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Anomaloglossus confusus, a New Ecuadorian Frog Formerly Masquerading as “*Colostethus*” *chocoensis* (Dendrobatoidea: Aromobatidae)

CHARLES W. MYERS¹ AND TARAN GRANT²

ABSTRACT

Anomaloglossus confusus, new species, is a small (21–26 mm SVL) riparian frog from the Pacific versant of the Andes in northwestern Ecuador. It inhabits rocky forest streams in an elevational range of about 600–1540 m. It is the only known *Anomaloglossus* in Ecuador, where it can be distinguished from all other dendrobatoids by the generic synapomorphy of a median lingual process. The only other named trans-Andean species of *Anomaloglossus* are the western Colombian *A. atopoglossus* and *A. lacrimosus*.

Anomaloglossus confusus was previously confused with “*Hylixalus*” or “*Colostethus*” *chocoensis* (currently in *Hyloxalus*), a rare species described by Boulenger on the basis of a subadult female from Pacific lowland Colombia. The first adult specimen of *Hyloxalus chocoensis*, an adult male, is described. The generic name *Hylixalus* is not “an incorrect subsequent spelling” as recently interpreted, but an emendation with its own authorship and date of publication (Boulenger, 1882); as such, it is a junior objective synonym of *Hyloxalus* and is an available name.

RESUMEN

Anomaloglossus confusus, especie nueva, es una rana ribereña pequeña (21–26 mm LRC) de la vertiente pacífica de los Andes del noroccidente del Ecuador. Se encuentra en quebradas rocosas en bosques de 600–1540 m.s.n.m. Es la única especie de *Anomaloglossus* conocida en el Ecuador, donde se distingue de las demás especies de Dendrobatoidea por poseer la sinapomorfia genérica

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del proceso medial lingual. Las únicas otras especies trans-andinas de *Anomaloglossus* son *A. atopoglossus* y *A. lacrimosus* del occidente colombiano.

Anomaloglossus confusus fue confundido anteriormente con “*Hylixalus*” o “*Colostethus*” *chocoensis* (actualmente en *Hyloxalus*), una especie escasa de las tierras bajas del pacífico colombiano descrita por Boulenger a partir de una hembra subadulto. Aquí se describe el primer ejemplar adulto de la especie, un macho. El nombre genérico *Hylixalus* no es una “ortografía incorrecta subsecuente,” como fue interpretado recientemente, sino una emendación con su propia autoría y fecha de publicación (Boulenger, 1882); por consiguiente, es un sinónimo menor de *Hyloxalus* y es un nombre nomenclaturalmente disponible.

INTRODUCTION

Nearly a century ago, G.A. Boulenger (1912) described the frog *Hyloxalus chocoensis* based on a single subadult female from the Río San Juan drainage in western Colombia. The species was assigned to several different genera over the years; it has been in *Colostethus* for the last several decades, but it recently was returned to *Hyloxalus* (Grant et al., 2006: 168). Despite the taxonomic shuffling, little is known about the species.

Myers (1991) redescribed and illustrated the *chocoensis* holotype and extended the geographic range north into Panama based on one specimen from that country. However, new material obtained in Panama by Roberto Ibáñez and colleagues shows that the isthmian frog represents still another secretive dendrobatoid (unpublished data).

Myers (1991: 1) also tentatively extended the range of *chocoensis* south into northwestern Ecuador, but pointed out that the Ecuadorian population “conceivably represents a different species [that] cannot be reliably diagnosed at this time.” However, our discovery of the “median lingual process” (Grant et al., 1997) in New World dendrobatoid frogs provided a definitive answer for this case. The holotype of *H. chocoensis* lacks a lingual process, whereas the Ecuadorian frogs possess one and were temporarily referenced as “*Colostethus* species (*C. chocoensis* auct.)” in Grant et al. (1997: 24, 35). All dendrobatoid frogs characterized by presence of the median lingual process are now referred to the genus *Anomaloglossus* Grant et al. (2006: 158).

We here provide the formal description of the only known Ecuadorian species of *Anomaloglossus*, followed by notes on the first adult specimen of *Hyloxalus chocoensis*. Institutional abbreviations are AMNH (American Museum of Natural History, New York, USA), BMNH

(Natural History Museum, London), ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia), KU (Natural History Museum and Biodiversity Research Center, the University of Kansas, Lawrence, USA), and MHNG (Muséum d’Histoire Naturelle, Geneva, Switzerland).

Anomaloglossus confusus, new species

Figures 1, 2 (upper), 3–5

Colostethus chocoensis (Boulenger): Myers, 1991 (part: Ecuadorian specimens, including figs. 1A, 8A–B); Coloma, 1995: 25–26, figs. 1 (hand and foot), 2D (dorsal color pattern), 5A (testes), 10 (map).

Colostethus species (*C. chocoensis* auct.): Grant, Humphrey, and Myers, 1997: 35.

A[nomaloglossus] “*chocoensis*” auctorum: Grant et al., 2006: 158.

HOLOTYPE: AMNH A-104819 (field no. CWM 15955), an adult female from about 7 air km SSW El Corazón, 800 m elev., Bolívar-Cotopaxi border, northwestern Ecuador, collected by Charles W. Myers, John W. Daly, and Eugene W. Schupp on November 13, 1979. The type locality is roughly 01°10’S, 79°09’W.³

PARATYPES: AMNH A-104820–104824, paratopotypes collected with the holotype. KU 166157, 166158 from 3.5 km NE Mindo, 1540 m, Pichincha, Ecuador, collected by W.E. Duellman on April 8, 1975. KU 221616 from

³Collection of specimens reported in this paper preceded civilian GPS satellite receivers. Coordinates for the type locality were estimated on the map *República del Ecuador 1:1,000,000*, Instituto Geográfico Militar, circa 1981. The type locality was 11 km by gravel road SSW El Corazón on the way to Moraspungo and Quevedo. Confusingly, Moraspungo is plotted about 8 km southeastward of El Corazón on earlier editions of official maps (*Mapa Geográfico de la República del Ecuador 1:500,000*, Instituto Geográfico Militar, 1956–1957).



Fig. 1. *Anomaloglossus confusus*, new species. Left- and right-side views of the adult female holotype in life (AMNH A-104819, 24 mm SVL). The blackish ground color appeared dark olive-green in sunlight. About 2.3× life size.

[San Francisco de] Las Pampas, [1800 m], Cotopaxi, Ecuador, collected by Giovane Onore. MHNG 2258.57–2258.63 from Tandapi, [1460 m],⁴ Pichincha, Ecuador, collected by G. Onora in December 1983.

REFERRED SPECIMENS: Additional specimens (not seen by us) identified by Luis Coloma as *Colostethus chocoensis*, from provinces of Carachi, Cotopaxi, and Pichincha, Ecuador (see Coloma, 1995: 68).

⁴Data in brackets are added from the gazetteer in Lynch and Duellman (1997: appendix 2).

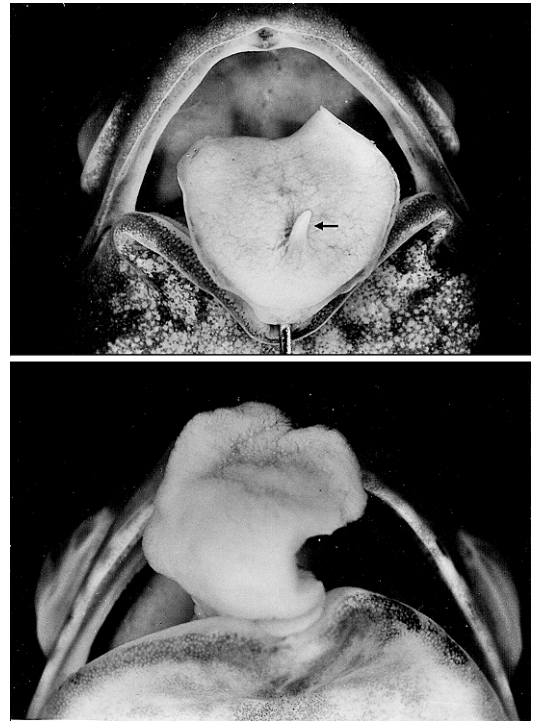


Fig. 2. The median lingual process as diagnostic character. **Upper:** Slender median process (arrow) present in *Anomaloglossus confusus*, new species (AMNH A-104820, ♀ paratopotype). **Lower:** Median lingual process absent in *Hyloxalus chocoensis* (Boulenger) (BMNH 1947.2.14.27, ♀ holotype).

ETYMOLOGY: The specific name *confusus* is the perfect passive participle of the Latin *confundo* (“to confound or mix together”), referring to the fact that this species was confused with another one.

DIAGNOSIS: The median lingual process (fig. 2) distinguishes *Anomaloglossus confusus* from all other dendrobatoid frogs known from Ecuador. The only other trans-Andean frogs with a median lingual process are *A. atopoglossus* and *A. lacrimosus* from western Colombia.

Anomaloglossus atopoglossus and *A. lacrimosus* are visually distinguished from *A. confusus* by a white oblique postocular stripe (absent in *confusus*) and by at least the anterior belly white in life (pale blue or bluish white in *confusus*; often dark spotted in *atopoglossus*). *A. confusus* is appreciably larger

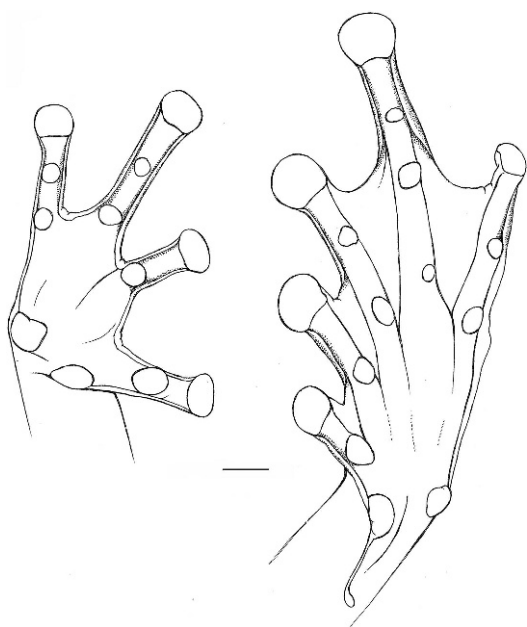


Fig. 3. Right hand and left foot of *Anomaloglossus confusus*, new species (AMNH A-104819, holotype). Scale line = 1 mm.

than *A. lacrimosus* and slightly larger than *A. atopoglossus*, as shown by comparison of snout-vent lengths (SVL):

A. confusus: ♂ 21.7 mm ($n = 1$), ♀ 23–26 mm ($\bar{x} = 24.2$, $n = 6$)

A. lacrimosus: ♂ 15.8 mm ($n = 1$), ♀ 17.7–19.6 mm ($\bar{x} = 18.7$, $n = 9$)

A. atopoglossus: ♂ 18.5–20.7 mm ($\bar{x} = 19.7$, $n = 19$), ♀ 21.7–25.2 mm ($\bar{x} = 23.3$, $n = 16$)

MEASUREMENTS (IN MM) OF HOLOTYPE: The specimen is an adult female, as shown by presence of convoluted oviducts and enlarged ova. Length from snout to vent 23.7; tibia length between heel and outer surface of flexed knee 12.1; greatest width of body ≈ 10 ; head width between angles of jaws, and between outer edges of upper eyelids, 8.2, 6.9 respectively; approximate width of interorbital area 2.5; head length (sagittal) from tip of snout to angle of jaw ≈ 7 ; tip of snout to center of naris (sagittal) 0.9; center of naris to anterior edge of eye 2.0; distance between centers of nares 3.2; eye length from anterior to posterior edge 3.2; horizontal diameter of tympanum about 1.5; corner of mouth to lower edge of

tympanic ring 0.7; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 6.8; width of disc of third finger (and width of penultimate phalanx below disc) 1.1 (0.7); width of discs (and penultimate phalanges below discs) of third and fourth toes 1.2 (0.8) and 1.2 (0.8), respectively.

DESCRIPTION

The type series comprises 16 specimens from four localities in northwestern Ecuador. One adult male and six adult females are included, the other specimens being juveniles. Size and proportions are summarized in table 1 for all specimens, including juveniles. Measurements and proportions given in the following description are for adults only.

MORPHOLOGY: Adult male (KU 166158) 21.7 mm SVL; testes unpigmented (white), large, right testis 3.8 mm long, slightly longer than eye (for illustration of large testes of referred specimen MHNG 19107 see Coloma, 1995: 10, fig. 5). Adult females 23.0–26.0 mm SVL ($n = 6$; $\bar{x} = 24.22 \pm 0.45$); oviducts of adults large and convoluted, unpigmented (white); mature ova yellowish brown (in contrast to white or cream immature ova) but lacking dark pigmented animal pole, large, approximately 3 mm in diameter (measured in KU 221616). An elongate, conical, smooth (nonpapillate), unretracted median lingual process with pit is present in all specimens (fig. 2, upper).

Dorsal surfaces weakly granular in life (fig. 1), becoming smooth in preservative; ventral surfaces smooth. A usually well-developed cloacal tubercle at base of each thigh (see Grant et al., 1997, p. 25, fig. 11); a small round postrictal tubercle. Head width between angles of jaws 34%–39% of SVL. Snout sloping, in profile slightly pointed to rounded, in dorsal and ventral view either rounded with median point or broadly rounded (outline drawings in Myers, 1991, figs. 8A, 8B). Canthus rostralis gently rounded (e.g., AMNH A-104820) to sharply defined (e.g., KU 221616). Loreal region flat or weakly concave, vertical or barely sloping outward to lip. Eye-naris distance 57–71% of eye length.

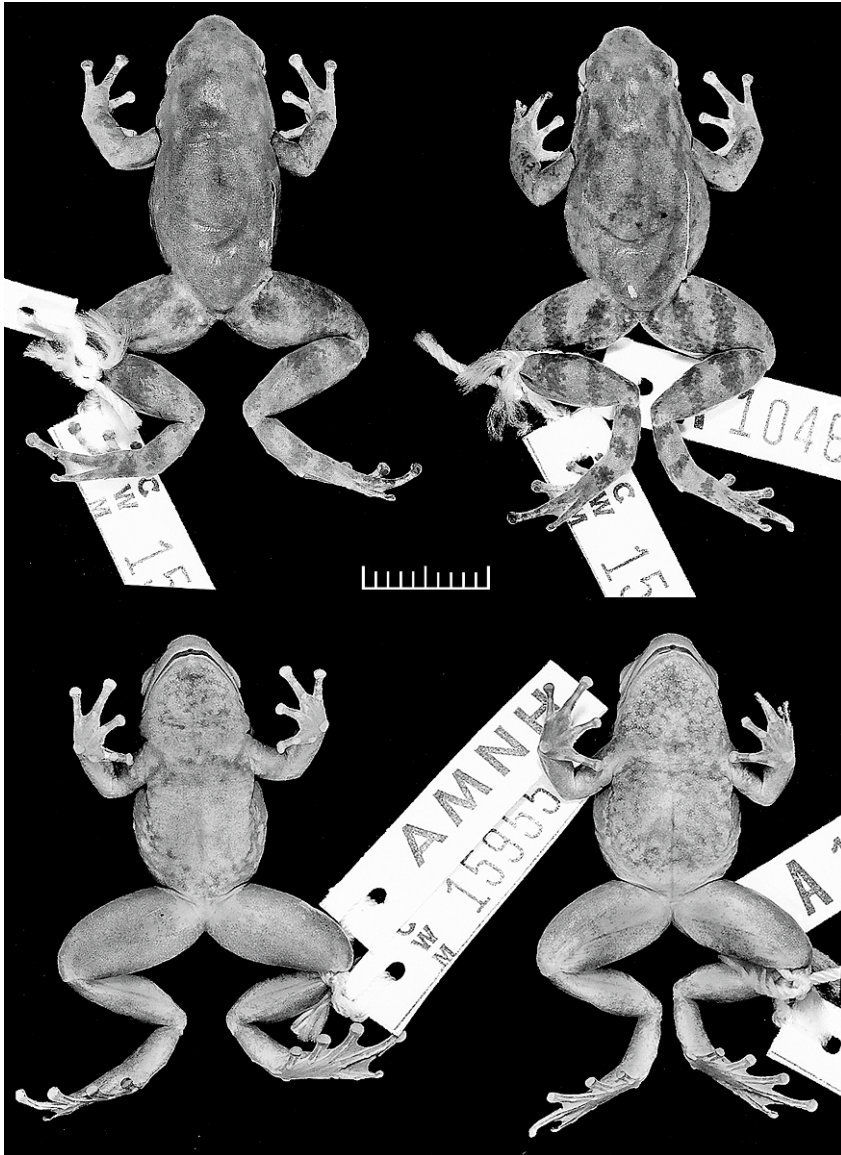


Fig. 4. *Anomaloglossus confusus*, new species. Dorsal and ventral views of two adult females, showing minor variation in color pattern. AMNH A-104819 (holotype) on left, AMNH A-104820 (paratopotype) on right. Scale = 10 mm.

Nares visible from in front, barely visible from above or below, slightly protuberant, directed posterodorsad. Tympanum well defined, concealed posterodorsally by low supratympanic bulge formed by superficial slip of m. depressor mandibulae. A pronounced, usually ventrally elongate or (in one specimen) round bulge at the anterior edge of the upper arm overlies the lower part of the m. latissimus

dorsi.⁵ Teeth present on maxillary arch.

⁵The m. dorsalis scapulae appears not to contribute to the bulge, as it is a narrow, relatively small muscle that lies anteriomedial to the large triangular m. latissimus dorsi. The latter originates as a broad thin sheet of muscle that thickens and bulges proximolaterad. When round (in AMNH A-104820), the bulge has the appearance of a diffuse preaxillary tubercle. (Dissections based on AMNH A-104820 and KU 221616, both adult females.)



Fig. 5. *Anomaloglossus confusus*, new species. Dorsal and ventral views of an adult male paratype (KU 166158). Scale = 10 mm.

Hand length 29%–31% of SVL, 76%–92% of greatest head width. Finger discs weakly to moderately expanded. Finger III not swollen. Fringes (sensu Grant et al., 2006: 66; see also Myers and Donnelly, 2008: 43) present on pre- and postaxial edges of all fingers of MHNG 2558.60–2558.61 and KU 221616 (three largest specimens); remaining specimens with weaker (but still well defined) fringes on preaxial edges of fingers II and III and strong dermal thickening (but not fringes) on other edges of fingers. Hand webbing absent. Metacarpal fold present. Appressed fingers I and II subequal in length (II usually slightly longer); II > I when measured from digit tip to base of palmar tubercle (Character 5, State 1 of Grant et al., 2006: 64). Finger II extends to middle of the distal subarticular tubercle of finger III; finger IV extends beyond the distal subarticular tubercle of finger III. Relative appressed finger lengths III > IV > II \approx I (fig. 3). Subarticular tubercles 1–1–2–2. All tubercles strongly protuberant; subarticular and thenar tubercles elliptical; palmar tubercle subcircular.

Tibia and foot length 47%–53% and 45%–52% of SVL, respectively. Relative lengths of appressed toes IV > III > V > II > I (fig. 3). Toe III extends to distal edge of ultimate

subarticular tubercles of toe IV; toe V extends approximately midway between penultimate and ultimate subarticular tubercles of toe IV. Extensive webbing present between all toes; webbing formula I 1–(1 $\frac{2}{3}$ –2) II 1–(2–2 $\frac{1}{2}$) III (1–1 $\frac{1}{2}$)–(1 $\frac{1}{2}$ –2 $\frac{1}{2}$) IV (2–2 $\frac{1}{2}$)–(1–1 $\frac{1}{3}$) V. Where the webbing fails to reach the disc, it extends distally as a narrow fringe, which turns downward on each side of toe IV and on the preaxial side of toe III. Outer metatarsal fold strong. Discs moderately expanded. Tubercles strongly protuberant. Subarticular tubercles 1–1–2–3–2. Inner metatarsal tubercle elongate. Outer metatarsal tubercle subcircular, diameter roughly one-half the length of inner metatarsal tubercle. Medial metatarsal tubercle absent, but thickening of skin is notable in some specimens (for discussion of relevance see Myers et al., 1991: 23–24). Tarsal keel well defined, straight or weakly curved, slightly enlarged proximally but not forming tubercle-like structure, extending diagonally from inner metatarsal tubercle along distal half of tarsus.

COLOR PATTERN: In life (fig. 1), the holotype and paratopotypes were very dark olive green—appearing virtually black in some light and in the photographs—with a few bronzy tan dots scattered on sides of body and with

TABLE 1
Size and Proportions of *Anomaloglossus confusus*, New Species

Character	N	Mean ± 1 S.E.	S.D.	C.V. (%)	Range
Snout-vent length (SVL) in mm	1 ad. ♂	21.70	—	—	21.7
	6 ad. ♀	24.22 ± 0.45	1.10	4.56	23.0–26.0
	9 juv.	15.63 ± 0.57	1.70	10.86	13.0–18.7
Tibia length ^a /SVL	1 ad. ♂	0.525	—	—	0.53
	6 ad. ♀	0.511 ± 0.010	0.024	4.71	0.47–0.53
	9 juv.	0.535 ± 0.013	0.038	7.03	0.50–0.62
Head width ^b /SVL	1 ad. ♂	0.355	—	—	0.36
	6 ad. ♀	0.353 ± 0.007	0.018	5.17	0.34–0.39
	7 juv.	0.378 ± 0.004	0.012	3.14	0.36–0.39
Center naris to edge eye/eye length	1 ad. ♂	0.613	—	—	0.61
	6 ad. ♀	0.637 ± 0.022	0.053	8.34	0.57–0.71
	6 juv.	0.608 ± 0.015	0.036	5.95	0.56–0.64
Hand length ^c /SVL	1 ad. ♂	0.300	—	—	0.30
	6 ad. ♀	0.301 ± 0.004	0.011	3.65	0.29–0.31
	6 juv.	0.287 ± 0.007	0.017	5.99	0.27–0.31
Hand length/head width	1 ad. ♂	0.844	—	—	0.84
	6 ad. ♀	0.853 ± 0.023	0.055	6.48	0.76–0.92
	6 juv.	0.761 ± 0.019	0.047	6.23	0.72–0.82
Width 3rd-finger disc/finger width below disc ^d	1 ad. ♂	1.667	—	—	1.67
	6 ad. ♀	1.518 ± 0.039	0.096	6.34	1.38–1.57
	6 juv.	1.317 ± 0.048	0.127	9.67	1.17–1.50

^aTibia length is the shank measured from heel to the convex surface of knee (with limb segments flexed at right angles), roughly approximating length of the tibiofibula.
^bGreatest head width as measured between jaw articulations.
^cHand length measured from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger.
^dDigit width measured near distal end of penultimate phalanx.

vague crossbands on the limbs. A pale mark atop the base of the arm appears (based on a color transparency of holotype) to have been golden bronze with a small area of pale blue. The throat and venter were pale blue; ventral limb surfaces were grayish brown, some with a slight suffusion of orange under the hind limbs. Iris pale green in the holotype, pale bronze in the other specimens, with dense black venation in all.

William E. Duellman (field notes) described KU 166157–166158 as brown with dark brown markings dorsally and with bluish cream flecks laterally; throat and ventral surfaces of limbs pale gray; belly bluish white with gray reticulations; iris dull bronze.

In preservative (figs. 4, 5), dorsum brown or pale brown, with dark brown markings varying from conspicuous, well-defined dark

brown interocular chevron, scapular “W,” and sacral bands (e.g., MHNG 2558.60) to faint, diffuse, and irregularly distributed blotches (e.g., AMNH A-104819). Pale lateral stripes absent, but flank often with small, scattered cream spots. Loreal region (and usually dorsal snout) dark brown, the dark color extending posteriorly through eye and above supratympanic bulge. Postocular region anterior and ventral to supratympanic bulge pale brown, lacking pale oblique postocular stripe. Upper lip area brownish tan, paler than adjacent loreal region but not forming a discrete stripe and lacking any pale spots.

Ventral coloration cream with dark brown reticulation, usually darker and more conspicuous on throat than on belly, not sexually dimorphic.

Exposed surfaces of arms brown or brown with dark brown blotches or crossbands.

Concealed surfaces of arms pale brown. Palmar surfaces pale brown. Hand dorsally brown. Fingers I and II dorsally cream or pale brown with brown blotches, fingers III and IV brown with cream blotches (i.e., inner fingers paler than outer fingers).

Exposed surfaces of legs brown or pale brown with variably defined dark brown transverse bands on thigh, shank, and foot that align on flexed limb. Anterior surface of thigh solid brown; posterior surface brown or pale brown with diffuse dark brown mottling. Pale paracloacal marks absent. Groin brown, lacking flash mark. Concealed surfaces of shank and foot cream or cream with diffuse brown stippling or mottling. Plantar surfaces pale brown. Webbing cream, often with brown stippling, stronger adjacent to toes.

DISTRIBUTION AND ECOLOGY

Anomaloglossus confusus occurs on the Pacific versant of the Andes in northwestern Ecuador, at known elevations of 600–1540 m (see distribution map [as *Colostethus chocoensis*] in Coloma, 1995: fig. 10).

Judged from the distribution, and observation at the type locality, the habitat is rocky clear-water streams in lower montane rain forest. The holotype and paratopotypes were found by day, mainly under rocks along the edge of a fast-flowing stream, but individuals also were seen moving actively among the rocks. At another locality, W.E. Duellman found two specimens (probably sleeping) perched on leaves of herbs 10 cm over water at night (Duellman's field notes for April 8, 1975).

At the type locality, *Anomaloglossus confusus* was microsympatric with *Hyloxalus infraguttatus* (Boulenger) and *Epipedobates tricolor* (Boulenger), although the latter occurred more commonly on slopes away from the stream. For other localities, Coloma (1995: 26) recorded sympatry with *Hyloxalus awa* (Coloma), *H. brevipartus* (Rivero and Serna), *H. toachi* (Coloma), and *Epipedobates espinosai* (Funkhouser).

DISCUSSION

There are only three named trans-Andean species of *Anomaloglossus*—*A. confusus*, new species from lower Andean slopes in north-

western Ecuador, and *A. atopoglossus* (Grant, Humphrey, and Myers) and *A. lacrimosus* (Myers) from western Colombia. The remaining 18 cis-Andean species comprise a Guayana Shield radiation, with species distributed north of the Amazon River between elevations of 50 m (e.g., *A. stepheni* [Martins]) and 2700 m (*A. roraima* [La Marca]). Due to lack of material trans-Andean species have not been included in quantitative phylogenetic analyses, but their placement in *Anomaloglossus* with the cis-Andean species is supported by the synapomorphic presence of the median lingual process (Grant et al., 2006).

As suggested by their extensively webbed feet and collection data, the three trans-Andean species of *Anomaloglossus* all appear to be riparian, occurring under and among rocks along clear-water streams in or near forest. The vocalization of *A. atopoglossus* is a frequency modulated series of high-pitched notes (Grant et al., 1997: 27–28, fig. 13); calls are unknown for *A. confusus* and *A. lacrimosus*. The cis-Andean species of *Anomaloglossus*—more diverse in terms of number of species, morphology, and life history—include robust, extensively webbed, riparian species like the trans-Andean taxa, small, slender species almost free of webbing, and phytotelm breeders with nidicolous and oophagous larvae (Grant et al., 2006).

The holotype and paratopotypes of *Anomaloglossus confusus* exuded a milky secretion from the dorsal and lateral body surfaces during fixation of the specimens in formalin; unfortunately, a skin sample in methanol had not been first obtained for analysis. Although secretions from dendrobatoid granular glands (Neuwirth et al., 1979) may contain defensive alkaloids having noxious or toxic properties, the mucous glands have not been ruled out as a source of some milky and possibly defensive secretions (e.g., Daly et al., 1987: 1065–1069). Skin alkaloids have not been documented in *Anomaloglossus* or in any other member of the family Aromobatidae (Grant et al., 2006: 157–163), but an extraordinary alternative form of chemical defense occurs in at least one species of the type genus. *Aromobates nocturnus* produces both a sticky mucus and a volatile compound that has a vile mercaptan-like odor (Myers et al., 1991: 14, 16). Field biologists need to be alert for new kinds of

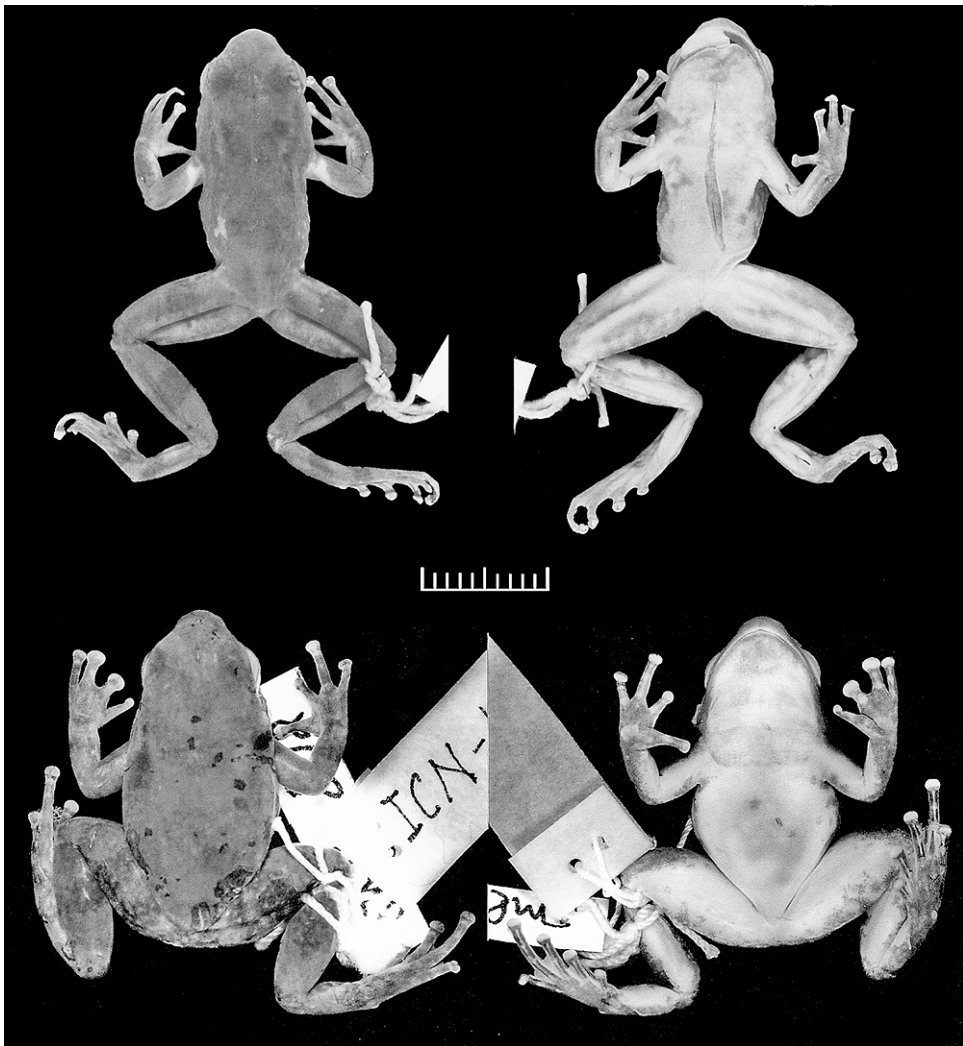


Fig. 6. *Hyloxalus chocoensis* (Boulenger) in dorsal and ventral view. **Upper:** Subadult female holotype (BMNH 1947.2.14.27). **Lower:** Adult male (ICN 47971). Scale = 10 mm.

chemical defense among dendrobatoids and other tropical frogs.

A NOTE ON *HYLOXALUS CHOCOENSIS* (BOULENGER)

Figures 2 (lower), 6

Hyloxalus chocoensis s.s. has long been known only from the holotype, a subadult female (fig. 6, upper), collected at Noanamá on the lower Río San Juan, Depto. Chocó, in western Colombia (Boulenger, 1912). The

specimen described below is the first adult specimen known to us that appears assignable to *H. chocoensis* (fig. 6, lower). The description below parallels Myers' (1991) redescription of the subadult female holotype (BMNH 1947.2.14.27).

The specimen (ICN 47971) is an adult male 26.0 mm SVL, with large paired vocal slits and a shallow subgular vocal sac; the right testis is white, 1.8 mm long. There is no median lingual process.

COLLECTION DATA: ICN 47971 (field no. JMR 892), collected near Campamento

Ingeominas (ca. 6°42'N, 76°27'W), near the headwaters of Río Amparradó, Municipio Dabeiba, Departamento Antioquia, Colombia, 805 m elevation, by Juan Manuel Renjifo.

MEASUREMENTS (IN MM): Length from snout to vent 26.0; tibia length between heel and outer surface of flexed knee 12.8; greatest width of body 11.8; head width between angles of jaws, and between outer edges of upper eyelids, 10.3, 8.0 respectively; approximate width of interorbital area 3.0; head length (sagittal) from tip of snout to angle of jaw 7.4; tip of snout to center of naris (sagittal) 1.0; center of naris to anterior edge of eye 2.3; distance between centers of nares 3.5; eye length from anterior to posterior edge 4.0; horizontal diameter of tympanum about 1.5 (estimated, posteriorly concealed); corner of mouth to lower edge of tympanic ring 0.5; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 7.5; width of disc of third finger (and width of penultimate phalanx below disc) 1.2 (0.7); width of discs (and penultimate phalanges below discs) of third and fourth toes 1.2 (0.8) and 1.3 (0.8), respectively.

MORPHOLOGY: Skin nearly smooth dorsally (under high magnification, appearing weakly granular posteriorly where patches of stratum corneum are lacking); skin smooth ventrally. Greatest head width (between angles of jaws) 40% of SVL. Snout sloping, rounded in profile, rounded in dorsal and ventral view. Nares visible from in front, barely visible from above or below; posterior rim of naris raised slightly and bearing a low, rounded prominence posterodorsad to naris. Canthus rostralis rounded; loreal region slightly concave, nearly vertical, sloping slightly outward to lip. Interorbital region slightly wider than upper eyelid. Length of snout in lateral view shorter (80%) than eye length; center naris to edge of eye 58% of eye length. Tympanum evident but concealed posterodorsally, seemingly one-third or more of eye length. Teeth present on maxillary arch.

Hand moderate, its length 29% of SVL, 73% of greatest head width. Relative lengths of appressed fingers on right hand (left malformed) $\text{III} > \text{IV} > \text{II} > \text{I}$; tip of finger I reaching disc of finger II; finger III not swollen. Discs of all fingers moderately expanded; third finger disc 1.7 times wider than distal end of adjacent phalanx. Base of palm with a large

rounded median metacarpal tubercle, a smaller elliptical inner metacarpal tubercle on base of first finger; one or two subarticular tubercles (one each on fingers I, II; two each on fingers III, IV); all tubercles low, with slightly rounded surfaces. A weak (narrow), fleshy keel-like fringe along sides of fingers; fringe on median side of first finger extending faintly to inner metacarpal tubercle; fringe on lateral side of fourth finger continuous with a weak outer metacarpal fold extending to large palmar (outer metacarpal) tubercle.

Hind limbs relatively long, with heel of appressed limb reaching between eye and tip of snout; tibia 49% of SVL. Relative lengths of appressed toes $\text{IV} > \text{III} > \text{V} > \text{II} > \text{I}$; first toe reaching middle of subarticular tubercle of second. Toe discs noticeably expanded, those on third and fourth toes 1.3–1.6 times wider than adjacent phalanges. Feet webbed to base of each toe disc, although the web is reduced to a fringe on medial sides of toes II–III and on both sides of toe IV distal to the second subarticular tubercle; the proximal part of the fringe tends to fold downward along each side of toe IV; a well-developed fringe along the outer free edges of toes I and V. One to three nonprotuberant subarticular tubercles; a small round outer metatarsal tubercle and a slightly larger elliptical inner metatarsal tubercle. A strong tarsal keel, on distal half of tarsus, is continuous with fringe on free edge of first toe; no tubercle or elevation at proximal end of tarsal keel.

COLOR PATTERN (FIG. 6 LOWER): Dorsal surfaces gray owing to detaching stratum corneum, under which the head and body appear to be covered overall in a very fine brown reticulum. (There is no discernible interocular bar or dorsal dark marking.) A few large irregular pale spots along the lower sides merge into the ventral color. (Oblique lateral and ventrolateral stripes lacking.) The forelimbs are brown, with vague crossbands; fingers I–II and tops of finger discs 1–3 are partly whitish. A well-defined pale axillary spot (flash mark). The hind limbs are brown with crossbands on thigh and shank; rear of thighs brown with vague mottling. Ventral surfaces whitish, with suffusions of pale brown on the chin and across throat. Palms and soles brown.

A pale ill-defined streak on snout, from near nostril to lower edge of eye; upper lip below

streak is brown, becoming pale and pigmentless along edge of mouth. An ill-defined pale area extending from the lower rear edge of the eye across the upper edge of the tympanum to the forelimb, forming a narrow, very vague post-ocular stripe.

SUMMARY NOTES ON *HYLOXALUS CHOCHOENSIS* (BOULENGER)

The genus *Hyloxalus* is currently defined by unambiguous DNA sequence transformations obtained from 17 of the 57 species currently assigned to the genus (Grant et al., 2006: 168–169). There are no unambiguous morphological synapomorphies. It should be noted that the two specimens of *H. chochoensis* seen by us lack one or two of the general characteristics listed for *Hyloxalus* by Grant et al. (2006: 169): (1) a pale oblique lateral stripe is lacking in these specimens; (2) there is no indication in either specimen that dorsal skin texture is “posteriorly granular” (however, skin granulation often is diminished in preservative and weak granulation may be lost).

The holotype of *Hyloxalus chochoensis* was judged by Myers (1991: 3) to be a “subadult or sexually inactive female” based on examination of the ovaries and oviducts. Although it was said to measure 26 mm in the original description, Myers obtained repeated measurements of 24.3 mm SVL with dial calipers. Adult female *Hyloxalus* are expected on average to be larger than males. Since the holotype is smaller than the adult male (26.0 mm) described above, we conclude that it had yet to reach sexual maturity and that it is indeed a “subadult.”

The specimen ICN 47971 is in general agreement with Myers’ (1991) redescription of the holotype. The holotype has two broad V-shaped blackish brown markings, one between the eyes and the other between the upper arms—but these are very ill defined and best viewed when the specimen is immersed in liquid. The stratum corneum is becoming detached on the adult male, giving it an overall gray appearance. Initially we saw no indication of dark dorsal markings when the specimen was immersed in liquid and examined under bright light, but a hint of vague dark markings was captured in the photograph (fig. 6, lower). The

dorsal coloration otherwise appears to consist of a very fine brown reticulum.

Differences appear to be minor. Both have a pale flash mark in the axilla, which extends dorsad onto the base of the arm in the holotype. The male has a broad pale brown band across the base of the throat, but it appears to be associated with the male vocal sac. The hands are similar, with very narrow keel-like fringes on the fingers; the fringe on the median side of finger I extends as a faint fold to the inner metacarpal tubercle; the fringe on the lateral side of finger IV is continuous with a weak outer metacarpal fold extending to the outer metacarpal tubercle (Myers, 1991: fig. 2). The feet also are similar, with extensive webbing that reduces to well-developed fringes along the medial sides of toes II–IV;⁶ however, the male also has the webbing reduced to a fringe on the lateral side of toe IV, although webbing is well developed on the lateral side of toe IV in the holotype (Myers, 1991: fig. 2).

A NOTE ON THE NAME *HYLIXALUS* BOULENGER, 1882

Boulenger (1912) originally described *Hyloxalus chochoensis* as “*Hylixalus*” *chochoensis*. The earlier-emended generic name *Hylixalus* Boulenger (1882: 137) was a presumed “correction” of *Hyloxalus* Jiménez de la Espada (1870), which had been explicitly derived from Greek *hylē* (forest) + *ixalos* (leaping).⁷ Nonetheless, *Hylixalus* Boulenger

⁶Myers and Donnelly (2008: 43) noted the presence of the usually overlooked character “folded flaplike fringes” in the holotype of *Hyloxalus chochoensis*, in which “the fringes along the distal half of toe IV are abruptly folded, as are the fringes on the medial sides of toes II and III and the outer fringing along toes I and IV” (see also Grant et al., 2006: 66).

⁷The etymology as given by Jiménez de la Espada (1870: 59) was “Υλη, sylvia; Ιξαλος, saltatorius” [sic, initial letters of the Greek words lack the aspiration marks usually shown nowadays]. Boulenger merely combined the transliterated *hylē* + *ixalos* by deleting the final letter in *hylē* and Latinizing *ixalos*, whereas Jiménez de la Espada had additionally added the connective -o- (as commonly done following Greek stems ending in a consonant) and also deleted the first letter of the second element (probably for euphony). With rare exceptions such as Linnaeus, few emenders ever published rules or principles for changing names whose constructions they thought objectionable; they relied on a “consent of the learned,” which (in the matter of botanical and especially zoological Latin and Greek) is not readily articulated in this day and age.

is an “unjustified emendation” of *Hyloxalus* under modern rules of nomenclature and therefore it is a junior objective synonym with its own author and date (ICZN, 1999: art. 33.2.3); it is an available name.

Hylixalus was incorrectly considered to be an “incorrect subsequent spelling” (ICZN, 1999: art. 33.3) by Grant et al. (2006: 11). However, Boulenger (1882: ix, 4, 137, 138) consistently referenced the original spelling *Hyloxalus* in the generic and two species synonymies—sufficient evidence that his “*Hylixalus*” was a “demonstrably intentional change in the original spelling” (ICZN, 1999: art. 33.2). Therefore, *Hylixalus* Boulenger, 1882, should be added to the list of available dendrobatoid genus-group names in Grant et al. (2006: 210, appendix 2).

It is to be noted that the spelling “*Hylexalus*” appears at one place in the index to Boulenger’s *Catalogue* (1882: 485). There is no internal evidence to interpret this as anything other than a simple misspelling (i.e., an “incorrect subsequent spelling”) of *Hylixalus*, which was used by Boulenger (1882, 1912, 1919) over a long period of time.

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