total length (CL), body length (BL), body width (BW, measured at the plane of the eyes), tail length (TL), fin height (FH, highest point), height of tail axis (TA; measured at highest point of fin), and body height (BH). Nomenclature of morphological features follows Altig and Johnston (1989), Altig and McDiarmid (1999), and McDiarmid and Altig (1999). The labial tooth row formula is according to Dubois (1995). The description of the coloration is based on living frogs and tadpoles.

Genetics.—We analyzed 16S rRNA from one *A. spinosus* (ZFMK 72000, female, Cameroon, Mt. Kupe) and five *A. sonjae* (two females, three juveniles, from the type locality, still alive). DNA was extracted using QuiAmp tissue extraction kits (Quiagen). We used the primers 16SA (light chain; 5'-CGC CTG TTT ATC AAA AAC AT-3') and 16SB (heavy chain; 5'-CCG GTC TGA ACT CAG ATC ACG T-3') of Kocher et al. (1989) to amplify a 560 bp section of the mitochondrial 16S ribosomal RNA gene. PCR cycling procedure was as follows. Initial denaturation step: 90 sec at 94°C; 33 cycles: denaturation 45 sec at 94°C, primer annealing for 45 sec at 55°C, extension for 90 sec at 72°C. PCR products were purified using Quiaquick purification kits (Quiagen). We sequenced single-stranded fragments using an automatic sequencer (ABI 377), comprising 546 bp homologous to the bp positions 3994–4554 of the *Xenopus laevis* mitochondrial genome (Roe et al., 1985). Sequences have been submitted to GenBank (*A. sonjae*: AF465437, *A. spinosus*: AF465438). Sequences were aligned manually using the computer program SEQUENCE NAVIGATOR (Applied Biosystems).

RESULTS

Acanthixalus sonjae, sp. nov.
Figs. 2–5

Holotype.—SMNS 09573, male, SRET station, transect X, large water-filled tree stump, secondary forest, 16 September 2000, 5°50'N, 7°20'W, Taï National Park, Ivory Coast, Ernst and Rödel coll.
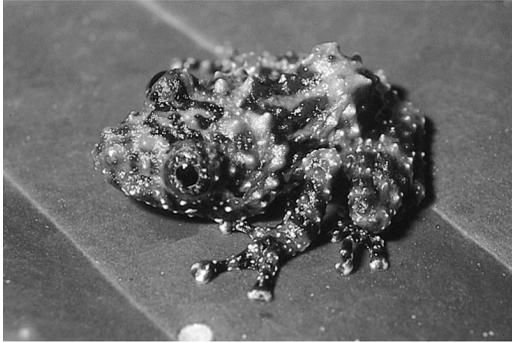
Paratypes.—SMNS 09574.1–2, 2 juveniles, Noë-

FIG. 3. Juvenile *Acanthixalus sonjae* sp. nov. (SMNS 09574.1, paratype).

Grid and same data as holotype; SMNS 09575.1–28, tadpoles, same data as holotype; ZSM 980/2001, young female, same data as holotype; PEM A7414, adult male, Forêt Classé de Haute Dodo, 4°54′03″N, 7°19′3″W; three males, two females, and four juveniles alive, same data as holotype; numerous tadpoles alive.

Diagnosis.—Warty tree frog with flattened body, long and pointed snout; protruding eyes with rhomboidal-shaped pupil; males apparently mute, with a pair of subgular glands and hook shaped tarsal spines; hands and feet webbed; toe and finger tips enlarged to discs; males differ from males of *A. spinosus* by wider heads; tadpoles differ from tadpoles of *A. spinosus* by much longer tails; *A. sonjae* differs from *A. spniosus* genetically.

Description of Holotype.—Adult male; body stout but flattened with a rather long snout (Fig. 2); SVL 33 mm; HW 11.4 mm; F 16.7 mm; TF 17 mm; foot incl. longest toe 24 mm; paired longitudinal, oval subgular glands, each 3 to 1.8 mm (Fig. 4); protruding eyes; pupils quadratic, rhomboidal-shaped; nostrils much closer to snout tip than to anterior border of eyes; tympanum absent; canthus rostralis present; loreal region slightly concave; dorsal skin and extremities strongly warty; dorsal warts with small black spinulae; ventral skin granular without black spinulae; four especially large warts in the shoulder region; two especially large warts in the sacral region; a transversal row of larger warts in the neck region, giving the appearance of a crown; 51 enlarged hooklike tarsal spines; toe and finger tips markedly enlarged to discs, discs broader than long; webbing formula of hand: 1 (1), 2 i/e (1-0), 3 i/e (1), 4 (1); webbing formula of feet: 1 (0), 2 i/e (1-0), 3 i/e (1-0), 4 i/e (1), 5 (0); margin of web always reaching toe and finger tips; relative finger length: 1 < 2 < 3 > 4; relative toe length: 1 < 2 < 3 < 4 > 5; large elongate inner metatarsal tubercle; small round outer metatarsal tubercle.
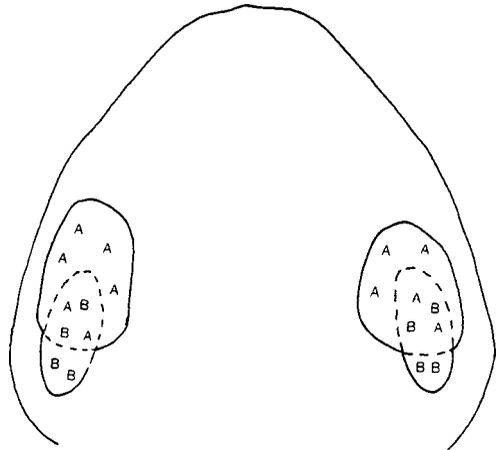

FIG. 4. Position and size of gular glands in male *Acanthixalus sonjae* sp. nov. (B = SMNS 09573, holotype) and *Acanthixalus spinosus* (A = ZMB 59354, syntype).
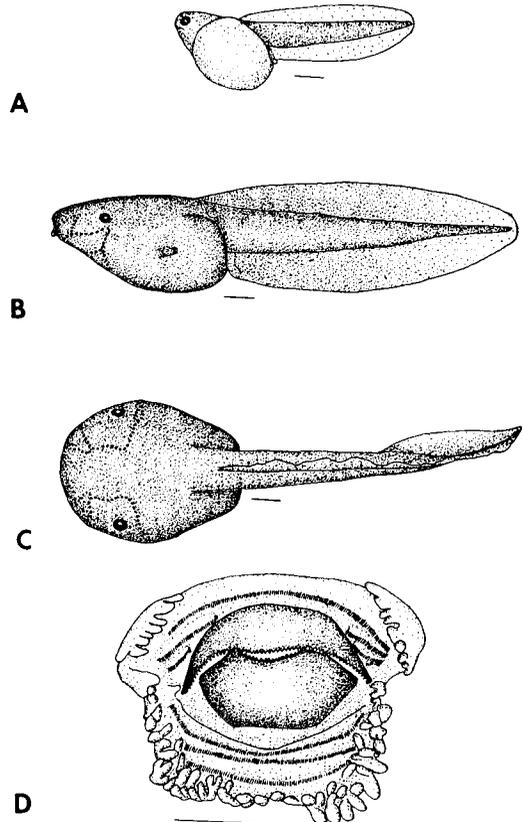

FIG. 5. Tadpoles of *Acanthixalus sonjae* sp. nov.; (A) prehatching stage (SMNS 9575.1; CL 8.7 mm); (B–C) stage 25 tadpole in lateral (B) and dorsal view (C); BL 6.7 mm; SMNS 9575.2); (D) oral disc of stage 27 tadpole (SMNS 9575.27; BL = 16.5 mm), keratodonts and side line system openings sketched, no accurate count; scale bar = 1 mm.

TABLE 1.   Measurements (mm) of male *Acanthixalus sonjae* sp. nov. and *Acanthixalus spinosus*; given are mean ± standard deviation and range; gland = size of gular gland (mm²); spines = number of large tarsal spines; for other abbreviations see the Material and Methods section.

Species	Sex	SVL	HW	F	TF	Gland	Spines	N
sonjae	m	35.1 ± 2.1	13.6 ± 1.0	16.9 ± 0.4	17.1 ± 0.3	6.6 ± 1.1	47 ± 5.0	4
		33–38	12.5–14.5	16.5–17.5	17.0–17.5	5.4–7.9	40–51	
spinosus	m	33.5 ± 2.3	11.8 ± 1.0	16.3 ± 1.2	17.4 ± 1.2	8.0 ± 3.3	48 ± 11	20
		30–38.3	11.0–14.6	14.5–18.8	15.9–19.7	3.0–15.9	36–76	
sonjae	f	35.5–38.5	12.0–12.5	17.0–19.0	17.0–18.5			2
spinosus	f	34.5 ± 1.0	12.0 ± 0.8	16.1 ± 1	16.9 ± 0.9			9
		32.2–35.5	11–13.5	15–17.9	16.1–17.5			

Color in Life.—Ground color of back and extremities is a clear yellow green; dorsal ground color broken by numerous black spots and lines and three larger black cross bands; a black triangle-like pattern is situated between the eyes, pointing caudad; in the shoulder region a pair of triangular-shaped black spots also point posteriorly; a black transversal band is present in the sacral region; black transversal bars are present on the upper lip, femur (4 and 5) and tibula fibula (4); flanks clear green to almost white; numerous white warts with a black spine on back and extremities; iris black with radial white stripes; anal region bright yellow; finger and toe tips white with a black spot; ventral surface of body and extremities gray brown with black meanders and numerous white warts without black spines; ventral part of discs beige; gular glands beige; heels orange to bright yellow. In sunlight, the light colors darkened within minutes, giving the frog an almost entire black appearance.

Color in Preservation.—Almost as in life; green colors turn brown; yellow and orange colors fade.

Variation.—Females lack gular glands and enlarged tarsal spines; discs on toes and fingers are smaller in females; dorsal coloration may change within minutes from almost green to nearly black; juveniles with much brighter colors (Fig. 3); often yellow to orange instead of green or brown; ground color of ventral side in juveniles orange; juveniles with four especially large yellow warts in the neck. Measurements are summarized in Table 1.

Tadpole Description.—Compact tadpole, body shape round in dorsal view, somewhat compressed in lateral view, caudal part of body higher than cranial part (Fig. 5B–C); long and muscular tail axis; moderately high tail fin, evenly curved; origin of tail fin slightly anterior to tail-body junction; tail tip broad round; tail length 1.6 times body length; side line system on the anterior region of body; subterminal oral disc; labial tooth row formula: 1 : 2 + 2 / 3 (Fig. 5D); both jaw sheaths wide and heavily serrated; upper jaw sheath with large medial convexity; lower jaw sheath U-shaped; uniserial lateral papillae row, a gap in the mouth angles; biserial caudal papillae row, medially uniserial; eyes laterally and very small; nostrils much closer to snout than to eyes; spiracle sinistral, hardly visible from dorsal view; median vent tube.

Color of tadpoles from natural tree holes was a fleshy violet. In sunlight, they quickly turned black. Back, flanks, and tail axis were uniform dark. Ventrum clearer or also dark. Tail fin dark, often lighter toward tail tip. In some tadpoles, the tip of the tail fin was nearly transparent. Measurements are summarized in Table 2.

Development.—Clutches seemed more or less flat shortly after oviposition. Very soon they became hemispheric, measuring 2–4 cm in diameter. Mean clutch size was 9.3 ± 2.9 eggs (5–13, N = 8, field observations and captive breeding). In our laboratory, one female deposited three clutches within 21 days, comprising 8, 10, and 11 eggs, respectively. The eggs were of a clear white gray color with a darker pole. Embryos first had a horizontal position within the clutch,

TABLE 2.   Indices of body measurements of 27 *Acanthixalus sonjae* sp. nov. tadpoles from Taï National Park, Ivory Coast (SMNS 09575.2-28; stage 25: N = 25, Stage 27: N = 2), one *Acanthixalus spinosus* tadpole from Mount Kupe, Cameroon (ZFMK 69604, stage 25), and measurements adopted from Lamotte et al. (1959) in italic (Stage 34); given are mean ± standard deviation and range.

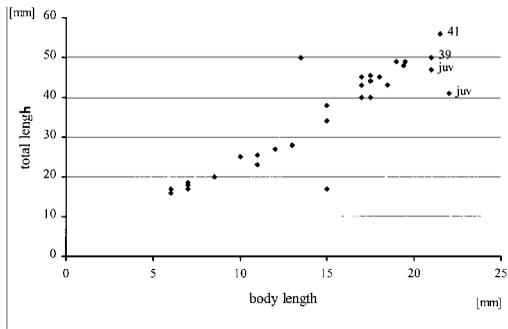| Species	Stage	TL/BL	BW/BL	FH/BL	FH/TA	BH/BL
sonjae	25 (N = 25);	1.6 ± 0.1;	0.7 ± 0.1;	0.6 ± 0;	2.7 ± 0.3;	0.5 ± 0;
	27 (N = 2)	1.4–1.9	0.6–0.8	0.5–0.7	2.2–3.2	0.5–0.6
spinosus	25 (N = 1)	*1.2–1.5*	*0.6–0.7*	*0.5–0.6*	*1.9–2.5*	*0.5–0.6*

FIG. 6. Body length/total length relation of randomly sampled *Acanthixalus sonjae* sp. nov. tadpoles from tree hole 1, Taï National Park, Ivory Coast (N = 30, 16 September 2000); if not stated otherwise all tadpoles of stage 25–27 (Gosner, 1960).

turning into a vertical one, head directed upward, later on (Fig. 5A; compare Perret, 1961, 1988). In the field as well as in captivity, tadpoles began dropping into water 11–14 days after oviposition. At that time, they measured 4.1–4.7 mm BL and 12.0–13.7 mm CL. Tadpoles of that stage still had a large yolk sac and a slightly open mouth. The jaw sheaths were black and evenly U-curved. The eyes were still covered with skin. Neither keratodonts, nor papillae, nor a spiracle were visible. In captivity CL was 16.3 ± 1.1 mm (15.0–18.0 mm, N = 14) 41 days after hatching. Two-month-old larvae measured 26.4 ± 1.8 mm CL (23.5–27.5 mm, N = 8). Two three-month-old tadpoles measured 47.5 mm and 49.5 mm CL, respectively. None of these tadpoles already showed any signs of hind limbs. Tadpoles remained in stage 25–27 until they reached a body length of more than 20 mm (Fig. 6). Stage 42 specimens (BL 21 mm; CL 47 mm) had already the color pattern of juveniles but still a smooth dorsal skin. Stage 44 tadpoles (BL 22 mm; CL 41 mm) had dorsal warts.

Natural History.—The first *A. sonjae*, a juvenile, was detected the 3 September 2000 on a leaf of a small tree in swampy primary rain forest. Our second locality was a fallen tree in secondary forest. The interior of the tree was completely rotten, forming a large water-filled cavity. The diameter of the water surface was about 40 cm. Water depth markedly exceeded 200 cm. The opening was directed sideward. Clutches were attached to the cavity's ceiling. At that place, we found more than six adults, of which four males and two females were captured, numerous juveniles and between 200 and 300 tadpoles of all sizes. It was impossible to get an accurate count of all specimens living in that tree hole, because all tadpoles and frogs were extremely shy and fled into the interior of the tree at the slightest disturbance. The color of the water was deep brown. No rotten vegetation could be detected. No other animal, neither culicid larvae nor oligochaet worms, otherwise very common in water-filled tree holes of TNP (pers. obs.) were detected. The second tree hole was located between the huge buttresses of a tree in a comparatively dry part of primary forest. The hole surface was completely exposed. Water surface was 25 × 40 cm. Water depth was 50 cm. The ground was covered with a deep layer, about 30 cm, of rotten leaves. The water was polluted by mammal excrements, probably from monkeys. Clutches were always attached to the same place on the wall. We only detected one adult *A. sonjae*. We cannot exclude the presence of further frogs or tadpoles. Adults at both holes often sat at the hole's ceiling or wall but immediately dived into water when we approached. At tree hole 2, we regularly observed a calling *Phrynobatrachus plicatus* male. We never observed the later species ovipositing in the tree hole. *Acanthixalus sonjae* shared tree hole 1 with a large cobra, *Naja melanoleuca*. On 20 September 2000, the walls of tree hole 2, including an *A. sonjae* clutch, were completely covered by foraging driver ants (*Dorylus* sp.). The next day we found the clutch still intact. Captured tadpoles made growling sounds and bit into our hands. In captivity, seven small to medium-sized tadpoles of *A. sonjae* (CL 20–30 mm) devoured 20 larvae of *Ptychadena aequiplicata* (CL 10–12 mm); 10 large *A. sonjae* tadpoles consumed 30–50 tadpoles of *P. aequiplicata* within one night. We never observed an attack on other tadpoles during daylight. Captive tadpoles fed on leaves, and commercial fish food. Freshly metamorphosed froglets measured 21–23 mm SVL (mean ± SE = 22.2 ± 0.7 mm, N = 6). After one month, they measured 21.5–24 mm (± SE = 23.2 ± 1.0, N = 5), after six months SVL was 29.5–32.5 mm (N = 4). We observed a death feigning behavior, already described and illustrated for *A. spinosus* by Perret (1961, 1979) and Schmitz et al. (1999). Disturbed frogs flattened their body, closed the eyes, and stretched a yellow tongue out of the otherwise closed mouth. We could not detect a strong odor during that behavior, described for *A. spinosus* by Schmitz et al. (1999).

Genetic Characterization.—The part of the 16S rRNA sequence of the holotype that corresponds to the nucleotides 3994–4554 of the *Xenopus laevis* mitochondrial genome (Roe et al., 1985) is available from M-OR upon request (GenBank accession numbers *A. sonjae*: AF465437, *A. spinosus*: AF465438). The analyzed specimens showed no intraspecific 16S rRNA variation. For specimens examined, see Appendix 1.

Distribution.—So far *A. sonjae* is only known from three localities around the SRET station in

FIG. 7. Female *Acanthixalus spinosus* from Mount Kupe, Cameroon (ZFMK 72000).

TNP, and from two forests adjacent to TNP (Fig. 1). On 15 March 2002, we found several adults and tadpoles in a large water-filled tree hole in the Forêt Classé de Haute Dodo (4°54′03″N, 7°19′3″W). On 25 April 2002, tadpoles were recorded in a water-filled cavity of a large buttress tree in the Forêt Classé de Cavally (6°05′53″N, 7°48′17″W; W.B. Branch and M.-O. Rödel, unpubl.).

Etymology.—The new species is dedicated to Sonja Wolters, who caught the first specimen of the new species and therewith initiated a closer investigation of larger water-filled tree holes.

DISCUSSION

Morphologically *A. spinosus* and *A. sonjae* sp. nov. are extremely similar (Fig. 2–3, 7–8; Table 1). Sexes are of equal size and show the same morphological differences: a pair of elongate gular glands, larger discs and a large number of strong tarsal spines in males (Fig. 8B; Perret, 1966). Although males of *A. sonjae* grouped separately from the other specimens investigated in a PCA (Fig. 8A), the only significant morphological differences between *A. sonjae* and *A. spinosus* was the HW of males (Table 1). Males of *A. sonjae* had wider heads. Mean gland size was larger in males of *A. spinosus*, and glands were located more craniad than in *A. sonjae* (Tables 1, 3; Fig. 4). However, gland size seems to change along with the reproductive stage of the males and the variation in males of *A. spinosus* was too large to give significant results. It is well possible that other morphological differences could simply not be detected because of the small sample size of *A. sonjae*. However, we feel that description of this taxon on the species level is justified. First, *A. sonjae* differs genetically from *Acanthixalus* from Cameroon at a level comparable to other amphibian species (e.g., Kobel et al., 1998; Veith et al., 1998, 2001). The overall sequence divergence for our 16S rRNA fragment is 4.6 %, with 18 transitions and seven trans-
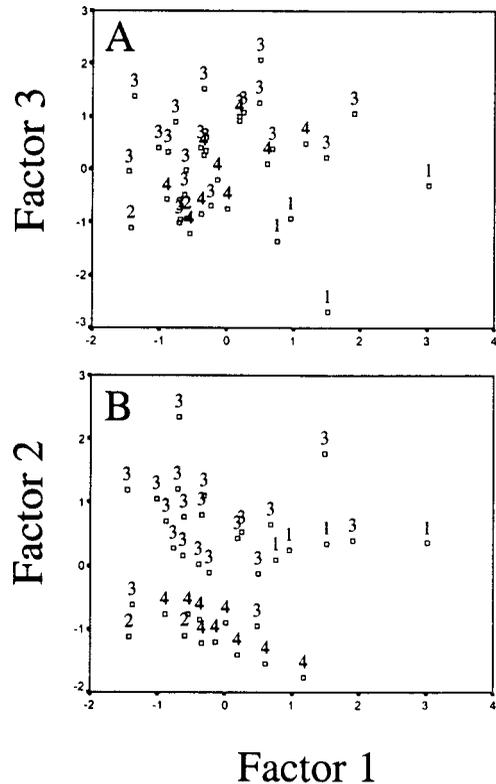

FIG. 8. Principal component analysis; 1 = male *Acanthixalus sonjae* (N = 4); 2 = female *A. sonjae* (N = 2); 3 = male *Acanthixalus spinosus* (N = 20); 4 = female *A. spinosus* (N = 9); (A) male *A. sonjae* are somewhat separated from the other specimens; (B) females and males are nearly separated by axis 2; for measurements taken into analyses see Table 3.

versions. Second, the new species occurs in an area more than 1700 km from the nearest known locality of *A. spinosus*, the Calabar region in southeast Nigeria (Fig. 1). It seems to be a common phenomenon that species pairs live in the Upper and Lower Guinean rain forest. Quite recently this has been shown for *Bufo tuberosus*

TABLE 3. Component matrix of axis values (PCA, only first four axis taken into consideration); % = % of explained variance, for abbreviations see the material and methods section; compare Figure 8.

Measure	Axis			
	1	2	3	4
HW/SVL	0.69	0.69	0.13	0.15
F/SVL	0.86	0.01	−0.32	−0.40
TF/SVL	0.82	−0.33	−0.32	0.35
GS/SVL	0.72	−0.31	0.62	−0.05
%	60.05	17.10	15.27	7.58

and *Bufo taiensis* (Rödel and Ernst, 2000; Tandy and Perret 2000). Because these forests have been separated longer than 10,000 years (Moreau, 1963, 1969; Guillaumet, 1967; Jahn et al., 1998), we believe that it is rather likely that other amphibians, being recorded in both regions, belong to different species, as well.

Clutch size, eggs and tadpoles of *A. sonjae* were also very similar to those of *A. spinosus* (Lamotte et al., 1959; Perret 1961; Largen and Dowsett-Lemaire, 1991). Tadpoles of *A. sonjae* have three labial tooth rows in the upper lip. Tadpoles of *A. spinosus* are reported to have four (Lamotte et al., 1959; Perret, 1961); however the single tadpole from Cameroon available to us, had only three teeth rows in the upper lip. Tadpoles of *A. sonjae* have longer tails than *A. spinosus* (Table 2). The upward deflection of the tail, originally thought to be characteristic for tadpoles of *A. spinosus* (Lamotte et al., 1959; Perret, 1961) is only a preservation artifact (Schiøtz, 1999). Both tadpole species fit into the arboreal type 2 of Altig and McDiarmid (1999; McDiarmid and Altig, 1999, erroneous by cite type 1).

With one exception, all *Acanthixalus* live in water-filled cavities of living trees or tree trunks from near ground to 5 m high (Lamotte et al., 1959; Perret, 1961; Affa'a, 1979; Amiet and Affa'a, 1985; Amiet, 1986; Reid et al., 1990; Largen and Dowsett-Lemaire, 1991; Schmitz et al., 1999). Amiet and Perret (1969) found one specimen and a clutch in a metal water-butt. These tree holes always seem to be comparatively large and often contained several frogs and tadpoles (Largen and Dowsett-Lemaire, 1991; Schmitz et al., 1999). However, none of the known *A. spinosus* localities ever gave home to such a large number of frogs and tadpoles as tree hole 1. Many *A. spinosus* localities were at higher altitudes (650–945 m a.s.l.; Amiet, 1986; Schmitz et al., 1999). There *A. spinosus* occurred in secondary and primary forest (Noble, 1924; Ahl, 1931; Perret, 1961; Amiet, 1986) and was even recorded from a cacao plantation (Amiet and Perret, 1961). Similarly, we recorded *A. sonjae* in dry and swampy, secondary and primary forest. It seems that the main requirement to be met for *Acanthixalus* to occur, are large water-filled cavities in wooded habitats, that probably have sufficient precipitation to assure water persistence during the dry season. The tree holes have to be relatively large, explaining why we never found any *Acanthixalus* in almost 70 small (water volume 3.8–824.7 ml) tree holes, occupied by *Phrynobatrachus guineensis* (Rödel, 1998; unpubl. data). One reason for this habitat choice might be the long period, tadpoles need until metamorphosis. According to Perret (1961) tadpoles of *A. spinosus* remain about three months

in the larval stage. Larval time in *A. sonjae* seemed to be even longer. In contrast tadpoles of *P. guineensis* metamorphose after about three weeks (Rödel, 1998; unpubl. data). Furthermore, adult *Acanthixalus* are at least partly aquatic and leave their holes only during night to forage for small arthropods (Perret, 1961; own data). Perret (1961) reported *A. spinosus* tadpoles to feed mainly on rotten leaves. According to our observations tadpoles of *A. sonjae* feed on everything they can get, including other tadpoles. At least at sites like our tree hole 1, where hundreds of tadpoles lived, food should be limited, and every possible food item should be taken by the larvae. Our captive tadpoles grew best on dead arthropods as food. Astonishingly we never observed any aggressive behavior between tadpoles of *A. sonjae* even if they differed by a factor of 2 in size and were not provided with other food. They therewith differed from other carnivorous tadpoles, to *Hoplobatrachus occipitalis* that become cannibalistic during periods of food shortage (Spieler and Linsenmair, 1997; Rödel, 2000). The only other anuran were tadpoles are known to generate noise is *Mantidactylus corvus* (Glaw and Vences, 1994). Tadpoles of that species are at least partly carnivorous as well but, in contrast to *A. sonjae*, behave also aggressive toward each other. In both tadpole species, the adaptive value for vocalization remains unknown.

Like *A. spinosus* (Perret, 1961; Drewes, 1984), *A. sonjae* is apparently mute. One of the most fascinating questions, still to be answered, therefore, is how sexes meet. Perret (1961) speculated that olfactory orientation might be a possible explanation in *A. spinosus*. His assumption was based on the observation of two specimens that appeared on the outside wall of a cage, containing his captive specimens. However, he did not record the sex of these visitors nor did he provide further data. We observed fighting between our captive specimens. However, the sex of the respective frogs was not detectable on the video tapes.

Large water filled cavities might be limited resources even in rain forests, and the question arises how *Acanthixalus* detect these habitats. Because single specimens of both species have been found far away from tree holes (e.g., Noble, 1924; SMNS 09574.1), we believe that some individuals migrate in search of new habitats, but it remains for future study to assess specific cues used by frogs while searching for new tree holes.

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APPENDIX 1

Additional Specimens Examined

Acanthixalus spinosus.—Cameroon: ZMB 8359, 59353–55 (syntypes), Cameruns, coll. Buchholz; ZFMK 67471, Mt. Kupe, NW-Flanke; ZFMK 69604 (tadpole), 67598, 72000, Nyasoso, Mt. Kupe; MHNG 1033.75, 1033.77–85, Foulassi, Cameroun, coll. Perret;

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.
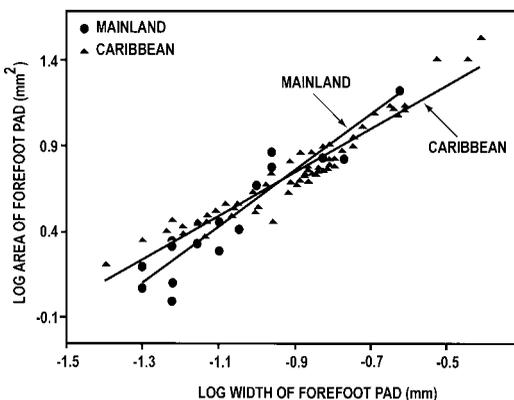

FIG. 1. Differences in shape of the forefoot toepad between Caribbean and mainland anoles. Lines on the plot represent linear regressions for the two groups of anoles.
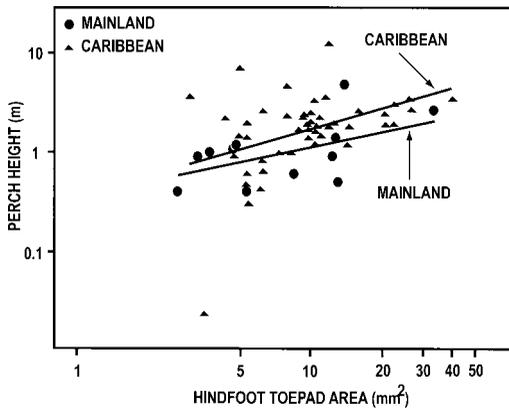
FIG. 2. The relationship between hind-foot toepad area and perch height for Caribbean and mainland anoles. Lines on the plot represent linear regressions for the two groups of anoles.

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.

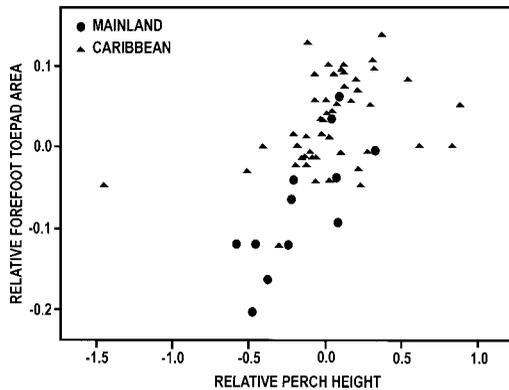| Characteristic vs. body size	Coefficient of determination	F ratio
Toepad width (ff)	$r^2 = 0.88$ $(+)$	$F_{1,77} = 570.52$***
Toepad width (hf)	$r^2 = 0.84$ $(+)$	$F_{1,77} = 424.48$***
Toepad area (ff)	$r^2 = 0.92$ $(+)$	$F_{1,77} = 847.87$***
Toepad area (hf)	$r^2 = 0.94$ $(+)$	$F_{1,77} = 1177.84$***
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.
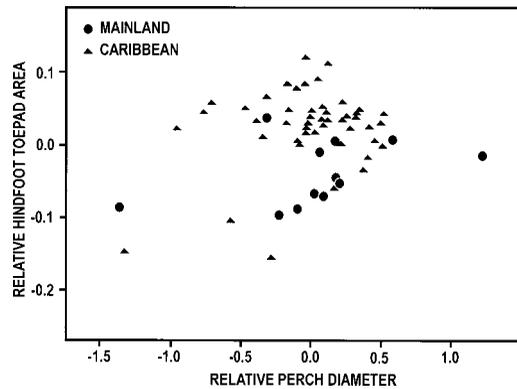

FIG. 4. The relationship between relative perch diameter and relative hind-foot toepad area for Caribbean and mainland anoles. Both variables are residuals from regressions against body size, as represented by SVL.

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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