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**John D. Lynch
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ISBN 0-89326-106-8

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ABSTRACT

Collections of frogs of the genus *Eleutherodactylus* from cloud forests of the Virolín region of Departamento Santander, Colombia (western flank of the Cordillera Oriental) include twelve species. Seven of those species are named here (one in the *fitzingeri* group and six in the *unistrigatus* group).

Although two species of *Eleutherodactylus* (*E. bogotensis* and *E. elegans*) were described in 1863 from the páramos near Bogotá, the Cordillera Oriental of Colombia has an apparently depauperate fauna in comparison to the other Andean cordilleras in northwestern South America. To date, only eleven species are known from the páramos and cloud forests of the Cordillera Oriental of Colombia north of Cerro Neiva (*E. affinis*, *E. anolirex*, *E. bicolor*, *E. bogotensis*, *E. elegans*, *E. frater*, *E. ingeri*, *E. lynchi*, *E. nicefori*, *E. prolixodiscus*, and *E. w-nigrum*).

In 1978, Pedro M. Ruíz and his students initiated a biological inventory of a very humid cloud forest region in Departamento Santander, Colombia, on the western flank of the Cordillera Oriental. At Dr. Ruíz's request, I here provide descriptions for most of the new species of *Eleutherodactylus* secured from the Virolín region.

Two major study sites were explored. The lower site (ca. 1750 m) has yielded *E. bicolor* (Rueda and Lynch, 1983), *E. ingeri*, *E. w-nigrum*, and four of the new species — *E. acutirostris*, *E. bacchus*, *E. lutites*, and *E. miyatai*. The higher site (ca. 2200-2400 m) has yielded *E. bicolor*, *E. ingeri*, and five of the new species — *E. acutirostris*, *E. grandiceps*, *E. merostictus*, *E. miyatai*, and *E. spilogaster*. Two other species secured by Ruíz are not named because the material is inadequate (one known from one adult female and one from two adult males).

Two intriguing questions remain: what are the relationships of these species and how compatible are those relationships with biogeographic theories about the tropics? The purpose of this paper is to attach names to the species and to suggest unrestrictive hypotheses of relationships. Dissections of the *M. adductor mandibulae* were made because Savage (1980) and Starret (1968) considered its variations of considerable importance. Each of the seven new species as well as *E. bicolor*, *E. ingeri*, and *E. w-nigrum* exhibits the "S" condition where the mandibular ramus of the trigeminal nerve passes lateral to the *m. adductor mandibulae posterior subexternus*.

MATERIALS AND METHODS

All specimens are housed in the amphibian collection of the Instituto de Ciencias Naturales (ICN), Bogotá, Colombia. All measurements were taken to the nearest 0.1 mm using dial calipers. The following abbreviations are used throughout: SVL (snout-vent length), HW (head width), IOD (interorbital distance), and E-N (distance between eye and nostril). Other terms and conventions follow Lynch and Duellman (1980). Frogs were sexed by gonadal examination; adults are those having swollen testes, vocal slits, and/or nuptial pads in the cases of males, or enlarged, convoluted, oviducts in the cases of females. I was able to examine live material (for all but one species) obtained in May 1983 and carried to Bogotá.

Eleutherodactylus acutirostris sp. nov.

Fig. 1A-B

Holotype — ICN 12374, gravid female, taken at "Cuchilla del Fara", near headwaters of Río Luisito, vereda Virolín, municipio Charalá, Depto. Santander, Colombia, 1780 m, in April 1983 by Rito Hernandez.

Paratypes — ICN 12373, topotype; ICN 4355, 4497-98, 5169, vereda El Reloj, 1740 m; ICN 4379-80, vereda El Taladro, 2300 m; all municipio Charalá, Depto, Santander.

Referred specimen — ICN 5490, El Brilante, finca El Pencil, sucesión Raimunda Hora, municipio Calarcá, Departamento Quindío, Colombia [I question the accuracy of the locality data for this frog and suggest it was mislabeled in the laboratory].

Diagnosis — (1) skin of dorsum shagreened, that of venter areolate; dorsolateral folds present; (2) tympanum visible, small, round; (3) snout acuminate in dorsal view, rounded in profile; canthus rostralis sharp; (4) no cranial crests nor eyelid tubercles; upper eyelid narrower than IOD; (5) vomerine odontophores low, small, widely separated; (6) males with vocal slits, subgular vocal sac; males with non-spinous nuptial pads on thumbs; (7) outer fingers bearing enlarged pads, 1.5 times as wide as digit; first finger shorter than second; (8) fingers lack lateral fringes; (9) indistinct ulnar tubercles present; (10) inner edge of tarsus with tubercle; minute tubercles on outer edge of tarsus and heels; (11) two metatarsal tubercles, inner oval, three times size of round outer; numerous supernumerary plantar tubercles; (12) toes with slight fringes, no webs; toe pads smaller than those of fingers; (13) cream with brown stripes on dorsum; lips white; venter white with a few dark spots; concealed surfaces of thighs yellow with brown reticulation; (14) adults small, 4 males 18.5-19.9 mm (\bar{x} = 19.0), 4 females 23.9-27.1 mm (\bar{x} = 25.6) SVL.

In dorsal color pattern, *E. acutirostris* is similar to *E. atratus* Lynch (Lynch, 1979a) but that species has a less acuminate snout, more ridges on the dorsum, more prominent vomerine odontophores, and dense black spotting in the groin and on the concealed surfaces of the hind limbs. *Eleutherodactylus variabilis* Lynch is similar in size and habitus but has narrower digital pads, lacks dorsolateral folds, and has very different coloration. No obvious relatives of *E. acutirostris* are known.

Description — Head as wide as body, longer than wide; HW 35.4-38.7 (\bar{x}

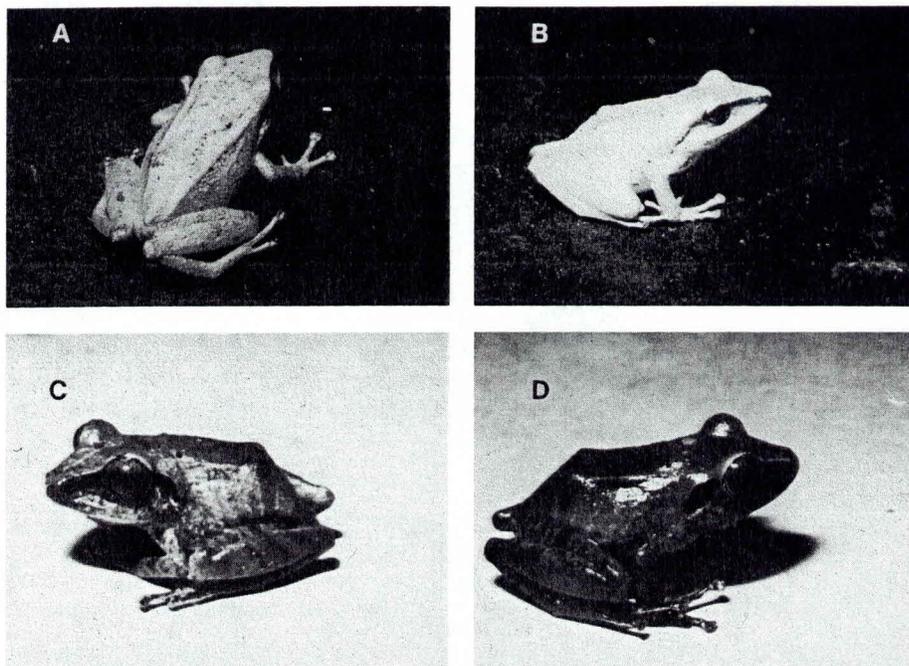


Figure 1. (A-B) *Eleutherodactylus acutirostris*, ICN 12372, young female, 23.3 mm SVL; (C) *E. bacchus*, ICN 12389, male, 29.3 mm SVL; (D) *E. bacchus*, ICN 12390, male, 29.0 mm SVL.

= 36.8, $n = 9$) % SVL; nostrils slightly protuberant, directed laterally; canthus rostralis sharp, essentially straight; loreal region concave, sloping abruptly to lip; lips not flared; E-N 85.7-96.3 ($\bar{x} = 91.7$, $n = 4$) % eye length in males, 88.6-106.9 ($\bar{x} = 99.1$, $n = 5$) in females; upper eyelid width 64.0-68.0 ($\bar{x} = 65.7$, $n = 3$) % IOD in males, 69.7-82.8 ($\bar{x} = 74.5$, $n = 5$) in females; supratympanic fold prominent, obscuring upper edge of tympanic annulus; tympanum separated from eye by $3/4$ to one tympanum length; tympanum length 33.3-35.7 ($\bar{x} = 33.9$, $n = 4$) % eye length in males, 35.3-44.8 ($\bar{x} = 38.4$, $n = 5$) in females; postrictal tubercles small, indistinct; choanae large, slightly longer than wide, partially concealed by palatal shelf of maxillary arch; vomerine odontophores low, scarcely evident in some specimens, medial and slightly posterior to choanae, each much smaller than a choana, separated on midline by a distance equal to $1\frac{1}{2}$ widths of a choana, bearing a small clump of teeth; tongue longer than wide, posterior end distinctly notched, posterior one-half free from floor of mouth; vocal slits of males posterolateral to tongue.

Skin of dorsum smooth in individuals long-preserved, finely shagreened in recently collected examples; dorsolateral folds low; skin of throat smooth; discoidal folds present; no anal sheath; palmar tubercle bifid, larger than oval thenar; supernumerary palmar tubercles pungent; subarticular tubercles prominent, pungent, round; edges of fingers bearing slight lateral keels;

pads on all fingers, that on thumb scarcely expanded, of II intermediate, of III and IV largest; pads of outer fingers broader than length of inner metatarsal tubercle, as large as tympanum; discs (broader than long) on ventral surfaces of all fingers.

Heel and tarsus bearing minute tubercles, not always evident; inner metatarsal tubercle about 2½ times as long as wide; supernumerary plantar tubercles not pungent, few on proximal portion of sole; subarticular tubercles round, pungent; third toe distinctly shorter than fifth; heels of flexed hind limbs overlap; shank 48.6-52.7 (\bar{x} = 50.2, n = 9)% SVL; heel of adpressed hind limb reaches to just in front of eye.

Cream to pale brown above with brown or reddish-brown stripes; stripes lateral to vertebral line, lateral to that (angling laterally from scapular region to contact eye), and below dorsolateral folds; limbs usually bearing oblique bands about one-half width of interspaces, but sometimes simply mottled with brown; brown to reddish brown canthal-supratympanic stripes; below stripes, lip white except for thin brown line at lip margin; venter and throat cream with faint to bold reddish-brown spots and open reticulation; undersides of limbs stippled with brown; in males, groin and posterior surfaces of thighs colorless except for brown stippling at periphery; in females, anterior and posterior surfaces of thighs more densely pigmented with brown so that these surfaces are brown with colorless spots, groin colorless.

In life, *E. acutirostris* is cream above with indefinite (and interrupted) brown paravertebral and dorsolateral stripes; canthal-supratympanic stripe darker brown; lip unmarked, paler cream than dorsum; fine brown reticulation in axillae extending onto anterior flanks; throat dull cream with brassy tint and olive-brown reticulation; venter white with brown spots and reticulation; groin bearing colorless patch; undersides of thighs and posterior surfaces of thighs yellow, latter reticulated with brown; iris pale powder blue with reddish horizontal streak.

Measurements of holotype — SVL 25.4, shank 12.6, HW 9.1, head length 9.9, upper eyelid width 2.2, IOD 3.0, tympanum length 1.3, eye length 2.9, E-N 3.1.

Etymology — Latin (*acutus* + *rostrum*), in reference to the acuminate snout.

Remarks — The only non-adult individual secured is ICN 12373, a young female (oviducts only slightly convoluted), 23.3 mm SVL.

Eleutherodactylus bacchus sp. nov.

Fig. 1C-D

Holotype — ICN 12389, adult male, one of series taken at "Cuchilla del Fara", near headwaters of Río Luisito, vereda Virolín, municipio Charalá, Depto. Santander, Colombia, 1780 m, 30 April 1983 by Pedro M. Ruíz *et al.*

Paratypes — ICN 12390-92, topotypes; headwaters of Río Luisito, vereda Virolín, 1750 m, ICN 6147-78, 6180-83, 6185, 6188-89, 12393-97; Hacienda Horizonte, vereda Virolín, 1800 m, ICN 5523; Río Luisito, vereda El Encino, ICN 4403; vereda El Reloj, 1740 m, ICN 5166, 5407; vereda El Taladro, 2300 m, ICN 4378.

Referred specimens (juveniles) — ICN 5406, vereda El Reloj; ICN 6179, 6186, headwaters Río Luisito, vereda Virolín; ICN 5541, Hacienda Horizonte, vereda Virolín; ICN 5450, Cerro Costilla del Fara, vereda Virolín.

Diagnosis — (1) skin of dorsum smooth, that of venter smooth; usually no dorsolateral folds; (2) tympanum prominent, round; (3) snout subacuminate in dorsal view; rounded in profile; canthus rostralis sharp; (4) no cranial crests; minute tubercles on upper eyelids; upper eyelid slightly narrower than IOD; (5) vomerine odontophores round, separated medially by width of odontophore; (6) males with vocal slits; subgular vocal sac; no nuptial pads in males; (7) outer fingers with enlarged pads, two times width of digit; first finger slightly shorter than second; (8) fingers with lateral keels; (9) no ulnar tubercles; (10) short inner tarsal fold; no tubercles on outer edge of tarsus or heel; (11) two metatarsal tubercles, inner oval, five times size of elongate outer; supernumerary plantar tubercles at bases of toes II-IV; (12) toes bear slight fringes, no webs; toe pads smaller than those of outer fingers; (13) brown above with dull yellow flecks; throat heavily dusted with brown, venter whitish with dark brown flecks; posterior surfaces of thighs deep brown; (14) adults moderate-sized, males 22.4-29.4 (\bar{x} = 26.3, n = 18) mm, females 32.0-34.9 (\bar{x} = 33.8, n = 6) mm SVL.

Eleutherodactylus bacchus is most similar to and easily confused with *E. savagei* Pyburn and Lynch, named from the Sierra de la Macarena in Amazonian Colombia; both are members of the *fitzingeri* group. Structurally, the two are nearly identical. However, *E. savagei* has white nuptial pads in males (absent in *E. bacchus*), a less prominent fold on inner edge of tarsus, more obvious basal webbing of the toes, and a copper iris with black reticulation. Additionally, *E. bacchus* is slightly larger, has a slightly longer and more acuminate snout, and has slightly larger tympani than does *E. savagei*.

Description — Head as broad as body, wider than long; HW 37.4-40.9 (\bar{x} = 38.7, n = 26) % SVL; E-N 85.4-100.0 (\bar{x} = 91.4, n = 18) % eye length in males, 93.2-107.7 (\bar{x} = 97.8, n = 8) in females; canthus rostralis sharp, sinuous; nostrils protuberant, directed laterally; loreal region concave, sloping abruptly to lips; lips not flared; minute tubercle on posterolateral portion of upper eyelid; upper eyelid width 69.7-96.9 (\bar{x} = 80.7, n = 18) % IOD in males, 64.3-82.2 (\bar{x} = 72.3, n = 8) in females; supratympanic fold prominent, obscuring dorsal and posterodorsal edges of tympanum; tympanum directed slightly dorsolaterally, separated from eye by a distance equal to 4/5 diameter of tympanum; tympanum length 30.0-45.0 (\bar{x} = 37.3, n = 25) % eye length, not sexually dimorphic; two elongate, non-conical, postictal tubercles below and slightly posterior to tympanum; choanae moderate-sized, not concealed by palatal shelf of maxillary arch, as long as wide; vomerine odontophores prominent, median and posterior to choanae, triangular in outline, bearing transverse row of 6-8 teeth, separated medially by a distance equal to an odontophore width, each nearly so large as a choana in adult females (proportionately smaller in males); tongue slightly longer than wide, posterior edge notched, posterior 2/5 free from floor of mouth; males with subgular, external vocal sac, long vocal slits lateral and posterolateral to tongue.

Skin smooth, although some individuals have minute thin ridges scattered on the dorsum and some individuals have subconical warts in the black scapular spots; very few individuals (e.g., ICN 6174) have short, low dorsolateral ridges bearing a row of tubercles in the scapular region; in most individuals, the superficial appearance of having dorsolateral folds is due to the pale dorsolateral stripes; discoidal folds present; no anal sheath; skin areolate only below and lateral to vent; no ulnar tubercles except for minute antebrachial; palmar tubercle bifid, much larger than oval thenar tubercle; palmar supernumerary tubercles present, scarcely elevated from palm; subarticular tubercles round, subconical; all fingers bearing pads, those of inner fingers small (ca. 1.5 times width of digit), those of outer fingers larger (ca. 2 times digit width); pads of outer fingers as large as tympanum, about equal in width to length of inner metatarsal tubercle; inner two fingers of nearly equal length (tip of pad of I reaches half way up the pad of II when equally adpressed).

Inner edge of tarsus bearing short fold (about as long as inner metatarsal tubercle) just proximal to inner metatarsal tubercle; non-pungent supernumerary plantar tubercles at bases of toes II-IV; subarticular tubercles subconical, longer than wide; heels of flexed hind legs overlap; shank 51.2-57.9 ($\bar{x} = 55.1$, $n = 18$) % SVL in males, 55.0-58.1 ($\bar{x} = 56.4$, $n = 7$) in females; heel of adpressed hind leg reaches nearly to nostril.

Above light to dark brown, usually with darker interorbital triangle, traces of a sacral chevron, and narrow pale dorsolateral stripes (from eye to about two-thirds of way between sacrum and groin); most individuals have darker brown or black scapular spots as well; canthal-supratympanic stripe dark brown, area below stripe only slightly more pale; no trace of labial marks except for cream flecks along upper lips; flanks less dark than dorsum, with thin, irregular slanting cream bars; anal triangle present, obscure (in pale individuals, there is a cream line above the anal triangle); limb bars dark brown, narrow (about half width of interspaces), those on shanks oblique; concealed surfaces of thighs, groin, and shank dark reddish-brown; throat, edges of venter, and undersides of limbs heavily peppered with brown; center of venter cream with little brown spotting or mottling; many individuals have a pale stripe on the underside of the thighs as well; in some individuals the brown markings on the ventral surfaces are less extensive (throat only spotted with brown, most of the ventral surfaces cream with scattered brown spots and blotches).

In life, *E. bacchus* is rust-brown above with dull yellow flecks and even fainter dorsolateral stripes; canthal-supratympanic stripe black, bordered below by dark brown; pale flecks on lips; postriatal tubercles dull straw-yellow; throat brown; venter whitish with dark brown flecks; undersides of thighs brown; anal triangle brown, bordered by cream line; posterior surfaces of thighs deep brown with some darker brown flecks; diffuse brown stippling behind arm, along lower edges of flanks, and in groin; iris blood red with black flecks/reticulation and black horizontal streak.

Measurements of holotype — SVL 29.3, shank 15.0, HW 11.4, head length 10.8, upper eyelid width 3.1, IOD 3.2, tympanum length 1.5, eye length 4.2,

E-N 3.9.

Etymology — Named for the Roman God of wine, in loose allusion to the blood-red eyes of *E. bacchus*.

Remarks — Specimens, including small juveniles, were collected between November and February. Three juvenile males are 17.6-19.9 mm and two small females are 15.1 and 19.6 mm SVL. Additionally, a female with non-convoluted oviducts (ICN 12391) is as large (33.2 mm SVL) as are gravid females. One other large female (ICN 5166, 32.6 mm SVL) is just coming into reproductive condition (thin, barely convoluted oviducts, small ova).

Based on similarities rather than synapomorphies, I consider *E. bacchus* most closely related to the recently described *E. savagei* (Pyburn and Lynch, 1981). Geographically, these frogs are separated by the higher elevations and páramos of the Cordillera Oriental of Colombia. *Eleutherodactylus savagei* occurs on the eastern flank of the Cordillera Oriental at elevations between 720 and 1560 m as well as on the Sierra de la Macarena.

Eleutherodactylus grandiceps sp. nov.

Fig. 2A-B

Holotype — ICN 12481, juvenile female, collected at "Bogotacito", km 55-56, Duitama-Charalá road, municipio Gambita, Depto. Santander, Colombia, ca. 2400 m, on 2 May 1983 by Pedro M. Ruíz *et al.*

Paratypes — ICN 12482-89, topotypes.

Diagnosis — (1) skin of dorsum smooth to finely shagreened, that of venter areolate; no dorsolateral folds; (2) tympanum visible, small, round; (3) snout subacuminate to ovoid in dorsal view, rounded in profile; lips flared; canthus rostralis moderately sharp; (4) no cranial crests; small tubercles on upper eyelids; upper eyelids narrower than IOD; (5) vomerine odontophores large, oval, narrowly separated; (6) males lacking vocal slits and nuptial pads; (7) outer fingers with larger pads, ca. 2.5 times as wide as digit; first finger slightly shorter than second; (8) fingers with lateral fringes; (9) ulnar tubercles present, low; (10) small tubercle on heel, another just proximal to inner metatarsal tubercle; (11) two metatarsal tubercles, inner oval, 5-6 times size of round outer; numerous supernumerary plantar tubercles; (12) toes with lateral fringes, basal web between toes IV and V; toe pads smaller than those of outer fingers; (13) dorsum brown with darker markings; flanks and thighs bear slanting dark lines; venter cream reticulated with brown; posterior surfaces of thighs reticulated with dark brown; (14) adults moderate-sized, one adult male 30.7 mm SVL, largest juvenile female 35.2 mm SVL.

Eleutherodactylus grandiceps is compared with a series of species in the *unistrigatus* group having flared lips (*E. aaptus*, *E. crenunguis*, *E. cruentus*, *E. latidiscus*, *E. loustes*, *E. muricatus*, and *E. rubicundus*). Lynch (1979b:502) listed features shared by all species then known but with the description of *E. aaptus* (Lynch and Lescure, 1980) two characteristics (narrowness of IOD and low cranial crests in females) were discarded. *Eleutherodactylus grandiceps* differs from all of these in having a comparatively broad head (HW

39.7-45.2 % SVL) and in having a sharper canthus rostralis and deeper snout. The skin of the dorsum of *E. grandiceps* is smoother (has fewer pungent tubercles and warts) than in the other species. The comparatively small eyes and broad interorbital space readily distinguish *E. grandiceps* from the other species, including *E. cruentus* which I view as its nearest relative.

Description — Head wider than body, wider than long; HW 39.7-43.1 (\bar{x} = 41.7, n = 5) % SVL in males, 43.6-45.2 % in two juvenile females; nostrils protuberant, directed laterally; canthus rostralis distinct (but keel rounded), sinuous; loreal region concave, sloping moderately rapidly to lips; lips flared throughout lengths; E-N 89.3-103.6 (\bar{x} = 97.3, n = 7) % eye length; upper eyelid width 78.6-84.6 (\bar{x} = 81.0, n = 5) % IOD in males, 64.6-67.6 % in 2 females; one or two small, non-conical tubercles on upper eyelid; supratympanic fold obscures upper edge of tympanum, bearing a few low tubercles; tympanum not prominent (annulus not pungent), separated from eye by distance equal $1\frac{1}{4}$ - $1\frac{1}{2}$ tympanum lengths; tympanum length 28.6-43.6 (\bar{x} = 34.6, n = 7) % eye length; two subconical postrictal tubercles posteroven-tral to tympanum; skin on rest of head smooth; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and psoterior to choanae, larger in larger specimens and more widely separated in smaller individuals, bearing clumps of up to 10 teeth; tongue longer

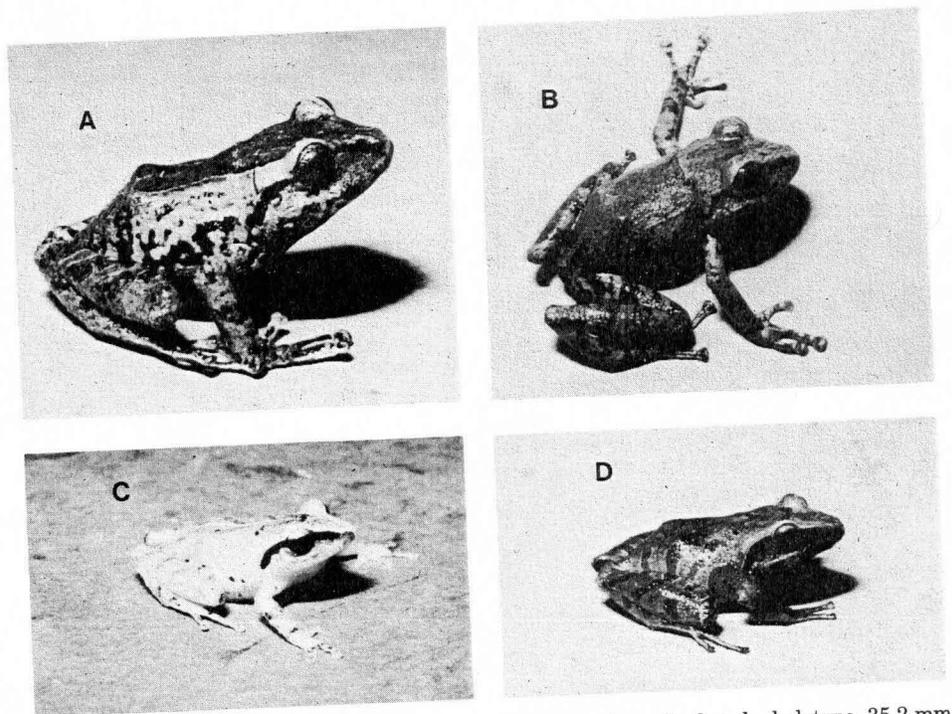


Figure 2. (A) *Eleutherodactylus grandiceps*, ICN 12481, juvenile female, holotype, 35.2 mm SVL; (B) *E. grandiceps*, ICN 12482, male, 30.7 mm SVL; (C) *E. merostictus*, ICN 12468, male, 30.7 mm SVL; (D) *E. merostictus*, ICN 12469, juvenile female, 22.0 mm SVL.

than wide, its posterior border notched, posterior 2/5 not adherent to floor of mouth.

Dorsum smooth or finely shagreened except for scattered low warts in areas bearing dark pigment; flanks areolate; throat feebly areolate; discoidal folds prominent; no anal sheath; no enlarged postanal tubercles; ulnar tubercles very low, sometimes not evident; palmar tubercle bifid, much larger than oval thenar tubercle; supernumerary tubercles pungent, non-conical; subarticular tubercles round, larger and more pungent than supernumeraries, non-conical; fingers with fleshy lateral fringes (also evident on outer edge of palm); discs on all fingers, all broader than long, round distally; pads not emarginate, scarcely wider than digit on I, almost twice digit width on II, more than twice as wide on III and IV; pad of fingers III or IV broader than length of inner metatarsal tubercle, larger than tympanum; when adpressed equally, tip of I reaches half-way up disc of II.

No tubercles on inner edge of tarsus except for that just proximal to inner metatarsal tubercle (which is twice as long as wide); sole with rows of supernumerary tubercles (most pungent distally); subarticular tubercles round, subconical; toe fringes coalesce at bases of toes, resulting webbing does not encompass basal subarticular tubercles except between toes IV and V; heels of flexed hind limbs overlap; heel of adpressed hind limb reaches to anterior one-half of eye; shank 50.2-56.4 ($\bar{x} = 53.6$, $n = 7$) % SVL.

Brown above with feeble dorsal pattern (blotch anterior to eyes, rectangular blotch between eyes extending to scapular region, sacral blotch, suprainguinal spots); bars on shanks and forearms as wide as interspaces, approximately transverse; flanks with steeply slanted dark stripes which coalesce and separate producing irregularly shaped pale spots; canthal-supratympanic stripe and labial bars brown; pale areas atop thighs (as bold blotches or as very pale interspaces) separated by dark brown bands on thighs; posterior surfaces of thighs pale cream with a few brown spots to cream with dense brown reticulation; throat and venter cream, latter more heavily reticulated with brown; the holotype has indefinite pale bands beginning on upper eyelids and extending posteriad, these fade away before sacrum; ICN 12484 has a pale vertebral raphe edged with dark brown.

In life, *E. grandiceps* was brown (washed with pale-rust, olive, or gray) above with indefinite markings; lower flanks reticulated with dark brown or pink ground color; concealed surfaces of limbs reticulated with dark brown or black on reddish ground color; venter pale yellow to off-white, flecked and/or reticulated with black; throat fleshy with black reticulation; in larger individuals the pink, yellow, and red areas are suffused with orange; iris bright copper with heavy black reticulation.

Measurements of holotype — SVL 35.2, shank 19.5, HW 15.9, head length 13.0, chord of head length 15.1, upper eyelid width 3.1, IOD 4.8, tympanum length 1.5, eye length 4.5, E-N 4.3.

Etyymology — Latin (*grandis* + *ceps*); a noun in apposition, referring to the broad head of the species.

Remarks — Lynch (1979b), Lynch and Duellman (1980), Lynch and Lescure (1980), and Lynch and Miyata (1980) discussed the relationships among the

several species currently assigned to the *rubicundus* assembly. This assemblage of species was grouped together because all shared the flaring of the lips. Lip flaring occurs in other *Eleutherodactylus* (e.g., *E. proluxodiscus* and *E. sulcatus*) not allied with the *rubicundus* assembly. If the trait should have evolved at least three times, there is little reason to continue to group members of the *rubicundus* assembly on the basis of a homoplasious trait. The oviducts of ICN 12481 are thin and not convoluted; the ovarian eggs are white and minute.

Eleutherodactylus lutitus sp. nov.

Fig. 3A

Holotype — ICN 5192, adult female, taken at the headwaters of the Río Luisito, municipio Charalá, Depto. Santander, Colombia, 1750 m, on 22 September 1979 by Pedro M. Ruíz.

Paratypes — ICN 5193, 6214 (topotypes).

Diagnosis — (1) skin of dorsum shagreened with numerous small pustules or warts, that of venter areolate; no dorsolateral folds; (2) tympanum prominent, round; (3) snout oval in dorsal view, round in lateral profile; canthus rostralis distinct; (4) no cranial crests; conical tubercle on eyelid; upper eyelid narrower than IOD; (5) vomerine odontophores slanted (teardrop-shaped), widely separated; (6) unknown; (7) first finger shorter than second; pads moderately large, those of outer fingers as wide as tympanum; (8) fingers with narrow lateral fringes; (9) row of subconical ulnar tubercles; (10) short inner tarsal fold; subconical tubercles on heel and outer edge of tarsus; (11) two metatarsal tubercles, inner oval, 5-6 times size of round outer; supernumerary tubercles at bases of toes II-IV; (12) toes with lateral keels, no webbing; toe pads almost as large as those of outer fingers; (13) dorsum brown with darker markings; limb bars broad; ventral surfaces cream with brown flecking, heaviest on throat; concealed surfaces of thighs barred cream and dark brown, dark areas coalescing on rear of thigh; (14) three adult females 23.7-28.0 mm SVL.

Eleutherodactylus lutitus is most similar to *E. incanus* named from the Amazonian slopes of the Andes in northern Ecuador (Lynch and Duellman, 1980:34-35), but differs in having more prominent eyelid tubercles, more distinct tympani, smaller digital pads, and in lacking glossy-white spots on the flanks, thighs, and shank.

Description — Head as wide as body, wider than long; HW 39.3-40.9 (\bar{x} = 40.1, n = 3) % SVL; nostrils protuberant, directed laterally; canthus rostralis weakly concave; loreal region concave, sloping abruptly to lips; lips not flared; E-N 94.6-103.2 (\bar{x} = 99.3, n = 3) % eye length; eyelid tubercle conical but small; upper eyelid width 75.0-87.9 (\bar{x} = 81.4, n = 3) % IOD; supratympanic fold distinct, with a few pustules, obscuring upper edge of tympanum; tympanum separated from eye by distance equal slightly less than length of tympanum; tympanum length 35.1-35.5 (\bar{x} = 35.3, n = 3) % eye length; postrectal tubercles subconical; small tubercles anterior to tympanum and on face; one tubercle between eyes; choanae large, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posteriad

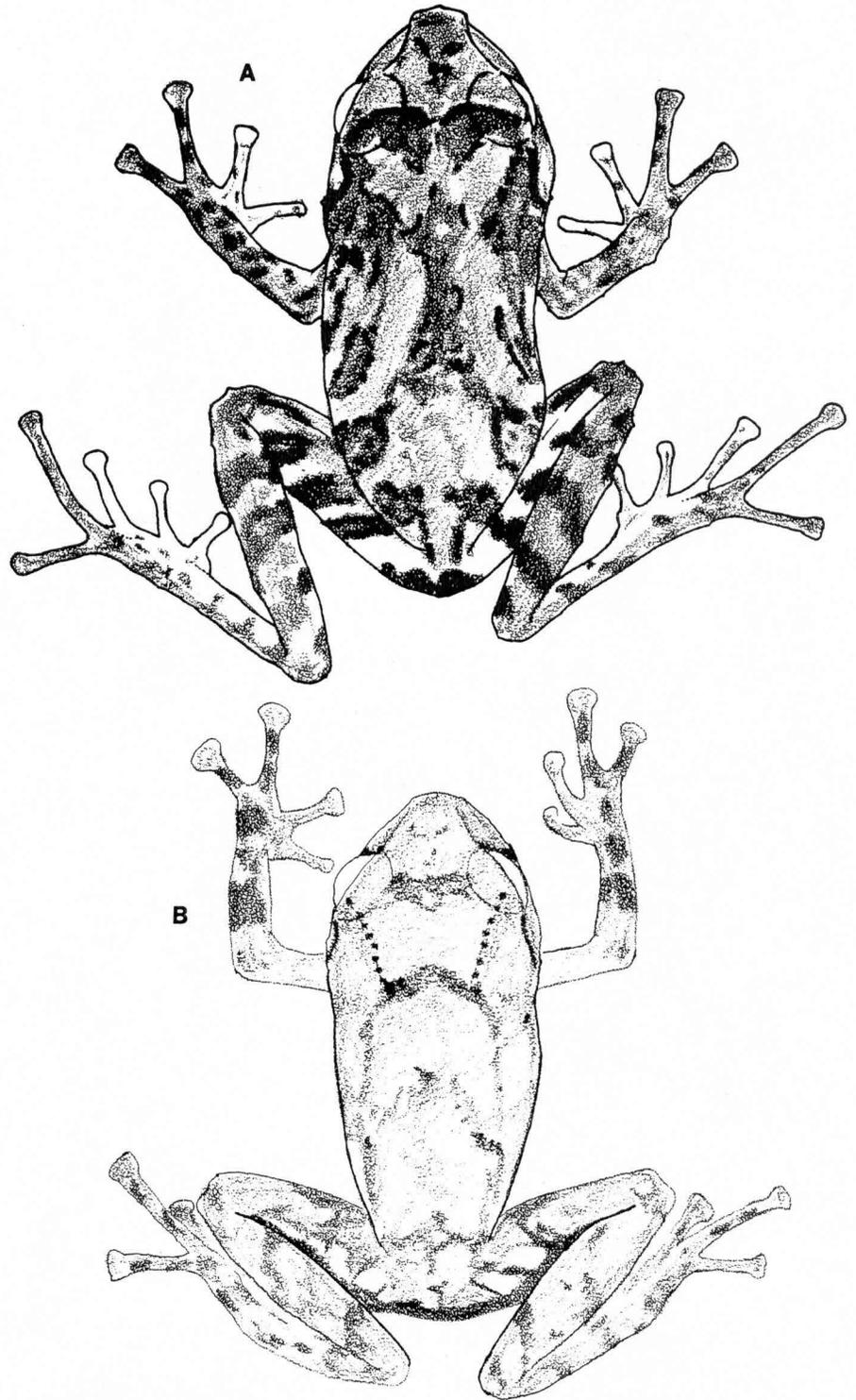


Figure 3. (A) *Eleutherodactylus lutitus*, ICN 5192, holotype; (B) *E. miyatai*, ICN 8527, adult female, 26.0 mm SVL.

to choane, separated medially by a distance equal to twice an odontophore width, each bearing an arched row at posterior end of 2-5 teeth; tongue longer than wide, posterior border not notched, posterior $\frac{1}{2}$ not adherent to floor of mouth.

Flanks areolate; enlarged postanal warts present, no anal sheath; ulnar tubercles slightly larger than pustules on forearm; palmar tubercle bifid, much larger than oval thenar tubercle; supernumerary palmar tubercles pungent, smaller than round nonconical subarticular tubercles; discs (broader than long) on ventral surfaces of all pads; pad of I scarcely wider than digit, that of II moderately wider, those of III-IV about twice as wide as digit and wider than length of inner metatarsal tubercle.

Inner tarsal fold about as long as inner metatarsal tubercle which is 2-2 $\frac{1}{2}$ times as long as wide; indistinct supernumerary plantar tubercles on sole, only those at bases of toes II-IV prominent; subarticular tubercles round, nonconical; heels of flexed hind legs overlap slightly; heel of adpressed hind leg reaches to between eye and nostril or almost to nostril; shank 51.4-55.7 (\bar{x} = 53.5, n = 3) % SVL.

Dorsum brown with darker brown markings (interorbital triangle and sacral triangle loosely forming hourglass-shaped mark, suprainguinal bar, scapular spots, supratympanic stripe, labial bars, and feeble canthal stripe); slanting brown bars on upper and anterior flanks (but not on lower posterior flanks which are colorless); broad oblique bars on shanks; all limb bars about as wide as interspaces; posterior surfaces of thighs barred cream and dark brown, dark areas coalescing on posterior edge of thigh; undersides of thighs and shanks cream with a few dark flecks/blotches; ventral surfaces cream with sparse brown flecking except for throat and breast where flecking is heavy.

Measurements of holotype — SVL 28.0, shank 14.4, HW 11.0, head length 10.0, upper eyelid width 2.9, IOD 3.3, tympanum length 1.3, eye length 3.7, E-N 3.5.

Etymology — Latin, meaning daubed with mud, in allusion to the spotted throat.

Remarks — Similarity is a poor gauge of relationship because plesiomorphic similarities outweigh apomorphic ones. Nevertheless, *E. incanus* is probably the nearest relative of *E. lutitus* and their widely separated distributions suggest that other species await discovery in the cloud forests on the Amazonian versant of the poorly collected Cordillera Oriental.

Eleutherodactylus merostictus sp. nov.

Fig. 2C-D

Holotype — ICN 12468, adult male, collected at Bogotacito, km 55-56, Duitama-Charalá road, municipio Gambita, Depto. Santander, Colombia, ca. 2400 m, on 2 May 1983 by Pedro M. Ruíz and students.

Paratypes — ICN 12466-67, 12469-75, 12478-79, topotypes.

Referred specimens — ICN 12476-77, 12480, topotypes in poor condition.

Diagnosis — (1) skin of dorsum shagreened, that of flanks and venter areolate; no dorsolateral folds; (2) tympanum visible, round; (3) snout acumi-

nate in dorsal view, round in lateral profile; canthus rostralis sharp; (4) no cranial crests; minute tubercle on upper eyelid; upper eyelid much narrower than IOD; (5) vomerine odontophores round, widely separated; (6) males with vocal slits, lacking nuptial pads; (7) first finger shorter than second; digits with moderately enlarged pads, pads round; (8) fingers with indistinct lateral keels; (9) low ulnar tubercles; (10) slight inner tarsal fold; small tubercles on heel, outer edge of tarsus; (11) two metatarsal tubercles, inner oval, 3 times size of outer; supernumerary plantar tubercles at bases of toes II-IV only; (12) toes with lateral keels, no webbing; pads on toes as large as those on fingers; (13) dorsum brown with darker markings; face dark; venter cream with black flecks; posterior surfaces of thighs black with numerous small yellow spots; (14) adult moderate-sized, males 16.5-22.5 (\bar{x} = 19.7, n = 11) mm SVL, one adult female 31.0 mm SVL.

Eleutherodactylus merostictus is most easily recognized by the color pattern on the concealed surfaces of the thighs. Similar patterns are known in the *fitzingeri* group (*E. conspicillatus*) and in the populations of *E. supernatis* found north of Medellín. Both *E. merostictus* and *E. supernatis* belong to the *unistrigatus* group but *E. supernatis* has cranial crests, a more granulate skin, and its males lack vocal slits (Lynch, 1980a).

Description — Head wider than body (not in gravid female), wider than long; HW 40.3-44.5 (\bar{x} = 42.4, n = 11) % SVL; nostrils protuberant, directed laterally; canthus rostralis sharp, straight or weakly sinuous; loreal region concave, sloping abruptly to lips; lips not flared; E-N 83.3-100.0 (\bar{x} = 92.6, n = 7) % eye length in males, 100.0-105.1 % in two females; upper eyelid width 63.3-82.8 (\bar{x} = 69.9, n = 7) % IOD in males, 62.5% in one female; supratympanic fold prominent, not concealing tympanum; tympanum separated from eye by distance equal to tympanum length; tympanic annulus not adpressed against skin; tympanum length 36.0-46.2 (\bar{x} = 40.5, n = 9) % eye length; postrectal tubercles subconical; normally no tubercles on head except eyelid, postrectals, and one behind eye (however ICN 12478 is more warty — head behind eyes is pustulate and there are a few tubercles anterior to tympanum); choanae round, relatively large, not concealed by palatal shelf of maxillary arch; vomerine odontophores oval, median and posterior to choanae, separated medially by a distance equal to an odontophore width in largest female, by twice width of an odontophore in males and juvenile females; each odontophore slightly smaller than a choana, with a clump of 5-8 teeth; tongue longer than wide, posterior edge feebly notched, posterior 2/5 not adherent to floor of mouth; vocal sac subgular, external; vocal slits short, near angle of jaws.

Skin of dorsum feebly granular, granules most distinct posteriorly, with large warts only in black scapular spots; skin of flanks and venter areolate; discoidal folds prominent; no anal sheath nor enlarged postanal tubercles; ulnar tubercles low, indistinct, except for elongate antebrachial; palmar tubercle bifid, much larger than oval thenar; supernumerary tubercles pungent; subarticular tubercles subconical, round; all fingers with discs (broader than long); no pad on thumb, pad on II ca. 1.5 times width of digit, pads on III and IV slightly more than 2 times width of digit; pads of outer fingers as wide as tympanum, as wide as length of inner metatarsal tubercle; first

finger much shorter than second; thumb of males swollen.

Skin of limbs smoother than that of dorsum; subconical tubercle on heel; no tubercles on outer edge of tarsus except in ICN 12478 (very warty individual); a single tubercle on inner edge of tarsus, sometimes part of an inner tarsal fold on distal one-half of tarsus; inner metatarsal tubercle $2\frac{1}{2}$ times as long as wide, outer subconical; subarticular tubercles subconical, longer than wide; pads on inner toes smaller than those on outer toes; heels of flexed hind legs overlap; heel of adpressed hind limb reaches to between anterior edge of eye and nostril; shank 52.4-58.6 ($\bar{x} = 55.2, n = 11$) % SVL.

Dorsum gray-brown to brown with brown scapular, sacral, and suprainguinal chevrons and interorbital bar; scapular spots and canthal-supratympanic stripe dark brown to black; canthal stripe fading towards lips (in some individuals, face black or dark brown; in others, labial bars are evident); anal triangle black; limb bars brown, narrower than interspaces, those on shanks oblique; posterior surfaces of thighs brown with numerous small cream spots; ventral surfaces cream, venter speckled with dark brown; undersides of tarsus, foot, and hand black. In some individuals (ICN 12471-72, 12478), the snout is pale gray and the body brown. A thin cream line running from the tip of the snout to the vent occurs in five individuals.

In life, *E. merostictus* is pale orange, light-brown, or reddish-brown above with black or rust markings; in most, face uniform black except for very black subocular bar; posterior surfaces of thighs black with pale rust to yellow spots; throat of males yellow; venter off-white to dirty cream with brown to black flecks; anal triangle black, edged above by cream line; iris pale green to pale yellow-bronze above, reddish below, bearing red horizontal streak and black flecking.

Measurements of holotype — SVL 20.8, shank 12.2, HW 8.7, head length 8.3, chord of head length 9.6, upper eyelid width 2.4, IOD 2.9, tympanum length 1.3, eye length 3.0, E-N 2.5.

Etymology — Greek (*meros* + *sticto*), in reference to the spotted pattern on the posterior surfaces of the thighs.

Remarks — At present, I know of no species likely to be confused with *E. merostictus* nor do I have any idea of its nearest relative. Its superficial color pattern recalls that of the Middle American *E. gollmeri* but the frogs are otherwise quite dissimilar.

Eleutherodactylus miyatai sp. nov.

Fig. 3B, 4A-B

Holotype — ICN 5165, adult female, taken on the road to El Reloj, vereda Virolín, municipio Charalá, Depto. Santander, Colombia, 1740 m, on 21 October 1979 by Pedro M. Ruíz.

Paratypes — ICN 5448-49, cerro Costilla del Fara, vereda Virolín; ICN 6184, 8527, headwaters of Río Luisito, vereda Virolín, 1750 m; ICN 12399, Río Luisito, 1750 m; ICN 12490-92, Bogotacito, km 55-56, Duitama-Charalá road, municipio Gambita, 2400 m; all Depto. Santander, Colombia.

Diagnosis — (1) skin of dorsum smooth, that of venter areolate; no dorsolateral folds; (2) tympanum round, mostly concealed; (3) snout round in dorsal

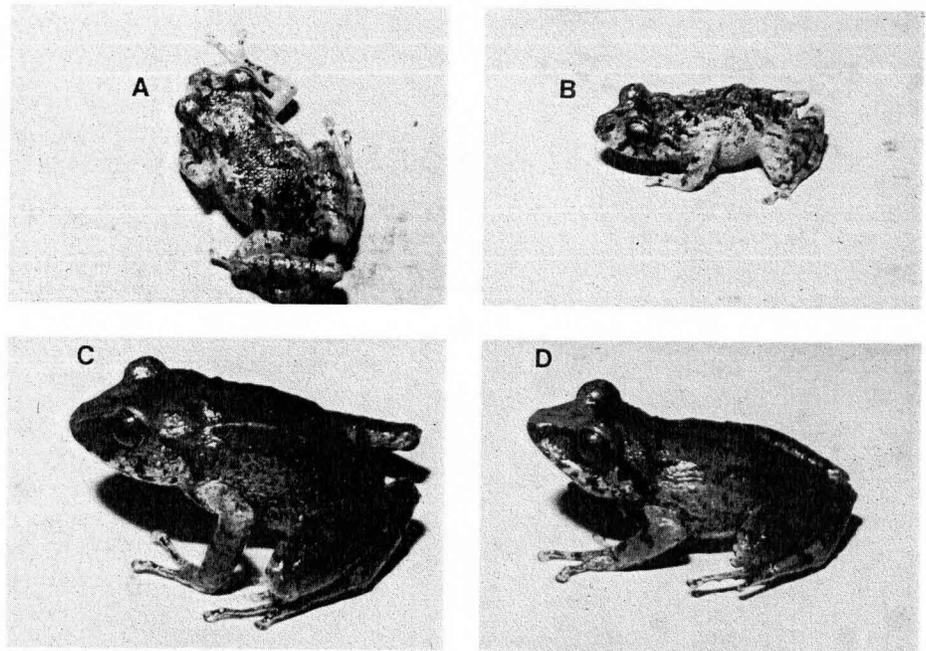


Figure 4. (A-B) *Eleutherodactylus miyatai*, ICN 12490, male, 20.2 mm SVL; (C) *E. spilogaster*, ICN 12420, juvenile female, 31.8 mm SVL; (D) *E. spilogaster*, ICN 12421, male, 29.7 mm SVL.

and lateral views; canthus rostralis not prominent; (4) no cranial crests; no tubercles on upper eyelids; (5) vomerine odontophores low, oval; (6) males with subgular vocal sac, vocal slits, white nuptial pads on thumbs; (7) fingers bearing enlarged pads, more than 2 times as wide as digit; first finger shorter than second; (8) fingers bear lateral keels; (9) antebrachial tubercle present; (10) tubercle on inner edge of tarsus; minute heel and outer tarsal tubercles; (11) two metatarsal tubercles, inner oval, 6-8 times size of round outer; numerous supernumerary plantar tubercles; (12) toes with slight lateral keels, no webs; toe pads as large as those of fingers; (13) brown above with slightly darker markings; no canthal stripe; groin and posterior surfaces of thighs brown with pale spots in females (surfaces cream-colored in males); venter stippled with brown; (14) adults small, males 16.9-20.2 (\bar{x} = 18.6, n = 4) mm SVL, females 24.0-26.7 (\bar{x} = 25.5, n = 4) % SVL.

Eleutherodactylus miyatai is most similar to *E. frater* (Werner), *E. ockenleni* (Boulenger), and *E. taeniatus* (Boulenger). The four species share the peculiar facial markings, simple dorsal patterns, and brown stippling on the venters. *Eleutherodactylus miyatai* is the only one with pale spots in the groin and on the posterior surfaces of the thighs (the others are uniform brown in these areas) and has a wider head than any of the others.

Description — Head as wide as to slightly wider than body; head wider than long; HW 39.7-41.4 (\bar{x} = 40.4, n = 4) % SVL in males, 40.4-44.6 (\bar{x} = 42.1, n = 5) % in females; nostrils weakly protuberant, directed dorsolaterally; tip of snout "mildly" pointed; canthus rostralis evident, but rounded,

gently concave; loreal region concave, slope to lips not abrupt but lips not flared; E-N 67.7-86.2 (\bar{x} = 74.5, n = 4) % eye length in males, 82.9-93.5 (\bar{x} = 88.0, n = 5) % in females, and E-N/eye ratio positively correlated (r = 0.736) with SVL; interorbital space flat, broad; upper eyelid width 80.8-95.6 (\bar{x} = 89.6, n = 4) % IOD in males, 66.7-96.0 (\bar{x} = 79.3, n = 5) % in females; supratympanic fold not prominent; tympanum concealed beneath skin but when skin dries out, annulus evident, separated from eye by a distance equal to 1½-2 tympanic diameters; tympanic annulus length 27.3-32.2 (\bar{x} = 30.0, n = 6) % eye length; postictal tubercles small, subconical; choanae large, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, small (smaller than a choana), oval, slightly elevated, separated medially by a distance less than one-half an odontophore width, with a clump or slanted row of 3-5 teeth; tongue longer than wide, posterior border not notched, posterior 2/5 not adherent to floor of mouth.

Skin of dorsum essentially smooth aside from slight shagreening (evident only under high magnification); no anal sheath or postanal tubercles; palmar tubercle bifid, much larger than oval thenar; supernumerary tubercles few, low; subarticular tubercles round, subconical; discs broad; pad of thumb ca. 1.75 times width of digit, of II ca. 2.25 times, of III and IV ca. 2.5 times; pads of outer fingers much wider than tympanic annulus, wider than length of inner metatarsal tubercle.

Inner tarsal tubercle approximately one length of inner metatarsal tubercle proximal to inner metatarsal tubercle whose length is 2½ times its width; outer metatarsal tubercle pungent; supernumerary plantar tubercles most prominent distally (bases of toes II-IV); subarticular tubercles round, relatively low; heels of flexed hind legs touch or slightly overlap; heel of adpressed hind limb reaches to anterior edge of eye or just beyond; shank 50.6-55.1 (\bar{x} = 52.8, n = 9) % SVL.

Cream to brown above with brown markings (interorbital bar, scapular W, rudiments of sacral chevron, suprainguinal bar) not well-defined in most specimens; shank bars oblique, narrower than interspaces; anal triangle brown; supratympanic stripe and labial bars brown; ventral surfaces pale to medium brown (uniform stippling of brown); in females, anterior and posterior surfaces of thighs brown, this pigment also forming bars atop thighs; on median part of thighs, interspaces are extremely pale (yellow in life); similar blotch on posterior flank; in males, posterior flanks and concealed surfaces of thighs cream with slight brown stippling (yellow in life).

In life, *E. miyatai* is brown, rust-brown, or olive above with dark brown markings; vocal sac off-yellow; concealed surfaces of limbs lemon yellow; venter pale brown; digital pads whitish above; iris pale gold above, gray below, reticulated with black and bearing reddish horizontal streak.

Measurements of holotype — SVL 24.0, shank 12.8, HW 9.8, head length 9.1, upper eyelid width 2.3, IOD 3.0, tympanic annulus 0.9, eye length 3.3, E-N 2.9.

Etymology — Named for the late Kenneth Miyata who so much enjoyed field work in cloud forests.

Remarks — I here propose that *E. frater*, *E. miyatai*, *E. ockendeni*, and *E.*

taeniatus form a monophyletic group of species. At present, all are allopatrically distributed. — *E. taeniatus* in the lowlands of eastern Panama and western (and possible northern) Colombia (Lynch, 1980b), *E. miyatai* from cloud forests on the western flank of the northern Cordillera Oriental, *E. frater* on the eastern flank of the Cordillera Oriental (Pyburn and Lynch, 1981), and *E. ockendeni* from the upper Amazon basin in southern Colombia, eastern Ecuador, and Amazonian Perú (Lynch, 1980c). These frogs are most easily recognized by a feature of their color pattern (no canthal stripe and no labial bars anterior to eye). Although this characteristic is proposed as a synapomorphy uniting these four species, I am skeptical of synapomorphies based on absences (of facial markings). I am not aware of any feature linking any pair or trio of this group.

Eleutherodactylus spilogaster sp. nov.

Fig. 4C-D

Holotype — ICN 12421, adult male, taken at Bogotacito, km 55-56, Duitama-Charalá road, municipio Gambita, Depto. Santander, Colombia, 2400 m, on 2 May 1983 by Pedro M. Ruíz and students.

Paratypes — ICN 12420, 12422-24, 12427-28, 12430-40, 12455-65, topotypes; ICN 5411, 5413, 5453-54, "Buena Vista", Hda. La Argentina, vereda Virolín, municipio Charalá, 2200 m; ICN 8528-31, vereda El Taladro, municipio Charalá, 2300 m; all Depto. Santander, Colombia.

Referred specimens — ICN 12425-26, 12441-52, juvenile topotypes.

Diagnosis — (1) skin of dorsum smooth, that of venter areolate; low dorsolateral folds present; (2) tympanum round, visible; (3) snout subacuminate in dorsal view, round in lateral profile; canthus rostralis sharp; (4) no cranial crests; non-conical tubercle on each eyelid; (5) vomerine odontophores round, narrowly separated; (6) males with vocal slits; males bearing small glandular nuptial pads; (7) first finger shorter than second; all digits with discs; pads of outer fingers 1.8-2.0 times width of digits; (8) fingers with thick lateral keels; (9) no ulnar tubercles except low antebrachial; (10) minute tubercle on heel; inner tarsal tubercle low; no tubercles on outer edge of tarsus; (11) two metatarsal tubercles, inner oval, 4-6 times size of round outer; supernumerary plantar tubercles at bases of toes II-IV; (12) toes with lateral fringes, without webbing; toe pads smaller than those of outer fingers; (13) olive to rust-brown above with darker dorsal markings and pale dorsolateral stripes; ventral surfaces brown with cream flecks; posterior surfaces of thighs brown with cream flecks; (14) adults moderate-sized, males 22.0-30.0 (\bar{x} = 27.6 \pm 0.6, n = 19) mm SVL, one adult female 36.7 mm SVL.

Eleutherodactylus spilogaster is most similar to *E. anolirex*. The two differ in that *E. spilogaster* has eyelid tubercles, a smooth dorsum, and cream flecks on the venter. *Eleutherodactylus anolirex* has a white stripe on the lips.

Description — Head as wide as or wider than body; head wider than long; HW 38.6-42.6 (\bar{x} = 40.6, n = 19) % SVL in males, 43.0% in one female; nostrils protuberant, directed dorsolaterally; canthus rostralis straight or sinuous; loreal region slightly concave, sloping abruptly to lips; lips not flared; E-N 76.7-100.0 (\bar{x} = 88.6, n = 20) % eye length; interorbital space broad, flat; upper eyelid width 66.7-93.9 (\bar{x} = 79.8, n = 20) % IOD; upper

edge of tympanum concealed by supratympanic fold, tympanum separated from eye by distance equal to tympanum length; tympanum 27.6-40.6 (\bar{x} = 36.9, n = 19) % eye length in males, 43.5% in one female; postrectal tubercles subconical; skin on head and face smooth; choanae moderate-sized, oval, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posteriad to choanae, elevated, separated medially by a distance equal one-half an odontophore width, each with a transverse row of 4-6 teeth; tongue longer than wide, posterior border feebly indented, posterior 2/5 not adherent to floor of mouth; vocal slits short, near angle of jaws.

Skin of dorsum smooth except for scapular warts and low dorsolateral folds (extending from a position just posterodorsal to tympanum to the sacral region), sometimes bearing another short fold lower on flank; discoidal folds present; no anal sheath or enlarged postanal tubercles; palmar tubercle bifid, much larger than oval thenar; supernumerary palmar tubercles low, few; subarticular tubercles round, non-conical, pungent; pads round, that on thumb scarcely wider than digit, that on II ca. 1.4 times digit width, those on III and IV ca. 1.8-2.0 times digit width; nuptial pads on thumbs difficult to see (same color as thumb), small; thumbs of males swollen at bases.

Inner tarsal tubercle elongate; inner metatarsal tubercle 2½ times as long as wide; basal subarticular tubercles longer than wide, more distal ones round, non-conical; heels of flexed hind legs overlap; heel of adpressed hind limb reaches vicinity of nostril; shank 50.7-58.5 (\bar{x} = 54.9, n = 20) % SVL.

Dorsal surfaces gray, light brown, or dark-brown with black or dark brown markings (interorbital bar, scapular spots, limb bars, dark stripes along dorsolateral folds, labial bars, canthal-supratympanic stripes); limb bars narrow, those on shanks oblique; occasionally traces of sacral chevron and occipital W-shaped mark; some vague slanted bars on flanks; anal triangle brown, edged above with cream line; venter cream or brown, heavily mottled with brown; throat and chest brown, flecked with whitish cream; groin and anterior surfaces of thighs cream with brown flecking; posterior surfaces of thighs brown with minute cream flecks.

In life, *E. spilogaster* is brown, olive, rust-brown, or olive-tan with a few dark marks between the dorsolateral folds (which tend to be paler than the ground color). Flanks have oblique dark brown bars. Undersides are dark brown with diffuse cream flecks. Posterior surfaces of thighs brown with tiny cream flecks. Iris bright copper with black flecks.

Measurements of holotype — SVL 29.7, shank 15.3, HW 12.2, head length 10.6, chord of head length 12.3, upper eyelid width 2.0, IOD 3.6, tympanum 1.6, eye length 4.3, E-N 3.2.

Etymology — Greek (*spilos* + *gaster*), in reference to the speckled venter.

Remarks — Lynch (1983) included five species in his *devillei* assembly and *E. spilogaster* appears to be another member. However, the *devillei* assembly must be viewed as a phenetic grouping because no synapomorphy for the group is known (Lynch, 1983:56). Four taxa (and *E. spilogaster*) share a feature (inner tarsal fold/tubercle) not shared by *E. briceni* (cladistically the most remote member) but the presence of this feature is scarcely likely

to be uniquely evolved inasmuch as tarsal folds and tubercles are common to most groups of *Eleutherodactylus* as well as other frogs. Until osteological characteristics and synapomorphy analyses are available, *E. spilogaster* can be regarded as a relative of *E. anolirex* and the *devillei* assembly.

ACKNOWLEDGMENTS

Pedro M. Ruíz encouraged me to describe his collections. He and Maria Cristina Ardila provided laboratory space and many courtesies in Bogotá and loaned material for study. Jennifer Lynch helped prepare the figures.

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