

**South American rocky habitat *Leptodactylus*
(Amphibia: Anura: Leptodactylidae)
with description of two new species**

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Abstract.—There are four groups of populations of *Leptodactylus* associated with rocky habitats in northern South America. The available data are most consistent with recognizing three species for these four units: *L. rugosus* and two new species, *L. lithonaetes* and *L. myersi*. A single specimen from Paraguay, although distinctive, is considered to be conspecific with *L. sypfax*, previously known from disjunct localities in eastern Brazil. Data are inadequate at present to determine whether the South American species of *Leptodactylus* associated with rocky habitats are a monophyletic group.

Charles W. Myers brought my attention to a distinctive new species of the frog genus *Leptodactylus* that he had collected from granitic outcrops in the State of Roraima, Brazil. As study of the material progressed, comparisons were made between the new species from northern Brazil with *Leptodactylus rugosus*, a species from granitic and sandstone habitats of the Guiana shield region. It became apparent that there was considerably more variation among populations of the Guiana shield frogs than recognized previously (Heyer 1979). From the other end of South America, a single specimen of *Leptodactylus* was collected several years ago from rocky outcrops in Paraguay; this specimen's affinities are problematic. The purpose of this paper is to re-evaluate the species status of the *Leptodactylus* associated with granitic and sandstone habitats in South America.

Methods and Materials

As aspects of variation in *Leptodactylus sypfax* have recently been addressed (Cardoso & Heyer 1995), members of that species are not treated in detail here. As many specimens as possible were borrowed of all

other granitic and sandstone habitat *Leptodactylus*. Data were taken on patterns of the dorsum, upper lip, posterior thigh, and upper shank using the standards described in Heyer (1979). In addition, belly and ventral thigh surface patterns were recorded. Information was noted on dorsal folds, texture of the dorsum, upper shank, outer tarsus, and foot, as well as male secondary sexual characteristics. The snout-vent length (SVL) was recorded for all specimens. For all adults and specimens near adult size, the following measurements were also recorded (following Heyer et al. 1990): head length (HL), head width (HW), eye-mid-nostril distance (E-N), tympanum diameter (TD), thigh, shank, and foot. Statistics were analyzed with SYSTAT for Windows, version 5 (1992). Museum abbreviations are those recommended by Leviton et al. (1985) with the addition of IND-AN = INDERENA, Ministerio de Agricultura, Bogotá, Colombia.

Variation in Northern South American Rocky Habitat *Leptodactylus*

As data were being collected on specimens from northern South America, it be-

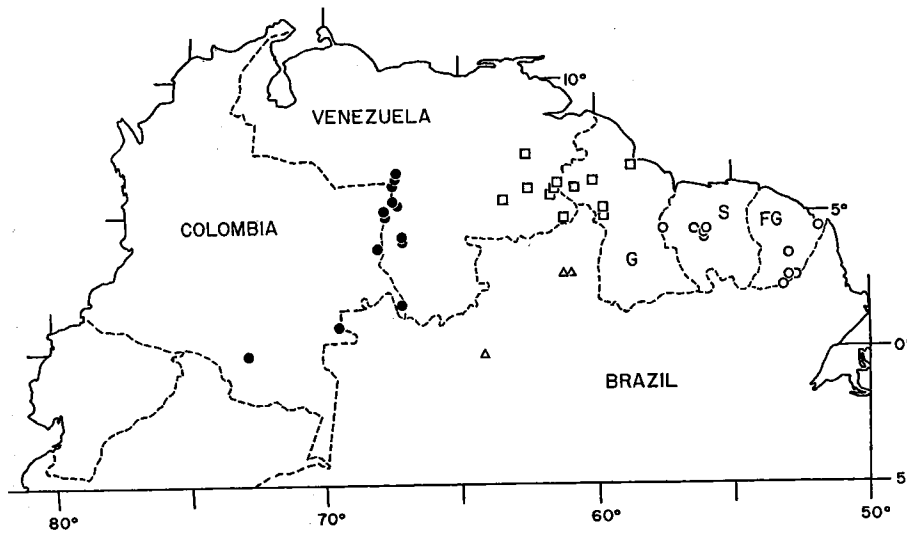


Fig. 1. Localities for Group 1-4 specimens from northern South America. Group I = dots (*L. lithonaetes*), Group II = squares (*L. rugosus*), Group III = triangles (*L. myersi*), Group IV = circles (*L. myersi*).

came apparent that there were four groups involved based on character states and geographic distributions. Each group is discussed in some detail and then decisions are drawn with respect to species limits. There are few tadpole samples; those that are available do not all contain Gosner (1960) stage 25-32 specimens. Tadpole characteristics described in this section are based on Gosner stage 33-42 specimens. Because recordings of advertisement calls exist for only Group 2 individuals, those data are not discussed.

Group 1.—Specimens in this group are from Colombia and Venezuela near the Colombian border (Fig. 1). Seventeen adult females, 31 adult males, 176 total specimens.

Dorsal patterns characteristically have a series of 3-4 (rarely 2) pairs of spots ranging from small to large in size and ranging from discrete to patterns of fusion with other spots both across, as well as, lengthwise along the dorsum (Heyer 1979, fig. 1, patterns H through K). About 10% of the individuals have a uniform dorsum.

Upper lip patterns show a continuum among the following states. Thirteen percent of the specimens have little pattern on

the upper lip (Heyer 1979, fig. 2, patterns C, E); 32% have some expression of alternating light and dark vertical bars (Heyer 1979, fig. 2, pattern J); 29% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); and 26% have some sort of irregularly defined light area in the loreal region to under the eye (Heyer 1979, fig. 2, pattern M).

The posterior thigh surface pattern also shows a complete continuum among the following conditions. The posterior thigh surfaces are indistinctly mottled in 39% of the individuals (Heyer 1979, fig. 3, pattern P); distinctly mottled with small light irregular marks in 17% of the individuals (Heyer 1979, fig. 3, patterns B, C, D); distinctly mottled with large light irregular spots and marks in 38% of the individuals (Heyer 1979, fig. 3, pattern A); 5% of the individuals have distinctly mottled thigh surfaces with some expression of light vertical marks or bars on the upper portions of the thigh surfaces (Heyer 1979, fig. 3, pattern D); one individual has a large light area on the lower thigh surface containing a few distinct dark spots; one individual has a large light area on the upper thigh surface.

One juvenile has a distinct lengthwise light band in the middle of the ventral thigh surface, 8% of the juveniles have a noticeable light band, whereas no adults have any indication of such a band; 76% of juveniles and 44% of adults have very light ventral thigh surfaces with few or no melanophores (Fig. 2); 9% of juveniles and 33% of adults have almost uniformly dark ventral thigh surfaces; 3% of juveniles and 12% of adults have lightly to moderately mottled ventral thigh surface patterns; 3% of juveniles and 10% of adults have the upper-lateral sector boldly mottled and the rest of the ventral thigh surface uniformly light.

Sixteen percent of the juveniles and 45% of the adults have relatively uniform gray/brown bellies, although in some, the posterior belly is lighter than the anterior; 50% of the juveniles and 2% of the adults have uniformly light bellies with very few melanophores (Fig. 2); 9% of the juveniles and 22% of the adults have dark bellies with moderate to low contrast light spots and/or vermiculations; 1% of the juveniles and 16% of the adults have a mottled pattern of smaller irregular lighter areas on a darker ground; and 24% of the juveniles and 14% of the adults have a bold mottled pattern of large light spots/flecks on a darker ground color.

Dr. Charles W. Myers (pers. comm.) provided life color information based on specimens AMNH 100656–100667 from the southwest sector of Cerro Yapacana, Amazonas, Venezuela: "Small white markings on lip. Rear of thigh usually suffused with orange (dotted pale tan on black in one specimen). Ventral surfaces grayish white. Juvenile (small specimen, 14875) [= AMNH 100666, 20.7 mm SVL] has pure white venter and bright orange under thighs, and a strong suffusion of orange on rear of thigh. Iris overall pale bronze, or pale bronze above and pale gray below—with overall dense black venation." Dr. John D. Lynch (pers. comm.) provided life color information based on specimens from Cueva Arévalo, Vichada, Colombia, es-

pecially ICNMMNH 13972–13974: "Dorsum brown with slightly darker brown and black spots on upper flanks. Patches on head and center of back rust. Pale brown (almost cream) interorbital bar and some marks on back. Face cream with black canthal stripe. Tympanum reddish-brown. Limb bands black. Yellow warts on flanks (glands). Venter and throat cream with brown spots and reticulation. Undersides of thighs pink. Posterior surfaces of thighs marbled black with faint rose spots. Iris bright copper above, gray below, flecked with black and bearing black horizontal streak. Other individuals may have posterior thighs black with small yellow spots above, becoming more rose below. Dorsum varies from tan to nearly black. In males the lateral $\frac{1}{3}$ of the gula is black (center white). Face generally pale (some dark individuals do not have the pale labial patch). Venter scarcely to heavily spotted with brown. Some dorsal patches have olive cast. Variation based on series of 15 individuals. . . ."

The degree of juvenile and adult pattern differences from individuals from the same localities, although noticeable in preserved specimens, is not striking. The most noticeable features are that the bellies and ventral thigh surfaces are lighter than in the adults, but these differences are more of degree than fundamentally different.

The commonest conditions for dorsolateral fold development are either no indication of dorsolateral folds or one short pair of ridges or elongate warts in the shoulder region. Some specimens have series of warts or ridges in the dorsolateral fold field, some extending the entire length of the dorsum from behind the eye, others extending only to the sacrum.

Most individuals have a shagreen together with black and/or white tubercles on the dorsum. When tubercles are present, they are more abundant on the posterior dorsum. Most juveniles (80%) either have a moderate to pronounced shagreen and/or small bumpy glands without any black and/or

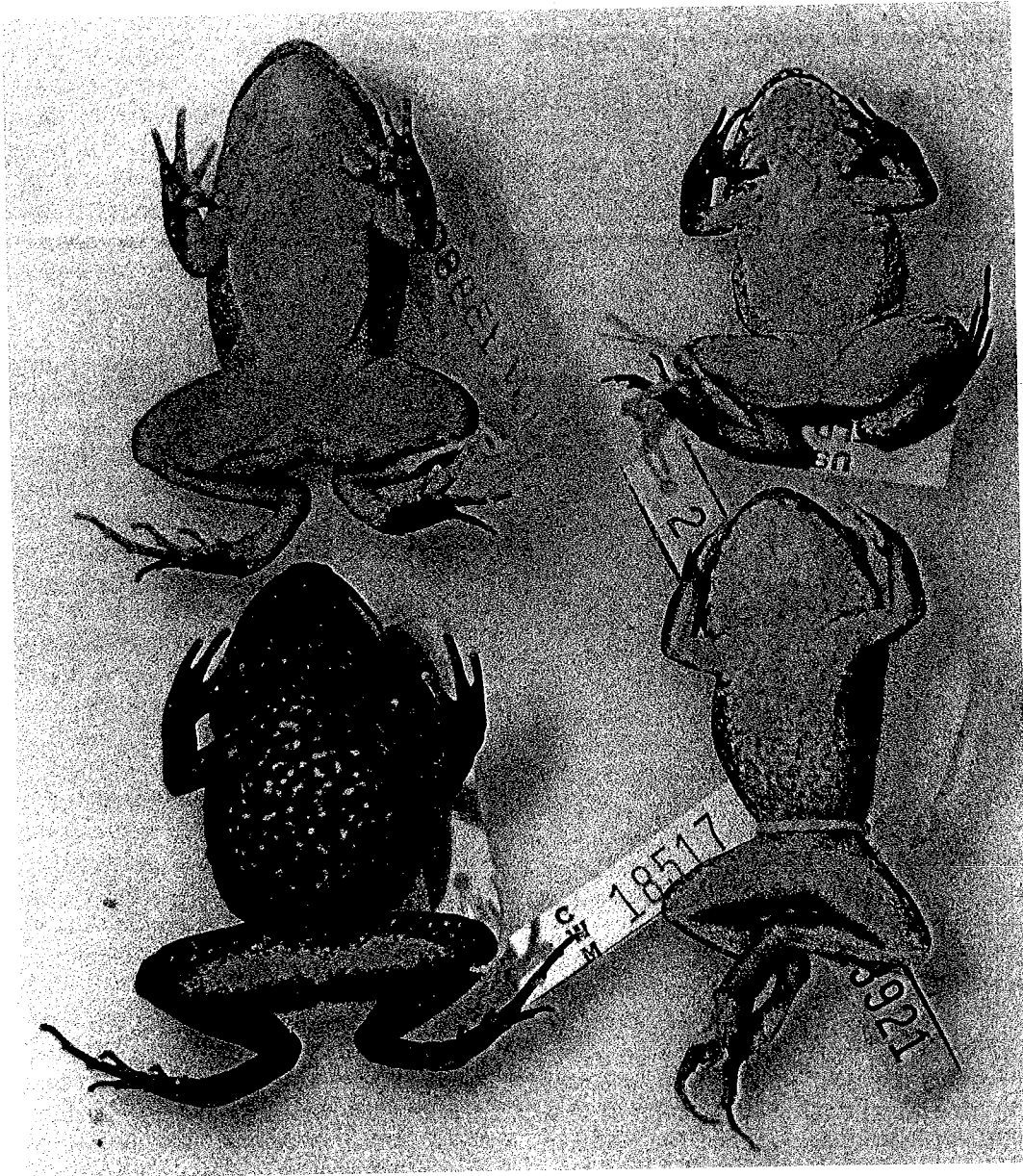


Fig. 2. Characteristic ventral patterns of juveniles. Upper left, Group I, ICNMNH 13980; upper right, Group II, USNM 291249; lower left, Group III, AMNH 128023; lower right, Group IV, RMNH 23921.

white tubercles; 31% of adults lack tubercles.

The upper shank surface may have a shagreen or not. Most specimens (93%) have few to many black and/or white tubercles; few specimens (7%) have very few or no tubercles.

The texture of the outer tarsus may be shagreened or not. Most specimens (81%) have few to many black and/or white tubercles; some specimens (19%) have very few or no tubercles.

Texture of the foot is usually smooth, lacking shagreen or tubercles (86%); some

individuals (12%) have no more than a few black and/or white tubercles; very few individuals (2%) have a weakly developed shagreen.

Adult males have one black thumb spine on each hand and a pair of chest spines. There is also a band of black tubercles across the chest in larger males. Males have a patch of black chin tubercles on the anterior portion of the throat. The vocal sacs are laterally expanded and darkly pigmented.

Adult females range between 54.8 and 78.4 mm SVL, adult males 45.3 and 71.4 mm SVL. A principal components analysis was run on the measurement data for adult specimens. No obvious outliers are evident on the resultant plot of individuals using the first two factors.

Two series of tadpoles are available, one well-preserved series of specimens from Cerro Patavá, Colombia, and two alcohol preserved dehydrated specimens from Canaripo, Venezuela. It is difficult to determine to what degree the differences observed between larvae from these two localities are due to preservation artifact. Tadpoles from both localities demonstrate the semiterrestrial ecomorph as described by Altig & Johnson (1989). The body length is 28–31% of the total length in the Cerro Patavá tadpoles, 31–32% in the Canaripo tadpoles. The anterior oral gap is 80–88% of the oral disk width in the Cerro Patavá specimens, 64–77% in the Canaripo specimens. The upper beak is highly arched; its depth is 27–37% of the upper beak width in the Cerro Patavá sample, 36% in the Canaripo sample. The body is flattened, with body depth 67–74% of body width in the Cerro Patavá larvae, 46–56% in the Canaripo larvae. Larvae have series of glandular ridges on the body above the abdominal cavity.

Habitat notes are available from AMNH 100656–100667 collected at Cerro Yapacana, Amazonas, Venezuela, 18–19 February 1978 (C. W. Myers, pers. comm.): "Mountain stream by night, sitting on the rock stream bed at or near edge of water.

... They are timid and quick to take cover in crevices and under large boulders if one's light is not kept on them while approaching; they seem to avoid diving into the water."

Group 2.—This group includes specimens from Guyana and southeastern Venezuela (Fig. 1). Seventeen adult females, 35 adult males, 126 total specimens.

Most specimens have a dorsal pattern of a series of 3–4 (rarely 2) pairs of large to small spots ranging from discretely defined to patterns of fusion with other spots both across the dorsum as well as lengthwise along the dorsum (Heyer 1979, fig. 1, patterns H through K). Twenty-seven percent of the individuals have uniform or almost uniform dorsal patterns.

Upper lip patterns represent a continuum among the following states. Eleven percent of the specimens have little pattern on the upper lip (Heyer 1979, fig. 2, patterns C, E); 8% have some expression of alternating light and dark vertical bars (Heyer 1979, fig. 2, pattern J); 43% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); 26% have some sort of irregularly defined light area in the loreal region to under the eye (Heyer 1979, fig. 2, pattern M); 7% have an irregularly defined light area in the loreal region, separated from light oblique bars behind the eye by irregular dark bars (Heyer 1979, fig. 2, pattern K); and 3% have extensive dark mottling on the upper lip, heaviest near the mouth.

Posterior thigh surface patterns are quite variable, with a continuum including the following states. The posterior thigh surfaces are indistinctly mottled in 8% of the individuals (Heyer 1979, fig. 3, pattern P); distinctly mottled with small light irregular marks in 4% of the individuals (Heyer 1979, fig. 3, patterns C, D); distinctly mottled with large light irregular spots and marks in 40% of the individuals (Heyer 1979, fig. 3, pattern A); the upper thigh surfaces have some sort of light vertical marks or bars in 15% of the individuals (Heyer 1979, fig. 3, patterns E, F); the lower thigh

surface has one or more extensive light area, sometimes with a few small dark spots in 22% of the specimens; and the upper thigh surface has a large light area in 10% of the individuals.

The ventral thigh surfaces are very light with few or no melanophores in 72% of the juveniles and 31% of the adults (Fig. 2); the ventral thigh surfaces are almost uniformly dark in 13% of the adults (no juveniles); the ventral thigh surfaces are lightly to moderately mottled in 5% of the juveniles and 37% of the adults; the ventral thigh surfaces have the upper-lateral sector boldly mottled with the rest of the thigh surface uniformly light in 23% of the juveniles and 18% of the adults.

Two percent of the juveniles and 21% of the adults have relatively uniform gray/brown bellies; 44% of the juveniles and 13% of the adults have almost uniformly light bellies with very few melanophores (Fig. 2); 3% of the juveniles and 8% of the adults have dark bellies with moderate to low contrast light spots and/or vermiculations; 17% of the juveniles and 45% of the adults have a mottled pattern of smaller irregular lighter areas on a darker ground; and 33% of the juveniles and 13% of the adults have a boldly mottled pattern of large light spots/flecks on a darker ground.

Donnelly & Myers (1991:22) provided color descriptions for specimens from Cerro Guaiquinima, Bolívar, Venezuela: "In life, some juveniles had white-edged dorsal blotches whereas others were uniformly blackish. The throat was heavily marked with gray mottling on white and there was less gray on the venter. The body glands of the groin and the ventral and posterior thigh surfaces had variable suffusion of orange that was bright in some individuals. The iris was bronze above, white on the medial ventral section, and brown between, with dense black venation overall." Dr. Robert P. Reynolds (pers. comm.) provided copies of his color notes for specimens from Kaieteur Falls, Guyana. A series of adults and small juveniles (USNM 291245–291250) had the

following: "Brown dorsally with warty rugose skin. . . . Venter cream with darker mottling. Rose-orange groin and undersurfaces of thighs. Bronze-gold iris." A female (USNM 291251) was: "Dorsally greenish with dark speckling throughout. Rims of eyelids yellowish with yellow band between eyelids. Three–4 light spots on lower eyelid. Yellowish with mottled brown between upper lip and eyelid. Tympanum rust brown. Iris bronze. Venter brownish with white throughout. Rear of thigh gold and brown mottled." A series of adults of both sexes (USNM 291252–291256) were: "Dorsally greenish brown with yellow mottling. Three distinct yellow lines from eye to lip. Yellow line between eyes on top of head and a line from rear of each eye back to rear of head. Rust wash over neck and shoulder area. Mottled light and dark venter. Undersides of legs rose tint with dark spots." A single male (USNM 342151) had: "Dorsum reddish brown, limbs with reticulate dark markings, light line between orbits, bronze eye, dark canthal stripe; chin, throat, chest and belly with dark grey spotting, underside of thighs and calfs salmon red."

The degree of juvenile and adult pattern differences from individuals from the same localities are striking with respect to ventral patterns, especially when small juveniles are compared with adults. The throats and bellies of juveniles are bright white in recently preserved specimens (Kaieteur National Park, Guyana), whereas the throats and bellies of adults are densely mottled dark gray; the ventral thigh surfaces of the juveniles lack melanophores and stand in contrast to the dark pigmented ventral thigh surfaces of adults. No differences in dorsal pattern between juveniles and adults are evident.

The commonest conditions for dorsolateral fold development are either no indication of dorsolateral folds or one short pair of ridges or elongate warts in the shoulder region. Three individuals were recorded as having two pair of short ridges and three

individuals were recorded as having a series of short ridges in the dorsolateral fold field.

Most individuals have a shagreen and black and/or white tubercles on the dorsum. When tubercles are present, they are more abundant on the posterior dorsum. Twenty-two percent (20 individuals) of the juveniles have a pronounced dorsal texture of a strongly developed shagreen with glandular warts; only 5% (2 individuals) of the adults have the same texture.

The upper shank surface may have a shagreen or not. Almost all specimens (122 of 124 recorded) have few to many black and/or white tubercles; only 2 individuals have very few or no tubercles.

The texture of the outer tarsus may be shagreened or not. Almost all specimens (98%) have few to many black and/or white tubercles; only 2 individuals (2%) have very few or no tubercles.

The texture of the foot is smooth, lacking shagreen or tubercles in 50% of the individuals; 49% of the specimens have no more than a few black and/or white tubercles; very few individuals (2%) have a weakly developed shagreen.

Adult males have one or two black thumb spines on each hand and a pair of chest spines. There is no distinctive band of black tubercles across the chest in larger males. Males lack a patch of black chin tubercles on the anterior portion of the throat. The vocal sacs are laterally expanded and darkly pigmented.

Adult females range between 53.6 and 73.5 mm SVL, adult males 50.9 and 71.6 mm SVL. A principal components analysis was run on the measurement data for adult specimens. There is a general cluster of points on the plot of individuals using the first two factors, but three individuals lie somewhat outside the general cluster. KU 166499 is an individual from a locality in which all other specimens lie in the general cluster of points. RMNH 23906 and USNM 258130 are the only adult individuals from each of two different localities. Re-examination of these specimens does not indicate

that any change should be made in their assignment to the geographically based four clusters.

Data were taken from a single tadpole from Cerro Auyantepui, Venezuela, a single tadpole from La Escalera, Venezuela (both alcoholic) and seven larvae from Kartabo, Guyana (formalin). These tadpoles demonstrate the semiterrestrial ecomorph as defined by Altig & Johnson (1989). The body length is 28–29% of the total length. The anterior oral gap is 75–81% of the oral disk width. The upper beak is highly arched; the upper beak depth is 33–40% of the upper beak width. The body is flattened; the depth is 64–70% the body width. Larvae have series of glandular ridges on the body above the abdominal cavity.

Habitat information specific for members of Group 2 has been published by Donnelly & Myers (1991:22) for specimens from Cerro Guaiquinima, Bolívar, Venezuela: "Adults were taken at night in the rocky stream bed at Camp 2 and in the north stream at Camp 1. At Camp 2, several adults were collected by night in water in the middle of small waterfalls. Juveniles were active both day and night. During the day, juveniles were commonly seen in exposed situations, sitting on rocks around small pools and jumping into the pools when disturbed." Robert P. Reynolds (pers. comm.) collected a series of specimens (including USNM 291245–291256) at night at Kaieteur National Park, Guyana, 29–30 March 1989, on a trail from the airstrip to the guest house above Kaieteur Falls. Some individuals were calling and others were not. On the afternoon of 7 April 1994, Reynolds collected USNM 342151–342160 on bedrock puddles, near the airstrip at Kaieteur Falls.

Group 3.—Specimens from this group are from northern Brazil (Fig. 1). Three adult females, 13 adult males, 47 total specimens.

The dorsal patterns characteristically have two large dark spots on the dorsum (Heyer 1979, fig. 1, pattern K). The spots may have fuzzy borders, or be well defined

with a black outline border, or be well defined by a contrasting light border. The spots may be fused with each other and the interocular spot. Nine percent of the individuals have a dark dorsum with a few small, discrete, irregular, lighter spots. One individual has paired series of dark dorsal spots (Heyer 1979, fig. 1, pattern H). No individual has a completely uniform dorsum.

Upper lip patterns demonstrate a continuum among the following states. Nine percent of the specimens have little pattern on the upper lip (Heyer 1979, fig. 2, patterns C, E); 49% have some expression of dark vertical bars (Heyer 1979, fig. 2, patterns A, J); 16% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); 20% have some sort of irregularly to regularly defined light area in the loreal region to under the eye (Heyer 1979, fig. 2, patterns L, M); and 7% have a mottled upper lip with small dark spotting.

The posterior thigh surface patterns grade among the following states. A single individual has an indistinctly mottled posterior thigh surface (Heyer 1979, fig. 3, pattern A); one specimen has an almost uniformly dark thigh surface; 70% have large light spots on the upper portion of the posterior thigh surfaces with or without smaller light spots on the lower portion of the posterior thigh surfaces; 15% have narrow vertical light stripes on the upper portion of the posterior thigh surface; and 11% have few to several distinct small light spots on the posterior thigh surface (Heyer 1979, fig. 3, patterns N, O).

Most juveniles (79%) have at least a noticeable lengthwise light band in the middle of the ventral thigh surfaces (very distinct in 38% (Fig. 2)), whereas only one adult has a faint indication of this band; one juvenile and most adults (69%) have almost uniformly dark gray or brown ventral thigh surfaces; 17% of the juveniles and 25% of the adults have lightly to moderately mottled ventral thigh surfaces.

No juveniles, but 29% of the adults, have relatively uniform gray or brown bellies; 63% of the juveniles, but no adults, have dark bellies with very contrasting distinct light spots (Fig. 2); 33% of the juveniles and 71% of the adults have dark bellies with moderate to low contrast distinct light spots or vermiculations.

Ronald I. Crombie (pers. comm.) took the following notes on a 79.4 mm SVL juvenile female (USNM 302192): "Light markings on back rich tan, especially on head, darker markings deep wood brown. Warts on side with reddish brown markings. Venter gray with lighter gray spots, lighter marks distinctly greenish in groin and under legs. Red-brown pustules under arms and near axilla (parasites?). Rear of thighs black with a few greenish blotches and some red-brown ones near anus. Soles of hands and feet dark gray, feet almost black. Iris gold with brassy vermiculations above, dark below." Crombie noted that on two other large juveniles (USNM 302194, 72.3 mm SVL; USNM 302195, 69.8 mm): "Considerable red spotting on anterior and posterior thighs." Charles W. Myers (pers. comm.) took color notes for adults and juveniles: "Adults [AMNH 128021-128022 = CWM 18514, 18516]: Throats blackish gray; rest of ventral surfaces gray, with or without small white spots. Thighs above with black bands separated by brown interspaces that may have a faint reddish suffusion (not bright as in juveniles). Rear of thigh black with a line of silvery white dots. Iris pale bronze with reddish brown horizontal stripe. Juveniles [AMNH 128023-128031 = CWM 18526-18534]: Throat and other ventral surfaces gray with irregular white spotting. Thighs with black bands and bright orange-red interspaces antero- and posterodorsally (red color not continuous across dorsal midline of thigh). Iris pale bronzy gray on upper half—above an ill-defined reddish brown horizontal stripe—and with a faint reddish suffusion on lower part of iris."

The degree of juvenile and adult pattern

differences from the same locality is striking in preserved specimens. The most noticeable differences occur on the thighs. The upper portion of the posterior thigh surfaces in juveniles have well defined large light spots (bright red in life), whereas such spots are not distinct or completely absent in adults. In most juveniles, there is a distinct light longitudinal band on the mid-ventral thigh surfaces; no such distinct light band occurs in adults. The belly spotting differences between juveniles and adults are not as striking as the thigh surface pattern differences—in juveniles, the dark bellies have more distinct light spots than adults.

No dorsolateral folds are evident in 16% of the individuals examined. In most specimens (77%) dorsolateral folds are distinct, but broken (not continuous) and range from short (extending only to the shoulder region) to long (entire length of back from behind eye to leg). Only two individuals have almost continuous dorsolateral folds extending to the sacrum, and only one specimen has a continuous dorsolateral fold extending to the leg.

Most specimens have a shagreen and white tubercles on the dorsum. When tubercles are present, they are more abundant on the posterior dorsum. Only in juveniles (60%) is a strong warty shagreen developed.

The upper shank usually has a shagreen (93%). Most specimens (87%) have few to many black and/or white tubercles; some (13%) have very few or no tubercles.

The texture of the outer tarsus is usually shagreened (85%). Most specimens (93%) have few to many black and/or white tubercles; a few (7%) have very few or no tubercles.

The texture of the sole of the foot is usually smooth (87%); 11% have a weak shagreen; only one individual has scattered white tubercles.

Adult males have one black spine on each thumb. There is no indication of chest spines, chest tubercles, or chin tubercles.

Vocal sacs are neither laterally expanded nor differentially patterned.

Adult females range from 103.8 to 112.9 mm SVL, adult males 74.2 to 116.8 mm SVL. The relatively small sample size does not justify analyzing the measurement data with principal components to identify potential outlier individuals.

No tadpoles are available for this group.

Habitat notes are available from two sets of collectors from the same rock outcrop from Mucajaí, Roraima, Brazil. Charles W. Myers (pers. comm.) indicated for specimens AMNH 128021–128031, collected on 11 July 1987: "On granite inselberg surrounded by humid scrubby forest with many palms. Some juveniles by day under granite flakes microsympatric with *Tropidurus hispidus* and *Leptodactylus fuscus*. Other juveniles by night, sitting on bare rock or in small pools of water (with sparse aquatic vegetation) on the bare rock. The four adults all in the small pools by night." On 30 May–1 June 1988, Ronald I. Crombie (pers. comm.) collected USNM 302066–302068, 302190–302203, MZUSP 660889 at night from on or under rock. Ronald I. Crombie (pers. comm.) documented that USNM 302267 from Colônia Apiaú, Roraima, Brazil, collected on the afternoon of 14 June 1988, was taken from under roofing tiles at an abandoned hunting camp in the forest, not near any rocky outcrop.

Group 4.—Specimens in this group are from French Guiana and Surinam (Fig. 1). One adult female, 1 adult male (both from French Guiana), 54 total specimens.

Most specimens have two large, dark, relatively well-defined blotches on the dorsum posterior to the dark interorbital blotch (Heyer 1979, fig. 1, pattern K); these blotches may be outlined by a white ring or a dark border. A few specimens have some paired large or small dark spots on the dorsum (Heyer 1979, fig. 1, patterns H, J). A few have fused blotches (Heyer 1979, fig. 1, patterns D, I). Uniform patterns (Heyer

