

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE
AMERICAN MUSEUM
OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2696

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Number 2696, pp. 1–24, figs. 1–5, tables 1–2

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A Taxonomic and Distributional Synopsis of the Amazonian Frogs of the Genus *Eleutherodactylus*

JOHN D. LYNCH¹

ABSTRACT

Twenty-four species of *Eleutherodactylus* are distributed in the Amazonian lowland forests (below 1000 m.) of South America; 23 of these occur within Haffer's (1969, 1974) Napo refugium. Primary distributional data or references to such reports are given for each of the 24 species, many of which have not been reported since their original descriptions. *Eleutherodactylus peruvianus* (Melin) is removed from synonymy with *E. conspicillatus* (Günther). *Hylodes gollmeri bisigna-*

tus Werner and *Eleutherodactylus crepitans* Bokermann are relegated to the synonymy of *E. fenestratus* (Steindachner). *Eleutherodactylus melini* Bokermann is relegated to the synonymy of *E. ockendeni* (Boulenger). *Eleutherodactylus malkini* is a new species reported from Brazil, Colombia, Ecuador, and Peru; it differs from all other Amazonian members of the *fitzingeri* group in having webbing between the toes.

INTRODUCTION

I earlier stated (Lynch, 1976) that the Neotropical frog genus *Eleutherodactylus* contains 340 recognized species. I now recognize (Lynch, in print, in press, and in preparation) more than three dozen additional species from Colombia and Ecuador. Of these approximately 380 species, nearly 200 occur in South America where they are primarily forest animals (although many species occur in the non-forested *páramos* of Colombia, Ecuador, and Venezuela).

Perusal of the literature reveals Ecuador to have the richest fauna. The high species density in Ecuador is partly a product of the attention given the fauna by Jiménez de la Espada and Boulenger in the late nineteenth century and by Andersson and Lynch during the mid-twentieth century and partly a product of great diversity associated with the Napo refugium (or high rainfall area) cited by Haffer (1969) and Müller (1973, 1974). I (Lynch, 1974) cited the sympatric (or near

¹Associate Professor, School of Life Science, the University of Nebraska–Lincoln.

sympatric) occurrence of 16 species of *Eleutherodactylus* in the Lago Agrio-Santa Cecilia area in Napo Province, Ecuador (the fauna was recently described in detail by Duellman, 1978a), whereas only a half-dozen species are reported from western Brazil (Lutz and Kloss, 1952; Lynch, 1975a, 1975b; Melin, 1941). I am aware of only 28 species of *Eleutherodactylus* distributed over the vast and varied forests of the central cis-Andean lowlands (hylaea) of South America.

The hylaea is bisected by a relatively dry belt extending from the Venezuelan llanos southeasterly to the Atlantic coast of Brazil east-southeast of the mouth of the Rio Amazonas (Haffer, 1974). The northeastern portion of the hylaea is not richly endowed with *Eleutherodactylus* (Hoogmoed, Lynch, and Lescure, 1977; Lynch and Hoogmoed, 1977) but most of the species are endemic. The endemicity may be a product of poor collections in northern Brazil west of the relatively dry belt. The Guyanan component of the hylaea harbors *E. chiastonotus* Lynch and Hoogmoed, *E. gutturalis* Hoogmoed, Lynch, and Lescure, *E. inguinalis* Parker, *E. lacrimosus* (Jiménez de la Espada), *E. marmoratus* (Boulenger), and *E. zeuctotylus* Lynch and Hoogmoed.

The larger component of the hylaea includes forested Amazonia (lowlands below 1000 m. drained by the Rio Amazonas and its major tributaries, viz., Rios Juruá, Madeira, Marañón, Napo, Negro, Purús, Solimões, Tapajóz, Tocantins, Ucayali, and Xingu). I am aware of 24 species of *Eleutherodactylus* in the larger unit, most of which are distributed within Haffer's (1969) Napo refugium. The Napo refugium has been extensively collected in Ecuador leading to the frequent recognition of an Amazonian fringe fauna (e.g., Duellman, 1972) (=preandine of Lutz, 1972).

The impetus for this report stems from study of the Collections of Harvey Bassler in the American Museum of Natural History, collected chiefly from the drainage of the Río Ucayali in Peru, and the recently acquired collections of Borys Malkin from the Rio Solimões area of Brazil and adjacent Peru as well as from localities in Ecuador and Co-

lombia. Malkin made large collections at several localities including Igarapé Belém, ca. 70 km. E Leticia, Territorio Amazonas, Brazil; Estirón, Río Ampiyacu (upstream from Pebas), Depto. Loreto, Peru; Yagua Indian village, headwaters of Río Loretoyacu (just west of the Colombian frontier), Depto. Loreto, Peru; and Cusuime, Río Cusuime, Prov. Morona-Santiago, Ecuador.

The functions of the present paper are (1) to provide systematic information and distributional data concerning Amazonian *Eleutherodactylus*, and (2) to document the geographic inequalities of species densities. The distributional data and geographic inequalities are pertinent to Haffer's (1969, 1974) refugia model and ultimately to an understanding of speciation in *Eleutherodactylus*, the largest vertebrate genus known.

ACKNOWLEDGMENTS

I am grateful to the following curators for loan of specimens and/or provision of working space at their institutions: Mr. Werner C. A. Bokermann, Dr. James R. Dixon, Dr. William E. Duellman, Dr. Josef Eiselt, Miss Alice G. C. Grandison, Ms. Brigitta Hansson, Dr. W. Ronald Heyer, Dr. Donald F. Hoffmeister, Dr. Arnold G. Kluge, Mr. Hyman Marx, Dr. Charles W. Myers, Dr. Ronald A. Nussbaum, Dr. Douglas Rossman, Mrs. Dorothy Smith, Ms. Greta Vestergren, Dr. Ernest E. Williams, Dr. John W. Wright, and Dr. Richard G. Zweifel. Travel to museums was made possible by grants from the University of Nebraska Research Council.

MATERIALS AND METHODS

I have examined approximately 3300 specimens of hylaeen *Eleutherodactylus*, including the extant holotypes or syntypes for all names except *E. brevicrus* Andersson, *E. carvalhoi* Lutz, *E. crepitans* Bokermann, *E. melini* Bokermann, and *E. nigrovittatus* Andersson. Abbreviations for institutions cited in the text are: AMNH (American Museum of Natural History), BM [British Museum (Natural History)], FMNH (Field Museum of Natural History), GNM (Göteborgs Na-

turhistoriska Museum), KU (University of Kansas Museum of Natural History), LACM (Natural History Museum of Los Angeles County), LSUMZ (Louisiana State University, Museum of Zoology), MCZ (Museum of Comparative Zoology, Harvard University), MZUSP (Museu de Zoologia, Universidade de São Paulo), NHW (Naturhistorisches Museum zu Wien), RMNH (Rijksmuseum van Natuurlijke Historie), SHNM (Royal Museum of Natural History, Stockholm), TCWC (Texas Cooperative Wildlife Collection, Texas A & M University), UIMNH (University of Illinois Museum of Natural History), UMMZ (University of Michigan Museum of Zoology), USNM (National Museum of Natural History; GOV and JAP refer to the Gustavo Orces-V and James A. Peters Collections), and WCAB (private collection of Werner C. A. Bokermann, São Paulo).

In the following accounts, snout-vent length is abbreviated SVL, interorbital distance is abbreviated IOD, and eye to nostril distance is abbreviated E-N.

THE AMAZONIAN *ELEUTHERODACTYLUS*

Eleutherodactylus acuminatus Shreve

Eleutherodactylus acuminatus Shreve, 1935, p. 217 (type-locality, Canelos, Prov. Pastaza, Ecuador; holotype, MCZ 19951, obtained by O. C. Felton in April 1932).

This small (males 17.1–22.6 mm. SVL, females 25.6–31.3 mm. SVL) green species of the *unistrigatus* group is distinguished from all other species by its protruding snout and concealed tympana. It has only been reported three times (Crump, 1974; Duellman, 1978a; Shreve, 1935) from localities in Ecuador, but ranges through eastern Ecuador into northern Peru and adjacent Colombia. I have seen 44 specimens from 12 localities in eastern Ecuador (provs. Morona-Santiago, Napo, and Pastaza) at elevations between 300 and 1000 m.

Outside of Ecuador, the species is known from Puerto Nariño, Comisaria Amazonas, Colombia (KU 153282), Santa Rosa de Sucumbios, Río San Miguel, Intendencia Pu-

tumayo, Colombia, 400 m. (AMNH 103428), and the Río Aguayita, Depto. Loreto, Peru (AMNH 42703). The distribution of the species is best matched with the Napo refugium rather than described as *Pre-Andine*.

Eleutherodactylus altamazonicus Barbour and Dunn

Eleutherodactylus altamazonicus Barbour and Dunn, 1921, p. 161 (type-locality, "Upper Amazon, probably collected by the Thayer Expedition at Nauta," Depto. Loreto, Peru; holotype, MCZ 2028).

Eleutherodactylus brevicrus Andersson, 1945, p. 40 (type-locality, Río Pastaza watershed, eastern Ecuador; holotype, SMNH [not examined], obtained by William Clarke-Macintyre). Placed in synonymy by Lynch (1974).

I (Lynch, 1974) reported *E. altamazonicus* from 21 localities in eastern Ecuador at elevations up to 1000 m.; the only non-Ecuadorian locality then known was the type-locality, "upper Amazon, probably near Nauta" (Barbour and Dunn, 1921). Since then I have seen specimens from slightly higher elevations (KU 123374–76, S slope Cordillera del Dué above the Río Coca, Napo Prov., Ecuador, 1150 m.; UMMZ 92130, Abitagua, Pastaza Prov., Ecuador, 1200 m.) and specimens from one locality in Colombia (AMNH 103429–103433, Santa Rosa de Sucumbios, Intend. Putumayo, 400 m.) and five localities in Peru (AMNH 42449, 42452, 42454, mouth of Río Santiago, Depto. Amazonas; KU 154759, Finca Panguna, Río Lullapichis, 4–5 km. upstream of Río Pachitea, Depto. Huánuco, 200 m.; AMNH 103417, Estirón, Río Ampiyacu, Depto. Loreto; AMNH 96283, Yagua Indian village, headwaters of Río Loretoyacu, Depto. Loreto; AMNH 42692, 42701, 43575, Río Utoquinia–Río Tapiche headwaters, Depto. Loreto).

The distributional area of *E. altamazonicus* is essentially congruent with that of *E. acuminatus*. *Eleutherodactylus altamazonicus* is a small (males 14.4–23.1 mm. SVL, females 23.6–33.9 mm. SVL) brown frog with bold red and black marbling in the groin

and red and black barring on the concealed shank.

Eleutherodactylus carvalhoi Lutz

Eleutherodactylus carvalhoi Lutz, in Lutz and Kloss, 1952, p. 642 (type-locality, Itacoai River, tributary of the Rio Javari, Estado Amazonas, Brazil; holotype, National Museum in Rio de Janeiro [not examined], obtained in 1950 by J. C. M. Carvalho).

Eleutherodactylus carvalhoi has been reported only once since its original description. I (Lynch, 1974) cited it as similar to *E. croceinguinis* and *E. martiae* and distinguished the three taxa. Much less information is available for *E. carvalhoi* than for *E. croceinguinis* and *E. martiae* but all are small frogs. Four gravid females of *E. carvalhoi* from western Brazil and adjacent Peru measure 17.4 to 24.0 mm. SVL (\bar{x} = 21.2).

The new locality records for *E. carvalhoi* (fig. 1) are BRAZIL, *Terr. Amazonas*: Igarapé Belém, near Rio Solimões, ca. 70 km. E Leticia (AMNH 96897-901); COLOMBIA, *Com. Amazonas*: Puerto Nariño (KU 153283-85); ECUADOR, *Prov. Pastaza*: Rio Villano (USNM JAP 6263); and PERU, *Depto. Loreto*: Yagua Indian village, headwaters of Río Loretoyacu (AMNH 96284-90). All records lie below 500 m. elevation in the Napo refugium of Haffer (1974). Duellman and Toft (1978) reported *E. carvalhoi* from east-central Peru; I have included their localities on the distribution map (fig. 1A). Their specimens of *E. carvalhoi* are smaller (two males 13.5 and 14.8 mm., two adult females 16.3 and 18.5 mm. SVL) than specimens from the Leticia region.

Eleutherodactylus conspicillatus
(Günther)

Hylodes conspicillatus Günther 1858, p. 92 (type-locality, Andes of Ecuador; holotype, BM 58.7.25.24 [reregistered as 1947.2.16.20] obtained by Mr. Fraser).

I (Lynch, 1975a) provided a redescription and distributional summary for *E. conspicillatus* and suggested that Melin's (1941) *Hylodes peruvianus* (type-locality Roque, Dep-

to. San Martín, Peru) was a synonym. The Bassler and Malkin Collections include many specimens of a frog from the upper Amazon Basin of Brazil, Ecuador, and Peru that resembles *E. conspicillatus* in habitus, proportions, skin texture, and most features of coloration, but which is distributed essentially parapatrically to what I previously considered *E. conspicillatus* in the eastern lowlands of Ecuador. All but one (the holotype of *peruvianus*) of the specimens reported by Lynch (1975a) are *E. conspicillatus*. I have seen 172 specimens of *E. conspicillatus* from 22 Ecuadorian localities and nine from five Colombian localities (all Intend. Putumayo). The new Colombian records are LACM 50497-98, 50520, near El Pepino, at jct. Pasto-Puerto Asis and Mocoa roads, and FMNH 54322, Rumiayaco. In addition to the three Peruvian records cited by Lynch (1975a), I have seen a specimen (AMNH 43224) from the headwaters of the Ríos Utoquinia and Tapiche, Depto. Loreto, near the Brazilian border in east-central Peru.

I am here proposing recognition of *E. peruvianus* (Melin) as a species distinct from *E. conspicillatus* although there is little evidence that the two behave as separate entities in nature. Unlike *E. conspicillatus*, *E. peruvianus* has brown, gray, or black spotting on the throat and anterior venter (least obvious in females), the underside of the shank is spotted (large pale spots [instead of dark marbling]), the pale spots on the posterior surfaces of the thighs are larger (smaller, usually smaller than pad of third finger, in *E. conspicillatus*), and a canthal streak and faint facial bars.

The only case of sympatry known is based on Bassler specimens from the upper Río Utoquinia in Depto. Loreto, Peru (I consider this a general rather than specific locality). At other localities in the upper Amazon Basin, one finds either *E. conspicillatus* or *E. peruvianus*. The four Peruvian localities for *E. conspicillatus* are generally well within the distribution area for *E. peruvianus* (fig. 4A) and well removed from the contiguous distribution of *E. conspicillatus* (northern Amazonian Ecuador and adjacent Colombia). The Peruvian records of *E. conspicil-*

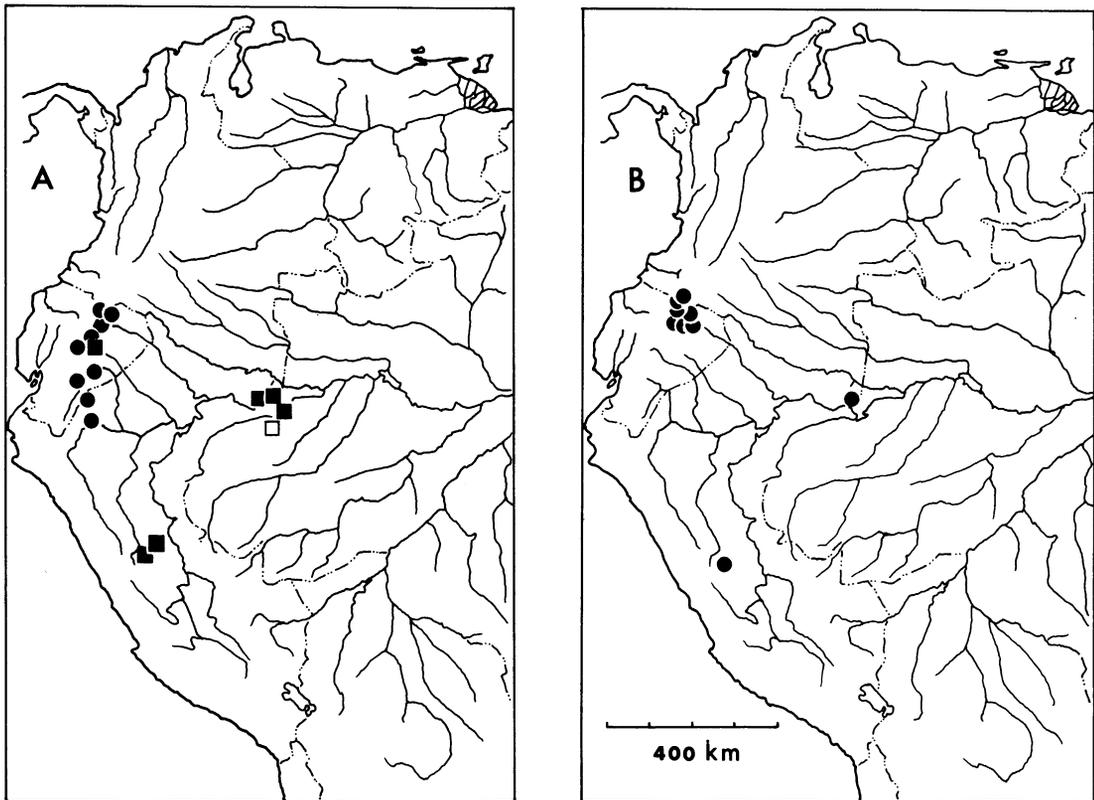


FIG. 1. (A) Distributions of *Eleutherodactylus carvalhoi* (squares) and *E. diadematus* (circles) in the upper Amazon Basin (open square is a literature record). (B) Distribution of *E. variabilis*.

latus are suggestive of a diffuse zone of macrosympatry (one species being uncommon and the two not ecologically sympatric). The two phenotypes (*conspicillatus* and *peruvianus*) differ only in coloration insofar as they are now known and exhibit a measure of geographic separation. Most other pairs of postulated nearest relatives in *Eleutherodactylus* are more sharply differentiated.

Eleutherodactylus croceinguinis Lynch

Eleutherodactylus croceinguinis Lynch, 1968, p. 133 (type-locality, Santa Cecilia, Napo Prov., Ecuador, 340 m.; holotype, KU 110789, obtained June 16, 1967 by John D. Lynch).

I have examined 257 specimens from 21 localities in Amazonian Ecuador (Prov. Morona-Santiago, Napo, and Pastaza) and one locality in Colombia (AMNH 103434, Santa

Rosa de Sucumbios, Río San Miguel, Intend. Putumayo, 400 m.). *Eleutherodactylus croceinguinis* is not known to co-occur with *E. carvalhoi* (a close relative) but is widely sympatric with another close relative, *E. martiae*. However, the critical areas of eastern Ecuador (<200 m.) have not been collected and the three are anticipated to occur together there. *Eleutherodactylus croceinguinis* is the smallest of the three (14 males 12.8–18.2 mm. SVL [\bar{x} = 14.6], 19 females 17.4–21.9 mm. SVL [\bar{x} = 19.8]).

Eleutherodactylus diadematus (Jiménez de la Espada)

Hylodes diadematus Jiménez de la Espada, 1875, pl. 3, figs. 3a–c (type-locality, not known; holotype, lost).

Hylodes platydactylus: Peracca, 1904, p. 27 (part).

Eleutherodactylus bufonius Andersson, 1945, p. 35 (type-locality, watershed, Río Pastaza, Ecuador; holotype, SHNM 1917, obtained by William Clark-Macintyre). Placed in synonymy by Lynch and Schwartz (1972).

Eleutherodactylus diadematus is the largest cis-andean member of the *unistrigatus* group (15 males 21.4–27.4 [\bar{x} = 23.5] mm. SVL, 19 females 35.4–44.5 mm. SVL [\bar{x} = 39.8]) and one of the least common. I have seen 60 specimens from eastern Ecuador and adjacent Peru (fig. 1): ECUADOR, eastern Ecuador, watershed of Río Pastaza (SHNM 1917); *Morona-Santiago Prov.*: Cusuime, Río Cusuime, 320 m. (AMNH 93489); Mendez, 580 m. (USNM JAP 6818); 10 km. S Mendez, 885 m. (USNM JAP 6902); 10–25 km. S Mendez, 915–1145 m. (USNM JAP 6906–07); 3.2 km. E Sucua, 825 m. (USNM JAP 2206, 2228); *Napo Prov.*: Bermejo No. 4, 15 km. ENE Umbaqui, 740 m. (KU 123379); Lago Agrio, 330 m. (KU 126132–47); Puerto Libre, Río Aguarico, 570 m. (KU 123380–84); Puerto Napo (UIMNH 55821); 2 km. W Puerto Napo (USNM JAP 2743); Río Suno (USNM GOV 7144); Santa Cecilia, 340 m. (KU 104598, 104617, 111180, 111186, 111188, 123377–78, 146096, 148884–88); *Pastaza Prov.*: Montalvo (USNM GOV 9656, 9663–64); 1 km. W Puyo, 1000 m. (MCZ 90019, 92032–33); Río Conambo (USNM GOV 9640); upper Río Oglán (USNM GOV 9644); Río Pastaza, 500 m. (UMMZ 92128); Río Pindo, trib. of Río Tigre (USNM GOV 9641); Río Pucayacu (USNM JAP 3870); mouth of Río Shyona at Río Conambo (USNM GOV 8999); PERU, *Depto. Amazonas*: Ayendama, Río Cenipa (AMNH 42038); mouth of Río Santiago (AMNH 43298).

Peracca's (1904) record of *Hylodes platydactylus* Boulenger (otherwise known only from southern Peru) is here referred to *E. diadematus*. Peracca's specimen is 44 mm. SVL and has a visible tympanum; *E. platydactylus* is much smaller and has concealed tympana (although the largest cotypes are somewhat desiccated and have partially visible tympana).

Eleutherodactylus fenestratus
(Steindachner)

Hylodes fenestratus Steindachner, 1864, p. 249 (type-localities, Río Mamoré, Estado Rondônia, Brazil; cotype, NMW 19940.1; and Borba, Estado Amazonas, Brazil; cotype, NMW 19940.2).

Hylodes gollmeri bisignatus Werner, 1899, p. 483 (type-locality, Chaco, Bolivia; holotype, NMW 16502). NEW SYNONYMY.

Eleutherodactylus crepitans Bokermann, 1965, p. 262 (type-locality, São Vicente, Cuiabá, Estado Mato Grosso, Brazil; holotype, WCAB 16144, obtained November 19, 1965 by M. Alvarenga, W. Bokermann, and F. M. Oliveira [not examined]). NEW SYNONYMY.

Although widespread in Amazonia (fig. 2), *E. fenestratus* has seldom been recognized or reported. Günther (1864) considered it a synonym of *Hylodes griseus* (Hallowell) and the latter name became entwined in South American literature. Günther was uncritically followed by Boulenger (1882), Nieden (1923), and Gorham (1966) although no specimens were involved. Savage (1974) showed that *griseus* is a synonym of *E. fitzingeri* (O. Schmidt) of Central American and Chocoan Colombia. It is unclear how or why a species having moderate toe webbing (*E. fitzingeri*) should have been confused so long with one having no toe webbing (*E. fenestratus*) in light of Cope's (1862a, 1862b, and 1863) comments on *griseus*.

Cope (1887) reported *E. fenestratus* as *Lithodytes conspicillatus* from Mato Grosso, Brazil. Boulenger (1898, 1903) reported specimens from northern Bolivia and Mato Grosso, Brazil, as *Hylodes gollmeri*. Rivero (1961) reported Bolivian specimens as *Eleutherodactylus longirostris*. Cochran and Goin (1970) reported Bolivian and Peruvian specimens as *E. conspicillatus*. Lutz and Kloss's (1952) report of *E. gollmeri* from extreme western Brazil may represent *E. fenestratus*, but is probably *E. peruvianus*. Hoogmoed, Lynch, and Lescure (1977) reported some frogs resembling the Guyanan *E. gutturalis* from Manaus and from SE of Santarem (Amazonas and Pará, Brazil);

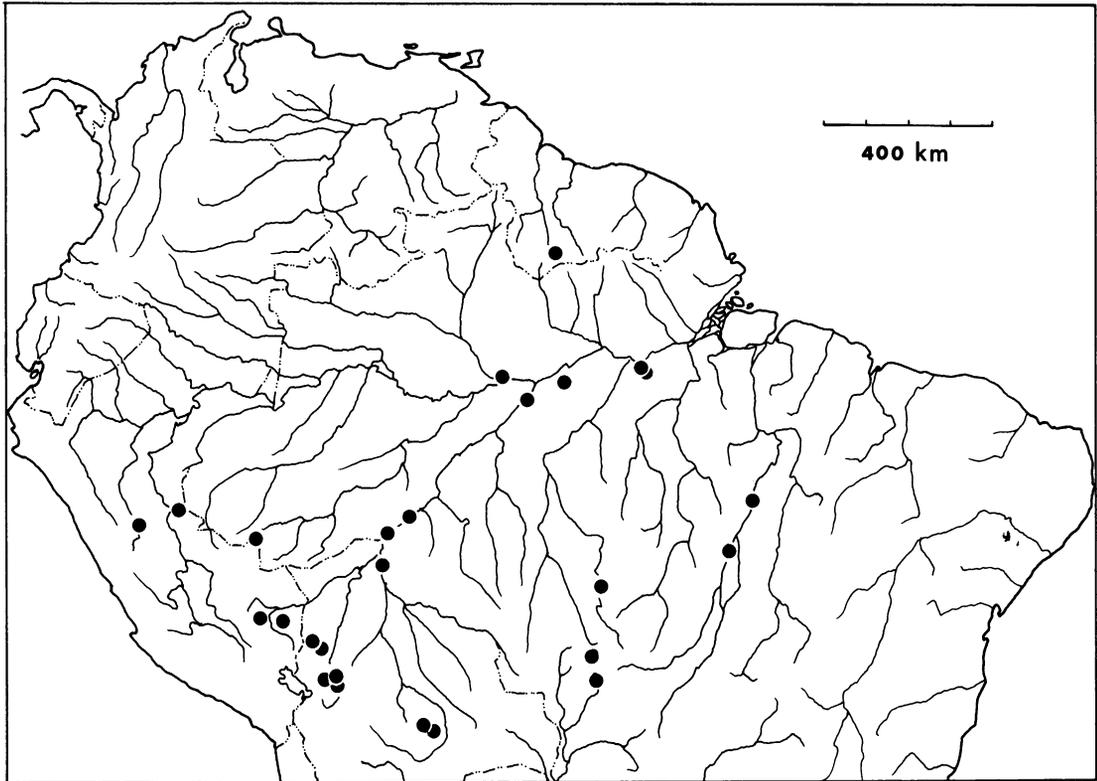


FIG. 2. Distribution of *Eleutherodactylus fenestratus*.

those specimens are *E. fenestratus*. Cope's (1874, p. 127) report of *Lithodytes conspicillatus* from Santarem probably is based on *E. fenestratus*.

Eleutherodactylus fenestratus is separable from *E. gollmeri* (Peters) of Costa Rica and Panama in that *fenestratus* has dilated, apically round digital pads, whereas *gollmeri* has narrow, pointed digital pads; *E. fenestratus* differs from *E. conspicillatus* and *E. peruvianus* in having scattered enlarged tubercles on the shagreened dorsum (rather than a uniformly shagreened dorsum), a less acuminate snout, prominent labial bars, and uniform brown posterior thigh surfaces (marbled or spotted in *conspicillatus* and *peruvianus*). *Eleutherodactylus fenestratus* resembles *E. gutturalis* Hoogmoed, Lynch, and Lescure,

E. lanthanites Lynch, *E. terraebolivaris* Rivero, and *E. vilarsi* (Melin) in having scattered enlarged tubercles on the shagreened dorsum and uniformly brown posterior surfaces of the thighs. *Eleutherodactylus gutturalis*, *E. lanthanites*, and *E. terraebolivaris* (usually evident only in males) have brown throats with a white gular stripe. *Eleutherodactylus lanthanites* and *E. vilarsi* are short-legged frogs (Lynch, 1975a), whereas *E. fenestratus*, *E. gutturalis*, and *E. terraebolivaris* are long-legged frogs. *Eleutherodactylus fenestratus* is moderate-sized (29 males 23.8–34.3 mm. SVL [\bar{x} 28.3 \pm 0.9 (mean \pm 2 standard errors)], 32 females 31.9–50.0 mm. SVL [\bar{x} = 41.5 \pm 1.5]).

Eleutherodactylus fenestratus is sympatric with few other species of the genus. In south-

ern Peru and Bolivia, *E. fenestratus* co-occurs with *E. cruralis* (Boulenger) and *E. granulatus* (Boulenger), members of the *discoidalis* group, and *E. platydactylus* (Boulenger) of the *unistrigatus* group at moderate elevations (1000–1800 m.). The distribution area of *E. fenestratus* is reasonably congruent with the drier forests of Amazonia (see Haffer, 1974, p. 17) having monsoon climates.

I here propose assignment of *Hylodes gollmeri bisignatus* Werner and *Eleutherodactylus crepitans* Bokermann to the synonymy of *E. fenestratus*. The confusion surrounding the identities of the *fitzingeri* group species of Amazonia led both Werner (1899) and Bokermann (1965) to describe the frogs as new without comparison to *E. fenestratus*. Each appears to have contrasted their specimens with Ecuadorian examples of *E. achatinus* (Boulenger), *E. conspicillatus* (Günther), and/or *E. w-nigrum* (Boettger). Such comparisons would support recognition of Bolivian or Brazilian material as distinct. Bokermann (1965) did not compare his material with Werner's (1899) description presumably because only frogs identified as *E. conspicillatus* or *E. gollmeri* had been reported from Mato Grosso.

The holotype of *Hylodes gollmeri bisignatus* is an adult female and except for having nearly smooth skin (probably an artifact of preservation) is not different from many adult females from Bolivia, Brazil, and Peru, except in having a pair of sinuous stripes in the scapular region. Bokermann's (1965) *E. crepitans* is described in great detail and illustrated. Bokermann cited the slight sexual dimorphism of *E. crepitans* as diagnostic (the holotype male and allotype female are 31.0 and 32.0 mm. SVL, respectively). Specimens in the British Museum from Mato Grosso (reported by Boulenger, 1898, 1903) exhibit more normal sexual dimorphism (two males, 23.3–23.4; three young females 30.9–33.3; two adult females, 31.9–34.5 mm.). Bokermann's two males are best regarded as abnormally large and his female as relatively small.

Eleutherodactylus lacrimosus
(Jiménez de la Espada)

Cyclocephalus lacrimosus Jiménez de la Espada, 1875, pl. 3, figs. 5a–b (type-locality, unknown; holotype, lost).

Lynch and Schwartz (1972) reported this species as ranging from Colombia and Ecuador east to the mouth of the Amazon. Lutz and Kloss's (1952) report of *Syrrhophus chalcus* (Peters) from Iuaretê, Amazonas, Brazil, is probably based on this species. The only distributional additions are KU 153286–88 from Petuna, Río Loreto-yacu, Com. Amazonas, Colombia, and AMNH 42080, from Mamayacu, Río Cenipa, Depto. Amazonas, Peru. *Eleutherodactylus lacrimosus* is a small member [lowland males 16.1–20.0 (\bar{x} = 18.5), females 20.6–24.4 (\bar{x} = 22.5) mm. SVL] of the *unistrigatus* group.

Eleutherodactylus lanthanites Lynch

Eleutherodactylus lanthanites Lynch, 1975, p. 10 (type-locality, Santa Cecilia, Prov. Napo, Ecuador, 340 m.; holotype, KU 146144, obtained on April 2, 1972 by William E. Duellman).

I (Lynch, 1975a) reported specimens from nine localities in Ecuador and adjacent Peru at elevations below 950 m. I have now seen 441 specimens from 25 localities in eastern Ecuador at elevations up to 1490 m. (2 km. SSW Río Reventador, Prov. Napo, KU 165885–93) as well as the following records outside of Ecuador: BRAZIL, *Terr. Amazonas*: Igarapé Belém, near Río Solimões (AMNH 96902). COLOMBIA, *Intend. Putumayo*: near El Pepino, jct. Pasto-Puerto Asis and Mocoa roads (LACM 50557) 10.3 km. W El Pepino, 1440 m. (KU 168834–45, 170172); ca. 10 km. S (airline) Mocoa, 700–800 m. (AMNH 84826); ca. 5 km. N Puerto Asis (0° 33' N, 76° 32' W) (LACM 50571); Santa Rosa de Sucumbios, Río San Miguel, 400 m. (AMNH 103435–103436). PERU, *Depto. Loreto*: headwaters of Río Loretoyacu (AMNH 96291–92). The distributional area of *E. lanthanites* is encompassed by the 3000 mm. annual rainfall isohyet (Haffer, 1974) in

the upper Amazon Basin. *Eleutherodactylus lanthanites* is moderate-sized [20 males 21.7–26.0 (\bar{x} = 23.5 \pm 0.6) mm., 32 females 27.5–44.8 (\bar{x} = 36.2 \pm 1.3) mm. SVL].

***Eleutherodactylus malkini*, new species**

HOLOTYPE: AMNH 94228, an adult male obtained at Estirón, Río Ampiyacu, Depto. Loreto, Peru, between March 28, and April 9, 1970 by Borys Malkin.

PARATYPES: AMNH 94229, taken with holotype; AMNH 94230–34, Yagua Indian village, headwaters of Río Loretoyacu, Depto. Loreto, Peru; AMNH 94220–23, Igarapé Belém, near Río Solimões, ca. 70 km. E Leticia (Colombia), Terr. Amazonas, Brazil; KU 175113, Río Yasuni, 200 (*sic*) km. upstream from Río Napo, Prov. Napo, Ecuador; AMNH 94219, Andoas, Río Pastaza, Prov. Pastaza, Ecuador; AMNH 94250, Intuto, Río Tigre, Prov. Pastaza, Ecuador; AMNH 94218, Santa Rosa, Río Tigre, Prov. Pastaza, Ecuador; AMNH 93686–87, 93690, Cusuime, Río Cusuime, Prov. Morona-Santiago, Ecuador, 320 m., AMNH 94213–17, eastern Ecuador.

REFERRED SPECIMENS: BRAZIL, *Terr. Amazonas:* Igarapé Belém, ca. 70 km. E. Leticia, AMNH 94224–27. COLOMBIA, *Com. Amazonas:* Puerto Nariño, KU 153920. ECUADOR, *Prov. Morona-Santiago:* Cusuime, 320 m., AMNH 93688–89; *Prov. Pastaza:* Río Bufe, Lower Río Bobonaza, USNM GOV 9031–32, 9034. PERU, *Depto. Loreto:* Mishana, Río Nanay, MCZ 89070–72; Yagua Indian village, headwaters of Río Loretoyacu, AMNH 94235–49; Roaboya, AMNH 43526; Yanamono, TCWC 41490.

DIAGNOSIS: A moderate-sized species of the *fitzingeri* group of *Eleutherodactylus* (11 males 30.4–37.2 [\bar{x} = 32.9] mm. SVL, nine females 41.5–47.9 [\bar{x} = 44.8] mm. SVL) having partially webbed toes (modal webbing of males I 2–2⁺ II 2–3⁺ III 3–4⁺ IV 4–2 ½ V, of females I 2–2⁺ II 2–3⁺ III 3–4[–] IV 4–2⁺ V) (webbing formula after Savage and Heyer, 1967); all digits bearing discs and non-emarginate pads; palmar tubercle bifid;

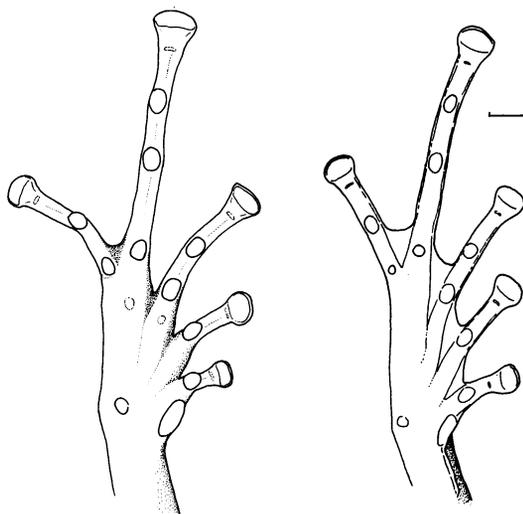


FIG. 3. Right feet of *Eleutherodactylus conspicillatus* (left, UIMNH 7381) and *E. malkini* (right, AMNH 94216). Scale equals 2 mm.

fold along distal one-half of tarsus; no calcar on heel; inner metatarsal tubercle much larger than outer; skin of dorsum shagreened with scattered enlarged tubercles, no dorso-lateral folds; tympanum prominent, its length one-third to two-fifths eye length; E–N usually less than eye length; males with vocal slits and nuptial pads, legs of moderate length, shank 52.7–64.4 percent SVL; throat spotted with gray; posterior surfaces of thighs cream, boldly reticulated with black; shank bars narrow, weakly oblique; dorsum gray with brown or black spots; labial bars not concealed by face mask.

The presence of appreciable webbing of the toes (fig. 3) distinguishes *E. malkini* from all species of the *fitzingeri* group except the assemblage of partially webbed species in Chococo Colombia and Central America [*E. andi* Savage, *E. anomalus* (Boulenger), *E. azueroensis* Savage, *E. brocchi* (Boulenger), *E. crassidigitus* Taylor, *E. fitzingeri* (O. Schmidt), *E. fleischmanni* (Boettger), *E. longirostris* (Boulenger), *E. matudai* Taylor, *E. merendionalis* Schmidt, *E. punctariolus* (Peters), *E. raniformis* (Boulenger), *E. ru-*

gulosus (Cope), *E. taurus* Taylor, and *E. vocalis* Taylor]. Of these, only *E. andi*, *E. crassidigitus*, *E. fitzingeri*, *E. fleischmanni*, *E. longirostris*, *E. merendionalis*, *E. punctariolus*, and *E. raniformis* have both nuptial pads and vocal slits in breeding males. Of these, only *E. fleischmanni* has comparable webbing and marbled posterior surfaces of the thighs. *Eleutherodactylus fleischmanni* is much larger than *E. malkini*, has rounded canthi rostrali, narrow digital pads, and a stronger inner tarsal fold (Savage, 1975).

DESCRIPTION: Head about as wide as body, as wide as long or slightly longer than wide; head width 36.0–40.5 (\bar{x} = 38.1, N = 19) percent SVL; snout acuminate in dorsal view, rounded in profile; nostrils weakly protuberant, directed dorsolaterally; E–N 78.4–95.6 (\bar{x} = 86.2, N = 8) percent eye length in males, 85.3–105.7 (\bar{x} = 94.6, N = 11) in females; canthus rostralis relatively sharp, weakly concave; loreal region weakly concave, sloping abruptly to lips; lips not flared; no cranial crests; upper eyelid width 100.0–129.0 (\bar{x} = 114.4, N = 8) percent IOD in males, 92.5–120.5 (\bar{x} = 106.6, N = 9) in females; upper eyelid shagreened (no enlarged tubercles); supratympanic fold prominent, concealing upper edge of tympanic annulus; tympanum higher than long, separated from eye by distance equal $\frac{3}{4}$ tympanum length; tympanum length 31.6–51.0 (\bar{x} = 43.6, N = 8) percent eye length in males, 41.2–58.3 (\bar{x} = 47.4, N = 11) in females; postrictal tubercles small; choanae moderate-sized, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores pungent, median and posterior to choanae, each slightly larger than a choana, separated on midline by distance equal to odontophore breadth, oval in outline, each bearing a transverse row of three to eight teeth (tooth counts for males three to seven per odontophore, \bar{x} = 4.7; for juvenile and young females, three to six, \bar{x} = 4.5; for adult females, four to eight, \bar{x} = 6.2); tongue slightly longer than wide, large, posterior edge feebly notched, posterior one-third to two-fifths not adherent to floor of mouth; males with short vocal slits near corner of jaw.

Skin of dorsum shagreened with scattered enlarged tubercles; no dorsolateral folds; large tubercles most numerous on flanks; skin of limbs relatively smooth; skin of venter smooth; discoidal folds prominent; skin below and lateral to vent areolate; antebra-chial tubercle present but otherwise no ulnar tubercles; palmar tubercle bifid, one and a half times size of oval thenar tubercle; supernumerary palmar tubercles proximal to subarticular tubercles; latter longer than wide, subconical; fingers lacking lateral fringes; fingers bearing broad discs on pads; pads twice width of digit below pad, rounded apically; no pad as large as tympanum; thumb much longer than second finger.

Heel and outer edge of tarsus lacking tubercles or folds; inner edge of tarsus bearing flaplike fold on distal one-half; inner metatarsal tubercle elongate (length three times width), not compressed, four times size of round outer metatarsal tubercle; no supernumerary plantar tubercles; subarticular tubercles longer than wide, subconical; toes bearing lateral fringes and basal webbing; webbing formulae (following Savage and Heyer, 1967) for males $I(2^- - 2) - 2^+ II(2^- - 2^+) - (3 - 3^+) III(2\frac{1}{4} - 3) - (4^- - 4\frac{1}{8}) IV(3\frac{3}{4} - 4) - (2\frac{2}{3} - 2) V$, for females $I(2^- - 2^+) - 2^+ II(2^- - 2^+) - (3 - 3^+) III(2\frac{1}{4} - 3) - (4^- - 4\frac{1}{8}) IV(3\frac{3}{4} - 4) - (2 - 2\frac{1}{2}) V$; toes bearing discs and pads; toe pads nearly as large as those of outer fingers; heels overlapping when flexed legs are held at right angles to sagittal plane; shrank 52.7–56.4 (\bar{x} = 54.4, N = 8) percent SVL in males, 57.0–64.4 (\bar{x} = 59.8, N = 11) in females.

Gray above with black or brown markings, viz., interorbital bar, scattered spots on back, loosely forming scapular W, sacral chevron, suprainguinal bar; supratympanic stripe black; three to four labial bars on brown to dark gray face; some pale spots on lip, pale vertical bar on snout tip; lowermost flanks reticulated with brown; this pattern continues into groin and along anterior edge of thigh and ventrolateral edge of shank; dorsal surfaces of limbs gray, barred with brown; bars on thighs narrower than interspaces, latter having thin brown line through

center; shank bars narrower than interspaces (latter not subdivided), weakly oblique; forearm, tarsus, foot barred; underside of tarsus heavily marbled with brown and black; posterior surfaces of thighs cream with bold black reticulation; venter white; throat moderately to heavily spotted with gray; undersides of limbs white although anterior edge of thighs and posterior edges of shanks invaded by gray marbling.

MEASUREMENTS OF HOLOTYPE (IN. MM.): SVL 33.8; shank 18.3; head width 12.5; head length 12.5; upper eyelid width 4.0; IOD 3.1; tympanum length 2.1; eye length 5.1; E-N 4.4. The thumb bears a non-spinous nuptial pad; vocal slits are present; the vomerine tooth counts are four and five; and the webbing formula is $I2^{-} - 2^{+} II2^{-} - 3^{+} III3^{-} - 4^{+} IV4^{-} - 2\frac{1}{2}V$.

ETYMOLOGY: The species is named for Borys Malkin in recognition of his outstanding collections from Amazonia and Colombia.

DISTRIBUTION: Known from low elevation rainforests in the upper Amazon Basin in Brazil, Colombia, Ecuador, and Peru (fig. 4).

Eleutherodactylus martiae Lynch

Eleutherodactylus martiae Lynch, 1974, p. 2 (type-locality, Santa Cecilia, Napo Prov., Ecuador, 340 m.; holotype, KU 152389, obtained May 4, 1973 by Martha L. Crump).

I (Lynch, 1974) reported *E. martiae* from seven localities in Napo and Pastaza provinces of Ecuador at elevations between 300 and 1300 m. *Eleutherodactylus martiae* ranges from extreme southern Colombia (AMNH 103437–103439, Santa Rosa de Sucumbios, Río San Miguel, Intend. Putumayo, 400 m.) through eastern Ecuador (157 specimens from 12 localities in Morona-Santiago, Napo, and Pastaza provinces) to south-central Peru. The Peruvian records are: *Depto. Loreto*: mouth of Río Contaya (AMNH 42568); *Depto. Junín*: Chanchamayo, 1220–1830 m. (AMNH 43442, 43447); *Depto. San Martín*: upper Biabo valley, 1070 m. (AMNH 43260); Chasita, Río Huallaga (AMNH 42791). *Eleutherodactylus martiae*

is a small (27 males 11.8–16.8 [\bar{x} = 15.1] mm. SVL, 33 females 18.3–23.0 [\bar{x} = 20.4] mm. SVL) species of the *unistrigatus* group only slightly larger than *E. croceinguinis*, a sympatric relative, and only slightly smaller than an apparently parapatric relative, *E. carvalhoi*.

Eleutherodactylus nigrovittatus Andersson

Eleutherodactylus nigrovittatus Andersson, 1945, p. 33 (type-locality, Abitagua, Río Pastaza, Prov. Tungurahua, Ecuador; holotype, SHNM [not examined], obtained in September 1937 by William Clarke-Macintyre).

Eleutherodactylus nigrovittatus has been reported from only four localities in Ecuador (Andersson, 1945; Duellman, 1978a; Lynch 1974) but is relatively widespread through the area of high rainfall in the Napo refugium. The species has one of the widest altitudinal ranges of any South American eleutherodactyline (100–1935 m.). The following have been examined: COLOMBIA, *Intend. Putumayo*: Santa Rosa de Sucumbios, Río San Miguel, 400 m. (AMNH 103440–103441). ECUADOR, *Morona-Santiago Prov.*: Cusuime, Río Cusuime, 320 m. (AMNH 93509–17); Macuma (USNM GOV 8902); Miazal (USNM JAP 3875); Río Yuquipa, Macas (USNM GOV 7210). *Napo Prov.*: S slope Cordillera del Dué above Río Coca, 1150 m. (KU 123503–42, 123544–65); La Bonita, 1935 m. (USNM JAP 4861); Lago Agrío, 330 m. (KU 126196); Loreto (USNM GOV 7692, 8897, 9544, JAP 3852–53, 8825–26); slope of Mount Sumaco (AMNH 22284, 22287–89, 22293–98, 22327, 22335–37); S slope Mount Sumaco (USNM GOV 8899–8900); Payamino (USNM GOV 7240); Puerto Libre, Río Aguarico, 570 m. (KU 123685–89); Puerto Napo (UIMNH 55817); Río Cotopino (UMMZ 92148); San José (AMNH 22169, 22172). *Pastaza Prov.*: Guache, Río Pastaza (near Peruvian frontier) (AMNH 21499); Mera, 1100 m. (KU 177356–57); Pucayacu, betw. Sarayacu and Montalvo (USNM GOV 8898); 5 km. SSE Puyo, 1000 m. (USNM JAP 2021, 2023, 2025); Río Rutuno, trib. Río Bobonaza (USNM GOV 7796–97); Río Villano

(USNM JAP 6255); 10 km. ESE Veracruz (MCZ 90311–14). PERU, *Depto. Amazonas*: Mamayacu, Río Cenipa (AMNH 42416); *Depto. Loreto*: Estirón, Río Ampiyacu (AMNH 103418); headwaters of Río Loretoyacu (AMNH 96293–98).

Andersson's (1945) holotype was obtained at an elevation of between 1200 and 1500 m. It agrees with the specimens from moderate elevations (900–1934 m.) in being of moderate-size (33 males 17.2–24.6 [\bar{x} = 21.4 \pm 0.6] mm. SVL, 21 females 25.0–30.5 [\bar{x} = 27.4 \pm 0.7] mm. SVL). Specimens from localities below 600 m. are small (eight males 13.3–19.4 [\bar{x} = 17.0 \pm 1.9], 9 females 19.7–22.1 [\bar{x} = 20.9 \pm 0.5] mm. SVL). Both high and low elevation populations agree in males lacking nuptial pads and vocal slits and in having the flesh at the tip of the snout and to a lesser degree along the side of the snout produced as a fleshy keel. The fleshy protuberance is reminiscent of that seen in males of some *Leptodactylus* suggesting that *E. nigrovittatus* may dig burrows for calling sites or nest building.

The *discoidalis* group is represented in northwestern South America by the low to moderate elevation *E. nigrovittatus*, a high elevation species on the Amazonian versant in southern Colombia and northern Ecuador (*E. elassodiscus* Lynch) and a moderate elevation species on the Cordilleras Central and Occidental in Colombia [*E. mantipus* (Boulenger)]. The distribution area of *E. nigrovittatus* lies within the 3000 mm. isohyet and probably extends into western Brazil.

Eleutherodactylus ockendeni (Boulenger)

Hylodes ockendeni Boulenger, 1912, p. 187 (type-locality, La Union, Río Huacamayo, Huacamayo, Carabaya, *Depto. Puno*, Peru, 600 m.; syntypes, BM 1907.5.7.19–21 [re-registered as 1947.2.16.88–90], collected by Mr. Ockenden).

Hylodes hylaeformis Melin, 1941, p. 48 (type-locality, Roque, *Depto. San Martín*, Peru; holotype, GNM [not examined] obtained in 1925 by Douglas Melin). NEW SYNONYMY.

Syrhophus calcaratus Andersson, 1945, p. 27 (type-locality, Río Cosanga near Archidona, Napo Prov., Ecuador, 800 m.; holotype, SHNM 1941, obtained in December 1937 by

William Clarke-Macintyre). Placed in synonymy by Lynch (1974).

Eleutherodactylus melini Bokermann, 1958, p. 95 (replacement name for *Hylodes hylaeformis* Melin, 1941, non *Phyllobates hylaeformis* Cope, 1875).

Eleutherodactylus anderssoni Lynch, 1968, p. 292 (replacement name for *Syrhophus calcaratus* Andersson, 1945, non *Hylodes calcaratus* Boulenger, 1908).

I (Lynch, 1974) provided a description and partial synonymy for *E. ockendeni*. The Harvey Bassler Collection provides specimens from 10 localities in *Deptos. Amazonas, Junín, Loreto, and San Martín*, Peru, and collections assembled by Catherine A. Toft (KU) produced specimens from *Deptos. Cuzco, Huánuco, and Madre de Dios*, Peru, bridging the distributional gap evident in Lynch's (1974) list of specimens examined. Borys Malkin secured specimens at Santa Rosa de Sucumbios, Río San Miguel, Intend. Putumayo, Colombia, 400 m. (AMNH 103442–103446), and at the Yagua Indian village at the headwaters of the Río Loretoyacu, *Depto. Loreto*, Peru (AMNH 96299–302) providing the northernmost and northeasternmost distributional records. I have examined 351 specimens from 35 localities at elevations below 1280 m.

Melin (1941) named *Hylodes hylaeformis* on the basis of a single specimen from Roque, *Dept. San Martín*, Peru, and except for Bokermann's (1958) proposal of a replacement name (*E. melini*), no primary literature has accumulated for the species. Melin's description is precise and provides no evidence to permit a distinction of *Hylodes hylaeformis* from *E. ockendeni* which is now known to occur in the Río Huallaga drainage; in the absence of differences, *E. melini* (and *H. hylaeformis*) is added to the synonymy of *E. ockendeni*.

Borys Malkin secured a long series of *E. ockendeni* at Cusuime, Río Cusuime, *Prov. Morona-Santiago*, Ecuador, 320 m. The frogs are remarkable for their small size. Specimens from southern Colombia, northern Amazonian Ecuador, and eastern, central, and southern Peru are significantly larger than those from southern Amazonian

TABLE 1

SIZES OF *Eleutherodactylus ockendeni*

(First row gives range of SVL in millimeters and sample size; second row gives mean \pm 2 standard errors.)

	Males	Females
Northern Ecuador ^a	17.9–21.3 (18) 19.4 \pm 0.5	24.6–31.1 (37) 27.2 \pm 0.5
Cusuime, Ecuador	15.3–19.3 (4) 17.3 \pm 1.0	22.2–24.7 (18) 23.4 \pm 0.3
Amazonian Peru	16.9–21.2 (3) 19.1	24.6–31.5 (12) 28.0 \pm 1.4

^aCrump (1974) reported slightly smaller examples from Santa Cecilia. [10 males 17.0–21.0 (\bar{x} = 18.8), 10 females 24.0–28.0 (\bar{x} = 26.3) mm. SVL.] The 55 examples reported here are from other localities.

Ecuador (table 1). The variation is inexplicable.

Eleutherodactylus orphnolaimus Lynch

Eleutherodactylus orphnolaimus Lynch, 1970, p. 221 (type-locality, Lago Agrio, Prov. Napo, Ecuador, 330 m.; holotype, KU 125332, obtained May 7, 1969 by Thomas H. Fritts).

One additional specimen (USNM GOV 8896, from just below Montalvo, Prov. Pastaza, Ecuador) provides the second record of the rarest species of eleutherodactyline frog in the Amazon Basin. The specimen is a gravid female 24.8 mm. SVL.

Eleutherodactylus paululus Lynch

Eleutherodactylus paululus Lynch, 1974, p. 6 (type-locality, Lago Agrio, Prov. Napo, Ecuador, 330 m.; holotype, KU 126209, obtained May 12, 1969 by William E. Duellman).

Two additional specimens have been found: USNM JAP 9202, from Don Tomás, 5 km. S Montalvo, Prov. Pastaza, and USNM JAP 9197, from the Río Rutuno, a tributary of the Río Bobonaza, Prov. Pastaza, Ecuador. These provide the fifth and sixth localities for this dwarf member of the *unistrigatus* group (nine males 13.6–17.1 [\bar{x} = 15.0], four females 16.5–19.4 [\bar{x} = 18.0] mm. SVL).

TABLE 2

GEOGRAPHIC VARIATION IN SIZE OF *Eleutherodactylus peruvianus*

(First line gives range of SVL in millimeters and sample size; second line gives mean \pm 2 standard errors.) Data for *E. conspicillatus* allow comparison

Species, locality	Males	Females
<i>Eleutherodactylus conspicillatus</i>		
Amazonian Ecuador	23.2–30.1 (29) 27.3 \pm 0.6	34.8–48.8 (19) 40.2 \pm 1.7
<i>Eleutherodactylus peruvianus</i>		
Igarapé Belém, Brasil	23.3–27.3 (21) 25.2 \pm 0.5	32.7–37.2 (13) 35.7 \pm 0.8
Cusuime, Ecuador	27.3–31.6 (16) 30.0 \pm 0.6	38.9–44.2 (7) 41.3 \pm 1.5
Peru (Bassler collection)	26.1–30.0 (8) 28.1 \pm 0.9	36.0–42.5 (9) 39.1 \pm 1.6

Eleutherodactylus peruvianus (Melin)

Hylodes peruvianus Melin 1941, p. 43 (type-locality, Roque, Depto. San Martín, Peru; holotype, GNM 490, obtained in July 1925 by Douglas Melin).

As mentioned above (account of *E. conspicillatus*), recognition of *E. peruvianus* as distinct from *E. conspicillatus* is done with little supportive data (different color patterns and anticipated sympatry). In spite of the apparent diffuse zone of sympatry in Amazonian Peru, the two may prove to be geographic variants. Some size variation is apparent within the distribution area of *E. peruvianus* (table 2). *Eleutherodactylus peruvianus* is a lowland forest frog over most of its distribution but invades moderate altitudes in southern Colombia, northern Ecuador, and probably also in Peru, surrounding the major distribution area of *E. conspicillatus* on the western, southern, and eastern fronts (fig. 4).

The lowland populations of the two are distinguished as follows:

Eleutherodactylus conspicillatus

- (1) face dark brown (no canthal streak or labial bars);

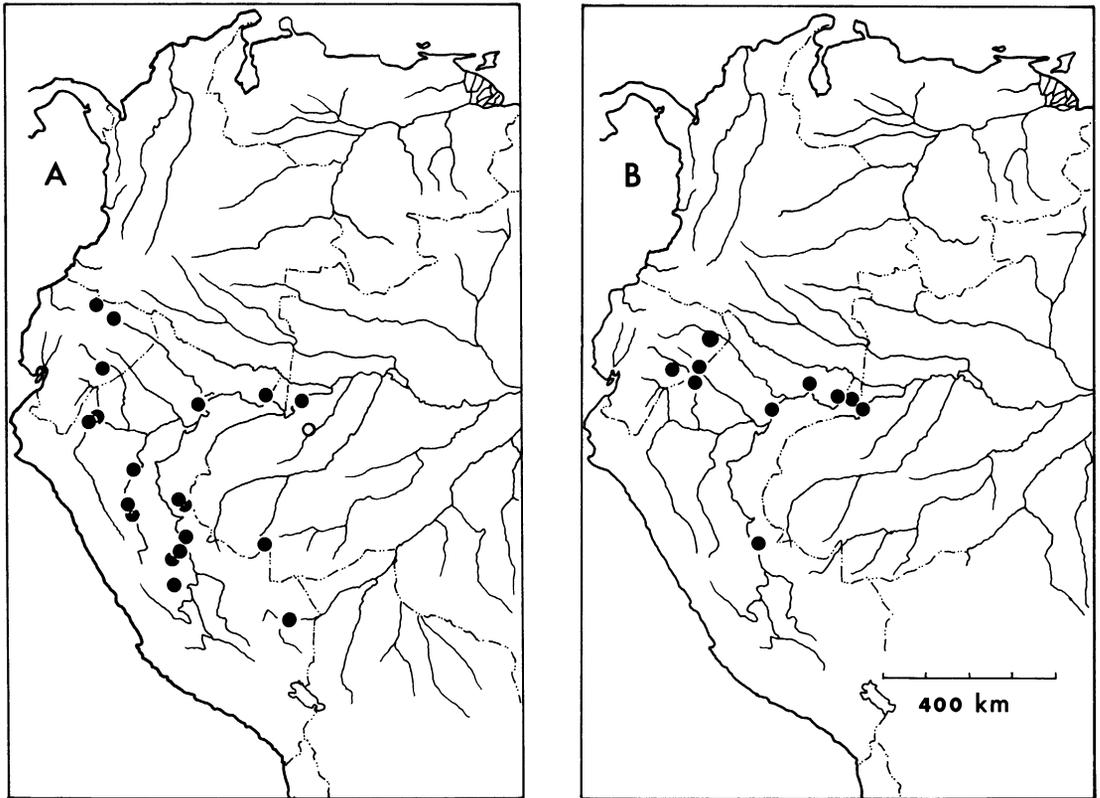


FIG. 4. (A) Distribution of *Eleutherodactylus peruvianus*; the open circle is a literature record. (B) Distribution of *E. malkini*.

- (2) throat usually white, stippled with brown in some large females;
- (3) belly immaculate;
- (4) spots on posterior thigh small (usually smaller than thumb pad);
- (5) underside of shank not spotted.

Eleutherodactylus peruvianus

- (1) canthal streak and frequently labial bars visible through brown wash on face;
- (2) throat usually stippled with brown, heaviest in males, which sometimes have dark gray throats;
- (3) belly frequently spotted (especially in males);
- (4) spots on posterior thigh larger than thumb pad;
- (5) underside of shank tan with cream spots.

The populations found on the Amazonian slopes of the Andes in Colombia and Ecuador are discussed by Lynch and Duellman (1980). Specimens from the lowlands include the following: BRAZIL, *Terr. Amazonas*: Igarapé Belém, near Rio Solimões (AMNH 96903–97042). ECUADOR, *Prov. Morona-Santiago*: Ashura village on Río Macuma, 10 km. above Río Morona, 300 m., (AMNH 94656–78); Cusuime, Río Cusuime, 320 m. (AMNH 93583–655). PERU, *Depto. Amazonas*: headwaters of Río Caterpisa, 457 m. (AMNH 42061); mouth of Río Cenipa (AMNH 42775, 43101); mouth of Río Santiago (AMNH 42041, 42093, 42118, 42749, 42973, 43483); *Depto. Huánuco*: Río Lullapichis, 4 to 5 km. upstream from Río Pachitea, Finca Panguana, 200 m. (KU 154835–47, 171867–76); S slope Serranía Sira, 690 m. (KU 154848–52); *Depto. Junín*: Chauncha-

mayo (AMNH 42284, 42919); *Depto. Loreto*: Balta, Río Curanja, 300 m. (LSUMZ 26070–79); Cashiboya (AMNH 42069); Iquitos (AMNH 42085, 42443); lower Río Aquaytia (AMNH 43321); Río Cashiboya, Ollanta (AMNH 42300); mouth of Río Contaya (AMNH 42992); Yagua village, headwaters of Río Loretoyacu (AMNH 96303–30); headwaters of and upper Río Utoquinia (AMNH 42242, 43310, 43374); Roaboya (AMNH 42042, 43521); Tacsha Huachiyacu, Río Morona (AMNH 43406); *Depto. Madre de Dios*: Cocha Cachu, Río Manú between Río Panagua and Río Cachiri, 400 m., (KU 154856–57); Manú, 365 m. (KU 154853–55); *Depto. San Martín*: Achinamisa, Río Huallaga, (AMNH 42596); Chasita, Río Huallaga (AMNH 43206); Río Mixiollo (AMNH 42903–04); Tocachi, 457–781 m. (AMNH 42719–20, 42722); “eastern Perú” AMNH 43276).

Eleutherodactylus pseudoacuminatus
Shreve

Eleutherodactylus pseudoacuminatus Shreve, 1935, p. 218 (type-locality, Sarayacu, Prov. Pastaza, Ecuador; holotype, MCZ 19948, obtained in 1933 by O. C. Felton).

Aside from Shreve's (1935) record from Sarayacu and those of Crump (1974) and Duellman (1978a) from Santa Cecilia, Prov. Napo, both in Amazonian Ecuador, no other primary references to this small frog exist. I have examined 44 specimens from localities in Napo Prov. (Lago Agrío, Puerto Libre, Puerto Ore, and Santa Cecilia), one in Pastaza Prov. (Sarayacu), and one in Colombia (20 km. SSE Mocoa, Intend. Putumayo, 560 m., AMNH 83950). The known altitudinal range is 330–570 m. Adults are small, 15 males are 12.7–17.6 (\bar{x} = 15.4) mm. and 21 females are 18.1–22.4 (\bar{x} = 19.9) mm. SVL.

Eleutherodactylus quaquaversus Lynch

Eleutherodactylus quaquaversus Lynch, 1974, p. 9 (type-locality, S slope of Cordillera del Due above Río Coca, Prov. Napo, Ecuador, 1150 m.; holotype, KU 123745, obtained August 3, 1968 by William E. Duellman and Stephen R. Edwards).

I have examined 170 specimens from 20 localities in eastern Ecuador at elevations between 320 and 1830 m. *Eleutherodactylus quaquaversus* is primarily distributed above 1000 m. but extends into the lowlands along the Río Aguarico in Napo Province (as low as Santa Cecilia [340 m.] where it is uncommon). Borys Malkin found a single specimen (AMNH 93656) at Cusuime in Morona-Santiago Province at 320 m. I think my earlier statement (Lynch, 1974) that it is an upland replacement for *E. ockendeni* remains reasonable. Too few lowland examples are known to see if size varies with altitude; specimens from 1000–1800 m. are moderate-sized—males 19.6–22.5 (\bar{x} = 20.7, N = 29) mm., females 24.6–31.3 (\bar{x} = 27.3, N = 20) mm. SVL.

Eleutherodactylus sulcatus (Cope)

Hylodes sulcatus Cope, 1874, p. 126 (type-locality, Nauta, Depto. Loreto, Peru; holotype, ANSP 11385).

Hylodes macrocephalus Peracca, 1904, p. 29 (type-locality, Valle Santiago, Prov. Morona-Santiago, Ecuador; lectotype, larger specimen of MZS 2930 [two individuals], obtained by E. Festa [lectotype designated by Lynch, 1975b, p. 42]). Placed in synonymy by Lynch (1975b).

Ctenocranius koki Melin, 1941, p. 45 (type-locality, Taracuá, Río Uaupés, Terr. Amazonas, Brazil; holotype, GNM 494, obtained April 1924 by D. Melin). Placed in synonymy by Lynch (1975b).

I (Lynch, 1975b) reported specimens from western Brazil, eastern Ecuador, and eastern Peru. I have now seen 146 specimens at elevations up to 1100 m. (KU 154800, S slope of Serranía Sira, Depto. Huánuco, Peru). Borys Malkin secured specimens at Igarapé Belém, Terr. Amazonas, Brazil, Santa Rosa de Sucumbios, Río San Miguel, Intend. Putumayo, Colombia, 400 m., Cusuime, Río Cusuime, Prov. Morona-Santiago, Ecuador, 320 m., and Estirón (Río Ampiyacu) and the Yagua Indian village (headwaters of Río Loretoyacu), Depto. Loreto, Peru. These records slightly extend the distribution area mapped by Lynch (1975b). Contrary to Lynch's statement of size, *E. sulcatus* fe-

males mature at SVL of approximately 42 mm.

Eleutherodactylus trachyblepharis
(Boulenger)

Hylodes trachyblepharis Boulenger, 1918, p. 429 (type-locality, El Topo, Prov. Tungurahua, Ecuador, 1280 m.; syntypes, BM 1912.11.1.58–60 [re-registered as 1947.2.17.2–4], collected by M. G. Palmer).

Eleutherodactylus trachyblepharis has not been reported since its description (Boulenger, 1918). The frog is not common in collections; I have seen 69 specimens from the following Ecuadorian localities: *Prov. Morona-Santiago*: Cusuime, Río Cusuime, 320 m.; *Prov. Pastaza*: Abitagua, 8 km. NW Mera, 1200–1300 m.; Canelos, 530 m.; Mera, 1140 m.; Puyo, 1000 m.; 5 km. SSE Puyo, 975 m.; Río Alpayacu, 1 km. E Mera, 1080–1100 m.; Sarayacu, 400 m.; Veracruz, 950 m.; 10 km. ESE Veracruz; *Prov. Tungurahua*: El Topo, 1280 m.; Río Negro, 1260 m. Native collectors secured the two Cusuime specimens (AMNH 93668–69) for Borys Malkin. In part, the relative rarity of *E. trachyblepharis* is probably due to its small size (20 males 12.1–15.8 [\bar{x} = 13.8] mm. SVL, 19 females 15.8–19.2 [\bar{x} = 17.2] mm. SVL). I collected 39 of the 69 known specimens in 1968. The frogs were collected at night as they perched on low herbs within 20 cm. of the forest floor. Specimens were not found in my normal search zone (0.5–2.0 m. above the forest floor); in that stratum, the larger *E. croceoinguinis* was especially abundant.

Eleutherodactylus variabilis Lynch

Eleutherodactylus variabilis Lynch, 1968, p. 129 (type-locality, Limón Cocha, Prov. Napo, Ecuador, 300 m.; holotype, KU 99011, obtained June 19, 1965 by Charles M. Fugler).

This species is now known from 378 specimens from 10 localities in the upper Amazon Basin in Colombia, Ecuador, and Peru at elevations between 100 and 1000 m. (fig. 1). The localities are as follows: COLOMBIA *Com. Amazonas*: Puerto Nariño; *Intend.*

Putumayo: Puesto de Bombeo Guamez, 1000 m.; Santa Rose de Sucumbios, Río San Miguel, 400 m. ECUADOR, *Prov. Napo*: Coca, 320 m.; Limón Cocha, 300 m.; Loreto; Puerto Libre, Río Aguatico, 570 m.; Santa Cecilia, 340 m. PERU, *Depto. Pasco*: Nevati, Oxapampa, 275 m. Where *E. variabilis* occurs it is a common forest-edge species (Duellman, 1978a); its apparent absence in southern Amazonian Ecuador is inexplicable. *Eleutherodactylus variabilis* is small: males 13.7–17.5 (\bar{x} = 16.3, N = 26), females 20.0–25.3 (\bar{x} = 22.8, N = 30) mm. SVL.

Eleutherodactylus ventrimarmoratus
(Boulenger)

Hylodes ventrimarmoratus Boulenger, 1912, p. 187 (cotypes, BM 1911.11.1.51–53 [re-registered as 1947.2.15.74–76], from El Topo, Prov. Tungurahua, Ecuador, 1280 m., collected by M. G. Palmer; and BM 1911.12.2.77 [re-registered as 1947.2.15.73], from Chanchamayo, Depto. Junín, Peru, obtained by G. Shunke).

Eleutherodactylus ventrivittatus Andersson, 1945, p. 33 (type-locality, Abitagua [=Abitagua], Río Pastaza, Prov. Tungurahua, Ecuador; holotype, SHNM [not examined], obtained in September 1937 by William Clarke-Macintyre).

Most records of *E. ventrimarmoratus* are from elevations of 1000–1300 m. I have examined the following from the Amazon lowlands: ECUADOR, *Prov. Morona-Santiago*: Ashura village on Río Macuma, ca. 10 km. above Río Morona, 300 m. (AMNH 94685–86). PERU, *Depto. Amazonas*: headwaters of Río Caterpisa, Manseriche range, 460 m. (AMNH 42435); *Depto. Huánuco*: Finca Panguana, Río Lullapichis, 4 to 5 km. upstream from Río Pachitea, 200 m. (KU 154801); *Depto. Loreto*: Río Utoquinia (AMNH 43376); Tipishca, opposite Contamana (AMNH 42938); *Depto. Madre de Dios*: Cocha Cachu, Río Manú between Río Panagua and Río Cachiri, 400 m. (KU 154803); Manú, 365 m. (KU 154802). In addition to these records, Lutz and Kloss (1952) reported this distinctive frog from Terr. Amazonas in Brazil; they suggested that *E. ventrivittatus* might be conspecific with *E. ventrimarmoratus*. I concur.

The relationships of *E. ventrimarmoratus* are probably with *E. diadematus*. Both have large digital pads, relatively coarse and tubercular skin on the dorsum, and relatively short legs. *Eleutherodactylus ventrimarmoratus* has bold red and black marbling on the venter and is smaller: eight males 17.8–25.5 (\bar{x} = 21.8) mm., nine females 33.3–43.8 (\bar{x} = 36.9) mm. SVL.

Eleutherodactylus vilarsi (Melin)

Hylodes vilarsi Melin, 1941, p. 45 (type-locality, Taracua, Rio Vaupes, Terr. Amazonas, Brazil; lectotype, larger specimen in GNM 491, obtained on March 5, 1924 by A. Vilars [lectotype designated by Lynch, 1975a, p. 9]).

Hylodes roseus Melin, 1941, p. 47 (type-locality, Rio Vaupes, north of Rio Japu, Terr. Amazonas, Brazil; holotype, GNM 492, obtained by natives). Placed in synonymy by Lynch (1975a).

Eleutherodactylus conspicillatus ileamazonicus Rivero, 1961, p. 63 (type-locality, Temiche, Mt. Marahuaca, Terr. Amazonas, Venezuela, 1234 m.; holotype, MCZ 30397, obtained in May 1950 by Juan A. Rivero). Placed in synonymy by Lynch (1975a).

Eleutherodactylus brachypodius Rivero, 1961, p. 61 (type-locality, upper Cunucunuma region, Terr. Amazonas, Venezuela; holotype, MCZ 28568, obtained in May or June 1950 by Juan A. Rivero). Placed in synonymy by Lynch (1975a).

Eleutherodactylus rosmelinus Gorham, 1966, p. 98 (replacement name for *Hylodes roseus* Melin nec *Hylodes roseus* Boulenger).

I (Lynch, 1975a) reported *E. vilarsi* from 13 localities in Brazil, Colombia, and Venezuela. I have examined 71 specimens from 20 localities. The only significant new record is AMNH 96339–40, Yagua Indian village at headwaters of Río Loretoyacu, Depto. Loreto, Peru. The distribution area of *E. vilarsi* is peripheral to that of most Amazonian *Eleutherodactylus*. It is comparable in size (males 25.4–31.5 mm., females 34.1–43.2 mm. SVL) to *E. conspicillatus*.

Eleutherodactylus zeuctotylus
Lynch and Hoogmoed

Eleutherodactylus zeuctotylus Lynch and Hoogmoed, 1977, p. 432 (type-locality, W slope, Vier

Gebroeders Mountain, Sipaliwini, Nickerie District, Suriname; holotype, RMNH 17701, obtained February 7, 1970 by M. S. Hoogmoed).

This recently described species is abundant in the wet rainforests of northeastern South America (Lynch and Hoogmoed, 1977) but is also known from two western hylaea localities in Brazil: Serra da Neblina (near the Brazil-Colombia-Venezuela border), Terr. Amazonas (WCAB 34157); and Cachoeira Santo Antonio (just upstream from Puerto Vehlo), Estado Rondonia (MZUSP [2], USNM [2]). Both upper hylaea localities are in the wetter Amazon and it seems judicious to assume that the distributional hiatus (800 or 1200 km.) may not be real although the collections of *E. fenestratus* and *E. vilarsi* in the intervening areas demonstrate that collectors of eleutherodactyline frogs have worked those areas. These distributional hiatuses do address our ignorance of the distribution of small and/or secretive Amazonian frogs.

OTHER AMAZONIAN
ELEUTHERODACTYLUS

In addition to the 24 species discussed above, *E. marmoratus* (Boulenger) may extend westward from the Guianas. M. S. Hoogmoed is currently studying some material from northern Amazonia that may prove to be *E. marmoratus*. There are some poorly preserved specimens in Borys Malkin's collections from Igarapé Belém (Brazil), the headwaters of the Río Loretoyacu (Peru), and Cusuime (Ecuador) that may represent undescribed species. The conditions of the specimens prevent identification at present.

Some species now known from cloud forests on the Amazonian slopes of central and southern Peru may invade the adjacent lowlands. Duellman (1978b, 1978c) reported some new taxa ranging from lowland localities well up into cloud forests. *Eleutherodactylus platydactylus* (Boulenger) may also invade the lowlands; most locality records have uncertain altitudinal limits and I have presumed the localities to be in cloud forests.

SPECIES IDENTIFICATION

The 24 Amazonian *Eleutherodactylus* belong to four species groups recognized by Lynch (1976). *Eleutherodactylus nigrovittatus* is a member of the *discoidalis* group and is distinguished from the other 23 species in having pointed discs and pads on the digits (frogs of this group have smooth skin in the venter and the first finger is longer than the second). *Eleutherodactylus sulcatus* is a member of the *sulcatus* group and is readily distinguished in having a broad head (head width > 45% SVL), flared lips, cranial crests, and in lacking discs and pads on the fingers. The *fitzingeri* and *unistrigatus* species group include more species, as follows:

KEY TO AMAZONIAN FROGS OF THE FITZINGERI GROUP

The *fitzingeri* group is represented in the Amazon Basin by seven species as well as two others which are extra-limital (*E. chias-tonotus* and *E. gutturalis* are species of the Guiana lowlands). *Eleutherodactylus conspicillatus*, *E. fenestratus*, *E. lanthanites*, *E. malkini*, *E. peruvianus*, *E. vilarsi*, and *E. zeuctotylus* occur in the Amazon Basin. All have smooth skin on the venter and the first finger is longer than the second (as in *E. nigrovittatus*) but these frogs also have broad, apically rounded digital pads and the discs are broader than long.

- 1. Posterior surfaces of thighs brown without prominent pale spots or marbling 2
- Posterior surfaces of thighs bearing prominent pale spots (small or large) or cream reticulation 5
- 2. Venter and throat gray (without darker markings) 3
- Throat bearing brown, black, or gray mottling or spots, venter creamy white without dark markings 4
- 3. Palmar tubercle round *E. zeuctotylus*
- Palmar tubercle bifid (partially divided distally) *E. vilarsi*
- 4. Throat bearing median pale streak; prominent tubercle on heel *E. lanthanites*
- Throat heavily stippled or spotted (lacking me-

- dian streak); no enlarged tubercle on heel ..
..... *E. fenestratus*
- 5. Toe webbing enclosing basal subarticular tubercles *E. malkini*
- Toes not webbed (or if basal webbing perceived, not enclosing basal subarticular tubercles between toes I-IV) 6
- 6. Large cream spots on underside of shank; canthal stripe visible; gray (or darker) spots on throat and breast *E. peruvianus*
- Underside of shank unicolor; canthal stripe not visible; throat and breast usually immaculate *E. conspicillatus*

NOTES AND KEY TO AMAZONIAN FROGS OF THE UNISTRIGATUS GROUP

Fifteen species of the *unistrigatus* group occur in the Amazon Basin: *E. acuminatus*, *E. altamazonicus*, *E. carvalhoi*, *E. croceoguinis*, *E. diadematus*, *E. lacrimosus*, *E. martiae*, *E. ockendeni*, *E. orphnolaimus*, *E. paululus*, *E. pseudoacuminatus*, *E. quaquaversus*, *E. trachyblepharis*, *E. variabilis*, and *E. ventrimarmoratus*. Identification of these frogs is often difficult because some are so small as to be taken for immature individuals (e.g., *E. paululus* and *E. trachyblepharis*). Many are easily recognized in life because they have a distinctive color pattern which is lost in preservative (e.g., *E. acuminatus* is green with dark canthal-supratympanic stripes, *E. altamazonicus* has red and black spotting and barring on the concealed surfaces of the hind leg, *E. carvalhoi* has a yellow spot in the groin, *E. croceoguinis* has a pair of orange spots in the groin, *E. variabilis* has a yellow area in the groin edged with black (sometimes confluent across the belly), and *E. ventrimarmoratus* has bold black and red marbling on the venter as well as on the concealed surfaces of the hind limbs).

All members of the *unistrigatus* group have areolate (granular) skin on the venter and short first fingers (shorter than second). All of these species have digital pads and discs although those of *E. lacrimosus*, *E. trachyblepharis*, and *E. variabilis* are comparatively narrow.

My preferred characteristics for species identification are qualitative characteristics.

Several taxa are readily distinguished on the bases of snout shape, skin texture, distinctness of the tympana, and presence or absence of small tubercles on the upper eyelid, heel, and outer edge of the tarsus. However, differences in concentrations of preservatives and degree of desiccation can make identification very difficult. Although none of these species is earless, several have concealed tympana; desiccation causes the skin on the side of the head to contract and the tympanic annulus may become quite distinct. Desiccation likewise may distort the digital pads and narrow fringes on the digits as well as render small conical tubercles less (or sometimes more) distinct than is the case in a well-preserved example. Misidentifications are frequently easily detected by comparing the sex and size of an example against that given in the species accounts above; species having similar morphologies (as cadavers) are often quite dissimilar in size.

- 1. No canthal stripe but labial bars present .. 2
Canthal stripe evident, or if not, entire face darkened and labial bars not evident ... 3
- 2. Posterior surface of thigh uniform brown; tubercles, if present, on eyelid and heel not prominent *E. ockendeni*
Posterior surface of thigh reddish, reticulated with brown; prominent tubercles (conical) on eyelid and heel *E. quaquaversus*
- 3. Tympana concealed beneath skin 4
Tympana distinct, annulus not concealed beneath skin 10
- 4. Groin and concealed surfaces of limbs boldly pattered with light and dark bars or spots 5
Groin and concealed surfaces of limbs not marked with contrasting pattern 6
- 5. Venter marbled light and dark; larger frogs (males 17.8–25.5 mm., females 33.3–43.8 mm. SVL) *E. ventrimarmoratus*
Venter and throat dark gray to black; smaller frogs (males 14.4–23.1 mm., 23.6–33.9 mm. SVL) *E. altamazonicus*
- 6. One or two colorless (yellow or orange in life) spots (as large as digital pad) in groin .. 7
Groin lacking distinct round spots, unicolor or diffusely reticulate 8
- 7. One spot in groin (yellow in life)
..... *E. carvalhoi*
Two spots in groin (orange in life)
..... *E. croceingunis*

- 8. Snout protruding in lateral profile; skin of dorsum shagreened; no labial bars
..... *E. acuminatus*
Snout rounded or truncate, skin not shagreened; labial bars present 9
- 9. Concealed thigh and groin brown; skin of dorsum bearing low warts; snout rounded in lateral profile *E. martiae*
Concealed thigh and groin pale with diffuse marbling; skin of dorsum smooth; snout truncate in lateral profile; tympanum visible through skin .. *E. pseudoacuminatus*
- 10. Digital pads large, those of outer fingers much larger than tympanum 11
Digital pads narrow, those of outer fingers not as large as typanum 12
- 11. Snout protruding, bearing large papilla at tip; conical tubercles on upper eyelid; concealed limb surfaces unicolor
..... *E. orphnolaimus*
Snout rounded; no conical tubercle on eyelid; concealed thigh surfaces and venter cream marbled with brown *E. diadematus*
- 12. Snout protruding in lateral profile
..... *E. paululus*
Snout rounded or truncate in laterae profile 13
- 13. Snout rounded in dorsal view
..... *E. lacrimosus*
Snout subacuminate to acuminate in dorsal view 14
- 14. Venter spotted with brown or black; colorless area in groin (yellow in life) edged with black or brown *E. variabilis*
Venter not spotted, no colorless area in groin edged with black 15
- 15. Posterior surfaces of thighs uniform brown; head longer than wide
..... *E. trachyblepharis*
Posterior surfaces of thighs pale, not uniform brown; head wider than long or as wide as long *E. pseudoacuminatus*

DISCUSSION

Contrary to Lutz's (1972) statement and Heyer's (1976) similar implication, the frogs of the Amazonian hylaea are not uniformly distributed. Species of *Eleutherodactylus* are clumped in upper Amazonia (fig. 5) in the area of the Río Marañon, Napo, and Ucayali (as are many other amphibian species [Lynch, 1979]). The comparatively depauperate *Eleutherodactylus* fauna of most of Amazonia (essentially populated by one or more of the following: *E. fenestratus*, *E. lac-*

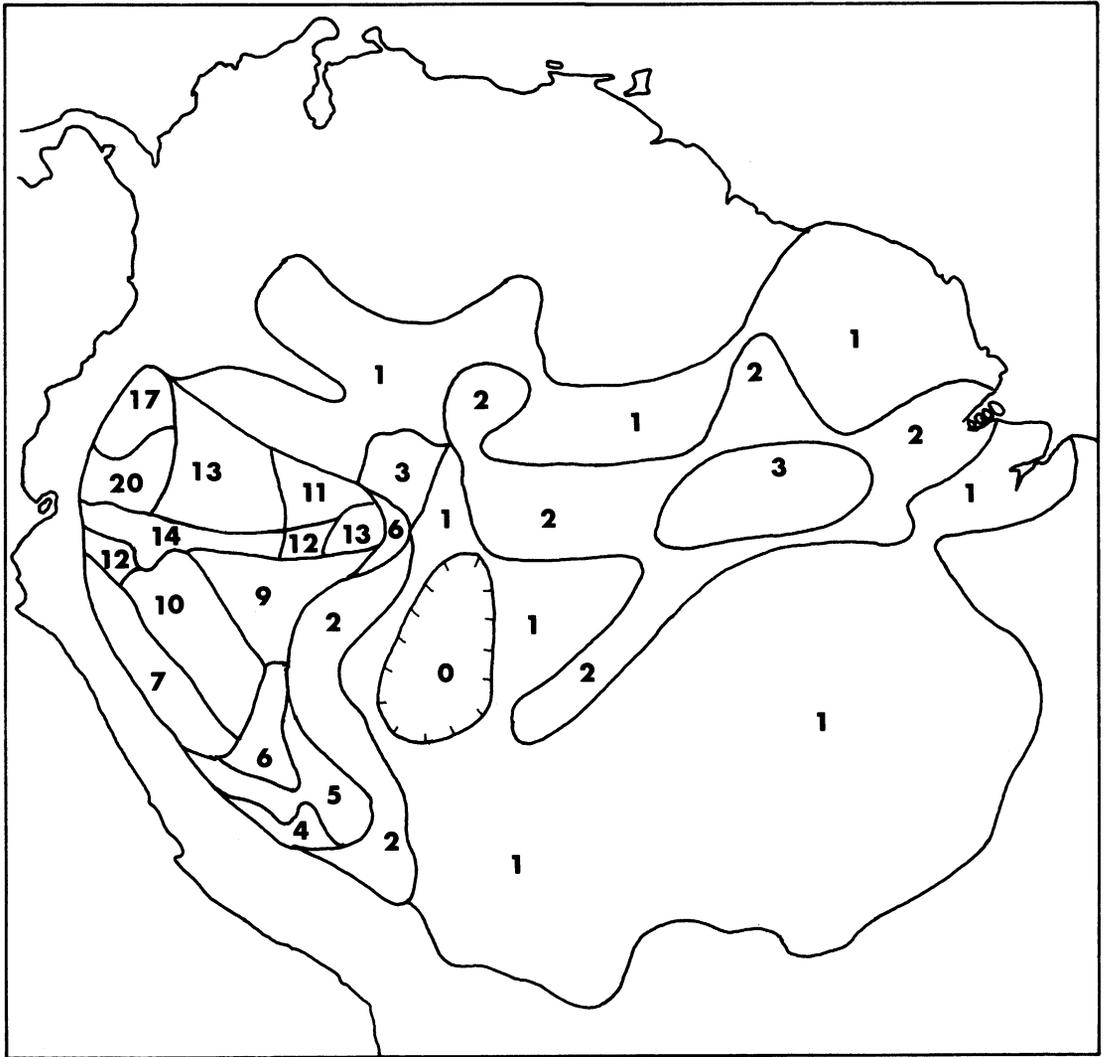


FIG. 5. Species density map for Amazonian *Eleutherodactylus*.

rimosus, *E. vilarsi*, and *E. zeuctotylus*—but never more than three of these) probably is real.

Lynch (1979) suggested that the low species density was a function of seasonal rainfall (monsoon climates). The reduction of numbers along the southwestern border of Amazonia is probably not real (see reports by Duellman, 1978b, 1978c, and Duellman and Toft, 1979).

The richest assembly of *Eleutherodactylus*

in the Amazon Basin is that found in east-central Ecuador (between the Río Napo and Río Santiago-Río Zamora). All Amazonian species except *E. fenestratus*, *E. variabilis*, *E. vilarsi*, and *E. zeuctotylus* occur in this area and *E. variabilis* may yet be found there. The richest single site is Borys Malkin's collection at Cusuime, on the Río Cusuime, ca. 60 km. SE Macas, Morona-Santiago Prov., Ecuador, 320 m. (*E. acuminatus*, *E. altamazonicus*, *E. croceoinguinis*, *E. dia-*

dematus, *E. lacrimosus*, *E. lanthanites*, *E. malkini*, *E. martiae*, *E. nigrovittatus*, *E. ockendeni*, *E. peruvianus*, *E. quaquaversus*, *E. sulcatus*, and *E. trachyblepharis*—14 species) although 15 species have been collected in the vicinity (within a 5 km. radius) of Puyo, Pastaza Prov., 1000 m. (the above minus *E. malkini* but also including *E. conspicillatus* and *E. ventrimarmoratus*).

To the north of this 20–21 species area we find the same fauna except that *E. carvalhoi*, *E. malkini*, *E. trachyblepharis*, and *E. ventrimarmoratus* drop out (but *E. variabilis* is abundant). The best collected localities are Lago Agrio and Santa Cecilia (16 species, see Duellman's 1978a account). Borys Malkin found nine of these at Santa Rosa de Sucumbios, Intend. Putumayo, Colombia (*E. acuminatus*, *E. altamazonicus*, *E. croceoinguinis*, *E. lanthanites*, *E. martiae*, *E. nigrovittatus*, *E. ockendeni*, *E. sulcatus*, and *E. variabilis*). To the east of this pair of species-rich areas, several species drop out (viz., *E. croceoinguinis*, *E. diadematus*, *E. orphnolaimus*, *E. paululus*, *E. pseudoacuminatus*, *E. quaquaversus*, and *E. trachyblepharis*). Yet farther east, *E. conspicillatus* and *E. martiae* drop out. Malkin's collection from the headwaters of the Río Loretoyacu, Depto. Loreto, Peru, includes *E. altamazonicus*, *E. carvalhoi*, *E. lanthanites*, *E. malkini*, *E. nigrovittatus*, *E. ockendeni*, *E. peruvianus*, *E. sulcatus*, and *E. vilarsi*.

The belt of slightly richer faunas to the south of the 20-13-11 series reflects the overlapping of ranges of the northern *E. lanthanites* and *E. nigrovittatus* and the southern *E. ventrimarmoratus*. Below the belt (areas with 7-10-9 species) the fauna consists of *E. acuminatus* and *E. altamazonicus* (not in western area), *E. carvalhoi* (NE only), *E. conspicillatus*, *E. fenestratus* (extreme S only), *E. malkini* (not in western area), *E. martiae*, *E. ockendeni*, *E. peruvianus*, *E. sulcatus*, *E. variabilis*, and *E. ventrimarmoratus*. The southwesternmost areas harbor some or all of the following: *E. conspicillatus*, *E. fenestratus*, *E. malkini*, *E. ockendeni*, *E. sulcatus*, and *E. ventrimarmoratus*.

One of the most intriguing questions

prompted by this distributional summary is "how do so many congeneric species manage to co-exist?" Although many man-months of fieldwork have been expended at Santa Cecilia in Napo Province, Ecuador, the applicable data are largely anecdotal (Duellman, 1978a). Duellman's data suggest that two species are entirely terrestrial (*E. nigrovittatus* and *E. sulcatus*), two others equally terrestrial and on low vegetation (*E. conspicillatus* and *E. lanthanites*), and the remaining 12 arboreal. Of the 16 species, only *E. conspicillatus*, *E. lanthanites*, and *E. nigrovittatus* appear to be active by day. Duellman found *E. acuminatus* to be a food specialist (ants) but his data for the other 15 species suggest they are generalists (at least in terms of crude food categories—arthropod orders). Duellman (1978a) concluded that the amphibian and reptile fauna at Santa Cecilia existed in the absence of interspecific competition.

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