

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

W. Ronald Heyer

Department of Vertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560, U.S.A.

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-

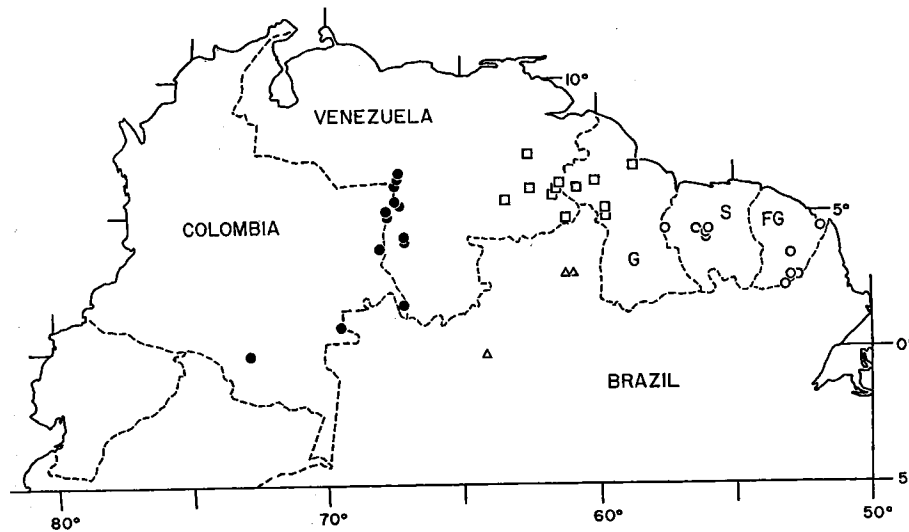


Fig. 1. Localities for Group 1-4 specimens from northern South America. Group I = dots (*L. lithonaetes*), Group II = squares (*L. rugosus*), Group III = triangles (*L. myersi*), Group IV = circles (*L. myersi*).

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

