

FIGURE 56. Dorsal views of striped (left, FMNH 128831) and unstriped (right, UPR 2641) *Leptodactylus longirostris*.



FIGURE 57. Lateral view of the heads of *Leptodactylus amazonicus* (left, lip stripe very distinct), *longirostris* (center, lip stripe moderately distinct), *poecilochilus* (right, no lip stripe, lip bar present).

SVL ratio $.545 \pm .026$, female $.553 \pm .031$) than *laurae* (male foot/SVL ratio $.649 \pm .039$, female $.628 \pm .028$); *longirostris* occurs in northern South America, *laurae* in mid-east and southern South America. Most individuals of *mystaceus* have distinct white tubercles on the sole of the foot; *mystaceus* occurs along coastal Brasil. Many individuals of *notoaktites* have white tubercles on the sole of the foot; *notoaktites* occurs in SE Brasil. *Leptodactylus longirostris* often has a distinct light lip stripe and lacks a dark suborbital bar, *poecilochilus* lacks a distinct light lip stripe and often has a dark suborbital bar (fig. 57).

Adult Characteristics ($N = 70$).—Dorsum uniform or spotted, spots sometimes elongate, fused (fig. 1, A, B, C, E, J); light mid-dorsal stripe present in 17% of individuals, presence not sexually dimorphic ($\chi^2 = .09$, $P = .76$); light lip stripe usually indistinct (60%), often distinct (40%), distinctiveness not sexually dimorphic ($\chi^2 = 2.94$, $P = .09$); dark suborbital bar absent; light stripe on posterior face of thigh usually distinct (80%), sometimes indistinct (20%), more females (100%) have distinct light stripes than males ($\chi^2 = 6.80$, $P = .009$); tibia barred; usually 4 well defined dorsal folds, 6 dorsolateral folds present when light mid-dorsal stripe present; dorsal surface of tibia lacking white tubercles; pos-

terior surface of tarsus almost always (99%) lacking white tubercles, presence not sexually dimorphic ($\chi^2 = .14$, $P = .71$); sole of foot lacking white tubercles (100%); male SVL 38.2 ± 1.8 mm, female 41.8 ± 2.4 mm, females larger than males ($F_{1, 68} = 49.7$, $P < .001$); male head length/SVL ratio $.394 \pm .012$, female $.387 \pm .014$, male head longer than female ($F_{1, 68} = 5.28$, $P = .025$); male head width/SVL ratio $.338 \pm .015$, female $.334 \pm .013$, not sexually dimorphic ($F_{1, 68} = 1.12$, $P > .05$); male femur/SVL ratio $.446 \pm .041$, female $.457 \pm .033$, not sexually dimorphic ($F_{1, 68} = 1.31$, $P > .05$); male tibia/SVL ratio $.512 \pm .024$, female $.527 \pm .031$, female tibia longer than male ($F_{1, 68} = 5.28$, $P = .025$); male foot/SVL ratio $.545 \pm .026$, female $.553 \pm .031$, not sexually dimorphic ($F_{1, 68} = 1.21$, $P > .05$).

Larval Characteristics.—Unknown.

Mating Call.—Dominant frequency modulated between 1500–3600 Hz; note duration about 0.8 s; note repetition rate 1.4 per second (from Rivero, 1971, fig. 58 reproduced here from same sonagram described by Rivero).

Karyotype.—Unknown.

Distribution.—Centered upon the Guiana Shield (fig. 55).



FIGURE 58. Sonagram of the mating call of *Leptodactylus longirostris*. Vertical scale marks at 1000 Hz intervals. Horizontal scale mark at 1 s. Specimen from Venezuela, La Escalera (sonagram courtesy of Juan A. Rivero).

BRASIL. AMAZONAS: Ponta Negra, Negro River, MZUSP 24880; Tapera, Rio Negro, MZUSP 37518.

PARÁ: Igarapé Jaramacaru, Campos do Ariramba, MZUSP 28401-04; Rio Mapuera, at equator, AMNH 46189-190 (3); Rio Mapuera, R. Trombetas, AMNH 46187-88.

GUYANA. Kartabo, USNM 118065-66; Kuyuwini Landing, AMNH 49349-351, 49353-54 (4); upper Rupununi River, AMNH 81355-56.

SURINAM. Brownsberg Nature Park, Brokopondo Dist., MCZ 89648; Brownsberg, RMNH 17531, 17535; Christian Kondre, MZUSP 24758, 24761, 24765, 24767-772; Kaiserberg Airstrip, Zuid River, FMNH 128827-832, 128913-18, 128920-23, RMNH 17527 (4), 17530, 17549 (5); Krakka, RMNH 17540 (2); road between Krakka and Phedra, RMNH 17537, 17539 (2); Powakka, CM 49482, 49484, 44265, 44272, 44274; Matta, RMNH 17558; Sabakoe Creek, between Berlijn and Zanderij, RMNH 15106; Sipaliwini, RMNH 15176, 15178 (2), 17524-26, 17528-29, 17532-33, 17547, 17569; Tibiti, RMNH 17555, 17563; Troeli Cr., 6 km S Matta, RMNH 15115 (2), 15133 (4); Zanderij, MCZ 35642, MZUSP 15869-870, USNM 159066-67.

VENEZUELA. BOLÍVAR: km 104-151 on El Dorado-Santa Elena de Uairén Road, KU-WED 40072, 40078, 40080, 40085, 40151, 40181-82, 40208-09, 40263, 40281-87, 40381; La Escalera, Serranía de Lema, MCZ 79907, UPR 2641, 2643-45, 2647.

LEPTODACTYLUS MARAMBAIAE IZECKSOHN 1976

Leptodactylus marambaiae Izecksohn 1976:527-530, fig. 1. (Type locality, Brasil: Rio de Janeiro; Restinga da Marambaia. Holotype personal collection of Izecksohn 4123, adult male.)

Diagnosis.—The species with light longitudinal stripes on skin-folds on the dorsal surface of the tibia (fig. 48) (if light stripes indistinct, folds are present where stripes occur in other individuals) are *geminus*, *gracilis*, and *marambaiae*. *Leptodactylus marambaiae* has a shorter leg (e.g. tibia 50% SVL) than *gracilis* (e.g. tibia average 58% SVL in males, 57% SVL in females). At present, *marambaiae* cannot be morphologically distinguished from *geminus*. The note repetition rate of the mating call is slower for *marambaiae* (6 per second) than for *geminus* (22 per second).

Adult Characteristics.—Dorsum striped; mid-dorsal light stripe always present; light upper lip stripe distinct; no dark suborbital bar; light stripe on posterior face of thigh usually distinct, sometimes indistinct; tibia partially barred with light longitudinal pin stripes present; 6 well defined dorsolateral folds; upper surface of tibia lacking white tubercles; posterior surface of tarsus lacking white tubercles; sole of foot lacking white tubercles; male SVL 36.8 mm, female 40.2 mm; male head length/SVL ratio .40, female .36; male head width/SVL ratio .34, female .34; male femur/SVL ratio .44, female .44; male tibia/SVL ratio .50, female .50; male foot/SVL ratio .56, female .54.

Larval Characteristics.—Unknown.

Mating Call.—Dominant frequency modulates between 3000-3700 hz (fig. 59); call without harmonic structure; call not pulsed (fig. 60); note duration about 0.02 s; note repetition rate about 6 per second.

Karyotype.—Unknown.

Distribution.—Known only from the type locality (fig. 55).

BRASIL. RIO DE JANEIRO: Restinga da Marambaia.

LEPTODACTYLUS MYSTACEUS (SPIX) 1824

Rana mystacea Spix 1824:27, plate 3, fig. 3. (Type locality, Brasil: Bahia [Salvador as designated by Bokermann 1966]. Types lost.)

Diagnosis.—Most individual *mystaceus* have a combination of a distinct light stripe on the posterior surface of the thigh and distinct white tubercles on the surfaces of the posterior tarsus and sole of foot; these states are shared with *albilabris*, *elenae*, *fragilis*, and *latinasus*. *Leptodactylus mystaceus* have distinct dorsolateral folds (at least indicated by color pattern), *fragilis* and *latinasus* lack distinct dorsolateral folds. *Leptodactylus mystaceus* has white tubercles on the dorsal surface of the tibia, the tibia is smooth in *elenae*. *Leptodactylus mystaceus* is found in east coastal Brasil, *albilabris* occurs in the West Indies.

Some individuals of *mystaceus* lack the white tubercles on the tarsus and sole of foot (light thigh stripe present), these states are shared with at least some individuals of *fuscus*, *geminus*, *gracilis*, *laurae*, *longirostris*, *notoaktites*, and *poecilochilus*. The tubercles on the dorsal surface of the tibia distinguishes *mystaceus* from all these species.

Adult Characteristics ($N = 38$).—Dorsum spotted or rarely uniform (fig. 1, A, C, 0); light mid-dorsal stripe usually absent (97%), presence not sexually dimorphic ($X^2 = .08$, $P = .78$); light lip stripe usually distinct (79%), distinctiveness not sexually dimorphic ($X^2 = .14$, $P = .71$); dark suborbital bar absent; light stripe on posterior face of thigh distinct (100%); tibia barred; usually 4 or 2 well defined dorsolateral folds, 6 dorsolateral folds present when light mid-dorsal stripe present; dorsal surface of tibia usually with many distinct white tubercles; posterior surface of tarsus usually with many distinct white tubercles (87%), tubercles sometimes lacking (13%), presence not sexually dimorphic ($X^2 = .43$, $P = .51$); sole of foot usually with many distinct tubercles (87%), tubercles sometimes lacking (13%), presence not sexually dimorphic ($X^2 = .43$, $P = .51$); male SVL 42.7 ± 2.3 mm, female 43.6 ± 3.0 mm, not sexually dimorphic ($F_{1, 36} = 1.18$, $P > .05$); male head length/SVL ratio $.379 \pm .015$, female $.375 \pm .022$, not sexually dimorphic ($F_{1, 36} = .40$, $P > .05$); male head width/SVL ratio $.344 \pm .018$, female $.342 \pm .029$, not sexually dimorphic ($F_{1, 36} = .15$, $P > .05$); male femur/SVL ratio $.434 \pm .032$, female $.461 \pm .037$, female femur longer than male ($F_{1, 36} = 5.61$, $.025 < P < .01$); male tibia/SVL ratio $.509 \pm .015$, female $.517 \pm .029$, not sexually dimorphic ($F_{1, 36} = 1.42$, $P > .05$); male foot/SVL ratio $.554 \pm .022$, female $.548 \pm .034$, not sexually dimorphic ($F_{1, 36} = .42$, $P > .05$).

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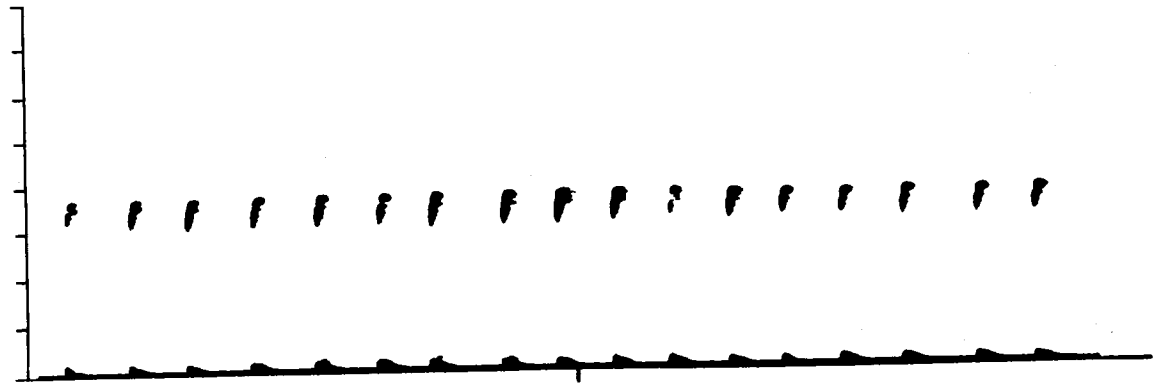


FIGURE 59. Sonagram of the mating call of *Leptodactylus marambaiae*. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. Specimen from Brasil, Restinga da Marambaia (tape courtesy of W. C. A. Bokermann).



FIGURE 60. Strip chart record of the mating call of *Leptodactylus marambaiae*. Line equals 0.01 s. See legend of Figure 59 for specimen data.

Larval Characteristics.—Unknown.

Mating Call.—Unknown.

Karyotype.—Unknown.

Distribution.—East coast of Brasil (fig. 61).

BRASIL. BAHIA: Copec. Ilhéus, MNRio 1724 (4), WCAB 45899–5919, 46570–6601, 47066–69; Itapetinga, WCAB 44885.

ESPÍRITO SANTO: Santa Teresa, CAS-SU 11787–88; São Mateus, MCZ 1298 (5).

RIO DE JANEIRO: Caxias, MNRio 1809 (5), 2374, 2861; Cidade dos Meninos, MNRio 1656 (3); Meriti, USNM 96222; Niteroi, Saco de São Francisco, USNM 96407–411, 99120; road to São Paulo, km 40, D. F., 97572; Serra de Friburgo, USNM 96467; Teresópolis, KU 92927–931, MNRio 397 (4), WCAB 12252.

LEPTODACTYLUS MYSTACINUS BURMEISTER 1861

Cystignathus mystacinus Burmeister 1861:532. (Type locality, Argentina. Holotype Martin-Luther-Universität, Halle (Saale), no number, male.)

Cystignathus labialis Cope 1878:90. (Type locality unknown. Presumed holotype USNM 31302, juvenile.)

Diagnosis.—The species having a combination of no light stripe on the posterior surface of the thigh and distinct white tubercles on the posterior surface of the tarsus are *bufonius*, *labrosus*, *mystacinus*, *troglydites*, and

ventrimaculatus. *Leptodactylus mystacinus* has distinct dorsolateral folds (at least indicated by color pattern), dorsolateral folds are indistinct or lacking in *bufonius* and *troglydites*. *Leptodactylus mystacinus* occurs east of the Andes, *labrosus* and *ventrimaculatus* occur west of the Andes.

Adult Characteristics ($N = 87$).—Dorsum uniform, striped, or slightly spotted (fig. 1, A, C, J, K); no light mid-dorsal stripe; light lip stripe usually distinct (86%), sometimes indistinct (14%), more females (100%) with distinct lip stripes than males ($X^2 = 4.10$, $P = .04$); dark suborbital bar absent; light stripe on posterior face of thigh usually absent (94%), rarely indistinct (6%), presence not sexually dimorphic ($X^2 = 1.17$, $P = .28$); tibia barred; usually 2 or 4 well defined dorsolateral folds; dorsal surface of tibia with many or scattered distinct white tubercles; posterior surface of tarsus almost always (94%) with many or scattered distinct white tubercles, absence not sexually dimorphic ($X^2 = .004$, $P = .95$); sole of foot usually with distinct scattered or many white tubercles (75%), sometimes absent (25%), presence not sexually dimorphic ($X^2 = .41$, $P = .52$); male SVL 53.0 ± 4.6 mm, female 56.5 ± 2.7 mm, females larger than males ($F_{1, 85} = 12.59$, $P < .001$); male head length/SVL ratio $.371 \pm .013$, female $.358 \pm .013$, male head

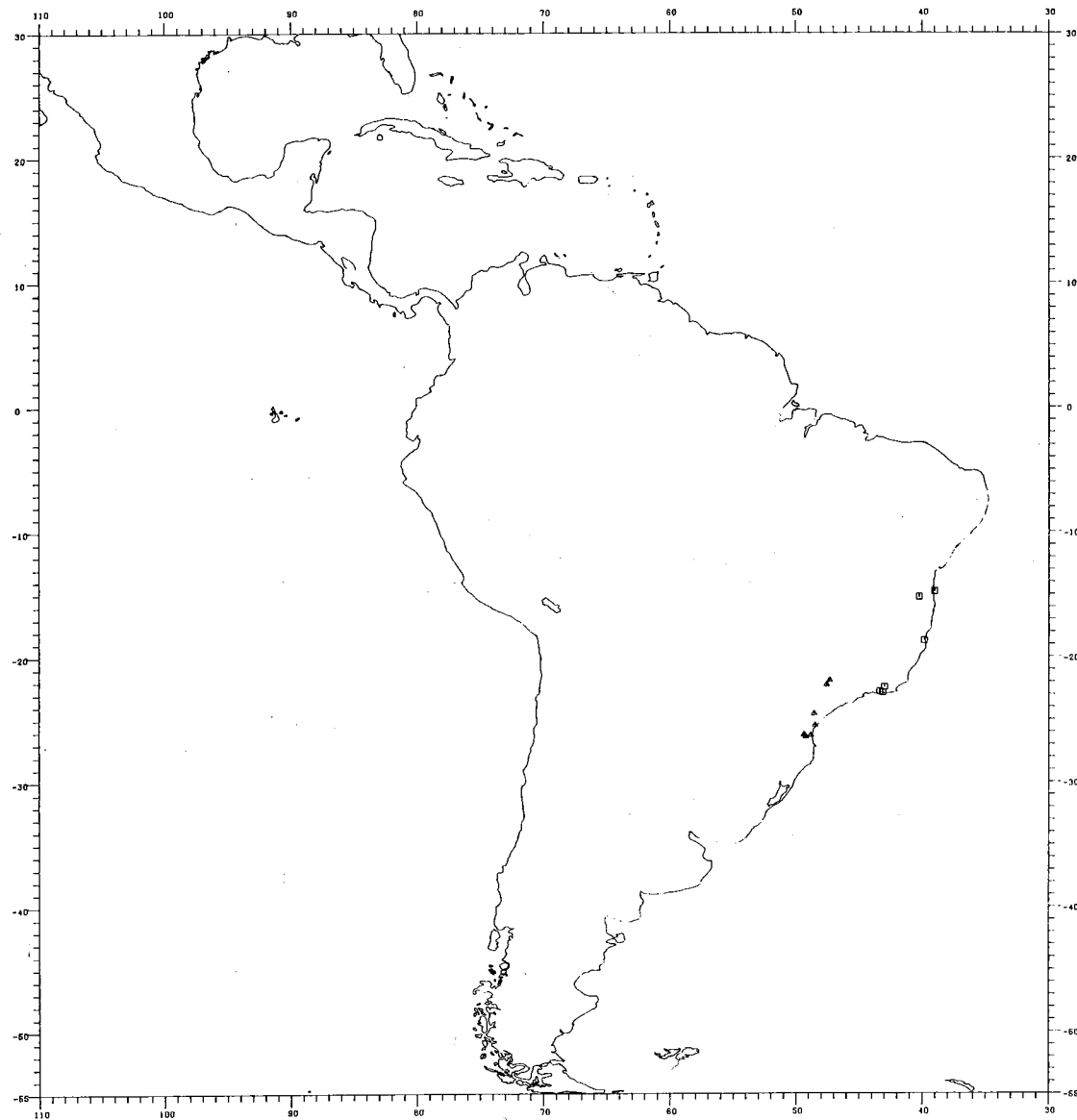


FIGURE 61. Distribution map of *Leptodactylus mystaceus* (squares) and *notoaktites* (triangles).

longer than female ($F_{1, 85} = 18.17, P < .001$); male head width/SVL ratio $.351 \pm .015$, female $.348 \pm .013$, not sexually dimorphic ($F_{1, 85} = .88, P = .94$); male femur/SVL ratio $.388 \pm .023$, female $.389 \pm .024$, not sexually dimorphic ($F_{1, 85} = 1.52, P > .05$); male tibia/SVL ratio $.421 \pm .013$, female $.416 \pm .018$, not sexually dimorphic ($F_{1, 85} = 2.34, P > .05$); male foot/SVL ratio $.428 \pm .021$, female $.423 \pm .022$, not sexually dimorphic ($F_{1, 85} = 1.06, P > .05$).

Larval Characteristics.—Sazima (1975) described and figured the larvae.

Mating Call.—Dominant frequency modulates between 2200–2500 Hz; note duration 0.1 s; note repetition rate 5–6.5 per second (Barrio 1965).

Karyotype.—Diploid number 22; 7 pair median, 3 pair submedian, 1 pair subterminal; secondary constriction on chromosome pair 11 (Bogart 1974).

Distribution.—Interior Brasil to and including the Gran Chaco, coastal southeast Brasil and Argentina (fig. 62).

ARGENTINA. BUENOS AIRES: Buenos Aires, MACN 4150.

CHACO: Ciervo Petizo, IML 243.

ENTRE RÍOS: Concepción del Uruguay, MACN 4530.

JUJUY: Sobre ruta entre Río San Francisco y La Realidad (5 km from Yuto), IML 1272; Ruta Yuto-Ledesma, IML 1273.

LA PAMPA: Conelo, MACN 1166; General Pico, MACN 4479, 4505, 4513.

MISIONES: Dos de Mayo, IML 2356; Puerto Piray, km 18,

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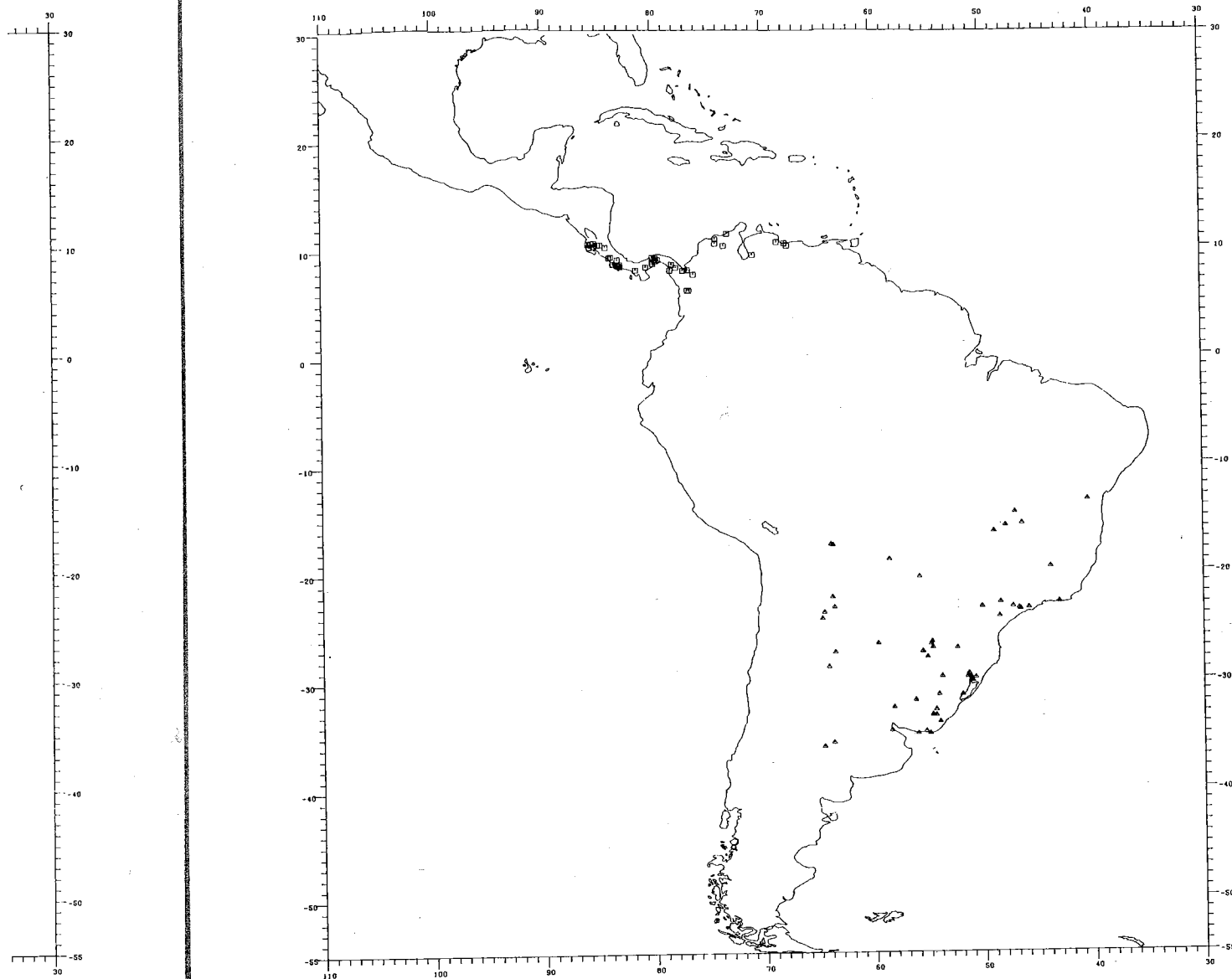


FIGURE 62. Distribution map of *Leptodactylus mystacinus* (triangles) and *poecilochilus* (squares).

MACN 2956; Río Parany, FMNH 9462-66; 10870; San Javier, Puerto Londero, MACN 2072; Santa Ana, MACN 5548. SALTA: Campo Aguaray, IML 1473; near Hickmann, IML 148, 433.

SANTIAGO DEL ESTERO: Caspi Corral, 96 km, IML 2188; Pajares, Simbol, Chichi Huarcunay y Guanaco, Depto. Atamisqui, IML 2230.

TUCUMÁN: Río Urueña, near border of Salta, IML 1428.

BOLIVIA. SANTA CRUZ: Buenavista, MCZ 12897, UMMZ 66479 (2), 66480, 66488; El Carmen, CM 36097, MCZ 29986; Río Surutú, CM 3811.

BRASIL. BAHIA: Maracás, WCAB 31825-28.

DISTRITO FEDERAL: Brasília, USNM 121292.

GOIÁS: Anápolis, AMNH 43847; Flôres, USNM 121270.

MATO GROSSO: Aquidauana, MZUSP 15800.

MINAS GERAIS: Lapa Vermelha, Lagoa Santa, MZUSP 15877; Urucua Riv., first waterfall, Buritis, MZUSP 25069.

PARANÁ: St. Antonio da Platina, MZUSP 24155.

RIO DE JANEIRO: Niteroi, Saco de São Francisco, AMNH 20308 USNM 99121.

RIO GRANDE DO SUL: Albardão, WCAB 16843; Bagé, WCAB 3878; 18 km S Farroupilha, FMNH 80374; Montenegro, MZUSP 16050; Pôrto Alegre, FMNH 80360-371, KU 92921-23, MZUSP 16048-49, 21688-89, WCAB 3876; 39 km N Rio Pardo, FMNH 80372-73; Sta. Maria, MZUSP 24153-54, USNM 121272, WCAB 5259; São Leopoldo, MZUSP 25478; São Lourenço, MZUSP 91, 1970; Viamão, MCZ 32695-96, WCAB 7137-178; Vila Nova, São Sepé, MZUSP 23707-08.

SANTA CATARINA: Nova Teutônia, MZUSP 8694-98.

SÃO PAULO: Botacatú, WCAB 4351; Ermelindo Matrazzo, MZUSP 8106; Faveiro, MZUSP 25423-26; Guapiara, WCAB 6119; Itu, FMNH 83235, KU 92923-24, WCAB 4306, 4311, 4314, 6223, 8230; Nova Itaperuna, WCAB 13660; Pe-

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URUGUAY. CANELONES: Carrasco, MZUSP 22640-41.

DURAZNO: 18 km NE Paloma, Arroyo del Estado, CM 57041-42.

LAVALLEJA: Río de Averías, Depto. Minas, FMNH 10400-01.

MALDONADO: Maldonado, FMNH 10155; Sierra de Animas, WCAB 7273.

ROCHA: 22 km SE Lascano, AMNH 71177.

TACUAREMBO: 3 km NE Tambores, Pozo Hondo, CM 55392-93.

30 Y 3: 8 mi E 30 y 3, FMNH 10465, 10470-72; Quebrada de los Cuervos, 45 km N 30 y 3, FMNH 10500.

LEPTODACTYLUS NOTOAKTITES NEW SPECIES

Figure 63

Holotype: MZUSP 25428, a female from Brasil; São Paulo, Iporanga. Collected by Nelson Papavero on 2 November 1963.

Diagnosis.—The species having a combination of a distinct light stripe on the posterior face of the thigh and a smooth posterior surface of the tarsus in some or all individuals are *amazonicus*, *fuscus*, *geminus*, *gracilis*,



FIGURE 63. Dorsal view of the holotype of *Leptodactylus notoaktites*.

laurae, *longirostris*, *marambaiae*, *mystaceus*, *notoaktites*, and *poecilochilus*. *Leptodactylus notoaktites* has a barred tibial pattern, the dorsal surface of the tibia has light stripes in *geminus*, *gracilis*, and *marambaiae*. Only individual *notoaktites* with a mid-dorsal light stripe have 6 dorsolateral folds; all *fuscus* and *laurae* individuals have 6 dorsolateral folds. *Leptodactylus notoaktites* has a shorter leg (e.g. male foot/SVL ratio $.587 \pm .033$, female $.583 \pm .036$) than *laurae* (male foot/SVL ratio $.649 \pm .039$, female $.628 \pm .028$). *Leptodactylus notoaktites* does not have the dorsal blotching of *L. fuscus*. Most *mystaceus* have white tubercles on the posterior surface of the tarsus. Some individual *notoaktites* have white tubercles on the sole of the foot, the sole of the foot is smooth in *longirostris* and *poecilochilus*. *Leptodactylus notoaktites* occurs in southeast Brasil, *longirostris* and *poecilochilus* are found in northern South America. Some *notoaktites* have a smooth sole of the foot and/or a light mid-dorsal stripe, all *amazonicus* have white tubercles on the sole of the foot and lack light mid-dorsal stripes; *amazonicus* occurs throughout the Amazon basin.

Description of Holotype.—Snout rounded-subelliptical from above, rounded in profile; canthus rostralis indistinct; loreal slightly concave; tympanum distinct, greatest diameter about $\frac{1}{2}$ eye diameter; vomerine teeth in slightly arched series posterior to choanae; finger lengths in order of decreasing size $I \approx III > II \approx IV$, $I \gg II$; inner metacarpal tubercle oval, smaller than rounded outer metacarpal tubercle; dorsum smooth above anteriorly, warty on sides and posteriorly; 1 pair of distinct dorsolateral folds from eye to groin, 1 pair of indistinct lateral folds; ventral texture smooth; belly disk fold distinct; toe tips not expanded; toes free, lacking fringe or web; subarticular tubercles moderately developed; outer metatarsal tubercle small, round, about $\frac{1}{4}$ oval inner metatarsal tubercle; tarsal fold indistinct; no metatarsal fold; posterior surface of tarsus smooth; sole of foot with 1 or 2 indistinct white tubercles.

SVL 56.1 mm, head length 20.6 mm, head width 18.4 mm, interorbital distance 3.7 mm, eye-nostril distance 5.0 mm, femur 27.0 mm, tibia 31.5 mm, foot 31.8 mm.

Dorsum brown with faint darker markings including an interorbital blotch and dorsal chevron; dorsolateral folds light outlined posteriorly; upper lip edge dark, bordered above by distinct light stripe from tip of snout passing under eye to angle of jaw; dark canthal stripe above light lip stripe from tip of snout to eye; venter immaculate; posterior surface of thigh mottled above, dark below with distinct light longitudinal stripe.

Etymology.—From the Greek *notos*, south, and *aktites*, coast dweller, in reference to the geographic distribution of the species in Brasil.

Remark.—This species was analyzed as south coastal *mystaceus*.

Adult Characteristics ($N = 18$).—Dorsum spotted,

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blotched, or striped (fig. 1, A, C, O, striped pattern not figured); light mid-dorsal stripes present in 11% of individuals, presence not sexually dimorphic (Fisher's exact test $P = 1.0$); light upper lip stripe usually distinct (78%), sometimes indistinct (22%), distinctiveness not sexually dimorphic (Fisher's exact test $P = .29$); no dark suborbital bar; distinct light stripe on posterior face of thigh present (100%); tibia barred; upper surface of tibia lacking white tubercles; posterior surface of tarsus lacking white tubercles (100%); sole of foot usually with scattered or very few white tubercles (78%), sometimes absent (22%), presence not sexually dimorphic (Fisher's exact test $P = 1.0$); male SVL 47.4 ± 3.4 mm, female 49.1 ± 3.0 mm, not sexually dimorphic ($F_{1, 16} = 1.21$, $P > .05$); male head length/SVL ratio $.368 \pm .014$, female $.375 \pm .011$, not sexually dimorphic ($F_{1, 16} = 1.60$, $P > .05$); male head width/SVL ratio $.336 \pm .013$, female $.334 \pm .014$, not sexually dimorphic ($F_{1, 16} = .10$, $P > .05$); male femur/SVL ratio $.470 \pm .037$, female $.450 \pm .032$, not sexually dimorphic ($F_{1, 16} = 1.57$, $P > .05$); male tibia/SVL ratio $.533 \pm .024$, female $.549 \pm .021$, not sexually dimorphic ($F_{1, 16} = 2.11$, $P > .05$); male foot/SVL ratio $.587 \pm .033$, female $.583 \pm .036$, not sexually dimorphic ($F_{1, 16} = .04$, $P > .05$).

Larval Characteristics.—Unknown.

Mating Call.—Unknown.

Karyotype.—Unknown.

Distribution.—Southeast Brasil (fig. 61).

BRASIL. PARANÁ: Paranaguá, WCAB 35170.

SANTA CATARINA: Colonia Hansa, Joinville, MZUSP 459, 1295; Humboldt (= Corupá), AMNH 15555; Rio Vermelho, WCAB 6717–723, 7929; Santa Luzia, prope Serra do Mar, MNRio 2148; São Bento, USNM 97176–78.

SÃO PAULO: Engenheiro Ferraz, MZUSP 25420; Iporanga, MZUSP 24149–150, 25428; Piraçununga, Cachoeira de Emas, MNRio 2107.

LEPTODACTYLUS POECILOCHILUS (COPE) 1862

Cystignathus poecilochilus Cope 1862:156–157. (Type locality, Colombia; Antioquia, Turbo. Holotype USNM 4347, male.)

Leptodactylus quadrivittatus Cope 1893:339–340. (Type locality, Costa Rica; Puntarenas, Buenos Aires. Holotype apparently lost.)

Leptodactylus maculilabris Boulenger 1896:404–405. (Type locality, Costa Rica; Guanacaste, Bebedero. Holotype BMNH 94.11.15.27.)

Leptodactylus diptychus Boulenger 1918:431. (Type locality, Andes of Venezuela. Holotype BMNH 94.8.31.11, female.)

Diagnosis.—The species having a combination of a distinct light stripe on the posterior surface of the thigh and smooth surfaces on the posterior tarsus and sole of the foot in some or all individuals are *fuscus*, *geminus*, *gracilis*, *laurae*, *longirostris*, *marambaiae*, *mystaceus*, *notoaktites*, and *poecilochilus*. The dorsal surface of the tibia lacks light longitudinal stripes in *poecilochilus*, such stripes are present in *geminus*, *gracilis*, and *marambaiae*.

ambaiae. Only individuals of *poecilochilus* with light mid-dorsal stripes have 6 dorsolateral folds (fig. 64), all individuals of *fuscus* and *laurae* have 6 dorsolateral folds. The leg of *poecilochilus* is shorter (e.g. male foot/SVL ratio $.514 \pm .029$, female $.508 \pm .029$) than *laurae* (male foot/SVL ratio $.649 \pm .039$, female $.628 \pm .028$). *Leptodactylus poecilochilus* lacks the scattered dorsal blotches characteristic of *fuscus*, does not have a light lip stripe, and often has a dark suborbital bar (fig. 57). No *longirostris*, *mystaceus*, or *notoaktites* have a dark suborbital bar and individuals often have distinct light lip stripes.

Adult Characteristics ($N = 133$).—Dorsum spotted, spots sometimes elongate, rarely fused (fig. 1, A, B, C, D, E) light mid-dorsal stripe present in 13% of individuals, presence not sexually dimorphic ($\chi^2 = .35$, $P = .55$); lip stripe indistinct; dark suborbital bar usually present (67%) or often absent (33%); light stripe on posterior face of thigh usually distinct (77%), sometimes indistinct (21%), rarely absent (2%), expression not sexually dimorphic ($\chi^2 = 1.31$, $P = .52$); tibia barred; usually 2 or 4 well defined dorsolateral folds present, 6 dorsolateral folds present when light mid-dorsal stripe present; dorsal surface of tibia lacking white tubercles; posterior surface of tarsus almost always lacking white tubercles (99%), presence not sexually dimorphic ($\chi^2 = .07$, $P = .80$); sole of foot almost always lacking white tubercles (93%), presence not sexually dimorphic ($\chi^2 = .63$, $P = .43$); male SVL 44.8 ± 2.2 mm, female 45.9 ± 3.4 mm, not sexually dimorphic ($F_{1, 131} = 3.75$, $P > .05$); male head length/SVL ratio $.380 \pm .010$, female $.376 \pm .011$, not sexually dimorphic ($F_{1, 131} = 3.48$, $P > .05$); male head width/SVL ratio $.340 \pm .013$, female $.340 \pm .011$, not sexually dimorphic ($F_{1, 131} = .03$, $P > .05$); male femur/SVL ratio $.424 \pm .024$, female $.427 \pm .025$, not sexually dimorphic, ($F_{1, 131} = .32$, $P > .05$); male tibia/SVL ratio $.489 \pm .024$, female $.488 \pm .024$, not sexually dimorphic ($F_{1, 131} = .06$, $P > .05$); male foot/SVL ratio $.514 \pm .029$, female $.508 \pm .029$, not sexually dimorphic ($F_{1, 131} = 1.47$, $P > .05$).

Larval Characteristics.—Eye diameter 9–14% head-body length; oral disk width 15–27% head-body width; oral papilla gap 45–65% oral disk width; 64–142 denticles on one side of split tooth row anterior to beak; head-body length 35–45% total length; total length, stage 41, 37 mm (Heyer 1970b, figs. 10, 15, 20).

Mating Call.—Dominant frequency modulates from 350–550 Hz; call lacks harmonic structure; note non-pulsatile; note duration 0.055 to 0.080 s; note repetition rate, 1.7 per second (Straughan and Heyer 1976).

Karyotype.—Unknown.

Distribution.—Lowlands of Costa Rica to north coastal South America as far as Venezuela (fig. 62).

COLOMBIA. ANTIOQUIA: Belén, 2½ h upstream Pto. Palacios, Río Arquía, LACM 51090–1110, 51138–148; Finca Chibigüí, Río Arquía, LACM 51112–137; Finca Los Llanos,

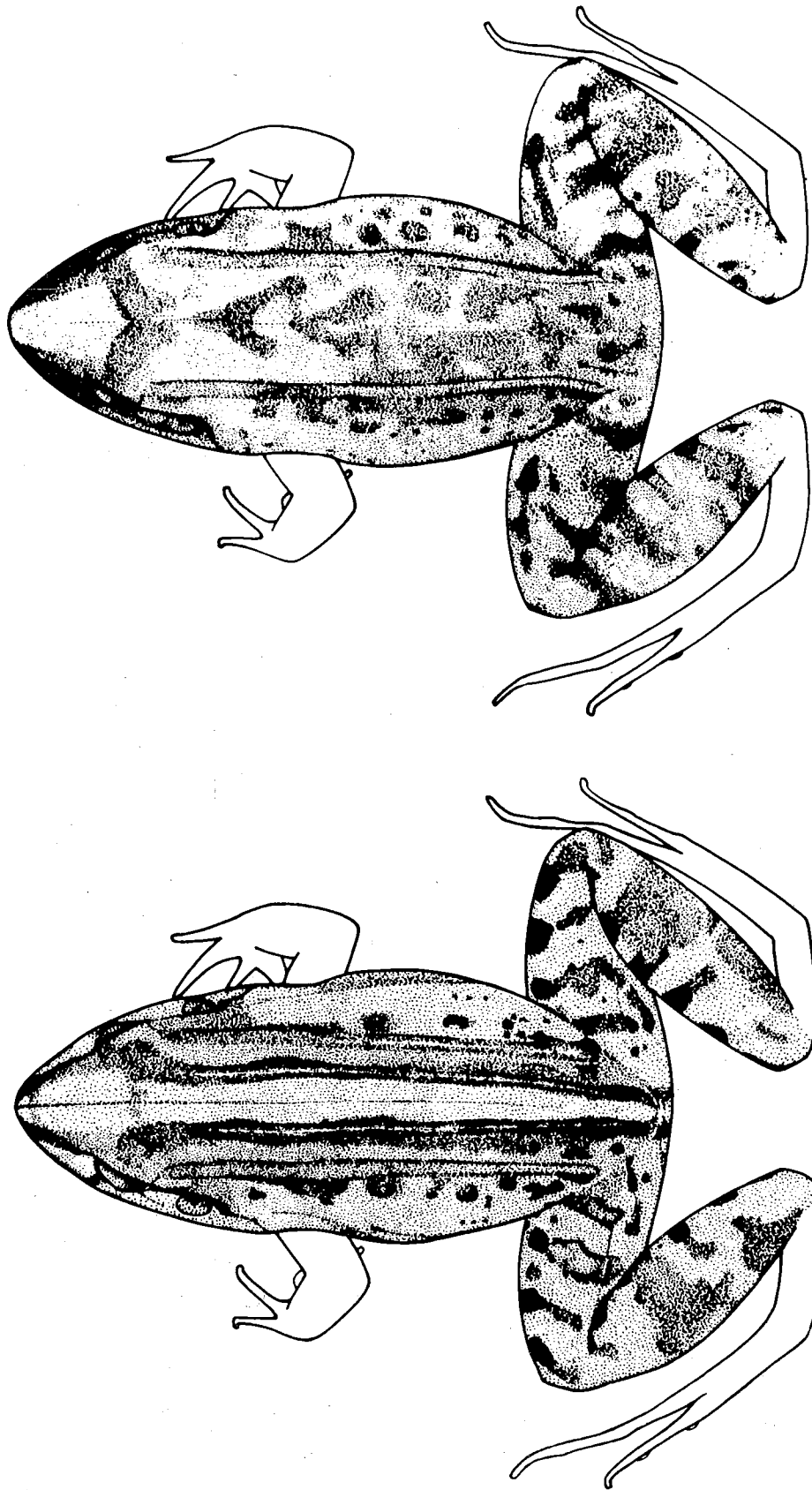


FIGURE 64. Dorsal views of striped (left, CRE 8039) and unstriped (right, LACM 51133) *Leptodactylus poecilochilus*.

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Río Arquia, LACM 51111; Pto. Palacios, Río Arquia, LACM 51089; Villa Arteaga, USNM 146437-38.

CHOCÓ: Golfo de Urabá, Unguía, FMNH 63846.

CÓRDOBA: Río Manso, trib. Río Sinú, USNM 151034-058.

GUAJIRA: Río Barbacoa, UMMZ 54599, 54602-03.

MAGDALENA: Fundación, UMMZ 48505-06, 48508, 51106, USNM 102408, 102410; Río Frio, MCZ 16069; Valencia, UMMZ 54604-08.

NORTE DE SANTANDER: Río Zulia, USNM 147070, 147072-73.

COSTA RICA. ALAJUELA: 3 km W La Fortuna, CRE 8078.

GUANACASTE: Arenal, CRE 6254; Finca Comelco, 30 km NNW Cañas, UMMZ 131908; near Liberia, CRE 8207; near Playa del Coco, CRE 8143, UMMZ 129248 (2); Río Sandillal, UMMZ 131909; 2 mi W Santa Cruz, CRE 8233; Hacienda Taboga, CRE 3086.

HEREDIA: Cariblanco, FMNH 175200.

PUNTARENAS: Coto, km 47 on rail from Golfito, CRE 176 (6), 178 (6), 180 (11); Finca Helechales, 15 km NE Potrero Grande, CRE 3126 (2), 8267-68; 6 km ESE Golfito, 10 m, CRE 7105; 8 km NE Potrero Grande, Finca del Sr. Treño, CRE 8279; near Rincón de Osa, CRE 705 (4), 750 (2), 3108, 6391 (2), 6545, 7228, 7236, LACM 53998-99, UMMZ 129258 (2); Villa Neily, 75 m, CRE 179, 8031, 8039.

SAN JOSÉ: Pozo Azul de Pirris, MCZ 7997-8001; 3 mi SSE San Isidro del General, CRE 8001; 13 mi WSW San Isidro del General, on Dominical road, 710 m, CRE 687.

PANAMA. CANAL ZONE: Cocoli, USNM 193340; Gatun, USNM 54177; near Madden Dam, FMNH 174061; near Paca, Military Road, FMNH 43577; Rosseau, KU 67960; Summit, MCZ 21834.

CHIRIQUÍ: Progreso, UMMZ 58267-272, 58275-283, USNM 118673.

COCLÉ: 1 km NE El Caño, 40 m, FMNH 22986.

DARIEN: Camp Creek, Camp Townsend, AMNH 41022; Ortiga, FMNH 170465, 170467; Río Canglón, UMMZ 125021 (3), 125022-29; Río Lara, FMNH 170304, 170392, 170436; Río Silugandí, UMMZ 113120-22 (3), 113123; Río Tuirá at Río Mono, KU 116829-831; Sambu Valley, Río Esaupe, MCZ 9161; Santa Fe Camp, FMNH 170269, 170308; S 6 VIII Camp, FMNH 170343.

PANAMÁ: Cermeño, MCZ 24880; Cerro Campana, FMNH 60500, MCZ 82072, USNM 139701; Río Itarare, FMNH 28856; Tapia, AMNH 18931.

SAN BLAS: SG VIII site, FMNH 170374.

VERAGUAS: Mojara, USNM 129841-42.

VENEZUELA. ARAGUA: near Maracay, Rancho Grande, AMNH 70688; near Ocumare, UMMZ 122374.

FALCÓN: 5 km S Palma Sola, UMMZ 55554; Soute Parriji, MCZ 25989; 19 km NW Urama, km 40, USNM field 1808, 5217, 5243, 5246.

GUÁRICO: Hato La Palmita, USNM 162702.

TRUJILLO: Sabana de Mendoza, UMMZ 57483.

LEPTODACTYLUS TROGLODYTES A. LUTZ 1926

Leptodactylus troglodytes A. Lutz 1926: 149-150, plate 32, fig. 12. (Type locality, Brasil; Pernambuco, Procedencia. Holotype Adolfo Lutz collection, no number, female.)

Diagnosis.—The species lacking a distinct thigh stripe and having distinct white tubercles on the posterior surface of the tarsus in some or all individuals are *albilabris*, *bufonius*, *labrosus*, *mystacinus*, *troglydytes*, and *ventrimaculatus*. *Leptodactylus albilabris* usually has at

least an indication of a light stripe on the posterior surface of the thigh. *Leptodactylus troglodytes* lacks distinct dorsolateral folds; distinct dorsolateral folds (indicated at least by color pattern) occur in *albilabris*, *labrosus*, *mystacinus*, and *ventrimaculatus*. *Leptodactylus troglodytes* and *bufonius* are morphologically similar and have similar dorsal patterns (fig. 65). All individuals of *troglydytes* have distinct white tubercles on the sole of the foot, almost all *bufonius* have smooth surfaces on the sole of the foot. *Leptodactylus troglodytes* occurs in northeast Brasil, *bufonius* has a distribution centered upon the Gran Chaco.

Remark.—This is the species referred to as "northern *bufonius*" in the morphological analysis.

Adult Characteristics ($N = 42$).—Dorsum with chevrons, spots, or blotches (fig. 1, A, B, C, G, L, N); no light mid-dorsal stripe; no light upper lip stripe; dark suborbital bar always present; light stripe on posterior face of thigh absent (100%); tibia barred; dorsolateral folds usually absent, 2 weak indistinct folds rarely present; dorsal surface of tibia with many distinct white tubercles; posterior surface of tarsus with distinct white tubercles (100%); sole of foot with white tubercles (100%); male SVL 48.8 ± 2.2 mm, female 49.9 ± 1.8 mm, not sexually dimorphic ($F_{1, 40} = 2.67, P > .05$); male head length/SVL ratio $.385 \pm .008$, female $.374 \pm .010$, male head longer ($F_{1, 40} = 16.17, P < .001$); male head width/SVL ratio $.344 \pm .011$, female $.339 \pm .011$, not sexually dimorphic ($F_{1, 40} = 1.92, P > .05$); male femur/SVL ratio $.400 \pm .020$, female $.393 \pm .015$, not sexually dimorphic ($F_{1, 40} = 1.38, P > .05$); male tibia/SVL ratio $.406 \pm .012$, female $.397 \pm .014$, male tibia longer ($F_{1, 40} = 5.51, .01 < P < .025$); male foot/SVL ratio $.395 \pm .011$, female $.386 \pm .016$, male foot longer ($F_{1, 40} = 5.38, .025 < P < .05$).

Larval Characteristics.—Unknown.

Mating Call.—Dominant frequency modulates from 2600-3200 hz (fig. 66); call without harmonic structure (fig. 67); call not pulsed; note duration .042 s; note repetition rate 1 per second.

Karyotype.—Unknown.

Distribution.—Northeast Brasil (fig. 68).

BRASIL. BAHIA: Andaraí, WCAB 43766-67; Barreiras, UMMZ 109980-81 (2); Carnaíba, WCAB 43867; Cocorobó, MZUSP 38278-79; Feira de Santana, WCAB 44085; Jeremoabo, MZUSP 38167; Maracás, WCAB 31813-824; Salvador, MZUSP 10715.

CEARÁ: Açude Amanari, Maranguapé, MZUSP 13589; Fortaleza, WCAB 19149.

GOIÁS: Cana Brava, MZUSP 20441-42.

MINAS GERAIS: Rio Pandeiros, MZUSP 24695, USNM 121300.

PARAÍBA: Piancó, WCAB 3626, 4976.

PERNAMBUCO: Bonito, UMMZ 132461; Exú, WCAB 39218.

PIAUÍ: 35 km N Valença, MZUSP field 750647-652.

RIO GRANDE DO NORTE: Natal, Areia Preta, USNM 97048-49; Ponta Negra, MZUSP 25017.

SERGIPE: Areia Branca, MZUSP 37825-837.

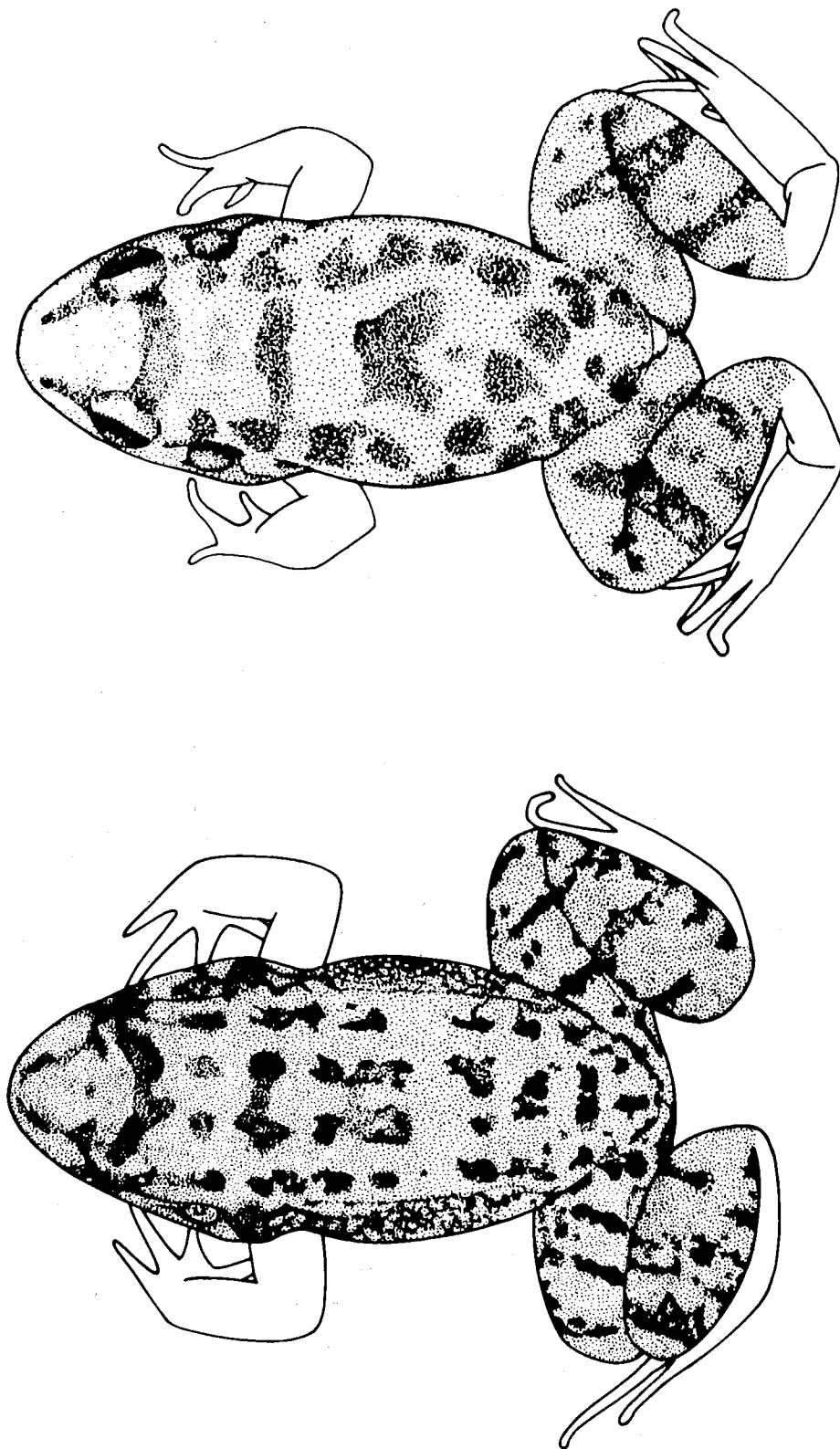


FIGURE 65. Dorsal views of *Leptodactylus bufonius* (left, LACM 91929) and *troglodytes* (right, USNM 121301).

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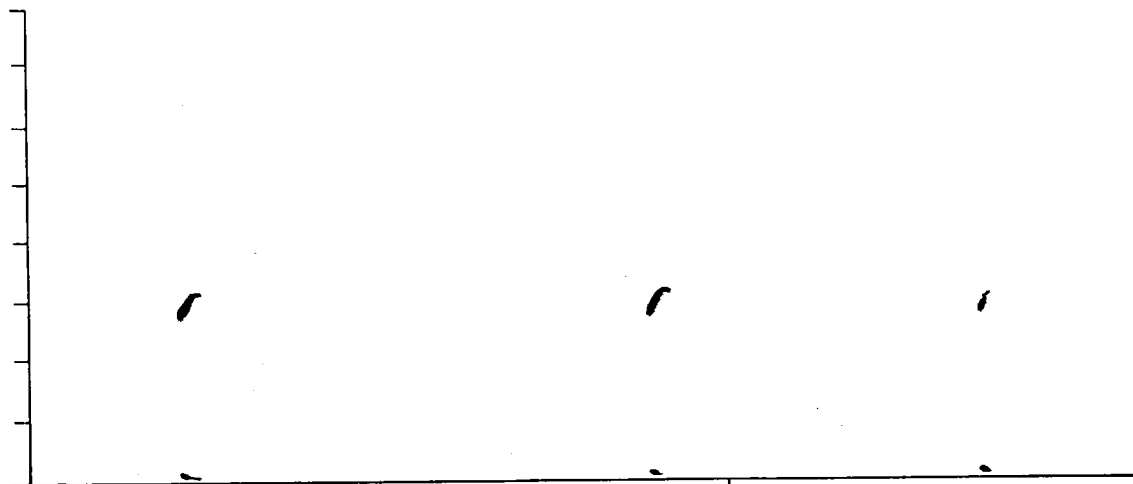


FIGURE 66. Sonagram of the mating call of *Leptodactylus troglodytes*, narrow band filter. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. Specimen from Brasil, Andarai, air temperature 24° C (WCAB tape).



FIGURE 67. Strip chart record of the mating call of *Leptodactylus troglodytes*. Line equals 0.01 s. See legend of Figure 66 for specimen data.

LEPTODACTYLUS VENTRIMACULATUS BOULENGER 1902

Leptodactylus ventrimaculatus Boulenger 1902:53. (Type locality, Ecuador, Bulun, 160'. Lectotype BMNH 1947.2.17.78, female.)

Diagnosis.—The species having a combination of no light stripe on the posterior surface of the thigh and distinct white tubercles on the posterior surface of the tarsus and sole of foot (fig. 69) in some or all individuals are *bufonius*, *labrosus*, *mystacinus*, *troglodytes*, and *ventrimaculatus*. *Leptodactylus ventrimaculatus* has distinct dorsolateral folds (indicated at least by color pattern), dorsolateral folds are absent or indistinct in *bufonius* and *troglodytes*. Some individuals of *mystacinus* lack white tubercles on the sole of the foot; *L. mystacinus* occurs east of the Andes, *L. ventrimaculatus* occurs west of the Andes along the wet coastal regions of Colombia to mid-Ecuador. Most *L. labrosus* have a smooth sole of the foot (fig. 69); *labrosus* occurs along the dry west coasts of South America from mid-Ecuador to Peru, including the northern interandean valley of northern Peru.

Adult Characteristics ($N = 38$).—Dorsum spotted, striped, or rarely uniform (fig. 1, A, B, C, J, K, striped

pattern not figured); no light mid-dorsal stripe; no light upper lip stripe; dark suborbital bar almost always present; light stripe on posterior face of thigh almost always absent (97%), rarely indistinct (3%), presence not sexually dimorphic ($\chi^2 = .03$, $P = .87$); tibia barred; usually 2 dorsolateral folds present; dorsal surface of tibia with many white tubercles; posterior surface of tarsus with many white tubercles (100%); sole of foot with scattered or very few white tubercles (at least some tubercles present in 100% of study sample); male SVL 50.4 ± 3.5 mm, female 51.9 ± 4.8 mm, not sexually dimorphic ($F_{1, 36} = 1.23$, $P > .05$); male head length/SVL ratio $.363 \pm .013$, female $.360 \pm .015$, not sexually dimorphic ($F_{1, 36} = .38$, $P > .05$); male head width/SVL ratio $.343 \pm .010$, female $.341 \pm .010$, not sexually dimorphic ($F_{1, 36} = .11$, $P > .05$); male femur/SVL ratio $.389 \pm .023$, female $.384 \pm .024$, not sexually dimorphic ($F_{1, 36} = .35$, $P > .05$); male tibia/SVL ratio $.420 \pm .019$, female $.409 \pm .020$, not sexually dimorphic ($F_{1, 36} = 2.50$, $P > .05$); male foot/SVL ratio $.457 \pm .022$, female $.447 \pm .021$, not sexually dimorphic ($F_{1, 36} = 2.0$, $P > .05$).

Larval Characteristics.—Unknown.



FIGURE 68. Distribution map of *Leptodactylus troglodytes* (squares) and *ventrimaculatus* (triangles).

Mating Call.—Unknown.

Karyotype.—Unknown.

Distribution.—Western South America, primarily west of the Andes, from mid-Ecuador to northern Peru (fig. 68).

COLOMBIA. CAUCA: Quebrada Guanguí, ½ km above Río Patía (upper Saija drainage), 100–200 m, AMNH 88529.

CHOCÓ: 2 km above Playa de Oro, upper Río San Juan, AMNH 87124–132; Quebrada Bochoramá, 180–190 m, LACM 44383; upper Río Buey, 110–160 m, LACM 44381.

NARIÑO: Imbilí, Río Mira, USNM 147457–480; near La Guayacana, LACM 50173–74; Río Satinga, USNM 147483–85; N Tumaco, Río Rosario, USNM 147488–89.

VALLE: Buenaventura (islet in Pacific), USNM 147077–78.

ECUADOR. ESMERALDAS: 1 km N Cachaví, USNM 196757 (7), 196758 (2); Hacienda Equinox, 30 km NNW Santo Domingo de los Colorados, 1000 ft, USNM 196755; 1 km NW Lita Station, USNM 196756; Río Pilatón, WCAB 276.

IMBABURA: Cachaco, USNM 196769; Lita, 520 m, KU 132805–06.

PICHINCHA: Hacienda Espinosa, 9 km W Santo Domingo de los Colorados, road to Chone, CAS-SU 10455–466; 5 km E La Palma, KU-WED 48227–233; 1 km E Mindo, farm of Julio Goetschel, 1400 m, USNM 196764–66 (2); Río Blanco, near mouth of Río Yambi, 700 m, USNM 196767; Río Toachi, USNM 196768; near Santo Domingo de los Colorados, KU 117794, 146186–87, USNM 196759–60 (6), 196761 (2), 196762 (2), 196763.

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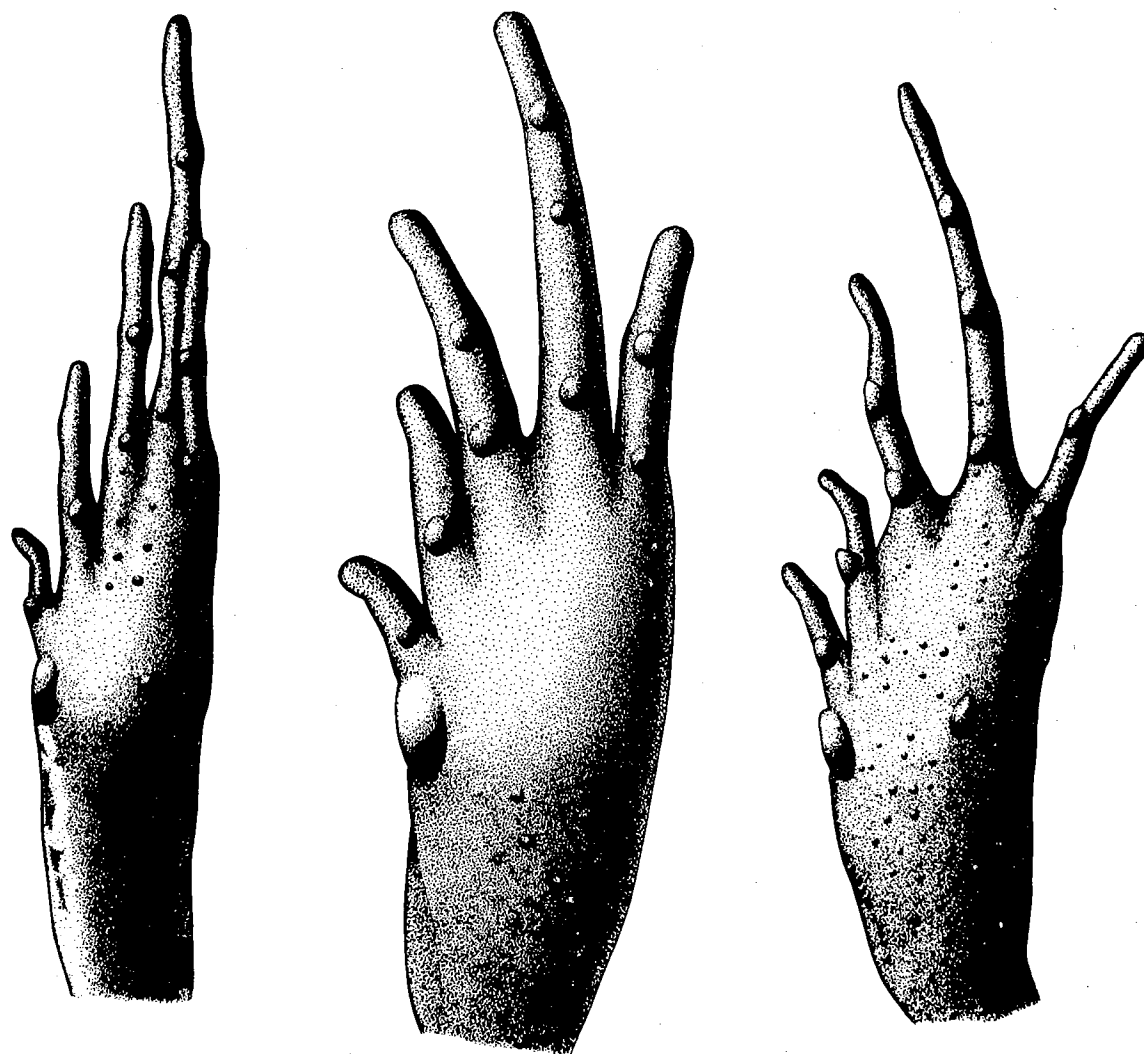


FIGURE 69. Tarsal and foot textures. Left, tarsus smooth, foot scattered with white tubercles (based on *L. fuscus*, LACM 92015, extreme development of foot tubercles for this species). Center, tarsus with many white tubercles, foot smooth (based on *L. labrosus*, LACM 49161). Right, tarsus and foot with many white tubercles (based on *L. ventrimaculatus*, AMNH 88529).

AN ARTIFICIAL KEY TO THE ADULT MEMBERS OF THE *LEPTODACTYLUS FUSCUS* GROUP

This key is designed to be used in conjunction with the diagnoses. For those species demonstrating variation in key characters, the most frequent condition is presented in the key; the diagnoses incorporate the range of variation of key characters.

- 1 A. Dorsal surface of tibia with distinct light longitudinal stripes (figs. 2, 48) 17
- 1 B. Dorsal surface of tibia barred, lacking light longitudinal stripes (figs. 2, 48) 2
- 2 A. Posterior surface of thigh lacking distinct light longitudinal stripe 3
- 2 B. Posterior surface of thigh with distinct light longitudinal stripe 7
- 3 A. Dorsolateral folds indistinct or absent 4
- 3 B. Dorsolateral folds distinct (indicated at least by color pattern) 5
- 4 A. Sole of foot smooth, Chacoan distribution *bufonius*
- 4 B. Sole of foot with white tubercles, northeast Brasil *troglydites*
- 5 A. Light upper lip stripe usually distinct, never a dark suborbital bar (fig. 57) *mystacinus*
- 5 B. No light upper lip stripe, usually a dark suborbital bar (fig. 57) 6
- 6 A. Sole of foot smooth, dry west coastal South America and interandean valley in northern Peru *labrosus*
- 6 B. Sole of foot with white tubercles, wet west coastal Colombia to mid-Ecuador *ventrimaculatus*

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- 7 A. Posterior surface of tarsus smooth (fig. 69) 8
 7 B. Posterior surface of tarsus with distinct white tubercles (fig. 69) 13
 8 A. Sole of foot with white tubercles (fig. 69) 9
 8 B. Sole of foot smooth (fig. 69) 10
 9 A. No individuals with a mid-dorsal light stripe, Amazonian distribution *amazonicus*
 9 B. Some individuals with a mid-dorsal light stripe, southeast Brasil *notoaktites*
 10 A. Leg noticeably long, all individuals with a mid-dorsal light stripe, southeast Brasil *laurae*
 10 B. Leg of normal proportions, most individuals without a mid-dorsal light stripe 11
 11 A. All individuals with 6 dorsolateral folds, dorsum usually with many irregular spots or blotches, widespread *fuscus*
 11 B. Most individuals with 2 or 4 dorsolateral folds, only individuals with a mid-dorsal light stripe having 6 dorsolateral folds, dorsum usually with a few more or less regular spots or blotches, Middle America and northern South America 12
 12 A. Light lip stripe often distinct, never a dark suborbital bar, Guiana Shield *longirostris*
 12 B. Light lip stripe indistinct, dark suborbital bar often present, Costa Rica through coastal Venezuela *poecilochilus*
 13 A. Dorsolateral folds indistinct or absent 14
 13 B. Dorsolateral folds distinct (at least indicated by color pattern) 15
 14 A. Texas throughout Middle America along coastal northern South America to Venezuela *fragilis*
 14 B. Gran Chaco and coastal Brasil *latinasus*
 15 A. Dorsal surface of tibia smooth, Chacoan distribution *elenae*
 15 B. Dorsal surface of tibia with white tubercles 16
 16 A. Tibia (male mean 43% SVL, female 44%) and foot (male mean 49% SVL, female 50%) shorter, West Indies *albilabris*
 16 B. Tibia (male mean 51% SVL, female 52%) and foot (male and female mean 55% SVL) longer, east coastal Brasil *mystaceus*
 17 A. Leg shorter, tibia 50% SVL *marambaiae*
 17 B. Leg longer, tibia 52–62% SVL *geminus* & *gracilis*

THE SIGNIFICANCE OF SEXUAL DIMORPHISM IN MEMBERS OF THE *LEPTODACTYLUS FUSCUS* GROUP

A surprising amount of sexual dimorphism was encountered in the morphological analysis. Many frogs demonstrate sexual dimorphism in size and various other secondary sexual characteristics, but to my knowledge, no one previously has demonstrated sexual dimorphism in limb proportions in frogs. The characters involved in secondary sexual dimorphism correlate with aspects of ecology and breeding biology in certain cases. Against the patchy background of available ecological information, tentative predictions can be made for some species for which ecological data are as yet unavailable.

In the species accounts section, sexual dimorphism was established at a significance level of 5%. Due to the degree of measurement error combined with the small sample sizes available, the 10% level of significance is used here to establish presence of sexual dimorphism in measurement and ratio characters (Table 4). *Leptodactylus geminus* is not included in this discussion as no validated specimens were available for analysis. The available series of *L. marambaiae* is too small to analyze.

Size.—In many species of frogs the female is larger than the male. The usual explanation for this phenomenon is that the larger female size allows for a greater clutch size and hence an increase in reproductive effort. In *Leptodactylus elenae*, *fragilis*, *fuscus*, *gracilis*, *la-*

brosus, *mystaceus*, *notoaktites*, *poecilochilus*, *troglo-*
dytes, and *ventrimaculatus*, the sexes are not dimorphic with respect to size. Both sexes of all these species must be under some environmental or developmental constraint selecting for the same size. What the constraint(s) is, is not known at present.

Head Length.—Members of the *fuscus* group deposit their eggs in underground chambers. In at least some species, these incubating chambers are constructed by the male. Males of the following species have either been observed constructing an incubating chamber, or have been observed calling in association with an incubating chamber: *amazonicus* (pers. obs.), *bufonius* (Philibosian, et. al. 1974), *fragilis* (Dixon and Heyer 1968), *mystacinus* (Sazima 1975). In all of these species the male's head is longer than the female's, reflecting the development of a rigid chisel-like snout that is used in the construction of the incubating chamber. The chamber is apparently excavated only in damp ground by males of these species. On the basis of snout morphologies, *albilabris*, *latinasus*, *laurae*, *longirostris*, *poecilochilus*, and *troglo-*
dytes males are also predicted to excavate the nest chamber in damp ground. For those species in which the head lengths of the sexes are the same, one would predict either that both sexes were involved in formation of the incubating chamber (or burrow construction) or that naturally occurring depressions are used for deposition of the foam nest with little modification on the part of the males. Based on head mor-

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bufonius
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fragilis
fuscus
gracilis
labrosus
latinasus
laurae
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TABLE 4

Occurrence of sexual dimorphism in members of the *fuscus* group. — = no sexual dimorphism, F = sexual dimorphism present, female elements longer or more distinct, M = sexual dimorphism present, male elements longer.

	Variables										
	SVL	Head Length	Head Width	Femur	Tibia	Foot	Mid-dorsal Stripe	Lip Stripe	Thigh Stripe	Tarsal Texture	Foot Texture
<i>albilabris</i>	F	M	—	F	F	F	—	—	—	—	—
<i>amazonicus</i>	F	M	M	—	F	F	—	F	—	—	—
<i>bufonius</i>	F	M	M	—	—	—	—	—	—	—	—
<i>elenae</i>	—	—	—	—	—	—	—	—	—	—	—
<i>fragilis</i>	—	M	M	F	F	F	—	—	—	—	—
<i>fuscus</i>	—	—	M	F	F	—	—	F	—	—	—
<i>gracilis</i>	—	—	M	—	—	—	—	—	—	—	—
<i>labrosus</i>	—	—	—	F	—	—	—	—	—	—	—
<i>latinasus</i>	F	M	—	—	—	—	—	F	—	—	—
<i>laurae</i>	F	M	M	—	—	—	—	—	—	—	—
<i>longirostris</i>	F	M	—	—	F	—	—	—	F	—	—
<i>mystaceus</i>	—	—	—	F	—	—	—	—	—	—	—
<i>mystacinus</i>	F	M	—	—	—	—	—	F	—	—	—
<i>notoaktites</i>	—	—	—	—	—	—	—	—	—	—	—
<i>poecilochilus</i>	—	M	—	—	—	—	—	—	—	—	—
<i>troglodytes</i>	—	M	—	—	M	M	—	—	—	—	—
<i>ventrimaculatus</i>	—	—	—	—	—	—	—	—	—	—	—

phology, *labrosus* is predicted to be a species in which both sexes are involved in the formation of incubating chambers or burrows. On the other hand, *elenae*, *fuscus*, *gracilis*, *mystaceus*, *notoaktites*, and *ventrimaculatus* are good candidates for foam nest deposition in natural depressions with little subsequent modification.

Head Width.—Not all species which show dimorphism of head length are also dimorphic with respect to head width, and vice versa. This suggests that head width is not associated with incubating chamber formation, but instead may be important with respect to such aspects as food niche separation or mating call broadcasting. Data are not available to test these hypotheses.

Limb Proportions.—The longer any of the hind limb elements are, the better a frog is at jumping (Zug 1972). Extreme jumping ability is usually associated with avoidance of vertebrate predators. The sexes of species demonstrating sexual dimorphism in leg length might have different abilities to escape predation, suggesting different selective forces operating on the two sexes. The most parsimonious explanation for the development of sexual dimorphism in hind limb length for members of the *fuscus* group takes into account: (1) relative fossoriality as relates to the general niche adaptations of the species; (2) fossoriality only in terms of incubating chamber formation by the males; and (3) exposure to above ground vertebrate predation. Members of the *fuscus* group appear to segregate into six groupings based on these three variables. The following groupings are not presented as groupings of fact, but rather as hypotheses which can account for limb length dimorphism. Hopefully, the hypotheses will focus attention on gathering data on differential predator success or exploration

of alternate hypotheses accounting for dimorphic limb lengths such as weight differences.

1. Fossorial niche, male under more vertebrate predatory pressure than female: *L. troglodytes*. This pattern suggests that most of the life activities of the species takes place under ground and the nest construction and/or calling activity of the male are the longest above ground activities in the adult life history. The longer limb of the male results from selective pressures exerted by vertebrate predation.

2. Fossorial niche, both sexes responding in the same way to vertebrate predatory pressure: *L. bufonius*, *mystacinus*, *ventrimaculatus*. This pattern indicates that most life activities take place fossorially but that both species spend about the same amount of time in above ground activities.

3. Fossorial niche, shorter leg of male the result of selection for fossorial activity of incubating chamber construction, longer leg of female the result of selection from vertebrate predators when above ground: *L. labrosus*. This pattern suggests that while many of the activities of the species are fossorial, relatively more time is spent above ground than for the species in the preceding pattern.

4. Above ground niche, longer head and shorter leg of male the result of selection for fossorial activity of incubating chamber construction, longer leg of female the result of selection pressure from vertebrate predators: *L. albilabris*, *amazonicus*, *fragilis*, *fuscus*, *longirostris*, *mystaceus*. Rather than being primarily fossorial as in the previous patterns, members showing this pattern are active above ground and incubating chamber construction is an important male activity.

5. Above ground niche, longer head of male the re-

sult of selection for fossorial activity of incubating chamber construction, both sexes responding in same way to selection from vertebrate predators: *L. latinasus*, *laurae*, *poecilochilus*. This pattern implies that selection from vertebrate predators is not important (*latinasus*, short legs), very important (*laurae*, long legs in both sexes), or that a different selective force is operating on limb length (all three species).

6. Above ground niche, male spends little or no energy in incubating chamber construction, both sexes responding equally to selection from vertebrate predators: *L. elenae*, *gracilis*, *notoaktites*. This pattern implies that neither sex is under selection that would result in shorter limb elements; males probably locate available depressions, holes, or burrows and make few if any modifications of them preparatory for use as incubating chambers.

Mid-dorsal Stripe.—This characteristic is not sexually dimorphic, suggesting that the character state is not involved in mate recognition.

Distinct Lip and Thigh Stripes.—A few species are dimorphic for these characteristics. In all cases, the stripes are more distinct in the females than in the males. Straughan (1966) has demonstrated that thigh pattern is important in mate recognition, acting as a species isolating mechanism. The *Leptodactylus* lip and thigh stripe data indicate that the males utilize this information in mate discrimination in several members of the *fuscus* group.

Texture of Tarsus and Foot.—The presence or absence of white tubercles is not sexually dimorphic in any species, indicating that these structures are not used in mate recognition but are probably important in how the frog physically interacts with the environment.

RELATIONSHIPS

The purpose of this section is to determine whether a pattern of phyletic relationship can be inferred among the species. Detailed relationships cannot be analyzed at this time for two reasons. The first is that there are several as yet undescribed species in this group, and the morphological information on *L. geminus* and *marambaiae* needs to be clarified. The second reason that detailed relationships cannot yet be determined is methodological. I prefer to deduce relationships on the basis of shared derived character state patterns (see Heyer, 1975, for fuller explanation). This method requires more derived character states than taxa for any detailed analysis. With the small number of characters presently available for analysis, only general hypotheses regarding relationships are possible.

The outgroup used for comparative purposes in determining the primitive states consists of members of the other species groups of *Leptodactylus* and members of the genera *Adenomera*, *Lithodytes*, and *Vanzolinius*. States common to the outgroup but variable within

members of the *fuscus* group are considered primitive. These four genera likely had a common ancestor. Only those characters for which the states are known for all species (*geminus* and *marambaiae* excluded) are analyzed in detail.

Character Analysis—Mid-dorsal stripe. *Character 1.*—State 0 = light mid-dorsal stripe absent in all individuals; State 1 = light mid-dorsal stripe present in some individuals; State 2 = light mid-dorsal stripe present in all individuals. Of the outgroup, only some members of the genus *Adenomera* have a light mid-dorsal stripe. The *Adenomera* light mid-dorsal stripe differs among *Adenomera* species and differs from the mid-dorsal stripe of members of the *fuscus* group, however. The most parsimonious explanation is that the common ancestor to all of the taxa considered had the genetic potential for a light mid-dorsal stripe. The direction of change of states is:

$$0 \rightarrow 1 \rightarrow 2.$$

Lip stripe. *Character 2.*—State 0 = light lip stripe indistinct; State 1 = light lip stripe distinct in at least some individuals. Members of the genera *Adenomera*, *Lithodytes*, *Vanzolinius* and the *melanonotus* species group lack light lip stripes. One species of the *ocellatus* group and two species of the *pentadactylus* group have light lip stripes. The *pentadactylus* group members have a stripe differing in detail from the *fuscus* group light stripe. The situation is analogous to the mid-dorsal stripe character. State 0 is considered the primitive state.

Thigh stripe. *Character 3.*—State 0 = no distinct light longitudinal stripe on the posterior surface of the thigh; State 1 = distinct posterior thigh stripe. Only some individuals of the other species groups of *Leptodactylus* approach state 1 in the outgroup. State 0 is considered the primitive state.

Dorsolateral folds.—The presence of at least a pair of distinct dorsolateral folds is common throughout the outgroup; the primitive state can not be determined from the outgroup. The condition of 6 dorsolateral folds is probably derived, but this character state is associated with the light mid-dorsal stripe in all *fuscus* group members except for *fuscus* itself. As the mid-dorsal stripe information is being analyzed, the dorsolateral fold information is not analyzed or used further.

Tarsal and foot texture.—Several members of the outgroup demonstrate all states regarding tarsal and foot texture. The outgroup provides no information on which state is primitive.

Size.—Members of the outgroup are both larger and smaller than members of the *fuscus* group; the primitive state can not be determined. In all likelihood, the moderate size of most of the *fuscus* group members is the primitive state.

Sexual dimorphism in size, head and limb proportions.—As discussed in the previous section, any sexual dimorphism of head and leg proportions is uncommon

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in frogs and is here considered the derived state. The exception is SVL, in which sexual dimorphism in size is considered the primitive state as discussed previously. For all characters listed below, state 0 is the primitive state.

SVL. Character 4.—State 0 = sexually dimorphic; State 1 = not sexually dimorphic.

Head length. Character 5.—State 0 = not sexually dimorphic; State 1 = sexually dimorphic.

Head width. Character 6.—State 0 = not sexually dimorphic; State 1 = sexually dimorphic.

Femur/SVL ratio. Character 7.—State 0 = not sexually dimorphic; State 1 = sexually dimorphic.

Tibia/SVL ratio. Character 8.—State 0 = not sexually dimorphic; State 1 = sexually dimorphic. As *trogodytes* is unique in that it is the male with the longer tibia, it is coded as 0 for analytic purposes.

Foot/SVL ratio. Character 9.—State 0 = not sexually dimorphic; State 1 = sexually dimorphic. See above for *trogodytes*.

The distribution of states among the species is presented in Table 5. With only 9 characters, detailed relationships can not be drawn, but the distribution of states and clustering patterns allow certain generalizations to be made. 1) There is a cluster of taxa characterized by having very few derived states, which do not demonstrate any meaningful patterns of relationships among themselves. These species, *L. bufonius*, *labrosus*, *trogodytes*, and *ventrimaculatus* are likely similar to the ancestor of the *fuscus* group and demonstrate the basic adaptive features of the ancestral stock of the entire *fuscus* group. Assuming this to be true, the ancestral stock of the *fuscus* group had a basic semi-fossorial adaptive set. As all members of this assemblage have white tubercles either on the tibia, tarsus, or foot, the *fuscus* group ancestor likely had tubercles also. 2) A

second assemblage of species is characterized by sharing the derived states of lip and thigh stripes: *L. albilabris*, *amazonicus*, *elenae*, *fragilis*, *fuscus*, *gracilis*, *latinasus*, *laurae*, *longirostris*, *mystaceus*, and *notoaktites*. Within this assemblage, *albilabris*, *amazonicus*, and *fragilis* together share the most derived states (5) within the data set. 3) *Leptodactylus mystacinus* and *poecilochilus* are intermediate between these two assemblages. There is no parsimonious way to include both of these species in the same evolutionary sequence leading to the second assemblage. As *L. mystacinus* bears more morphological similarity to members of the first, supposed primitive, assemblage of species, it does provide at least an example of how the transition between the first two assemblages could have occurred.

ZOOGEOGRAPHY

When the distributions of species (excluding those known only from single localities) are outlined and overlaid, two results are apparent. First, most species of the *fuscus* group occur south and east of the Amazon basin. Second, the areas of greatest present species densities do not appear to coincide with local areas of speciation. There are four areas where the ranges of five species overlap. Two of these are in the dry interior portions of Argentina. The species coexisting in these two areas are: (A) *bufonius*, *elenae*, *fuscus*, *latinasus*, *mystacinus*, and (B) *elenae*, *fuscus*, *gracilis*, *latinasus*, *mystacinus*. A third area is in southeast Brazil in the São Paulo region. The species that occur in sympatry there are *fuscus*, *gracilis*, *laurae*, *notoaktites*, *mystacinus*. The fourth area is the border region between southeast Brazil and Uruguay. The species are *fuscus*, *gracilis*, *latinasus*, *laurae*, *mystacinus*. Clearly, the high numbers of species that coexist in these regions reflect overlap in the ranges of widespread species. There are no

TABLE 5
Distribution of character states among members of the *fuscus* group. Character numbers and states as used in text.

	1	2	3	4	5	6	7	8	9
<i>albilabris</i>	1	1	1	0	1	0	1	1	1
<i>amazonicus</i>	0	1	1	0	1	1	0	1	1
<i>bufonius</i>	0	0	0	0	1	1	0	0	0
<i>elenae</i>	0	1	1	1	0	0	0	0	0
<i>fragilis</i>	0	1	1	1	1	1	1	1	1
<i>fuscus</i>	1	1	1	1	0	1	1	1	0
<i>gracilis</i>	2	1	1	1	0	1	0	0	0
<i>labrosus</i>	0	0	0	1	0	0	1	0	0
<i>latinasus</i>	0	1	1	0	1	0	0	0	0
<i>laurae</i>	2	1	1	0	1	1	0	0	0
<i>longirostris</i>	1	1	1	0	1	0	0	1	0
<i>mystaceus</i>	1	1	1	1	0	0	1	0	0
<i>mystacinus</i>	0	1	0	0	1	0	0	0	0
<i>notoaktites</i>	1	1	1	1	0	0	0	0	0
<i>poecilochilus</i>	1	0	1	1	1	0	0	0	0
<i>trogodytes</i>	0	0	0	1	1	0	0	0	0
<i>ventrimaculatus</i>	0	0	0	1	0	0	0	0	0

small circumscribed geographic areas characterized by having a number of endemic species.

When the distributions of *fuscus* group species are compared with the distributions of broad vegetation types, a general correlation is evident. There are certain distributions that do not correlate, however.

Two peripheral populations of *L. amazonicus* do not fit the general distribution pattern of the remaining populations: the population in north coastal Venezuela and the population in northeast Brasil (fig. 34). Both of these populations occur in mesic forest regions, but are separated from the mesic forest associated Amazon populations by dry forests. No information is available on the mating calls of individuals from these populations to determine whether they are sibling species or disjunct populations of *L. amazonicus*. Vanzolini (1974) suggested that there was broad continuity between the Atlantic and Amazonian forests until relatively recently. If the population in northeast Brasil is a disjunct population of *L. amazonicus*, its presence there can be accounted for if the Amazonian and Atlantic forests were in recent contact. I have no explanation for the Venezuelan population.

The distribution of *L. elenae* is Chacoan with a single exception of a sample of two frogs from Tocache Nuevo, Río Huallaga, Peru. Further sampling and knowledge of the mating call of frogs from this area are needed.

Two disjunct populations of *L. latinasus* are apparent (fig. 51), a southern series and a northeast Brasil series. No mating calls are available from the northeast Brasil specimens. They may represent a sibling species of the southern *latinasus*.

The individual distribution patterns (figs. 34, 42, 44,

47, 51, 55, 61, 62, 68) were compared with the vegetation map of South America by Hueck and Seibert (1972). Because most *Leptodactylus* locality records do not include specific data on associated vegetation, only broad associations can be made. The occurrence by species within Hueck and Seibert's (1972) broad categories are shown in Table 6. Most species occur in more than one broad vegetation type. The three species which occur within only one vegetation category are restricted to tropical and subtropical rainforest. Vanzolini (1970) grouped the individual vegetation units of Hueck (1966) into broad units which differ in part from the broad categories later recognized by Hueck and Seibert (1972). For those species occurring east of the Andes and in the greater Amazon basin southeastward, excluding those species known from but a single locality, distributions by broad vegetation types are shown in Table 7. According to the Vanzolini modification, several species are associated with a single broad vegetation category; thus the Vanzolini modification (1970) describes the distributions by vegetation types of *Leptodactylus* species better than the Hueck and Seibert (1972) classification.

Three conclusions may be drawn from the data in Tables 6 and 7: (1) Some species are restricted to wet forest or open habitat vegetation formations, (2) more species are associated with mesic forest vegetation types than xeric vegetations, (3) several species show distribution patterns associated with more than one major vegetation type. In the discussion that follows, open formations as used here contrast with closed canopy forests. Open formations include the open vegetation formations such as cerrado and caatinga, natural and man-

TABLE 6
Species occurrence within general vegetation types of Hueck and Seibert (1972).
Occurrence of *L. elenae* in tropical rainforest is at single Peruvian locality, see text.

	Tropical and Subtropical Rainforest	Deciduous, Mesophytic, Tropical and Subtropical Forests	Dry Forests	Savannas, Palm Savannas, and Palm Forests	Bush and Grass Steppe; Half and Full Deserts
<i>albilabris</i>	X	X	X		
<i>amazonicus</i>	X				
<i>bufonius</i>		X	X		X
<i>fragilis</i>		X	X		
<i>elenae</i>	(X)		X	X	
<i>fuscus</i>	X	X	X	X	X
<i>gracilis</i>	X	X	X		X
<i>labrosus</i>	X		X		X
<i>latinasus</i>		X	X		X
<i>longirostris</i>	X	X		X	
<i>laurae</i>	X	X			X
<i>mystaceus</i>	X				
<i>notoaktites</i>	X	X			
<i>mystacinus</i>	X	X	X	X	X
<i>poecilochilus</i>	X		X		
<i>troglydites</i>			X		X
<i>ventrimaculatus</i>	X				

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TABLE 7

Species occurrence within general vegetation types using Vanzolini's (1970) modification of Hueck's (1966) scheme. Species with West Indian, distributions west of the Andes, and primarily Middle American distribution patterns omitted.

	Hylea	Atlantic Forest and Araucaria	Cerrado	Caatinga
<i>amazonicus</i>	X	(X)		
<i>bufonius</i>			X	
<i>elenae</i>	(X)		X	
<i>fuscus</i>	X	X	X	
<i>gracilis</i>		X	X	
<i>latinasus</i>		X	X	
<i>longirostris</i>	X			
<i>laurae</i>		X		
<i>mystaceus</i>		X		
<i>notoaktites</i>		X		
<i>mystacinus</i>		X	X	
<i>trogodytes</i>				X

made openings in closed canopy forests, and river flood plains. If the only data one had were museum specimens, localities, and a vegetation map, one would logically look in the forest for such species as *L. amazonicus* or *longirostris* on a field trip. But there is a paradox: Although several species in the *fuscus* group are associated geographically with wet forest formations, not one (to my knowledge) is found within the forests themselves. These species occur in the open formations within the forest systems, such as along river banks. The paradox can be resolved by recognizing a scheme of two basic zoogeographic patterns.

The first zoogeographic pattern involves species occurring only within dry forest vegetations (e.g. cerrado and caatinga). The distributions of *L. bufonius* and *trogodytes* are typical of species associated with the diagonal band of open formations (Vanzolini 1974, which see for comparable distribution patterns in lizards). Characteristically, two closely related populations are found in the diagonal; one in the Chaco, one in northeast Brasil. Speciation of these xeric adapted forms undoubtedly followed the classical allopatric model. However, the stability of the open formations throughout the probable period of speciation of members of the *fuscus* group (Solbrig 1976) has provided limited opportunities for speciation. Looking at it another way, if one removed the members of the *fuscus* group that are associated with mesic forest, the group would consist of only four or five species. If *bufonius*, *labrosus*, *trogodytes*, and *ventrimaculatus* reflect the original distribution of members of the group as postulated in the relationships section, then the ancestral group must have had a broader distribution historically than is reflected by the four remaining species populations. The intervening areas (Amazonia) must have had dry corridors; extensive dry corridors may have existed up until the Miocene, when there was still a lowland area in the forming Andean chain, about where Ecuador is today (e.g. Solbrig 1976, fig. 2.2). After the uplift of the Andes, any mesic period

(such as now) would eliminate the extensive dry corridors in Amazonia, resulting in elimination of the ancestral *fuscus* group stock from the Amazon basin.

A second zoogeographic pattern involves the species associated with wet forests. The open formations found within wet forest systems are distinctive from the open formations of dry forest systems. Further, the open formations of different wet forest units must differ in soil characteristics, standing water, etc., so that given time, the adaptations to open formations within different wet forest units will differ. The key to the relatively large number of species in the *fuscus* group is that evolutionary histories of many of the species have been associated with the histories of the Neotropical mesic forests. The mesic forest units have been a dynamic system, providing greater opportunity for speciation than the dry forests for the *fuscus* group. The critical point is that the open formation *Leptodactylus* species of the mesic forests have the same evolutionary histories as the fauna of the forests. In other words, the evolutionary-environmental-geographic unit consists of the wet forests and their associated open habitats, not just the forests themselves. The distributions of *Leptodactylus* species associated exclusively with wet forests can be correlated with the location of supposed Pleistocene forest refugia (e.g. compare fig. 4, Vuilleumier 1971, with the distributions of *longirostris*, *notoaktites*, and *ventrimaculatus*). The dynamic expansion, contraction and fragmentation of the mesic forests and their associated open formations has provided the opportunity for speciation in many members of the *fuscus* group.

In regions characterized by both wet and dry forests, it is likely that the differentiation of species has been associated with presence of the open formations within a given wet forest system. The species subsequently spread to adjacent open habitats in drier forests. The distribution in drier forest open habitats could occur in association with the gallery forests along the rivers. For example, if *amazonicus* only occur in association with

gallery forests along the rivers in cerrado, the result would be a case of symmetry to the network of open formations in closed forests. In such instances, the microhabitats utilized by the species within the open formations of mesic closed forest and galleries of dry forest would be similar.

The zoogeographic hypotheses invoke mesic and xeric associations. For didactic purposes, the zoogeographic patterns have been explained separately. This does not infer that the zoogeographic patterns are the result of two separate processes. The single process of historic climatic fluctuations has produced all of the zoogeographic patterns.

In a previous section (see Relationships), *L. mystacinus* was cited as an example of how evolution could have proceeded from the more primitive member species to the more derived. The distribution of *L. mystacinus* is also exemplary in this regard. The species occurs in open formations in dry and wet forests. The pattern demonstrates that an ancestral member of the *fuscus* group, which was adapted to dry forest open habitats could have invaded the openings within wet forests. Once such open habitats were occupied, the species range could expand during periods when the forests were extensive. During drier times, some of the populations were likely isolated in open habitats within forest islands.

One difficulty in understanding the zoogeography of this group (or any other large species group) is what might be termed the palimpsest factor (term and following discussion suggested by P. E. Vanzolini). There are three possible historical times to date certain zoogeographic distributions for the *fuscus* group: (1) A possible Miocene distribution of the ancestral *fuscus* stock, (2) A Pliocene distribution event for *fragilis* and *poecilochilus*, and (3) A very recent (hundreds of years) wet climax providing continuity of the hylaeon and Atlantic forests accounting for the present distribution of *amazonicus*. So much of what happened between these end points has been erased and written over, there is no hope of unravelling the history.

EVOLUTIONARY HYPOTHESES

The *fuscus* group ancestral stock was semi-fossorial, adapted to the kind of open, xeric vegetation formation that now occurs in the Gran Chaco (this does not infer that the origin of the group was necessarily in the Chaco). The extant species of the *fuscus* group that are the most primitive in morphology and habits are still primarily associated with this ancestral vegetation formation. The burrowing adaptations of the semifossorial ancestral stock served as a preadaptation for placement of the foam nest in an underground chamber. It is possible that the ancestral stock formed their own underground burrows for retreats or aestivating sites and the males simply made use of these chambers as calling sites with consequent deposition of the foam nest. The place-

ment of the foam nest in an underground chamber was a preadaptation for the expansion of the group into adjacent, less harsh, vegetation formations. In more mesic habitats, more activities were carried out above ground, and the principal function of burrowing became the formation of the chamber in which the foam nest is placed. This nesting activity had by now become solely a male activity. Distinctive lip and thigh stripes presumably became important at this evolutionary stage because the male is expending considerable energy into reproductive activities, the success of which depend on selection of a proper mate. In the previous evolutionary stage, there was much less energy specifically channeled into reproductive activities by males, for the latter utilized chambers formed for another purpose. Presumably females also made the same kind of burrows or chambers, for the snout shapes of *L. labrosus* suggest that individuals of both sexes engage in burrow or chamber formation in this species. Once the formation of an incubating chamber becomes a strictly male activity, selection should reinforce any mechanism that assures that the male makes the correct species choice in mate selection. The female chooses the male on the basis of call; but the male must make a choice based upon the females that he encounters. Observations on *L. mystacinus* (Sazima 1975) corroborate this series of events. The male calls to attract a female. The male does not initiate chamber formation until a female approaches. Once the male starts chamber formation, he stops frequently and makes contact with the female. Apparently this frequent interruption of chamber formation is for reinforcement from the female, either tactile or visual. Males of some species of the *fuscus* group form the incubating chamber before females are called in. In these cases, proper species mate recognition would be at a premium; it would appear that the thigh and lip stripes function in this role.

PRELIMINARY COMMENT ON SIBLING SPECIES

There are two sibling species complexes in the *fuscus* group as now constituted (the new species being described by South American workers may provide additional cases). A sibling species complex is operationally defined herein as a group of biological species which are indistinguishable morphologically, with or without the aid of sophisticated statistical techniques. The two cases of sibling species pair complexes are *L. fragilis* - *latinus* and *L. geminus* - *gracilis* - *marambaiae*. Although more data are needed concerning the *geminus* - *gracilis* - *marambaiae* problem, it appears that the *fragilis* - *latinus* pair and *geminus* - *gracilis* - *marambaiae* group had very different evolutionary origins. All that is essentially required as a mechanism for sibling species formation in frogs is the evolution of distinctive mating calls. If polyploidy accompanied mating call differentiation, such as in the sibling species pair *Hyla chrysoscelis* - *versicolor*, reproductive isolation would be

immediate. The *geminus* - *gracilis* - *marambaiae* sibling triad suggests that call differentiation, unaccompanied by polyploidy, has led to reproductive isolation. In contrast, the *fragilis* - *latinasus* morphologies apparently are due to convergence. As indicated in the relationships section (and data in Table 5), the two species are not particularly closely related to each other. In fact *fragilis* has several closer related species than *latinasus*. This is substantiated by the karyotype data, in that *latinasus* is unique in the *fuscus* group in having a pair of terminal chromosomes. The similarities in size and morphology of these two species apparently are due to parallel selective pressures in similar habitat types. The *fragilis* - *latinasus* example points out the need for caution in assuming that because two species of frogs are morphologically most similar to each other, they are necessarily most closely related to each other.

RESUMEN

Se analizan detalladamente trece caracteres de la morfología externa para las especies comprendiendo el grupo *fuscus* (género *Leptodactylus*). El método principal del análisis de los datos es el aplicación del análisis multivariante de función selectiva en serie (multivariate stepwise discriminant function analysis). Se comparan los resultados del análisis morfológico con la información conocida respecto a los cantos nupciales, las larvas, y los cariotipos. Basándose sobre todos los datos obtenibles, se extraen conclusiones taxonómicas.

La nomenclatura del grupo se describe detalladamente, asociando los nombres propuestos con las unidades de especies reconocidas en este estudio. Cada y cuando que fuese posible fué re-examinado el material de los tipos originales para este estudio. De los diez y

nueve especies reconocidos en el grupo *fuscus*, cuatro se describen como especies nuevas.

Para cada especie, se provee la siguiente información: una sinonimia de los nombres primarios, un diagnóstico para los adultos, sumarios de las características morfológicas de los adultos y las larvas, descripciones diagnósticas de los cantos nupciales, descripción diagnóstica del cariotipo, y distribución incluyendo localidades y los respectivos números de clasificación de los ejemplares de museos para las especies examinadas. Se provee una clave al final de las descripciones de las especies.

El orden compuesta del grupo es enorme, con distribución de Texas hasta Argentina en ambos lados de la Cordillera de los Andes y ciertas islas de las Antillas.

Varios caracteres utilizados en el análisis son sexualmente dimorfos. Queda postulado que el dimorfismo sexual en las proporciones de los miembros traseros se debe a la selección diferencial, el miembro más corto del macho es el resultado de la selección para la actividad de hacer madrigueras relacionada a la formación de cámaras de incubación, el miembro más largo de la hembra es el resultado de la selección para evitar vivientes de repaña. El dimorfismo sexual que ocurre en las rayas del labio y del muslo de varias especies es explicado por el hipótesis que los machos están usando la información a diferenciar entre las hembras en el reconocimiento aparear.

El linaje hereditario del grupo *fuscus* es presumido haber sido cavadoramente adaptado a una área con un tipo vegetativo parecido a este ahora encuentro en el Gran Chaco. Los hechos evolutivos dentro el grupo de las especies tienen correlación con las adaptaciones a las ambientes más húmedas.

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Accepted for publication November 23, 1977.