

NEW SPECIES OF FROGS (*ELEUTHERODACTYLUS*: LEPTODACTYLIDAE) FROM THE CORDILLERA ORIENTAL OF NORTE DE SANTANDER AND SANTANDER, COLOMBIA

por

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Resumen

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Se describen tres especies más de *Eleutherodactylus* de los bosques andinos de la parte norte de la Cordillera Oriental. La primera pertenece al grupo *E. conspicillatus* y aparentemente esta relacionada con una especie ampliamente distribuida, *E. w-nigrum* pero es alopátrica de ella. La segunda es parecida superficialmente a *E. tubernasus* pero parece tener parentesco con otras especies de las cordilleras Central y Occidental. Se re-evalúa el grupo *E. tubernasus* en el cual, de las cuatro especies originales, solamente dos son válidas y no muestran parentescos cercanos. La tercera especie parece tener parentesco con *E. ganonotus* (de los bosques andinos del oriente de Ecuador) y *E. viridis* (parte norte de la Cordillera Occidental).

Palabras clave: *Eleutherodactylus*, taxonomía.

Abstract

Three additional species of *Eleutherodactylus* are described from the Andean forests of the northern Cordillera Oriental. One is a species of the *E. conspicillatus* species group, apparently related to the wide-spread *E. w-nigrum*. A second superficially resembles *E. tubernasus* but appears related to other frogs from the Central and Occidental cordilleras. The *E. tubernasus* species group is re-evaluated and the four species once-recognized are reduced to two species, not closely related. The third new species appears to be related to *E. ganonotus* (Andean forests of eastern Ecuador) and *E. viridis* (northern part of the Cordillera Occidental).

Key words: *Eleutherodactylus*, taxonomy.

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Introduction

The Cordillera Oriental of Colombia is the least species-rich of the three cordilleras in terms of the frog genus *Eleutherodactylus* (Lynch et al., 1997). In spite of my having devoted most of my attention these past 25 years to the Cordillera Central and, especially, the Cordillera Occidental (Lynch, 1998), I remain convinced that the eastern cordillera is more impoverished than the other two, primarily based on the number of species recovered from single localities. That said, it must be admitted that the intensity of fieldwork carried out by my colleagues M. Cristina Ardila, J. Vicente Rueda, and the late Pedro M. Ruiz, and me, at least in terms of intense transects, was much more extensive in the Central and Occidental than in the Oriental.

In the past few years, following study of material collected in the northern portion of the Cordillera Oriental by persons from the Universidad de Antioquia (Juan Manuel Daza), Universidad de Atlántico (Daniel Cuentas), and the Universidad Industrial de Santander (Martha Patricia Ramírez and her students), I have learned that this cordillera harbors more species than have been reported (and this conclusion is further reinforced by the largely unreported surveys carried out in the Parque Nacional Natural Cordillera de Los Picachos [M. C. Ardila] and on the road leading from Florencia, Caquetá, to Huila [Lynch, Restrepo, & Ruiz] Lynch & Suárez, 2000, Suárez, 2000). This contribution is the second (after Lynch, 2003, with two more to follow) to deal with recent discoveries from the northern portion of the Cordillera Oriental and deals with three new species sharing very little except geographic location.

Materials and methods

Methodology and terminology follow Lynch & Duellman (1997). Specimens mentioned here are deposited in six collections: ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá), KU (Natural History Museum, University of Kansas, Lawrence), MHUA (Museo de Herpetología, Universidad de Antioquia, Medellín), SCNLS (Sociedad de Ciencias Naturales La Salle, Caracas), UIS-A (Universidad Industrial de Santander), and UPR-M (Universidad de Puerto Rico-Mayagüez).

A. A new Andean species of the *E. conspicillatus* group

The *E. conspicillatus* group (defined by Lynch, 1994) is a conspicuous element of the fauna in the wet lowlands

of South America (ignoring eastern Brasil and the *conosur*) but the group is also present in montane situations in Colombia, Ecuador, and northern Peru. In the eastern cordillera, the only known species are *E. carregerorum* Lynch from two localities in Boyacá, *E. eparcus* Lynch & Suárez from western Caquetá, *E. savagei* Pyburn and Lynch from eastern Cundinamarca and Meta, and the widespread *E. w-nigrum* (Boettger), known in the Cordillera Oriental from Caquetá, Cundinamarca, and Santander. Recently, I had the opportunity to examine yet another species in collections of the Museo de Herpetología of the Universidad de Antioquia. It is here named.

Eleutherodactylus ixalus sp. nov.

Holotype: ICN 47886, a subadult female, one of a series collected 10-12 October 2001 by Juan Manuel Daza and Eliana M. Muñoz (gift from MHUA, original number MHUA 1814).

Paratopotypes: MHUA 1821-22, 2311, adult males.

Type-locality: COLOMBIA, Departamento de Santander, Municipio de Betulia, vereda Palma de Oro, Finca La Antigua, 1300-1700 msnm., 6° 57' N, 73° 19' W.

Referred specimens: MHUA 1819, 1823, juveniles taken with the type-specimens.

Etymology: Greek, *ixalos*, meaning bounding or springing, in reference to the long hindlegs and my suspicion that this is an active jumper, like most other species of the group.

Diagnosis: (1) skin of dorsum shagreen, that of venter smooth; no dorsolateral folds; (2) tympanum round, 40–45 % length of eye; (3) snout subacuminate or acuminate in dorsal view, round in lateral profile; canthus rostralis distinct; (4) upper eyelid narrower than IOD, without pungent tubercles; no cranial crests; (5) vomerine odontophores subtriangular in outline, median and posterior to choanae, separated by width of an odontophore, smaller than choanae; (6) males lacking vocal slits; nuptial pads ill-defined; (7) first finger longer than second, moderate sized disks on fingers III and IV; (8) fingers bearing lateral keels; (9) ulnar tubercles, excepting antebrachial, absent; (10) conical tubercle on heel, smaller tubercles along outer edge of tarsus; (11) two metatarsal tubercles, inner oval, outer 1/5–1/4 size of inner; (12) toe V slightly longer than toe III; toes bearing lateral keels, lacking webbing; few supernumerary plantar tubercles; (13) Brown above with vague brown markings; throat pigmented, with white raphe, venter white, posterior surfaces of thighs brown with some cream flecks and dark spots along upper edge; (14) adults

of moderate size, three males 23.1—31.3 mm SVL, one young female 45.4 mm SVL.

Eleutherodactylus ixalus is most similar to *E. w-nigrum*, from which it differs in having a longer snout (Fig. 1), heel and outer tarsal tubercles, absence of vocal slits, and in the coloration of the posterior surfaces of the thighs (yellow with black spots in *E. w-nigrum*).

Description: Head broader than body, longer than wide; HW 37.4—38.6 % SVL; snout almost acuminate in dorsal view, rounded in lateral profile; nostrils not (or very weakly) protuberant, directed laterally; E-N 100.0—105.00 % eye length in males, 121.2 % in female; canthus rostralis obvious, edge rounded; loreal region concave, sloping abruptly to lips; lips not flared; upper eyelid without pungent tubercles, its width 74.0—100.0 % IOD; no cranial crests; supratympanic fold distinct, obscuring upper edge of tympanum, ending behind tympanum; tympanum round, its length 40.0—45.0 % eye length; 2 or 3 conical postrectal tubercles; choanae not concealed by palatal shelf of maxillary arch, triangular in outline; vomerine odontophores median and posterior to choanae, subtriangular in outline in female, slanted in males, separated medially by distance equal width of an odontophore, bearing a slanted row of 3-5 teeth; posterior edge of tongue notched, posterior 1/5 not adherent to floor of mouth; no vocal slits in males.

Skin of dorsum fine shagreen (fine tubercles, closely spaced); no dorsolateral nor postocular folds; flanks shagreen, ventral surfaces smooth; discoidal folds anterior to groin; no anal sheath nor subanal tubercles; ulnar surfaces without tubercles except for antebrachial tubercle; palmar tubercle bifid, much larger than oval thenar tubercle; one non-conical supernumerary palmar tubercle/ digit;

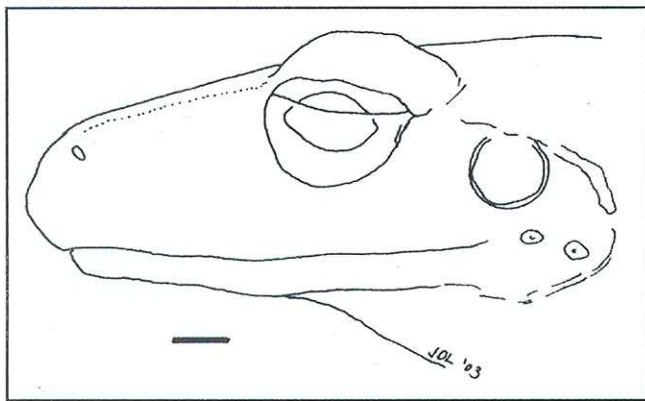


Figure 1. Side of head of *Eleutherodactylus ixalus* (ICN 47886). Scale equals 2 mm.

subarticular tubercles round, subconical; first finger longer than second when each appressed; all digits bearing circumferential grooves defining ventral pads on disks; disks of fingers I and II scarcely wider than digit below disk, of fingers III and IV, circa 2X width of digit; fingers bearing lateral keels; nuptial pad not distinctive but present.

Conical (but small) tubercle on upper edge of heel; series of smaller tubercles along outer edge of tarsus; inner edge of tarsus with elongate tubercle on distal 1/6th; inner metatarsal tubercle 2 1/2 times as long as wide, oval, outer round, 1/4—1/5 size of inner; plantar supernumerary tubercles just below subarticulars, 1—2/ digit; subarticular tubercles longer than wide (basals of toes IV—V) or round, non-pungent; toes with narrow lateral keels, no webbing; Toe V extends just beyond distal edge of penultimate subarticular tubercle of Toe IV, Toe III to proximal 1/2 of same tubercle; disks of toes expanded, nearly so large as those of outer fingers, with circumferential grooves on pads; hindlimbs long, shank 57.1—57.8 % SVL in males, 68.3 % in female, when hindlimbs flexed and held perpendicular to sagittal plane, heels overlapping substantially.

Coloration in alcohol: Brown above with interorbital bar/ triangle and some vague spots on body; limb bars of legs evident in female (not males), edged with cream and oblique to axis of shank; canthal stripe and supratympanic stripe dark brown; pair of pale subocular bars; slanted bars on flanks; venter nearly white but some concentration of brown stippling on throat of MHUA 1822 (with white raphe) and the holotype; venter with few clusters of stipples; posterior surface of thigh with dark spots near upper edge—rest of surface brown with diffuse cream spots.

Coloration in life: Dorsum pale brown with upper lip golden; throat pale gray with faint white line; upper surface of disks golden; plantar surface black; black spots on concealed surface of shank; iris golden with dark horizontal stripe.

Measurements of the holotype in mm: SVL 45.4, shank 31.0, HW 17.5, head length 17.5, chord of head length 17.8, upper eyelid width 3.7, IOD 5.0, tympanum length 2.3, eye length 5.2, E-N 6.3.

Natural history: Little is known except that three paratypes were calling at night in early October and that small (11.0-13.5 mm SVL) juveniles were found at the same time. These data suggest that reproduction is aseasonal. Males were calling, early in the evening (6-8 PM, but not later) on the ground (not on vegetation) near a stream in a very humid forest.

Remarks: My initial, cursory (through the bottle), examination of these specimens resulted in their misidentification as *E. w-nigrum*, a judgment corrected when I removed them from their jar and examined them under a stereoscope. This is not evidence of relationship (rather, of my slothfulness). Nevertheless, *E. ixalus* is considered here as a close relative of the widespread *E. w-nigrum* (Lynch, 1979, Lynch & Duellman, 1997). Departamento de Santander has not yet been adequately collected to assert that *E. ixalus* has a small distributional area (like *E. actites* Lynch of western Ecuador, Lynch & Duellman, 1997). The nearest locality record for *E. w-nigrum* is in southern Santander (municipio de Charalá). At least tentatively, it appears that these three species depart partially (and significantly) from Mayr's model of peripatric speciation—speciation without ecological shifts (Lynch, 1999).

B. The dismantling of the *E. tubernasus* group and a new species similar to *E. tubernasus*

Rivero (1984) proposed the *Eleutherodactylus tubernasus* species group, named three Venezuelan species (*E. chlorosoma*, *E. pulidoi*, and *E. tubernasus*), and included *E. prolixodiscus* Lynch (a Colombian species) in the group as well. Lynch (1978), in his initial concept of *E. prolixodiscus*, included material from the Sierra Nevada de Santa Marta and from the cloud forests of Santander, Colombia. Subsequently, Lynch & Ruiz (1985) pointed out that the specimens from the Sierra Nevada de Santa Marta were not conspecific with specimens from Santander and named the former as *E. tayrona*. Rivero's proposal was based on material from the Sierra Nevada de Santa Marta (*E. tayrona*) and not the species from the Cordillera Oriental (and Venezuela), *E. prolixodiscus*. He

borrowed specimens from the University of Kansas, where the types are deposited (unfortunately he did not borrow some paratypes).

In the early 1990s, I had occasion to wonder about the *E. tubernasus* group and its included species and noted Rivero's error (deriving from an error of my own—confusing *E. prolixodiscus* and *E. tayrona*). Thus, I requested the loan of all type specimens of the three species named by Rivero (1984) to settle ambiguities. Through the good offices of Enrique La Marca, I also had the opportunity to examine specimens assigned to one or more of these names from other localities on the Cordillera de Mérida. Rivero (1984) assumed that Lynch (1978) was correct in assigning Santa Marta specimens to *E. prolixodiscus*—thus he confidently named three species from Venezuela and even provided a cladogram for the four species (here rejected).

All of these frogs live in bromeliads—frequently being seen plastered between the leaves of bromeliads. Their flattened bodies might be taken for evidence of relationship (Rivero, 1984) or as an adaptation for living in bromeliads (a worry of Lynch & Duellman, 1997:92). Reporting the results of my study languished until I visited the Universidad de Antioquia and the Universidad Industrial de Santander in early 2002 and had the opportunity to examine specimens of similar frogs collected in the departments of Norte de Santander and Santander.

Rivero (1984) defined the *tubernasus* complex because its species possessed (1) a tubercle (or papilla) on the tip of the snout, (2) a large tympanum (wider than long, and more prominent ventrally), (3) an indistinct canthus rostralis, concave loreal region, a tendency to



Figure 2. Photographs of *Eleutherodactylus uisae*. (left) The holotype (ICN 47882) and (right) a paratype (ICN 47884), illustrating the two color morphs.

flared upper lips, (4) the lack of dorsolateral folds, and other trivial characters, including color in life. He noted that "*E. prolixodiscus*" did not match in all of the characters (but recall that his "*E. prolixodiscus*" were subsequently re-identified as *E. tayrona*).

In 1978, I dealt with specimens long-preserved but had no experience with any of these organisms. In 1983, 1986, and 1992, I had the opportunity to collect, and closely observe, *E. prolixodiscus* and *E. tayrona*. Rivero (1984) had 27 specimens of the three species that he reported for Venezuela (20 *E. chlorosoma*, five males and 15 females, two females of *E. pulidoi*, and one male and four females of *E. tubernasus*)—in spite of his descriptions, I doubted that he had three species or that they were closely related. Subsequent study of all of his material, and additional collections, resolved my concerns (hence, this report).

Lynch & Ruiz (1985) reported *E. prolixodiscus* from western Venezuela and Ruiz *et al.* (1996), with no further comment, reported *E. tubernasus* from Cerro Tamá (Colombia-Venezuela border), but did not mention the other two names (*E. chlorosoma* and *E. pulidoi*) published by Rivero, because, by then, I had arrived at the conclusions, following examination of the type-specimens, that *E. chlorosoma* and *E. pulidoi* were synonyms of *E. prolixodiscus* and *E. tubernasus*, respectively (see Commentary), and that *E. tubernasus* was a species not related to *E. prolixodiscus*, causing the *E. tubernasus* species group to evaporate, for lack of evidence.

During the 1980s and the early 1990s, I had encountered bromeliad-dwelling frogs in the cloud forests of the Cordillera Central (and its equivalent in Ecuador, there-called the Cordillera Real), the Cordillera Occidental, and the Sierra Nevada de Santa Marta. Likewise, I (Lynch, 1978) had associated *E. prolixodiscus* with this complex and Rivero (1984) had named four taxa as well from the Cordillera Mérida and/or Cordillera Oriental. By the mid 1990s, I had concluded (but not published) that *E. prolixodiscus* and *E. tubernasus* were not closely related to species from the other cordilleras (and that two of the taxa named by Rivero were synonyms).

Nonetheless, collections by students from the Universidad Industrial de Santander revealed the presence of another species similar to *E. tubernasus*, but probably allied with species from the western cordilleras of Colombia, in cloud forests on the western flanks of the Cordillera Oriental in the Departamento de Santander; this species is here named.

Eleutherodactylus uisae sp. nov.

Holotype: ICN (amphibian collection) 47882, a female, part of a series collected by Sandy Arroyo 13 August 2002, formerly UIS-A 2428.

Paratopotype: ICN 47883, a male collected with the holotype (formerly UIS-A 2429).

Paratypes: ICN 47884-85 (formerly UIS-A 2430-31), UIS-A 1876, 2241-46, 3008, 3010, 3012-18, 3022, Santuario de Fauna y Flora Guanentá—Alto Río Fonce, 2400 m (Santander, municipio Charalá)

Type-locality: COLOMBIA, Departamento de Boyacá, Municipio de Paipa, Hacienda La Sierra, dentro el Santuario de Fauna y Flora Guanentá—Alto Río Fonce, antigua escuela, 2700 m.

Referred specimens (juveniles and material dissected or destined to be dissected): UIS-A 1301, 1308, 1310, 1319, 1329, 1339, 1341, 1343, 1345, 1362, 1376, 1386-87, 1389-90, 1395, 1397, 1400, 1402-03, 1584, 1594, 1606, 1853, 1858, 1861, 1872-73, 1892, 1894-95, 1897-901, 1907-08, 2024-25, 2041, 2056, 2063, 2065-68, 2072, 2077, 2084, 2087, 2098-99, 2101, 2104-05, 2173-75, 2190-93, 2195-99, 2204, 2207, 2219, 2221, 2233, 2240, 2264-65, 2268, 2272, 2328, 2331, 2334, 2336-39, 2347, 2350-52, 2488, 2491, 2496, 2500, 2502, 2505-06, 2508, 2510-11, 2514-16, 2521, 2524, 2526-27, 2533-34, 2537-39, 2541, 2544, 2550, 2557, 2559, 2561, 2589, 2654-56, 2659, 2662, 2665, 2668, 2672-74, 2676, 2684-85, 2694, 2696, 2698-99, 2701, 2712-13, 2715-16, 2718, 2720-22, 2727, 2732, 2743-46, 2750, 2760, 2762, 2769, 2771-75, 2778, 2787, 2774, 2801, 2806, 2820, 2822, 2825, 2831, 2835, 2837, 2839, 2844, 2846, 2848-49, 2855, 2869-71, 2874-76.

Etymology: The name is derived from the acronym of the Universidad Industrial de Santander (UIS) and is used as a noun used in apposition. The name intends to honor my colleague, Martha Patricia Ramírez, and her students, for their dedication to learn what frogs occur in the cloud forests above Bucaramanga and things about their ecology.

Diagnosis: (1) Skin of dorsum nearly smooth except for low warts on lower back, that of venter areolate; no dorsolateral folds; (2) tympanum round, 1/3-1/2 length of eye; (3) snout subacuminate to nearly round in dorsal view, pointed in lateral profile, bearing papilla at tip; canthus rostralis distinct, straight or slightly concave; (4) upper eyelid narrower than IOD, bearing small conical tubercle; no cranial crests; (5) vomerine odontophores oval, slanted;

(6) males with vocal slits and nuptial pads; (7) first finger shorter than second, disks of fingers expanded, but small; (8) fingers bearing lateral keels; (9) series of small ulnar tubercles along outer edge of forearm; (10) small tubercle on heel, smaller tubercles along outer edge of tarsus; (11) two metatarsal tubercles, inner oval, outer round, 1/5 size of inner; supernumerary plantar tubercles present; (12) toes bearing lateral fringes but no web, disks expanded, about size of those of hand, fifth toe very long; (13) dorsum brown with darker brown spots; ventral surfaces cream; posterior surfaces of thighs pale brown with some small cream spots; (14) adults small, males 17.0-20.7 (\bar{x} = 18.9 \pm 0.3, N = 16) mm SVL, females 26.3-31.2 (\bar{x} = 27.6 \pm 0.5, N = 9) mm SVL.

Eleutherodactylus uisae is not thought closely related to *E. tubernasus* (as one might assume from geography) but rather to a series of small frogs found on the Cordillera Central, Cordillera Occidental, and western slope of the Macizo Colombiano and northern Cordillera Real of Ecuador (*E. angustilineatus*, *E. baiotis*, *E. boulengeri*, *E. brevifrons*, *E. dorsopictus*, *E. eremitus*), none known in the era of Cochran & Goin (1970). Of these, only *E. brevifrons*, *E. dorsopictus*, and *E. eremitus* have tubercles on the upper eyelid and on the heel and outer edge of the tarsus. *Eleutherodactylus angustilineatus*, *E. baiotis*, and *E. dorsopictus* are readily distinguished in having bifid subarticular tubercles. *Eleutherodactylus brevifrons* is smaller, has a concealed tympanum, and has larger eyes (as reflected by the upper eyelid/IOD ratio). *Eleutherodactylus eremitus* has larger eyes, more prominent vomerine odontophores, and is green in life. The geographically nearer *E. tubernasus* has sharply slanting tympani (in both sexes) and a notably flatter head than *E. uisae*.

Description: Head broader than body; head wider than long; HW 34.8-38.4 (\bar{x} = 37.1 \pm 0.2, N = 16) % SVL in males, 36.9-40.3 (\bar{x} = 38.2 \pm 0.4, N = 9) % in females; snout nearly rounded in dorsal view in females (more subacuminate in males) except for conical tubercle at tip, pointed (due to tubercle) in lateral profile; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis straight or weakly concave, sharp; E-N 70.4-88.0 (\bar{x} = 80.1 \pm 5.4, N = 16) % eye length in males, 81.8-106.9 (\bar{x} = 93.4 \pm 2.3) % in females; loreal region concave, sloping abruptly to lips; lips not flared in males, somewhat in females; small subconical tubercle on upper eyelid and most individuals also have numerous minute tubercles scattered over upper eyelid; width of upper eyelid 50.0-85.7 (\bar{x} = 70.0 \pm 2.4, N = 16) % IOD in males, 57.1-87.5 (\bar{x} = 67.8 \pm 2.9) % in females; interorbital space flat (no cranial crests) but with small tubercle midway between

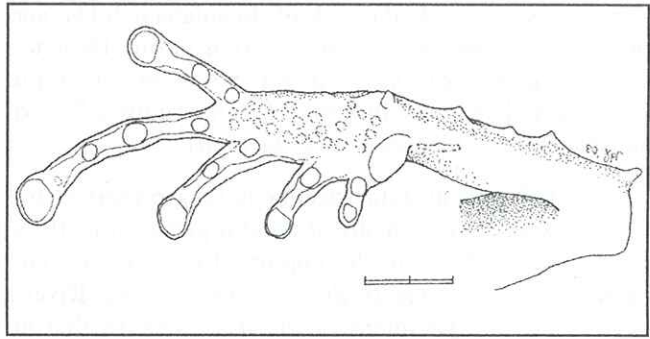


Figure 3. Foot (and tarsus) of *Eleutherodactylus batrachites* (MHUA 1776). Scale equals 2 mm.

two upper eyelids; supratympanic fold ending at midlevel of tympanum; tympanum round, its length 31.8-47.8 (\bar{x} = 39.5 \pm 1.2) % eye length in males, 36.4-58.6 (\bar{x} = 47.3 \pm 2.3) % in females, separated from eye by slightly less than tympanum length; in males, tympanum is nearly vertical whereas in females it is slanted nearly dorsolaterally; two subconical postrictal tubercles; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, slanted in males, more elevated and oval in females, each bearing row of 2-5 teeth; odontophores separated medially by distance 1 1/2-2 times width of an odontophore; posterior edge of tongue with shallow notch; posterior 1/3 of tongue not adherent to floor of mouth; long vocal slits lateral to tongue; vocal sac large, subgular.

Skin of head and anterior trunk smooth, that of lower back bearing many small low tubercles, flanks more noticeably tuberculate, of venter coarsely areolate; no discoidal folds; no anal sheath; series of 3-5 ulnar tubercles in row; palmar tubercle bifid, much larger than oval thenar; numerous low supernumerary palmar tubercles; subarticular tubercles round, conical; narrow lateral keels on fingers; disks of fingers I-II scarcely expanded, of outer fingers 1.5 times width of digit below disk; disks round apically; circumferential grooves complete, defining ventral pads; first finger shorter than second; nuptial pad on thumb of male.

Small tubercle on heel and series of smaller tubercles along outer edge of tarsus; elongate tubercle (or short fold) just proximal to inner metatarsal tubercle on inner edge of tarsus; inner metatarsal tubercle twice as long as wide; outer metatarsal tubercle round, 1/6 size of inner; numerous supernumerary plantar tubercles, non-conical; subarticular tubercles round, simple, non-conical; lateral fringes on toes, no webbing; tip of toe V to distal edge of

distal subarticular tubercle of toe IV, tip of toe III to distal edge of penultimate subarticular tubercle of toe iv; disks of toes slightly smaller than those of outer fingers—ca 1 ¼ times width of digit below disk; circumferential grooves complete; heels overlapping when flexed hindlegs held perpendicular to sagittal plane; shank 46.5—52.9 (\bar{x} = 49.7 ± 0.4, N = 16) % SVL in males, 47.1—52.8 (\bar{x} = 50.3 ± 0.8, N = 9) % in females.

Coloration in alcohol: dorsum brown with darker dorsal markings (interorbital bar, scapular W, inverted Y-shape mark above sacrum, sometimes inguinal spots); canthal stripe present but labial bars only beneath eye; shank bars narrower than interspaces, transverse on shank; flanks paler than dorsum, venter cream with brown stippling; posterior surfaces of thighs pale brown, sometimes with small cream spots.

Coloration in life: dorsum brown to orange brown with darker brown markings, edged in cream; individuals with a *dorsoconcolor* pattern have a cream to reddish-brown dorsum, stripes, if present, are brown, and dark brown flanks; iris golden with brown flecking.

Measurements of holotype in mm.: SVL 27.5, shank 13.7, HW 10.5, head length 9.4, chord of head length 10.0, upper eyelid with 2.5, IOD 3.5, tympanum length 1.2, eye length 3.3, E-N 2.7.

Natural history: *Eleutherodactylus uisae* is somewhat unusual for a species of the *bosque andino* in that it is active both by day and night. **Gutiérrez L.** (2003) found males calling at night as well as in the afternoons. Although some specimens were found in, or perched on, bromeliads, there is no credible evidence that the species is some sort of bromeliad-dwelling frogs (in contrast to many species loosely associated in the bromeliad-dwelling group). Adults (and juveniles) are found normally perched upon broad-leaves or less commonly in the leaf-litter (the latter by day). The study by **Gutiérrez L.** (2003) was an ecological one—she found *E. uisae* to be much more abundant in native forests than in restored (*Quercus*) forests 30 years old. Furthermore, *E. uisae* was found as well in *Pinus* forests near a *cabaña* of the reserve (type-locality).

Remarks: As is the case for many *Eleutherodactylus*, *E. uisae* is pattern-polymorphic. The species exhibits only two polymorphisms in my judgment—a spotted pattern (81 % of individuals) and a *dorsoconcolor* pattern (19 %). Some individuals of the *dorsoconcolor* pattern have no markings on the dorsum, others have a single vertebral band, broadest anteriorly, and yet others have thinner

paravertebral dark bands (the last variant accounts for 75 % of *dorsoconcolor* morphs). To date, too few specimens have been captured in the reforested areas (of *Pinus* or of *Quercus*) to decide if polymorph frequencies might correlate with habitat.

Commentary: My study of the type specimens from Venezuela did not conform to Rivero's reports. The papilla (or tubercle) at the tip of the snout was seen in only the types of *E. pulidoi* and *E. tubernasus*. **Rivero** (1984) reported a cladogram relating the taxa as follows: (((*pulidoi tubernasus*) *chlorosoma*) *prolixodiscus*). He considered the following characters as derived: (a) nuchal depression, (b) tubercular skin, (c) granular loreal region, (d) tympanum close to eye, (e) metatarsal tubercle prominent, (f) cutaneous folds on digits, (g) black testes, and (h) tarsal tubercles. The types of *E. chlorosoma* have a pointed snout but lack a terminal papilla (a character not included in his analysis). Only females are available for *E. pulidoi*, hence, it is not possible to report pigmentation of the mesorchium for this taxon (character g). White testes must be considered as primitive within the genus *Eleutherodactylus* (**Lynch**, 1993), hence this character is *contra* Rivero's hypothesis. Rivero opined that characters b, c, e, f, and h supported his hypothesis but did not recognize that characters a, f, and g were against it. Rivero had no evidence available to assert that *E. chlorosoma* was more closely related to *E. pulidoi* + *E. tubernasus*, except using a most parsimonious treatment of (a), where the derived condition must be reversed in *E. pulidoi* (a claim never made by Rivero).

Based on published results, there seems no reason to doubt Rivero's arguments. However, my study of his specimens (and many others) reveals that the "nuchal depression" (a) cannot be recognized as a character and the distance between the eye and tympanum (d) is equal for all four taxa. This means that *E. pulidoi* and *E. tubernasus* cannot be distinguished. Furthermore, *E. chlorosoma* and *E. prolixodiscus* are united by sharing black mesorchia (a derived character achieved repeatedly in *Eleutherodactylus*, and other frogs).

Rivero (1984) was a victim of an error that **Lynch** (1978) reported—that frogs (*E. prolixodiscus*) from Santander were conspecific with frogs from Magdalena. Nevertheless, Rivero made additional errors (in distinguishing *E. chlorosoma* from whoever's *E. prolixodiscus* and in distinguishing *E. pulidoi* from *E. tubernasus*) and in grouping the two (or four) taxa. Among all the specimens reported by **Lynch** (1978), **Lynch & Ruiz** (1985), and **Rivero** (1984), there are only three species—*E. prolixodiscus* (in Colombia and Venezuela), *E. tayrona*

(endemic to the Sierra Nevada de Santa Marta), and *E. tubernasus* (Colombia and Venezuela)—*E. chlorosoma* and *E. pulidoi* are synonyms of other species.

Necessary taxonomic housecleaning

Eleutherodactylus chlorosoma Rivero 1984

This taxon was recognized by **Rivero** (1984) because it exhibited two characters (a) nuchal depression and (f) lateral fringes on the digits. I do not recognize a nuchal depression as a character and attribute the digital fringe character to Rivero's confusion as to what is *E. prolixodiscus* (actually, my fault, **Lynch**, 1978, for confusing *E. prolixodiscus* and *E. tayrona*). Direct comparisons of the types of *E. chlorosoma* and *E. prolixodiscus* (1992) fail to reveal any differences. Therefore, *Eleutherodactylus chlorosoma* (**Rivero**, 1984) is placed in the synonymy of *Eleutherodactylus prolixodiscus* (**Lynch**, 1978).

Eleutherodactylus pulidoi Rivero 1984

Direct comparison of the holotypes (and/or paratypes) of *E. pulidoi* and *E. tubernasus* do not reveal differences (and, additional specimens confirm this conclusion). **Rivero** (1984) claimed that the latter possessed a nuchal depression lacking in the former and that the former had a tympanum less separated from the eye than did the latter. As mentioned previously, I cannot confirm the existence of a nuchal depression (as a character) and do not see any difference in the separation of the eye and tympanum in these specimens. Accordingly, *Eleutherodactylus pulidoi* Rivero is assigned to the synonymy of *Eleutherodactylus tubernasus* Rivero (the latter has page priority over the former and is a descriptive name as well—I exercise my prerogative as first revisor, in any case).

The conclusions just presented mean that only two biological species are involved—*E. prolixodiscus* (including *E. chlorosoma*) and *E. tubernasus* (including *E. pulidoi*). However, there is at least one other species loosely involved—a species found in the cloud forest of western Santander (*E. uisae*). Even more important is the assertion (on the part of **Rivero**, 1984) that *E. prolixodiscus* and *E. tubernasus* form a group (i.e., are sister species).

My observation that *E. chlorosoma* and *E. pulidoi* do not constitute biological entities requires a summary (and I believe that such a summary begins at the level of species). I am prepared to recognize only three biological (or phylogenetic) species at this point—*E. prolixodiscus*, *E. tubernasus*, and *E. uisae*:

Eleutherodactylus prolixodiscus Lynch

This species is now known from eleven localities west of the Táchira Depression (nine localities in NE Colombia) and six localities east of the Táchira Depression on the southeastern flanks of the Cordillera de Mérida (see Specimens Examined for data). As mentioned by **Rivero** (1984), and based on my own experiences, this is a frog of bromeliads. At night, individuals can be found perched on vegetation only a short distance from a bromeliad—by day, individuals (and egg clutches) are found in the axillae of bromeliads.

Rivero (1984) reported the sizes of *E. chlorosoma* as five males 22.0–22.5 mm and 15 females 18.2–26.0 mm SVL; however, many of his specimens are immature. My study of his specimens revealed nine adult males and four other adult males were obtained from other collections. These males (all with vocal slits and all but one with nuptial pads) are 19.9–25.8 mm SVL (mean = 23.4 ± 0.4). Nearly all of Rivero's females are juveniles—only five are adults. The La Salle collection includes an additional adult female. The six adult females are 24.1–25.8 mm SVL (mean = 25.2 ± 0.3). The two males from Barinas are small (19.9–21.9 mm SVL) in comparison with the specimens from most other localities (see below, for data on specimens from Departamento Cesar, Colombia) but are otherwise indistinguishable. Taking all of the data (except Depto. Cesar) available reveals that males average 23.7 ± 0.3 mm SVL (range 19.3–25.8, N = 34) and females average 25.8 ± 0.3 mm SVL (range 24.1–28.2, N = 12).

A small collection from Departamento Cesar, Municipio de La Jagua de Ibirico, corregimiento de La Victoria de San Isidro, vereda Alto de Canta Rana, 1810–1850 m (260 kms. N of the next-nearest record), is peculiar for the small sizes of the frogs (eight males 17.8–21.9 mm SVL, six females 18.7–22.4 mm SVL). The data are even more peculiar when the frogs are separated into the two elevations—1810 m (four males 20.4–21.9 mm, three young females 21.2–21.7 mm, two gravid females 21.9–22.4 mm) and 1850 m (four males 17.8–20.4 mm, four gravid females 18.7–20.6 mm). These samples are also peculiar for the near absence of sexual dimorphism in size.

Eleutherodactylus tubernasus Rivero

This species, also a bromeliad endemic, has been found at only four localities (two in Colombia and two in Venezuela—see Specimens Examined for data) and three of these lie to the west of the Táchira Depression. As noted by **Rivero** (1984) this species is readily distinguished from *E. prolixodiscus* in having the tympanum oriented dorsolaterally rather than

laterally. Such a character is also seen in *E. lacrimosus*, a species that was not considered by Rivero—I think that *E. tubernasus* is an Andean species of the *E. lacrimosus* group. Males average 23.2 ± 0.4 mm (range 20.1—25.5, $N = 14$) and females 26.6 mm (range 24.8—28.3, $N = 4$).

***Eleutherodactylus uisae* Lynch**

See description (above).

C. A new species allied to *E. ganonotus* and *E. viridis*

***Eleutherodactylus batrachites* sp. nov.**

Holotype: ICN 47887, adult female, one of a series collected by Juan Manuel Daza and Eliana M. Muñoz 21 August 2001 (original numbers JMD 661, MHUA 1607).

Paratopotypes: ICN 47888-92 Original numbers MHUA 1605-06, 1608-10), MHUA 1572-73, 1575-76, 1578-88, 1590-97, 1600-01, 1603-04, 1775-80, 2023, UIS-A 2280, 2283, same collectors, between 13 and 21 August 2001.

Type-locality: COLOMBIA, Departamento de Norte de Santander, municipio de Cucutilla, vereda Carrizal, sitio Sisavita, 2180—2250 msnm. $7^{\circ} 13' N$, $72^{\circ} 51' W$.

Referred specimens: MHUA 1574, 1577-78, 1589, 1598, 1602, from the type-locality (all are juveniles).

Etymology: Greek, a stone of frog-green color.

Diagnosis: (1) Skin of dorsum smooth or very minutely granular, that of venter finely granular; no dorsolateral folds; (2) tympanum round, its length $1/3$ — $3/5$ eye length; (3) snout acuminate in dorsal view, protruding in lateral profile; canthus rostralis sharp, weakly concave; (4) upper eyelid narrower than IOD, without tubercles; no cranial crests; (5) vomerine odontophores very low, not evident in males; (6) long vocal slits, subgular vocal sack, nuptial pads in males; (7) first finger shorter than second, disks on fingers II-IV; (8) fingers bearing lateral fringes; (9) series of prominent, subconical ulnar tubercles; (10) conical tubercle on heel, row of subconical outer tarsal tubercles; (11) two metatarsal tubercles, inner oval, outer round, $1/3$ size of inner; numerous supernumerary plantar tubercles; (12) Toe V slightly longer than Toe III, toes bearing lateral fringes, no webbing, toe disks almost as large as those of outer fingers; (13) cream above with almost no markings; venter cream with brown spots, most dense on underside of hindlegs; posterior surface of thighs brown with cream spots; green in life; (14) a minute species, males 14.0—17.0 ($x = 15.6 \pm 0.3$, $N = 16$) mm SVL, females 17.9—21.7 ($x = 19.9 \pm 0.3$, $N = 13$) mm SVL.

Although the fifth toe in *E. batrachites* is only slightly longer than the third, I consider *E. batrachites* a near relative of *E. ganonotus* and *E. viridis*. The three species share the shape of the head, size, and color in life but, none of these could be a synapomorphy—hence, my decision here is phenetic. *Eleutherodactylus batrachites* is readily distinguished from the other two by virtue of having series of ulnar and tarsal tubercles and a conical heel tubercle.

Description: Head as wide as body (males) or narrower than body (females); head slightly wider than long (males), or longer than wide (females); HW 33.3—42.8 ($x = 37.2 \pm 0.6$) % SVL in males, 32.7—36.3 ($x = 34.4 \pm 0.3$) % in females; snout acuminate in dorsal view, protruding in lateral profile; nostrils not protuberant, directed laterally; canthus rostralis sharp, slightly concave; E-N 95.0—117.6 ($x = 105.1 \pm 2.0$) % eye length in males, 111.1—136.8 ($x = 123.7 \pm 2.4$) % in females; loreal region nearly flat, sloping abruptly to lips; lips not flared; no tubercles on upper eyelid, interorbital space flat, no cranial crests; upper eyelid width 40.0—68.4 ($x = 56.6 \pm 1.9$) % IOD in males, 43.5—62.5 ($x = 53.9 \pm 1.8$) % in females; no supratympanic fold; tympanum directed laterally, round or slightly higher than long, its length 29.4—47.6 ($x = 37.6 \pm 1.4$) % eye length in males, 35.0—63.2 ($x = 47.1 \pm 2.1$) % in females; no postrectal tubercles; choanae small, round, not concealed by palatal shelf of maxillary arch; in females vomerine odontophores median and posterior to choanae, each smaller than a choana, oval, separated on midline by distance equal choana width, bearing 1 or 2 teeth, odontophores not apparent in males; posterior border of tongue with feeble notch, posterior $1/3$ - $1/2$ not adherent to floor of mouth; long vocal slits lateral to tongue; vocal sac large, subgular.

Skin of dorsum smooth but under magnification, very finely shagreen; no dorsolateral folds; skin of venter areolate; discoidal folds not apparent; no anal sheath; pair of prominent subanal tubercles; antibrachial tubercle small, large, subconical tubercles along outer edge of forearm; palmar tubercle bifid, larger than oval thenar; few supernumerary palmar tubercles, at bases of fingers II-III; subarticular tubercles round, non-pungent; narrow lateral fringes on fingers; all fingers with ventral pads (defined by circumferential grooves); disks on fingers II-IV, $1 \frac{1}{4}$ - $1 \frac{1}{2}$ times width of digit below disk; first finger shorter than second; males with nuptial pads on thumbs.

Conical tubercle on heel; outer edge of tarsus with row of subconical tubercles; short inner tarsal fold on distal $1/4$ of tarsus; inner metatarsal tubercle $2 \frac{1}{2}$ times as long as wide, outer round, subconical, $1/4$ size of inner;

plantar surface bearing numerous supernumerary tubercles; basal subarticular tubercles longer than wide, distal ones round, all non-pungent; toes bearing lateral fringes but no webbing; all toes with ventral pads; disk of I not expanded, of II-V expanded ($1\frac{1}{4}$ - $1\frac{1}{2}$ width of digit below disk); tip of toe III to distal edge of penultimate subarticular tubercle of toe IV, tip of toe V to $\frac{1}{2}$ way between distal and penultimate subarticular tubercles of toe IV; heels overlapping when flexed hindlimbs held perpendicular to sagittal plane; shank 45.0–53.0 ($x = 49.8 \pm 0.6$) % SVL in males, 44.2–51.3 ($x = 47.6 \pm 0.6$) % in females.

Coloration in alcohol: Above cream with little or no trace of pattern (light stippling between eyes in some specimens); canthal stripe brown, thin; anal triangle dark brown; no limb bars except brown band across wrist; in 2003, some specimens have the cream washed with red; brown spotting on venter, underside of thighs, shanks, arm; posterior surfaces of thighs brown with irregularly shaped cream spots. The mesorchium of adult and juvenile males is black.

Coloration in life: Dorsum and upper surfaces of limbs lemon green delimited ventrally by a non-continuous chocolate brown stripe, venter transparent, flecked with white spots, throat pale yellow with small gray spots; canthal stripe chocolate brown.

Measurements of holotype in mm.: SVL 19.0, shank 9.6, HW 6.5, upper eyelid width 1.0, IOD 2.3, length of tympanum 0.8, eye length 1.8, E-N 2.1.

Natural history: Most of the available specimens are adults (males with obvious vocal sacs, gravid females) but in the MHUA sample, there are three very small juveniles (MHUA 1578, 1598, 1602). These were not sexed but measure 5.9–8.1 mm SVL. Three other juveniles are larger (MHUA 1574 and 1589, juvenile males, 13.0–13.5 mm SVL, and MHUA 1577, juvenile female, 12.5 mm SVL). The presence of reproductive adults and two classes of immature frogs, strongly suggests that reproduction in *E. batrachites* is aseasonal. *Eleutherodactylus batrachites* called during the day as well as at night but in more dense chorus during the day (however, the frogs were very cryptic by day). All specimens were found along a trail on ground covered with a moss blanket—none was found within the forest proper or open areas at the type-locality. The frogs appear to have some affinity for the moss—when sitting on/in the moss, the frogs become nearly invisible. At night, frogs were more easily seen perched on ferns, up to one meter above the ground. The collectors found *E. batrachites* to be

very abundant and report finding more than 30 in a half an hour—they declined to preserve most specimens found, assuming the species to be well-known.

During the visit to Sisavita, the site was normally shrouded in fog and most specimens were either collected under cover of fog or at night. MHUA 1600-02 were collected one morning and were found in full sun.

Remarks: My association of *E. batrachites* here with *E. ganonotus* and *E. viridis* is done in the absence of synapomorphies (and must thus be viewed with some skepticism). If my association is correct, there is another complex of frogs that exhibits as disjunct a pattern of distribution as does the *E. galdi* group (Lynch, 1996, Lynch & Rueda-A., 1997).

Discussion

With these three descriptions, the *Eleutherodactylus* fauna (found above 1000 m) of the Cordillera Oriental, climbs to 38 species (four of which, *E. cornutus*, *E. dolops*, *E. hernandezii*, and *E. pugnax*, are shared with the Cordillera Central and one, *E. w-nigrum*, is shared by all three cordilleras). The Cordillera Oriental is a massive cordillera yet its *Eleutherodactylus* fauna is impoverished in comparison with the Cordillera Central and Cordillera Occidental (each with 80 species above 1000 m).

The impoverishment of the Cordillera Oriental is probably real rather than an artifact of the intensity of investigation (I am aware of yet other undescribed species from all three cordilleras but more from the Cordillera Oriental than the others). Explaining this impoverishment remains a serious challenge for the future. The yet smaller Cordillera de Mérida (Venezuela) is also species impoverished and notably isolated from the Cordillera Oriental (they share on two species of *Eleutherodactylus*, *E. prolixodiscus* and *E. tubernasus*, each discussed in this paper).

Although one of the new species described here is from Norte de Santander, this paper hardly begins to address distribution patterns for *Eleutherodactylus* in that Departamento. Two species described herein are from the Departamento de Santander (as is the recently described *E. adercus*, Lynch, 2003). My previous fieldwork in Santander was confined to revisiting some of the localities previously studied by my deceased colleague, Pedro M. Ruiz (the area of Virolín, municipio de Charalá, 1700–2200 m and the municipio de Tona) and our joint fieldwork on the road between Bucaramanga and Cúcuta (2000–2750 m). The recent fieldwork by students from the Universidad Industrial de Santander has enlarged measurably our

understanding of the frogs of the *bosque andino* and *subpáramo* of this department. Arroyo (2002) and Suárez Badillo (2003) studied the frogs of the *Estación Experimental y Demonstrativa El Rasgón* (municipio Piedecuesta) and Gutiérrez L. (2003) frogs from *el Santuario de Fauna y Flora Guanentá—Alto Río Fonce* (municipio Charalá, above the area ["Virolín"] studied by Ruiz and his students). Five studies have been carried out (six, including the collections by Juan Manuel Daza from the Universidad de Antioquia in municipio Betulia, which remain to be studied in detail) of the frog fauna on the western face of the Cordillera Oriental in Santander. Several species suggest that this is not a single region—*E. adercus* and *E. ixalus* are known only from Betulia, positioned on an Andean spur, perhaps explaining their uniqueness; *E. anolirez*, *E. douglasi*, *E. jorgevelosai*, and *E. prolixodiscus* are known from northern transects but not from el Santuario de Fauna y Flora Guanentá—Alto Río Fonce, nor from areas lower than their apparent distributional limits; and *E. uisae*, the most common frog in the Santuario de Fauna y Flora Guanentá—Alto Río Fonce, remains endemic to the *santuario*. Some of these observations can be dismissed as results of collectors with different levels of experience and search-image, combined with microhabitat preferences (or rarity) of certain species (for example, *E. ingeri* has yet to fall into the collections of students of the UIS, an observation probably consonant with their lack of experience, but others are not be so easily dismissed). It appears certain (as certain as one can be with "negative" evidence) that *E. uisae* is not present in the seemingly equivalent forests to the north-northwest of the *Santuario de Fauna y Flora Guanentá—Alto Río Fonce* and that the *Santuario de Fauna y Flora Guanentá—Alto Río Fonce* lies beyond the distributional limits of *E. anolirez*, *E. douglasi*, and *E. prolixodiscus* (and possibly of the rare *E. jorgevelosai* as well). The northeastern extent of *E. w-nigrum* remains the forests near the town of Virolín and the absence of this species in *El Diviso*, *El Rasgón*, *el Santuario de Fauna y Flora Guanentá—Alto Río Fonce*, and Tona probably serve as evidence of a range limit.

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leave granted by the University of Nebraska (1992). Study of material in the herpetological collections of the University of Antioquia was facilitated by Vivian Paéz (and her students), of those of the Universidad Industrial de Santander by Martha Patricia Ramírez (and her students), and of those of the Universidad de Los Andes (Mérida, Venezuela) by Enrique La Marca. Specimens from the Museo de La Salle (Caracas, Venezuela) were loaned by A. Paolillo.

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Appendix (Specimens examined)

Eleutherodactylus prolixodiscus

COLOMBIA, Depto. Cesar: Municipio de La Jagua de Ibirico, correg. La Victoria de San Isidro, vereda Alto Canta Rana, 1810 m (ICN, field nos. PR 16950-8), 1850 m (ICN, field nos. PR 16966-81, 17101). Depto. Norte de Santander: Municipio Chinácota, Alto de Mejuey, 2500-2550 m (ICN 15157-73); Municipio Cucutilla, vereda Carrizal, Sisavita, 2180-2250 m (UIS-A 2275); Municipio Herrán, Parque Nacional Natural Tamá, vicinity of cabaña Orocué, 2300-2400 m (ICN 10102-19). Depto. Santander: 30 km ENE Bucaramanga, road to Cúcuta, 2485 m (KU 132724-33, holotype and paratypes of *E. prolixodiscus*); Municipio de Piedecuesta, Estación Experimental y Demostrativa El Rasgón, 2200-2400 m, 2450-3000m, 3200-3450 m (UIS-A 1159-61, 1164, 1214, 1456, 2006, 2019, 2132-33, 2135-38, 2140-43, 2145, 2147, 2149-50, 2153, 2913-23; Municipio tona, El Diviso, 1890-2050 m (ICN 15174-81).

VENEZUELA, Edo. Barinas: Altamiras, Soledad "900 m" (UPR-M 6900, 6998-99). Edo. Mérida: camino de Pregonero, Boca de Monte, 2393 m (UPR-M 4484-86, 4615-16, 4746, 5929); Selvas de San Eusebio, 2316 m (UPR-M 4958); 3 km SW Bailadores, Qda. El Capador, 2000 m (ELM 1985, 1995); carretera El Molino-Estanques, ca. Estanques, 2400 m (ELM 2438-39). Edo. Táchira: Distrito Junín, Betania (SCNLS 8383-84); camino de El Zumbador a Queniquea, 2240 m (UPR-M 4954-57, 5678); La Loma, entre El Zumbador y Queniquea, 2225 m (UPR 4960-69).

Eleutherodactylus tubernasus

COLOMBIA, Depto. Norte de Santander: Municipio Cucutilla, vereda Carrizal, Sisavita, 1950-2000 m (MHUA

1668-72, UIS-A 2284); municipio Herrán, Parque Nacional Natural Tamá, vicinity of cabaña Orocué, 2300 m (ICN 10483).

VENEZUELA, Edo. Barinas: Altamira, Soledad "900 m" (UPR-M 6894-97). Edo. Mérida: camino de Pregone-ro, Boca de Monte, 2390 m (UPR-M 4349, 4613, holotype and paratype of *E. tubernasus*). Edo. Táchira: Delicias, Matamula, 1120 m (UPR-M 6085-86, holotype and paratype of *E. pulidoi*); Laguna de García, 2.4 km del cruce vías Bailadores—Lago García—Pregonero, 1900 m (ELM 1490-96).

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