

THE *ELEUTHERODACTYLUS* OF THE *TAENIATUS* COMPLEX IN WESTERN COLOMBIA: TAXONOMY AND DISTRIBUTION

por

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Resumen

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Eleutherodactylus taeniatus previamente se confundió con otras especies del género establecidas en alturas moderadas; una de las especies nuevas está confinada a la parte norte de la Cordillera Occidental donde aparentemente sustituye a *E. ptochus*. La otra especie se encuentra en el altiplano antioqueño de la Cordillera Central, mientras que *E. taeniatus* se encuentra por debajo de los 1500m al norte del Chocó biogeográfico y en el Magdalena Medio. Actualmente se conocen siete especies de este complejo en la zona trans-andina de Colombia.

Palabras clave: *Eleutherodactylus* grupo *taeniatus*, Leptodactylidae, Nuevas especies, Distribución, Colombia.

Abstract

Eleutherodactylus taeniatus was confused previously with two other species found at moderate to intermediate elevations. One of the new species is confined to the northern part of the Cordillera Occidental where it apparently replaces *E. ptochus*. The other species is found on the Antioquian altiplano of the Cordillera Central. *Eleutherodactylus taeniatus* occurs at elevations below 1500 m in the northern part of the Chocó biogeographic and in the Magdalena Medio. Presently, seven species of this complex are known in trans-andean Colombia.

Key words: Colombia, *Eleutherodactylus*, Leptodactylidae, New species.

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Introduction

A complex of small, drab *Eleutherodactylus* termed the *frater* Assembly by Flores & Vigle (1994) has grown in number but remains a boring yet challenging complex of species. Perhaps the initial serious sorting out of the confusion was by Lynch (1980) who identified *E. frater* (Werner) as a small species found in the eastern piedmont of Colombia and *E. taeniatus* (Boulenger) as an element of the biogeographic Chocó. However, Lynch's *E. taeniatus* was a mixture of species largely grouped on the basis of size and two features of coloration: the posterior surfaces of the thighs are uniformly brown and the frogs lack a canthal stripe and labial bars anterior to the eyes (drawings in Lynch, 1980, 1998). These two features allow ready sorting of small *Eleutherodactylus* but may be irrelevant in organizing the species of this very diverse genus of frogs.

Here, we are not concerned with the cis-Andean species currently recognized in this assembly (or group) [*E. frater*, *E. incomptus* Lynch & Duellman (including *E. kirklandi* Flores), *E. librarius* Flores & Vigle, *E. martiae* Lynch, *E. ockendeni* (Boulenger), *E. quaquaversus* Lynch, or *E. pecki* Duellman & Lynch] except as concerns some character states of those taxa. This paper concerns the species distributed in the Caribbean and Pacific drainages of Colombia. Five species are recognized currently: *E. miyatai* Lynch from the western flanks of the Cordillera Oriental of Colombia, *E. ptochus* Lynch from the Serranía de los Paraguas and adjacent Risaralda in the Cordillera Occidental of Colombia, *E. suetus* Lynch & Rueda-A. from the eastern flanks of the northern part of the Cordillera Central, *E. taeniatus*, a species restricted to the lowland forests of eastern Panamá, the drainages of the Río Atrato and Río San Juan of western Colombia, and the middle Magdalena, and *E. viejas* Lynch & Rueda-A., a species of low and moderate elevations on each side of the Middle Magdalena. The reports of Lynch (1980) of *E. taeniatus* intermediate elevations of the northern parts of the Cordillera Central and Cordillera Occidental are based on material of species described herein.

Materials and methods

Terminology follows Lynch & Duellman (1997). In the following accounts, we use some abbreviations: E-N (eye to nostril distance), HW (greatest width of head), IOD (interorbital distance), SVL (snout-vent length).

Characters

Snout. Flores & Vigle (1994) summarized the distinguishing features for nine species but failed to note that snout length varies sexually (males have shorter snouts than do females, expressed as the ratio of E-N to eye length, Table 1). Round snouts (in dorsal view) occur in *E. ptochus*, *E. suetus*, and females *E. zophus* whereas all others have subacuminate snouts (Figure 1). In male *E. zophus*, the snout appears subacuminate (Figure 1) because the tip is pointed. Flores & Vigle (1994) considered *E. librarius* to have an acuminate snout but we record its state as subacuminate.

Flores & Vigle distinguished various taxa as having round (*E. frater*, *E. incomptus*, *E. miyatai*, and *E. pecki*) versus sharp canthus rostralis (five others including *E. taeniatus*). The prominence of a canthus rostralis is difficult to quantify because in none of these taxa is there a sharp break between the plane of the top of the snout and the loreal plane. Rather, one encounters a curved surface that is more or less rounded. Among the species from the Caribbean and Pacific drainages of Colombia, only *E. ptochus*, *E. suetus*, and *E. zophus* have distinctly rounded canthi rostrali – in the other species, the canthus is more or less distinct.

Frogs can also be distinguished based on the length of the snout (short versus long) and the associated head shape (round dorsally or subacuminate) but one must take care to note sexual differences. Additionally, there are obvious differences in the sizes of the digital disks and minor (easily overlooked) differences in the tuberculation of the tarsus. Lastly, some differences in body size and proportions emerge from the study of series (some have very short hindlimbs).

Sizes of digital disks and tarsal tuberculation. Although these frogs are very similar structurally to one another, some other minor structural differences are apparent when direct comparisons are made. As noted by Lynch & Rueda-A (1999), *E. viejas* has narrower disks on the fingers than do *E. miyatai* or *E. taeniatus*. *Eleutherodactylus paisa* (named herein) is like *E. viejas* whereas the other five trans-Andean species have larger finger disks (Figure 2).

Two species (*E. ptochus* and *E. taeniatus*) lack outer tarsal tubercles (or these are very poorly developed) whereas the other five species have a series of rounded tubercles along the outer edge of the tarsus. *Eleutherodactylus suetus* and *E. zophus* (Figure 3) have a single round inner tarsal tubercle in contrast to having

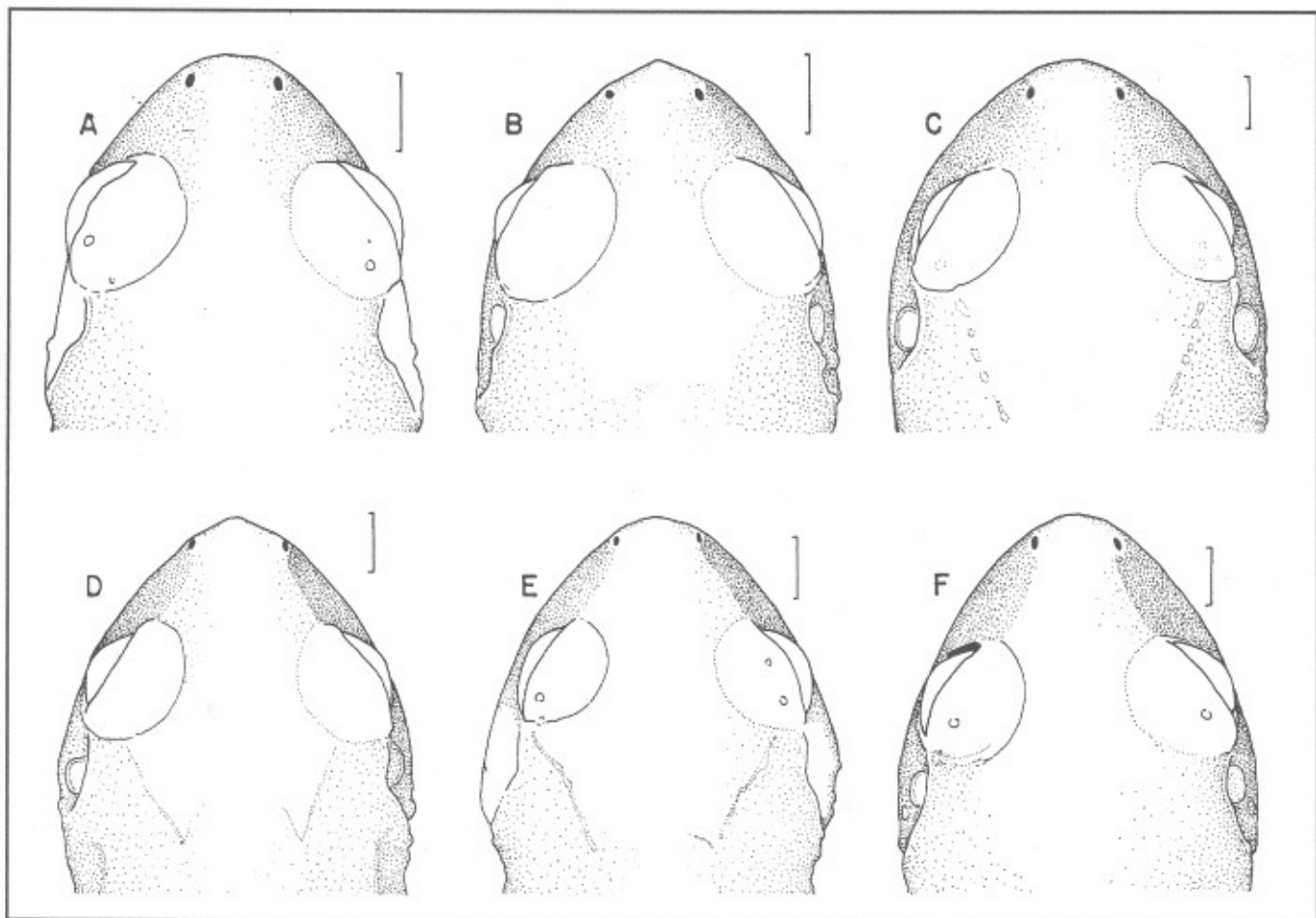


Figure 1. Dorsal views of heads of species of the *Eleutherodactylus taeniatus* complex. (A) *E. suetus*, ICN 41740, (B) *E. zophus*, male, ICN 20198, (C) *E. zophus*, female, ICN 20196, (D) *E. paisa*, ICN 9995, (E) *E. viejas*, ICN 42426, (F) *E. taeniatus*, ICN 31855. Scales equal 2 mm.

an elongated fold-like tubercle (Figure 3), the state seen in *E. miyatai*, *E. paisa*, *E. ptochus*, and *E. viejas*). *Eleutherodactylus taeniatus* differs from all of these in having two or three inner tarsal tubercles (Lynch, 1980).

Coloration: Although most of these frogs have uniformly brown posterior surfaces of the thighs (as preserved specimens), this description conceals three variations: (1) uniform brown surfaces, (2) brown surfaces but bearing small cream flecks, and (3) brown surfaces of the posterior surfaces enclosing large cream (yellow to orange in life) spots.

Sizes and proportions: Two species are small (*E. ptochus* and *E. suetus*) and each has a short snout, rounded in dorsal view. The other five species are all larger (their

largest juvenile females are the sizes of adult females of the small species) but the differences in sizes of adults of the five "large" species are not significant given the sample sizes available (Table 1). Three of the larger species differ significantly from the others in one aspect of proportions or another.

Eleutherodactylus miyatai differs from the other six species in having small tympani in females (and in lacking sexual dimorphism in tympanum size), *E. viejas* has significantly longer legs than seen in the other six species, and *E. zophus* has significantly shorter hindlegs than the other six species. In all seven, females have slightly wider heads than do males (usually significantly so) and in five species (excepting *E. miyatai* and *E. ptochus*), females

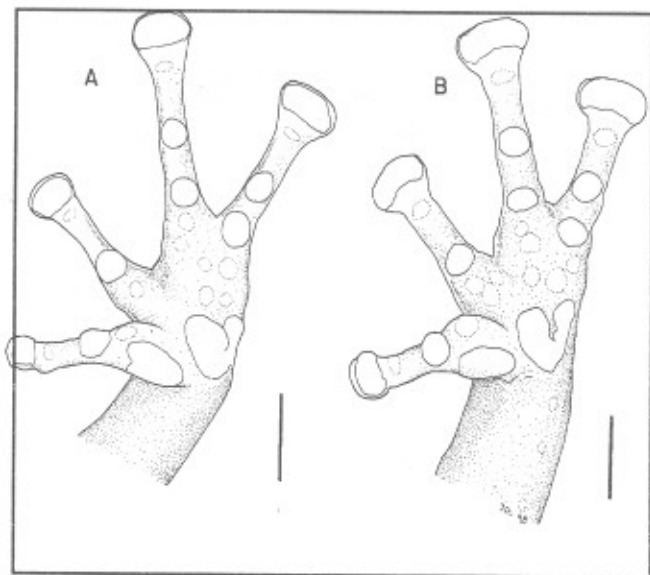


Figura 2. Palmar views of hands of *Eleutherodactylus paisa* (ICN 9993) and *E. zophus* (ICN 36046). Scales equal 2 mm.

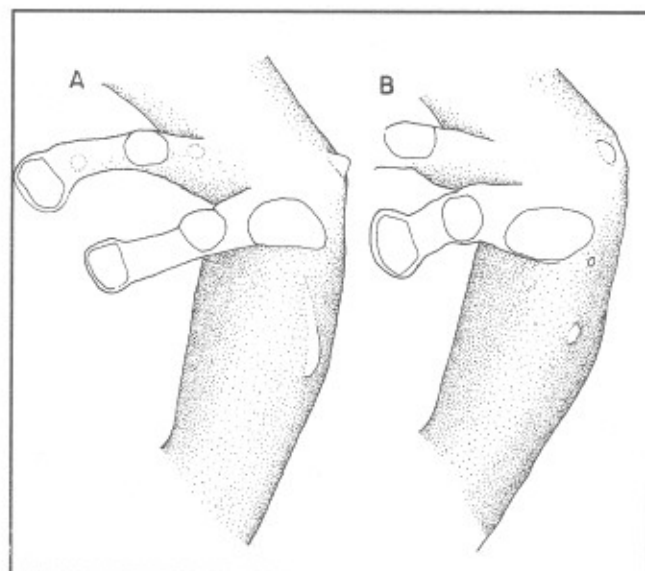


Figura 3. Ventral views of tarsi of *Eleutherodactylus paisa* and *E. zophus*.

have larger tympani than do males. The snout is longer in females than in males in all species although the differences for *E. suetus* are only marginally significant. Males usually have larger eyelid/IOD ratios than do females which we think reflects the broader IOD seen in females. However, the variances for this proportion are so great that little reliance can be placed in the "character".

Accounts of species

Eleutherodactylus miyatai Lynch

This species was described originally from the vicinity of Virolín, Santander (Lynch, 1984) but is now known to occur more widely along the western flanks of the Cordillera Oriental of Colombia at elevations between 1720 and 2440 m (Figure 4).

Eleutherodactylus paisa sp. nov.

Eleutherodactylus taeniatus (in part): Lynch, 1980: 183, 185, 187.

Holotype: Amphibian collection of the Instituto de Ciencias Naturales 9992, an adult female, one of a series collected by J. D. Lynch and P. M. Ruiz on 8 June 1981 (field number JDL 13028).

Paratopotypes: ICN 3551, ICN 9993-94 (adult females).

Type-locality: COLOMBIA, Departamento de ANTIOQUIA, municipio Medellín, north slope Cerro Padre Amaya, 6.2 km from paved road, 2670 m.

Paratypes: Males, ICN 9996-98, female, 9995 (ANTIOQUIA, Bello, Serranía Las Valdías, 6.6-8.1 km WSW San Felix, 2820-3100 m), males, ICN 43814-5, females, MHUA 62, 64, 66-67, 72 (ANTIOQUIA, Caldas, vereda La Clara, Alto San Miguel, 1800-2300 m), female, ICN 10001 (ANTIOQUIA, Sonsón, Sonsón, 2525 m), males ICN 39566-67 (ANTIOQUIA, Sonsón, vereda San Francisco y Sirgua, 2420-3100 m).

Referred specimen Antioquia, Yarumal: el Colgado-ro, Hacienda Las Convenciones (ICN 1178).

Diagnosis. (1) Skin of dorsum smooth with low tubercles laterally and posteriorly, that of venter areolate; dorsolateral folds incomplete; (2) tympanum round, not prominent, 25-43% eye length; (3) snout subacuminate in dorsal view, long; (4) upper eyelid narrower than IOD, bearing low tubercle; no cranial crests; (%) vomerine odontophores oblique; (6) males with vocal slits and nuptial pads; (7) first finger shorter than second; disks expanded, round; (8) fingers bearing lateral keels; (9) ulnar tubercles in row, not prominent; (10) nonconical tubercles on heel, outer edge of tarsus; fold-like tubercle on inner edge of tarsus; (11) two metatarsal tubercles, inner elongate, six times size of subconical outer; supernumerary plantar tubercles at bases of toes; (12) toes

bearing lateral keels, no webbing; toe disks smaller than those of outer fingers; fifth toe very long; (13) posterior surfaces of thighs uniformly brown; no white line above anal triangle; (14) adults small, males 19.9-24.2 ($x = 21.5 \pm 0.6$) mm, females 27.5-30.7 ($x = 28.9 \pm 0.6$) mm SVL.

Etymology. The specific epithet is used as a noun in apposition and is Spanish. It is given to the species because it occurs on the "altiplano" of the Departamento de Antioquia, whose inhabitants are called paisas.

Description (see table 1 for proportions). Head slightly narrower than (females) to as broad as (males, young females) body, wider than long; snout subacuminate in dorsal view, rounded in lateral profile; nostrils weakly protuberant, directed laterally; canthus rostralis relatively sharp, straight or weakly concave; loreal region weakly concave, sloping abruptly to lips; lips not flared, even in large females; low tubercle on posterior part of upper eyelid; upper eyelid narrower than

IOD; no cranial crests; supratympanic fold evident above and behind tympanum; tympanum round, not prominent, separated from eye by 1.5 times its diameter; postrectal tubercles subconical; choanae round, well median of maxillary arch; vomerine odontophores median and posterior to choanae, oblique, separated medially by distance equal width of an odontophore, each about 2/3 size of a choana, bearing 3-4 teeth in a slanted row; tongue longer than wide, posterior edge notched, posterior 2/5 not adherent to floor of mouth; males with subgular vocal sac, short vocal slits posterolateral to tongue.

Skin of dorsum nearly smooth with low tubercles, especially laterally and posteriorly; tubercles becoming larger on flanks; dorsolateral fold ill-defined, not reaching supratympanic fold nor above groin; skin of venter coarsely granular; discoidal folds well anterior to groin; no anal sheath or perianal warts; ulnar tubercles not prominent but present, decreasing in size toward elbow; palmar tubercle bifid, twice size of oval thenar; super-

Table 1. Sizes (in mm) and proportions of seven species of the *taeniatus* complex of *Eleutherodactylus* in the Caribbean and Pacific drainages of Colombia. First line provides range of values (and sample size); second line reports mean ± 1 standard error of the mean

SPECIES	SEX	SVL	SHANK/SVL	HW/SVL	EYELID/IOD	TYMP/EYE	E-N/EYE
<i>E. miyatai</i>	males	16.9-20.2 (8)	46.7-55.1 (8)	37.4-41.4 (8)	68.0-95.6 (8)	20.0-32.3 (6)	67.7-87.0 (8)
		18.2 \pm 0.4	52.0 \pm 0.9	39.8 \pm 0.4	86.5 \pm 3.4	28.0 \pm 1.8	78.4 \pm 2.5
	females	24.0-28.5 (8)	47.7-53.3 (8)	39.8-43.7 (8)	66.7-96.0 (8)	23.7-30.6 (7)	81.8-93.6 (8)
		26.1 \pm 0.5	51.1 \pm 0.6	41.8 \pm 0.6	76.9 \pm 3.5	27.5 \pm 1.0	87.0 \pm 1.4
<i>E. paisa</i>	males	19.9-24.2 (7)	43.4-53.8 (7)	37.1-39.4 (7)	80.0-100.0 (7)	25.0-37.0 (7)	77.8-89.3 (7)
		21.5 \pm 0.6	49.1 \pm 1.5	38.0 \pm 0.3	89.7 \pm 2.6	30.6 \pm 1.6	82.2 \pm 1.5
	females	27.5-30.7 (6)	47.1-49.1 (6)	37.9-40.7 (6)	69.4-81.2 (6)	31.2-42.9 (6)	94.1-100.0 (6)
		28.9 \pm 0.6	47.9 \pm 0.3	38.9 \pm 0.4	75.6 \pm 2.0	38.0 \pm 1.7	97.0 \pm 1.1
<i>E. ptochus</i>	males	16.7-19.8 (29)	45.6-52.9 (28)	35.4-38.9 (28)	68.0-100.0 (28)	23.1-41.7 (28)	69.2-91.7 (28)
		18.5 \pm 0.2	49.2 \pm 0.4	37.0 \pm 0.2	86.4 \pm 1.7	29.3 \pm 0.7	74.4 \pm 0.9
	females	20.7-25.5 (7)	46.8-54.3 (15)	36.5-40.8 (15)	69.2-100.0 (15)	15.2-37.9 (15)	72.7-81.5 (15)
		23.0 \pm 0.6	49.7 \pm 0.6	38.3 \pm 0.3	84.5 \pm 2.3	30.1 \pm 1.5	76.8 \pm 0.8
<i>E. suetus</i>	males	13.9-18.2 (26)	47.5-54.0 (19)	34.8-39.8 (19)	75.0-100.0 (19)	18.2-33.3 (19)	65.4-86.4 (19)
		16.5 \pm 0.2	49.8 \pm 0.4	37.1 \pm 0.3	88.2 \pm 1.6	27.4 \pm 1.1	75.8 \pm 1.1
	females	20.7-23.0 (10)	47.3-55.3 (12)	37.3-40.6 (12)	78.3-100.0 (12)	26.1-40.6 (12)	65.6-92.3 (12)
		22.0 \pm 0.2	50.0 \pm 0.6	39.0 \pm 0.3	88.3 \pm 2.5	33.8 \pm 1.0	80.9 \pm 2.0
<i>E. taeniatus</i>	males	15.3-22.2 (37)	50.5-59.5 (31)	35.8-41.9 (31)	72.0-100.0 (31)	26.1-40.6 (31)	73.1-100.0 (31)
		19.5 \pm 0.2	55.2 \pm 0.4	39.1 \pm 0.3	85.0 \pm 1.3	31.2 \pm 0.5	83.4 \pm 1.0
	females	23.0-31.6 (20)	49.3-57.2 (19)	38.3-42.9 (19)	65.8-111.1 (19)	29.3-41.6 (19)	82.9-100.0 (19)
		27.3 \pm 0.4	53.8 \pm 0.5	40.0 \pm 0.3	85.0 \pm 3.4	34.8 \pm 0.8	91.5 \pm 1.4
<i>E. viejas</i>	males	15.3-19.1 (9)	57.1-61.4 (9)	35.4-41.0 (9)	60.0-85.7 (9)	26.1-36.0 (9)	77.8-100.0 (9)
		17.7 \pm 0.5	58.8 \pm 0.5	39.0 \pm 0.6	73.9 \pm 3.0	29.9 \pm 1.0	86.4 \pm 2.7
	females	24.0-29.1 (11)	52.7-61.4 (15)	338.0-43.5 (15)	59.1-86.7 (15)	29.0-40.0 (15)	85.2-108.6 (15)
		26.8 \pm 0.5	57.1 \pm 0.7	40.6 \pm 0.4	73.7 \pm 2.0	32.8 \pm 0.9	97.5 \pm 1.8
<i>E. zophus</i>	males	18.7-23.0 (18)	42.7-51.4 (18)	36.4-40.5 (16)	72.0-96.0 (16)	25.9-40.0 (17)	65.5-90.9 (17)
		21.0 \pm 0.3	46.9 \pm 0.6	38.6 \pm 0.3	84.3 \pm 2.1	32.7 \pm 1.1	80.0 \pm 1.4
	females	25.5-31.2 (21)	43.3-50.6 (21)	37.7-42.3 (21)	61.1-90.3 (19)	31.2-41.2 (20)	75.7-100.0 (20)
		28.3 \pm 0.3	46.5 \pm 0.4	40.1 \pm 1.2	74.7 \pm 2.2	35.8 \pm 0.7	88.4 \pm 1.4

Eleutherodactylus taeniatus (Boulenger)

Lynch (1980) rescued this name from oblivion and pointed out that the frog often identified as *E. ockendeni* from Panamá was this species. At the same time, Lynch confused specimens of *E. paisa* and *E. zophus* with *E. taeniatus*. This confusion does not affect the description given by Lynch but does affect his data on body size.

Although we characterize this species as a lowlands frog, it also enters moderate elevations (to about 1500 m). In the biogeographic Chocó, *E. taeniatus* is distributed from Panamá to just north of Buenaventura. The more southern record given by Lynch (1980) in western Ecuador represents specimens of *E. ockendeni* with incorrect locality data (Lynch & Duellman, 1997). *Eleutherodactylus taeniatus* also occurs across the northern foothills of the western Cordilleras and enters the Middle Magdalena. The distribution of *E. taeniatus* (Figura 6) is remarkably like that of *E. raniformis* (Lynch & Myers, 1983) suggesting that these two species have responded in precisely the same way to the ecological and geological changes that have shaped the isthmian bridge in spite of belonging to different subgenera, one Middle American and the other presumably South American in origin.

Eleutherodactylus viejas Lynch & Rueda-A.

This recently described species (Lynch & Rueda-A., 1999) apparently is distributed in a discontinuous fashion at elevations between 565 and 1800 m (Figure 4). One system of populations is known along the eastern base of the northern part of the Cordillera Central and the other is found on the opposite side of the Magdalena valley.

Eleutherodactylus zophus sp. nov.

Eleutherodactylus taeniatus (in part): Lynch, 1980: 183, 185, 187 (AMNH specimens from western Antioquia).

Holotype: Amphibian collection of the Instituto de Ciencias Naturales 20149, an adult female, one of a series collected by M. C. Ardila, J. D. Lynch, P. M. Ruiz, and R. Sánchez 4 June 1988 (original field number JDL 16934).

Paratopotypes: Males, ICN 20155, 20158-61, 20164, 20170, 20173, 20187, 20197-98; females, 20151-53, 20171, 20185-86, 20189-90, 20196, 20200.

Type-locality: COLOMBIA, Departamento de ANTIOQUIA, municipio de Urrao, carretera Urrao-Caicedo, vereda El Chuscal, Quebrada "La Nevera", 2680 m.s.n.m.

Paratypes: ICN 20148 (ANTIOQUIA, límite entre municipios Caicedo and Urrao, "Alto de Caicedo", 2700-2740 m), 20141, 20144, 20147 (ANTIOQUIA, Urrao: 15.7 km by road from Urrao, Qda. La Nevera, 2430 m), 41670-82 (ANTIOQUIA, Betania: vereda Piedra Alta, Hda. Agua Linda, 5° 44' N, 76° 01' W, 2030-2200 m).

Referred specimens (juveniles and poorly-preserved specimens). Topotypes (ICN 20150, 20154, 20156-57, 20162-63, 20165-69, 20172, 20174-84, 20188, 20191-95, 20199). **Antioquia**, Andes (AMNH 14091, 14095). Urrao: El Chuscal (ICN 1208-13, 1215-16, 1219, 1227), La Nevera, 2560 m (ICN 1179, 1182, 1187, 1189, 3499), 15.7 km by road from Urrao, 2430 m (ICN 20142-43, 20145-46).

Etymology. Greek, *zophus*, meaning darkness or gloom. The name is used in reference to the drab coloration of this small frog and in reference to its habit of becoming very active soon after sunset.

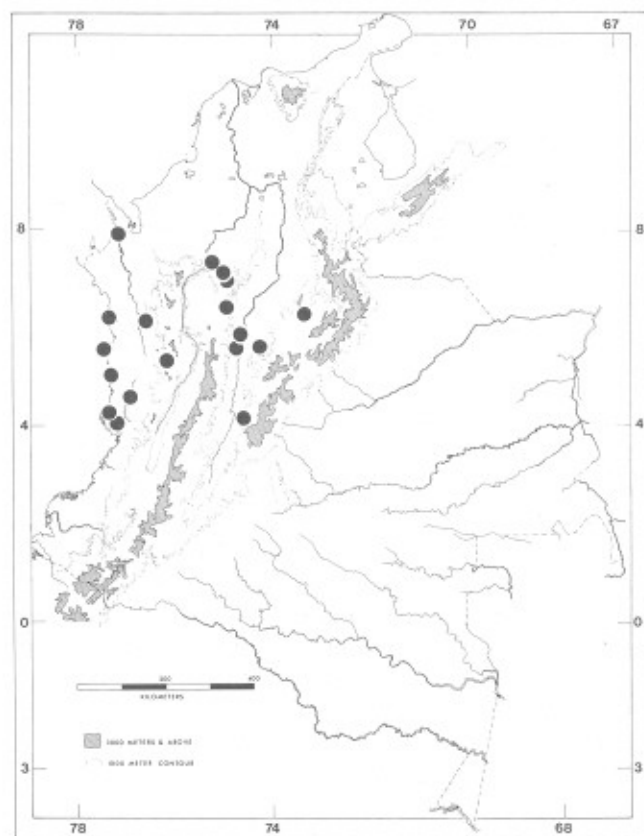


Figura 6. Distribution of *Eleutherodactylus taeniatus* in western Colombia. Specimens examined

Diagnosis. (1) Skin of dorsum smooth except for flattened warts associated with color pattern, that of venter areolate; no dorsolateral folds; (2) tympanum round, 26-41% eye length; (3) snout subacuminate in dorsal view in males, round in females, short; (4) upper eyelid narrower than IOD, bearing low warts; no cranial crests; (5) vomerine odontophores low, oval; (6) males with vocal slits and nuptial pads; (7) first finger shorter than second; digital disks expanded, round; (8) fingers bearing lateral keels; (9) row of ulnar tubercles present; (10) nonconical tubercles on heel, outer edge of tarsus, one on inner edge of tarsus; (11) two metatarsal tubercles, inner oval, ca six times size of subconical outer; numerous supernumerary plantar tubercles; (12) toes bearing lateral keels, no webbing; toe disks as large as those of outer fingers; fifth toe very long; (13) dorsum brown with darker brown markings; venter brown; posterior surfaces of thighs brown with cream flecks; (14) adults small, males 18.7-23.0 ($x = 21.0 \pm 0.3$) mm, females 25.5-31.2 ($x = 28.3 \pm 0.3$) mm SVL.

Eleutherodactylus zophus is most similar to *E. ptochus* but is larger than *E. ptochus* (males 16.7-19.8, $x = 18.5 \pm 0.2$, females 20.7-25.5, $x = 23.0 \pm 0.6$ mm SVL) with shorter legs (*E. zophus* shank/SVL 46.9 \pm 0.6 in males, 46.5 \pm 0.4 in females versus *E. ptochus* 49.2 \pm 0.4 in males, 49.7 \pm 0.6 in females), a larger tympanum, and longer snout. Additionally, the skin of the dorsum in *E. zophus* bears more prominent warts than that of *E. ptochus* (nearly smooth), males of *E. zophus* have a subacuminate, not round, snout in dorsal view, *E. zophus* has lateral keels on the fingers, ulnar tubercles, and small tubercles on the heel and outer edge of the tarsus. In *E. zophus*, the anal triangle is not bordered above by a cream line.

Description (see table 1 for proportions). Head as broad as body in males, narrower than body in adult females; head broader than long; snout of males weakly subacuminate in dorsal view, of females round, in lateral view rounded in each; nostrils very slightly protuberant, directed dorsolaterally; canthus rostralis round in females, slightly more evident in males, concave; snout short; loreal region weakly concave, sloping to upper lip; lips weakly flared in females; upper eyelid bearing few low tubercles; no cranial crests; supratympanic fold evident above and behind tympanum; tympanum round; tympanum separated from eye by distance equal its diameter; postrectal tubercles subconical; choanae small, round, well median of palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, low, oval, slanted, separated medially by distance equal one-half width of an odontophore, each bearing 2-3 teeth;

odontophores smaller in males than in females, in females slightly larger than a choana; tongue longer than wide, its posterior border notched, posterior 2/5 not adherent to floor of mouth; vocal slits posterolateral to tongue; vocal sac subglular.

Dorsum smooth except for warts associated with color pattern and continuing onto flanks; no dorsolateral folds; skin of limbs bearing warts in dark markings; venter coarsely areolate; discoidal fold evident, just anterior to groin; no anal sheath; pair of subanal tubercles; ulnar tubercles forming row, diminishing in size from antibrachial tubercle; palmar tubercle bifid, occasionally divided, twice size of oval thenar tubercle; supernumerary palmar tubercles numerous; subarticular tubercles round, nonconical; fingers bearing lateral keels and round disks; disks about twice as wide as digit below disk except on thumb; disk of thumb obviously expanded; first finger shorter than second; large white nuptial pad on thumb in males.

Nonconical tubercle on heel with row of smaller tubercles along outer edge of tarsus; one tubercle on distal 1/4 of inner edge of tarsus, sometimes with smaller tubercles proximal and distal to it; inner metatarsal tubercle twice as long as wide, about six times size of subconical outer; numerous supernumerary plantar tubercles; subarticular tubercles round, nonconical; toes bearing lateral keels but no webbing; disks of toes as large as those of outer fingers, round; tip of III reaches distal edge of penultimate subarticular tubercle of toe IV, tip of V to distal edge of distal subarticular tubercle of toe IV; hindlimbs short, heels touching or nearly touching when flexed hindlimbs held perpendicular to sagittal plane.

Coloration in ethanol. Dorsum brown with darker brown ill-defined scapular and sacral chevrons and suprainguinal spots; limb bars about equal in width to interspaces, more or less transverse on shanks; posterior surfaces of thighs brown with cream flecks; groin and anterior surfaces of thighs uniform brown; supratympanic stripe and labial bars brown, edged with cream.

Coloration in life. "Venters all dark brown as are concealed surfaces of limbs. Dorsum varies greatly in ground color: one is pale cream-gray; most are brown; another has much rust color scattered on dorsum. Green enters dorsum of several. Iris gray with black reticulation and hint of reddish horizontal streak." (fieldnotes JDL, 4 June 1988). "Iris is either very pale green or pale brassy color above with red horizontal streak and gray below, all reticulate with black. Concealed thigh, groin brown

with cream flecks. Venter brown (somewhat more dirty yellow with brown stipple in larger females). Dorsum colored with browns (yellowish brown to reddish brown). Some have dorsoconcolor type pattern with very dark flanks." (fieldnotes, JDL, 16 June 1997).

Measurements of holotype in mm. SVL 29.0, shank 13.5, HW 11.4, head length 10.4, chord of head length 11.4, upper eyelid width 2.5, IOD 3.5, tympanum length 1.3, eye length 3.2, E-N 3.0.

Natural history. In the vicinity of the type-locality in June 1988, *E. zophus* was found on vegetation within the forest as well as along the forest-edge and on low vegetation in the bed of the quebrada La Nevera. The call was described as a "series of musical bonks (banging bamboo stick together)." Males called from the tops of leaves with the body elevated off the surface of the leaf. Males called sporadically the night of 16 June 1997 in municipio Betania in the forest at 2030-2200 m. All were found on very low vegetation within 20 cm of the forest floor in dense forest (none was found along the forest edge or in the pastures).

Females smaller than 24.5 mm are juveniles (straight oviducts with no thickening, small ovarian eggs) except for ICN 20148 (24.0 mm SVL) which has some convolutions of her oviducts and is scored as a young female. Males smaller than 18.5 mm SVL do not have nuptial pads and were not calling.

Distribution: Known only from two localities (2030-2680 m) in the northern part of the Cordillera Occidental of Colombia (Figura 5).

Specimens examined

Eleutherodactylus miyatai.

Boyacá: Monquirá: Km 21, carretera Barbosa-Arcabuco, 15 km W Arcabuco, 2440 m (ICN 29922). Toquí: Finca Versalles, 1720 m (ICN 38738). **Santander:** Bolívar: corregimiento La Hermosura, Km 3 carretera Hermosura - Puerta de Los Cerros, 1800 m (ICN 39108-20). Charalá: vereda Virolín, Cañaverales, 1770 m (ICN 22476-77), Cerro del Fara (ICN 5448-49), carretera a El Reloj, 1740 m (ICN 5165), Río Luisito, 1750 m (ICN 12399), cabeceras Río Luisito, 1750 m (ICN 6184, 8527). Gambita: Km 55-56, carretera Duitama-Charalá, Bogotacito, 2400 m (ICN 12490-92). Tona: Km 22, carretera Bucaramanga-Pamplona, Finca El Diviso, 1890-2050 m (ICN 15266-82).

Eleutherodactylus ptochus.

Chocó: San José del Palmar: 20.5-22.5 km del cementario de El Cairo, 2080-2200 m (ICN 38772-79, 39826-27) **Risaralda:** Apía: sector "Colgaderos" (ICN 31290). **Valle del Cauca:** El Cairo: vereda Las Amarillas, 2100-2200 m (ICN 39780-825), Cerro Ingles (UVC 9155-60).

Eleutherodactylus suetus

Antioquia: Sonsón: 8 km E (por carretera) Sonsón, 2780 m (ICN 10002). **Caldas:** Pensilvania: transecto altitudinal desde Km 18 hacia Km 28 de la carretera Pensilvania-Arboleda, 2000-2650 m (ICN 41748). **Samaná:** corregimiento de Florencia, El Estadero, 1850-1950 m (ICN 41698-746, 41747, 41749).

Eleutherodactylus taeniatus

Antioquia: Amalfí: vereda El Mango, Quebrada El Caiman, 1200 m (MHUA 742), vereda La Guyana, 1400 m (MHUA 597, 677-86). Anorí: alto de los Tauros, 700 m (ICN 43654). Puerto Arquia: Río Arquia, Belén (LACM 46883), Finca Chiribiquí (LACM 46884). Puerto Triunfo: Qda. Las Mercedes, 500 m (ICN 39561-65.). Valdivia: Puerto Valdivia, vereda La China, 800 m (MHUA 393). Yolombo: Bosque Normandia, Quebrada Guaduas, 1000 m (MHUA 671). **Caldas:** La Victoria: vereda Cañaveral, finca "La Cuba", Qda. La Juanita, 1100 m (ICN 42403-05). **Samaná:** corregimiento Norcasia, campamento El Diamante (proyecto Miel I), 520-620 m (ICN 41178-91, 41196-98, 42414), Km 23, carretera La Victoria - Samaná, campamento La Miel II, cerca la desembocadura Qda. Tasajos en la Río de la Miel, 700-880 m (ICN 41192-95, 41199-202, 42400); carretera Samaná a La Cristalina, Km 5.8-7.0, 1430-1500 m (ICN 42397-99); carretera Samaná a Florencia, Km 4.4, La Palma, 1385 m (ICN 42406-08); carretera Samaná a vereda California Alta, Km 1.6-3.0 (ICN 42401-02). **Chocó:** Boyajá: hills near upper Río Napapí (LACM 46885-93); Camino de Yupe, 350-400 m (LACM 73206-08), 420-625 m (LACM 73209, 73211-12, 73214-24), 420-720 m (LACM 73225); upper Río Opogodó above Río Merendó (LACM 46894-95); Serranía de Baudó, ridges paralleling Río Yupe (LACM 46896-902), camino de Yupe, entre alto Río Opogodó y alto Río Domingadó (ICN 565). Ciudad Mutis: Alto de Buey, N slope, 420-1070 m (LACM 47231-32, 47229); Nuquí: Estación Biológica Amargal, 100-300 m (MHUA 363-64). Docordó: Quebrada Docordó, 10 km above boca del Río San Juan, 120 m (AMNH 87120-21). Istmina: Noanamá, Río San Juan (BM 1947.2.16.99); Quebrada Vicordó, 10 km above Noanamá, 80-110 m

(AMNH 87111-12, 87116-19). Pizarro: Pizarro (CMNH 44074). Río Sucio: Parque Nacional Natural Kátios, Alto El Limón, 500 m (IAvH 1969-70), vereda Sautata (IAvH 2252). **Cundinamarca:** Yacopí: Inspección de Policía Guadalito, hacia Guadalito, Río Aldana, 1050 m (PR 16356, 16365-66), vereda Cabo Verde, 1100 m (PR 16454-55, Quebrada La Fortuna (PR 16413-14), vereda Sardinas, finca Matacaña, 1120 m (PR 16424), via vereda Pasurcha, ca. cementario (PR 16355).

Risaralda: Mistrató: sector Puerto de Oro, 900-1200 m (ICN 31855). **Tolima:** Icononzo y alrededores (ICN 43323-24). **Valle del Cauca:** Buenaventura: Bahía Málaga (UVC 8918).

Eleutherodactylus viejas

Antioquia: Amalfí: vereda El Jardín, bosque Quebradoncita, 1100 m (MHUA 453). Guatapé: vereda Santa Rita, Hda. Montepinar, 1840 m (ICN xxxxxx [jdl 21374-75]). San Carlos: carretera San Carlos a vereda Patio Bonito, Hda. Las Vegas, 1180 m (ICN 32426-44). San Rafael: bosque San Rafael (ICN 42436-40, 42446). **Caldas:** Samaná: Km 23, carretera La Victoria a Samaná, quebrada Tasajos con Río La Miel, 700 m (ICN 42409-10), carretera Samaná a Florencia, Km 1.7, 1375 m (ICN 42412-13), carretera Samaná a vereda California alta, Km 1.6-3.0 (ICN 42411). **Cundinamarca:** Yacopí: Inspección de Policía de Guadalito (ICN 42992), Cerro Colorado, 1190 m (ICN 42987), 1502 m (ICN 42980-81); vereda Barbascales, finca Montebello, 820 m (ICN 42983-84, 42991, 43003); vereda Sardinas, finca Matecaña, 1100-1120 m (ICN 42982, 42988-90, 42998-99). **Santander:** Landázuri: Km 19 [de] Cimitarra – Escuela La Esperanza, vereda El Azufrado, Qda. Torova, 565 m (ICN 39123).

Discussion

Although we can not identify synapomorphies for this assembly (the *E. frater* group) nor for the trans-Andean species, our suspicion is that each component is monophyletic. If they represent a monophyletic group, the pattern of distribution is largely consistent with allopatric models of speciation except that *E. taeniatus* and *E. viejas* are sympatric at several localities along the edges of the Middle Magdalena.

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