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A NEW SPECIES OF SEMIARBOREAL TOAD WITH A SALAMANDER-LIKE EAR (ANURA: BUFONIDAE: *RHINELLA*)

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Abstract: We describe a new species of the *Rhinella acrolopha* group (previously *Rhamphophryne*) from mid-elevations (1800–2500 m) of the Cordillera Occidental of Colombia. It is found exclusively in cloud forest habitats and is not associated with streams or other bodies of water. The species is characterized by possessing eight presacral vertebrae, fusion of the sacrum and urostyle, and nuptial excrescences in adult males, and in lacking conspicuous cranial ornamentation and vocal slits. The most striking characteristic of this species is its middle ear, which lacks a tympanic membrane and annulus but possesses a short stapes that articulates with the palatoquadrate and squamosal in a manner similar to the middle ear of many salamanders. A population of this species in the Serranía de los Paraguas seems to be stable despite drastic declines in many sympatric species.

Resumen: Describimos una nueva especie perteneciente al grupo *Rhinella acrolopha* (anteriormente *Rhamphophryne*) de elevaciones medias (1800–2500 m) en la Cordillera Occidental de Colombia. La nueva especie ha sido encontrada exclusivamente en hábitat de bosques nublados y no está asociada con quebradas u otros cuerpos de agua. La especie se caracteriza por poseer ocho vértebras presacrales, fusión del sacro y el uróstilo, excrecencias nupciales en machos adultos, ausencia de crestas craneales agrandadas y ausencia de hendiduras vocales en machos adultos. La característica más destacada de la nueva especie es su oído medio, el cual carece de membrana timpánica y anillo timpánico pero presenta un estribo reducido que se articula con el palatocuadrado y el escamoso, semejante a lo que se encuentra en salamandras. Una población de esta especie en la Serranía de los Paraguas al parecer se mantiene estable, a pesar de la disminución drástica de poblaciones de especies simpátricas.

Key words: Amphibia; Andes; Colombia; Cordillera Occidental; Middle ear; South America; *Rhinella acrolopha* Group; Systematics; Taxonomy

Fieldwork and detailed study of existing natural history collections continue to reveal new species of Colombian amphibians, especially in cloud forest habitats at moderate elevations of the three Andean cordilleras (Lynch et al., 1997). It is not uncommon for newly discovered species to challenge prior understanding as a result of their unexpected phylogenetic positions or morphological or behavioral characteristics. Here, we describe a new species of bufonid from the Pacific slopes of the Cordillera Occidental that possesses a middle ear unlike that of any other anuran but that resembles that of many salamanders.

After decades of stagnation, bufonid generic taxonomy is being extensively amended to reflect phylogenetic relationships. Previously, this new species would have been referred to *Rhamphophryne* Trueb, 1971 (type species: *Rhamphophryne acrolopha* Trueb, 1971), a group of nine recognized species (Fouquet et al., 2012; Frost, 2014), eight of which occur in Colombia (Grant, 2000 "1999"). On the basis of consideration of their own results and those of Frost et al. (2006) and Pramuk (2006), however, Chaparro et al. (2007) placed *Rhamphophryne* in the synonymy of *Rhinella* Fitzinger, 1826, a heterogeneous group presently composed of 86 species (Frost, 2014), to rectify the paraphyly of *Chaunus* Wagler, 1828 sensu Frost et al. (2006). The authors did not challenge the monophyly of *Rhamphophryne*, which is supported by limited morphology (see Frost et al., 2006:217) and has been upheld in phylogenetic analyses of DNA sequences (Van Bocxlaer et al., 2010; Pyron and Wiens, 2011; see "Phylogenetic relationships," below). Consequently, we follow Chaparro et al. (2007) in describing this toad as a new species of *Rhinella* and, to facilitate comparisons, refer to the species of

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TABLE 1.—Measurements in mm (minimum–maximum, $\bar{X} \pm$ SE) of sampled adult *Rhinella paraguas* sp. nov. See text for measurement definitions.

	Males (n = 12)	Females (n = 20)
Snout–vent length	31.3–41.7, 35.5 ± 0.8	40.6–51.4, 45.1 ± 0.7
Forearm length	7.4–10.6, 8.6 ± 0.2	10.1–13.3, 11.2 ± 0.2
Hand length	7.3–10.2, 8.8 ± 0.3	11.1–13.5, 12.1 ± 0.2
Shank length	9.8–12.8, 11.4 ± 0.3	13.3–16.9, 14.8 ± 0.2
Foot length	9.5–13.5, 11.8 ± 0.3	13.3–18.2, 15.8 ± 0.3
Head width	10.2–14.6, 11.8 ± 0.3	13.1–16.7, 14.9 ± 0.2
Head length	9.6–11.8, 10.6 ± 0.2	12.2–14.4, 13.0 ± 0.1
Eyelid length	3.9–4.7, 4.4 ± 0.1	4.8–5.7, 5.3 ± 0.1
Eye–naris distance	2.0–2.9, 2.5 ± 0.1	2.6–3.5, 3.0 ± 0.1
Internarial distance	3.5–4.3, 3.9 ± 0.1	4.0–4.8, 4.5 ± 0.1
Snout length	4.7–5.8, 5.2 ± 0.1	5.4–6.4, 6.1 ± 0.1
Interorbital distance	3.1–5.0, 4.2 ± 0.2	4.3–5.8, 5.0 ± 0.1
Naris–snout distance	2.3–3.1, 2.7 ± 0.1	2.3–3.5, 3.1 ± 0.1

the former *Rhamphophryne*—including *R. acrolopha* (Trueb, 1971), *R. festae* (Peracca, 1904), *R. lindae* (Rivero and Castaño, 1990), *R. macrorhina* (Trueb, 1971), *R. nicefori* (Cochran and Goin, 1970), *R. rostrata* (Noble, 1920), *R. ruizi* (Grant, 2000 "1999"), *R. tenrec* (Lynch and Renjifo, 1990), and *R. truebae* (Lynch and Renjifo, 1990)—as the *Rhinella acrolopha* group.

Materials and Methods

Diagnostic comparisons are restricted to the *R. acrolopha* group (see Appendix for specimens examined). The diagnosis follows that of Trueb (1971), as modified by Grant (2000 "1999"). Measurements (±0.1 mm) were taken with dial or digital calipers. Unless otherwise noted, measurements and proportions are reported for adults only, as determined by examination of gonads and secondary sex characters. Males with well-developed nuptial excrescences and enlarged testes were scored as adults, those with inconspicuous nuptial excrescences (visible under high magnification as a small, slightly swollen patch of skin) and weakly enlarged testes as subadults, and those lacking nuptial excrescences altogether as juveniles. Females with expanded, convoluted oviducts and enlarged ova were considered to be adults, those with only weakly expanded, non- or weakly convoluted oviducts and poorly differentiated ova to be subadults, and those with small, undifferentiated ova and unexpanded, straight oviducts to be juveniles. Statistical summaries of measurements are reported as mean ±1 SE. The following measurements-were taken: snout–vent length (SVL); forearm length between flexed elbow and proximal edge of palmar tubercle; hand length between proximal edge of palmar tubercle and tip of Finger IV; shank length from outer edges of flexed knee to heel; foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV; head width between angle of jaws; head length diagonally from corner of mouth to tip of snout; upper eyelid length; eye–naris distance from anterior corner of eye to center of naris; internarial distance between centers of nares; snout length between anterior corner of eye and tip of snout; interorbital distance; and naris–snout distance between center of naris and tip of snout.

For hand morphology, we followed Fabrezi and Alberch (1996) in considering digit I of other tetrapods to be absent in Anura and number fingers accordingly. The webbing formulation is that of Savage and Heyer (1967), whereby webbing is quantified by the number and proportion of free phalanges (see also Myers and Duellman, 1982; Savage and Heyer, 1997), with fingers renumbered according to Fabrezi and Alberch (1996). Jaw muscle terminology follows that of Haas (2001). To examine middle ear anatomy, cartilage and bone in the otic region were stained with 30 mL of acetic acid, 70 mL of ethanol, and 20 mg of alcian blue for ca. 60 min and, following neutralization in a saturated sodium borate solution, a concentrated solution of alizarin red S dissolved in 70%

ethanol (cf. Springer and Johnson, 2000) for ca. 30 min.

The WGS84 datum is used for all coordinates. Institutional abbreviations are CD (Colección Vertebrados de Docencia, Universidad del Valle, Cali, Colombia), CSJ (Colegio San José, Medellín, Colombia), ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia), KU (University of Kansas Natural History Museum, Lawrence, USA); LACM (Natural History Museum of Los Angeles County, Los Angeles, USA), MHUA (Museo de Herpetologia Natural, Universidad de Antioquia, Medellín, Colombia), MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil), and UV-C (Colección de Anfibios y Reptiles, Universidad del Valle, Cali, Colombia).

Species Description

Rhinella paraguas *sp. nov.*
(Figs. 1–4)

Holotype.—ICN 28816 (field number JDL 18968), an adult female collected in Colombia, Depto. Chocó, Mpio. San José del Palmar, Paso de Galápagos, 20.2 km NW La Carbonera, ca. 4°53′N, 76°16′W, 2100 m, 28 June 1991 by John D. Lynch, Jorge H. Restrepo, Pedro M. Ruiz, and Ricardo Sánchez.

Paratopotypes.—ICN 28811, 28812 (cleared and stained [C&S]), 28813, 28814 (C&S), 28815, 28817, all taken with the holotype.

Paratypes.—All from Colombia. ICN 18266, UV-C 8117–19, 8120 (C&S), 8497, 9314, 9365, 9569, 11474 (C&S), Depto. Chocó, Mpio. San José del Palmar, Paso de Galápagos, ca. 4°53′N, 76°16′W, 2000 m; CD 1503, 2843, UV-C 6971, 9120 (C&S), Depto. Valle del Cauca, Mpio. El Cairo, Reserva Natural Cerro del Inglés, 2150–2500 m; ICN 28797–802, Depto. Chocó, Mpio. San José del Palmar, near border with Depto. Valle del Cauca, 20–24 km from El Cairo cemetery, 1900–2250 m; ICN 28803–08, Depto. Valle del Cauca, Mpio. El Cairo, Vda. Las Amarillas, El Boquerón, 2200–2250 m; UV-C 9163, 9165, 12953–56, 14888–89, 14901, 14907, 14911, 14918–19, 14921–28, 15702, 15703 (C&S), Depto. Valle del Cauca, Mpio. El Cairo, Vda. Las Amarillas, El Boquerón, near border with Depto. Chocó, 4°47.196′N, 76°13.877′W, 2220 m; UV-C 6734–37, Depto. Chocó, eastern slope of Cerro del Torrá, 1900–1940 m; ICN 28809–10, Depto. Chocó, Mpio. San José del Palmar, 5.7 km W summit at El Boquerón, 26 km from El Cairo cemetery, 1900 m; UV-C 14864, Depto. Valle del Cauca, Mpio. El Cairo, forest ca. 1.5-h hike from town of El Cairo, 4°47.170′N, 76°13.791′W, 2140 m; CD 869–70, UV-C 12994–99, 15069–700, 15701 (C&S), Depto. Valle del Cauca, Mpio. Dagua, Cgto. El Queremal, Hda. San Pedro, 1850–2000 m.

Diagnosis.—*Rhinella paraguas* differs from all other species of the *R. acrolopha* group in possessing a short stapes (= columella, plectrum) that articulates with the palatoquadrate and squamosal and lacking a tympanic annulus and tympanic membrane (stapes, tympanum, and tympanic annulus absent in most species; middle ear complete in *R. lindae* and *R. truebae*). The fusion of the sacrum and urostyle further distinguishes *R. paraguas* from all species of the *R. acrolopha* group except *R. festae* and *R. rostrata* (bicondylar articulation in other species), and it differs from *R. festae* and *R. rostrata* in possessing eight presacral vertebrae (seven in *R. festae* and *R. rostrata*).

Additionally, *Rhinella paraguas* is considerably smaller than *R. lindae*, *R. tenrec*, and *R. truebae* (maximum female SVL = 51.4 mm in *R. paraguas,* 60.8 mm in *R. tenrec*, 64.0 mm in *R. lindae*, and 65.9 in *R. truebae*). It further differs from *R. acrolopha*, *R. nicefori*, and *R. ruizi* by having eight presacral vertebrae (seven in those species), and from *R. acrolopha*, *R. festae*, *R. lindae*, *R. macrorhina*, *R. nicefori*, and *R. truebae* by bearing poorly developed cranial ornamentation (well developed in those species). In possessing nuptial excrescences in adult males, *R. paraguas* differs from *R. acrolopha*, *R. festae*, *R. nicefori*, *R. ruizi*, and *R. tenrec* (absent in those species).

Description.—A moderate-sized species of the *Rhinella acrolopha* group (Table 1): adult male SVL 31.3–41.7 mm ($\bar{X} = 35.5 \pm 0.8$ mm; $n = 12$); adult female SVL 40.6–51.4 mm ($\bar{X} = 45.1 \pm 0.7$ mm; $n = 20$). (1) Eight presacral vertebrae; (2) sacral vertebra fused with

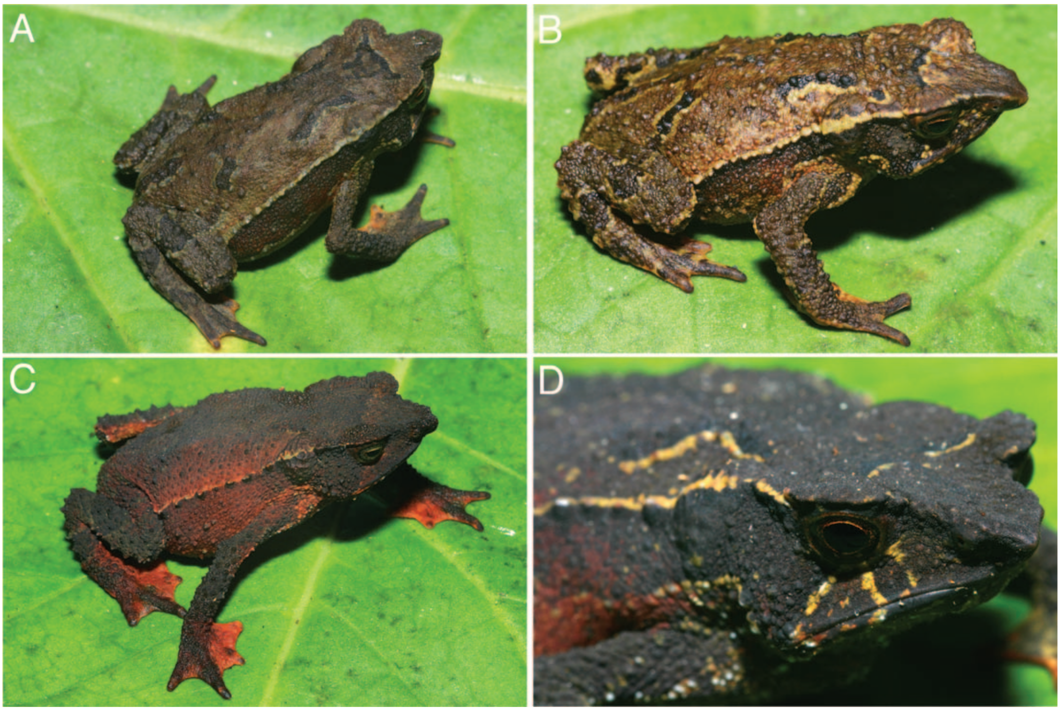

FIG. 1.—*Rhinella paraguas* sp. nov. in life. (A) UV-C 14919, juvenile female, 30.8 mm SVL. (B) UV-C 14911, adult male, 31.3 mm SVL. (C) UV-C 14918, adult female, 43.8 mm SVL. (D) UV-C 14910, adult female, 43.5 mm SVL. (A color version of this figure is available online.)

urostyle; (3) snout long, protuberant, directed anteroventrad; (4) supraorbital crests low; (5) postorbital crests low; (6) supratympanic crests present; (7) pretympanic crests present; (8) occipital crests absent; (9) dorsal tubercles small, conical; (10) oblique-lateral row of tubercles extending from groin to upper eyelid; (11) hands and feet extensively webbed, digits long; (12) subarticular tubercles diffuse or indistinguishable; (13) supernumerary tubercles present; (14) m. tensor fasciae latae elongate; (15) vocal slits absent; (16) nuptial excrescences present in adult males.

Measurements of holotype (in mm).—ICN 28816, adult female. SVL 46.3; forearm length

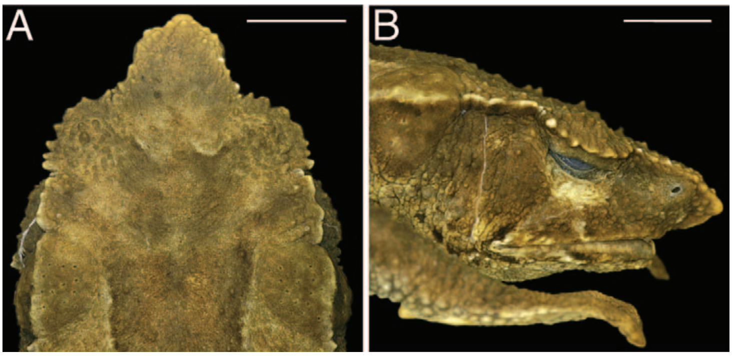

FIG. 2.—The head of *Rhinella paraguas* sp. nov. adult female holotype ICN 28816 in (A) dorsal and (B) lateral views. Scale = 5 mm. (A color version of this figure is available online.)

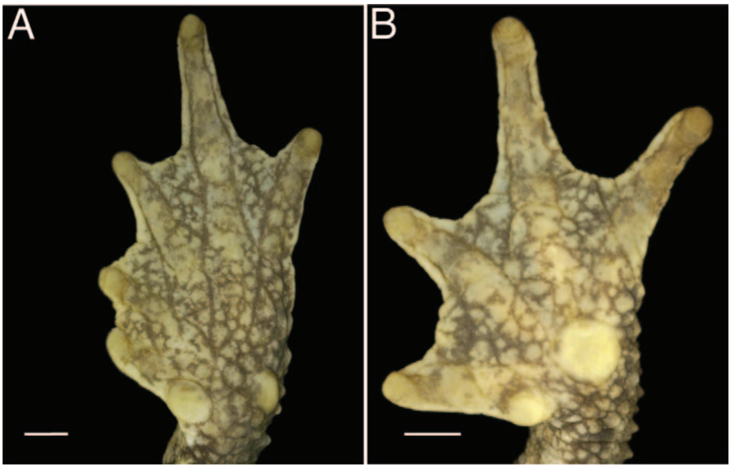

Fig. 3.—The foot (A) and hand (B) of *Rhinella paraguas* sp. nov. adult female holotype ICN 28816. Scale = 2 mm. (A color version of this figure is available online.)

11.7; hand length 12.7; shank length 14.8; foot length 16.8; head width 15.3; head length 13.3; upper eyelid length 5.4; eye–naris distance 2.9; internarial distance 4.8; snout length 6.2; interorbital distance 5.2; naris–snout distance 3.3.

Morphology.—The following is a composite description based on the 74 specimens of the type series. Adult male SVL 31.3–41.7 mm ($\bar{X}$ = 35.5 ± 0.8 mm; n = 12); UV-C 14921 is a juvenile male of 27.0 mm SVL. Mature testes large, granular, dark brown or black with white reticulation. Vocal slits absent. Adult female SVL 40.6–51.4 ($\bar{X}$ = 45.1 ± 0.7 mm; n = 20); UV-C 14907 is a subadult female of 39.5 mm SVL, and the largest juvenile female (UV-C 14928) is 38.2 mm SVL, suggesting that female maturity is reached at approximately 40 mm SVL.

Dorsal surfaces finely spiculate with scattered conical tubercles, sparse on mid-dorsum. Flanks finely spiculate with scattered, large conical tubercles and conspicuous, oblique lateral row of large, conical tubercles, extending from groin, over parotoid macroglands, along supratympanic ridge to outer edge of upper eyelid. Ventral surfaces granular. Tensor fasciae latae muscle short, originating at midlength of ilium. Adductor longus muscle absent.

Head (Fig. 2) triangular in dorsal view. Head width 1.1–1.3 times head length in females, 1.0–1.2 times head length in males, 30–36% of SVL in both sexes. Head length 26–31% of SVL in females, 28–32% of SVL in males (i.e., relative head width similar in both sexes; relative head length greater in males). Snout length 42–51% of head length in females, 45–51% of head length in males. Eye–naris distance in females 44–59% of snout length, 48–69% of upper eyelid length; in males 44–54% of snout length, 45–63% of upper eyelid length. Snout acuminate, often bearing sagittal ridge ventrally between tip of snout and lip. Canthus rostralis elevated to form weak crest, angular in section, exaggerated by tuberculation along canthus rostralis. Loreal region concave, vertical. Nares weakly protuberant, not visible in dorsal view. Pre-, supra-, and postorbital crests not visible externally (i.e., obscured by texture of dermal structures). Occipital crests absent. Supratympanic crests low. Pretympanic crests well defined. Tympanic membrane absent (see description of middle ear, below). Parotoid macroglands well defined, triangular, commencing immediately posterior to supratympanic ridge. Upper eyelids bearing many tubercles of various sizes; conspicuous lateral crenulation continuous with dermal ridge and tubercles that extend from groin, over parotoid macroglands, and along supratympanic ridge. Dorsal and lateral surfaces of head

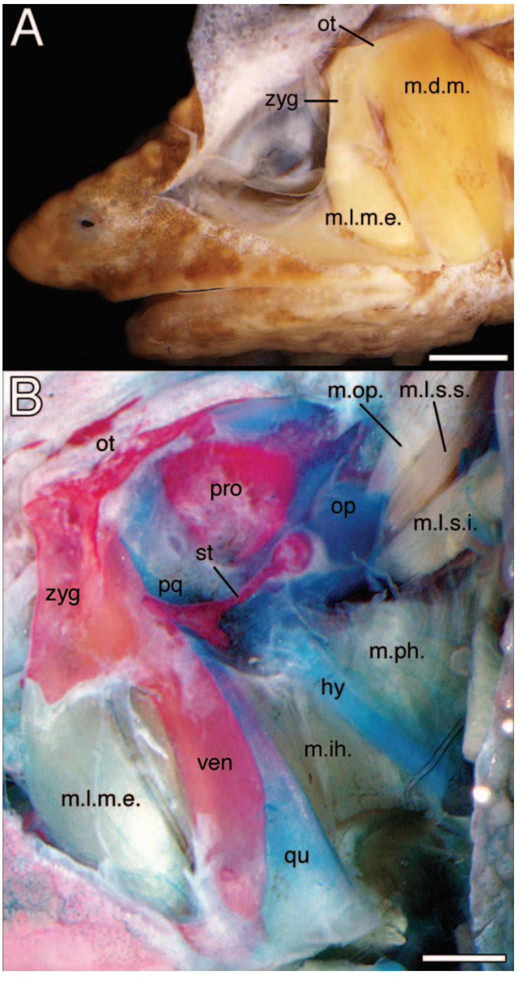

FIG. 4.—The otic region of *Rhinella paraguas* sp. nov. (A) Lateral view of adult male paratype CD 870 with skin deflected (scale = 2 mm). (B) Lateral view of adult female paratype CD 1503 with skin deflected and musculature (m. depressor mandibulae and tendon of the m. petrohyoideus) removed to reveal the middle ear; alizarin red S and alcian blue were applied to differentiate bone and cartilage, respectively (scale = 1 mm). Abbreviations: hy, hyale; m.d.m., musculus depressor mandibulae; m.ih., musculus interhyoideus; m.l.m.e., musculus levator mandibulae externus; m.l.s.i., musculus levator scapulae inferior; m.l.s.s., musculus levator scapulae superior; m.op., musculus opercularis; m.ph., musculus petrohyoideus; op, operculum; ot, otic ramus of the squamosal; pq, palatoquadrate; pro, prootic; qu, quadrate; st, stapes; ven, ventral ramus of the squamosal; zyg, zygomatic ramus of the squamosal. (A color version of this figure is available online.)

bearing many low tubercles, often with enlarged postrictal tubercles.

Hand length 22–30% of SVL. Relative appressed finger lengths II < III < V < IV. Nuptial excrescences present in adult males as a swollen patch of spiculate skin on the preaxial surface of the proximal portion of Finger II, absent in adult females and juveniles. Webbing extended to tip of digit II on postaxial side, to midlength of digit III on preaxial side and base of distal phalanx on postaxial side, to base of penultimate phalanx of both sides of digit IV and preaxial side of digit V, giving the following formula: II 0–2 III 1–2 IV 2–2 V. Free portions of all fingers bearing well-defined lateral fringes (better developed distally). Discrete subarticular tubercles absent, skin forming diffuse pads. Palmar tubercle round, well defined. Thenar tubercle elliptical, well defined, approximately 1/2 size of palmar tubercle. Forearm length 22–28% of SVL. Dorsal surfaces of arms spiculate with densely scattered conical tubercles. Finger tips round.

Foot (Fig. 3) and shank lengths 29–41% and 30–37% of SVL, respectively. Toes extensively webbed, with the following formula: I 0–0 II 0–1.5 III 1–3 IV 3–1 V. Relative lengths of appressed digits 1 < 2 < 3 < 5 < 4 (e.g., holotype ICN 28816) or 1 < 2 < 3 = 5 < 4 (e.g., ICN 28806). Free portions of all toes bear well-defined lateral fringes. Discrete subarticular tubercles absent, skin forming diffuse pads. Inner metatarsal tubercle large, round or slightly elliptical, weakly protuberant. Outer metatarsal tubercle elliptical, smaller, and more protuberant than inner metatarsal tubercle. Toe tips round. Exposed surfaces of thigh, shank, and foot spiculate with large, conical tubercles.

Jaw levator musculature.—The m. levator mandibulae externus is undivided and the path of the mandibular ramus of the trigeminal nerve (V_3) passes medial (deep) to this muscle in most specimens (43 of 52 specimens), with the following teratologies: (1) On one side of six specimens (ICN 28799, 28809, 28813, 28816–17, UV-C 12954) and both sides of one specimen (UV-C 8118), V_3 passes between some fibers of the m. levator mandibulae externus, but the muscle is not divided into distinct slips. (2) In UV-C 6971, the m. levator mandibulae externus is greatly reduced relative to the normal condition, consisting of only a few fibers and V_3 emerging anterior to the m. levator mandibulae longus and extending directly to the mandible without crossing the m. levator mandibulae externus medially or laterally. (3) In UV-C 9120, V_3 is lateral (superficial) to the m. levator mandibulae externus on the right side but medial on the left side.

Middle ear.—The tympanic membrane and annulus are absent (Figs. 1, 2B). Deflection of the skin of the otic region reveals a slight depression and small space between the squamosal and m. depressor mandibulae that corresponds to the position normally occupied by the middle ear cavity (Fig. 4A); however, the space is superficial, both the middle ear cavity and Eustachian tube are absent, and the depressor musculature must be removed to expose the middle ear (Fig. 4B). The operculum is cartilaginous, approximately twice the size of the stapedial footplate, and occupies the posterior portion of the fenestra ovalis. The m. opercularis attaches to the posterior edge of the operculum via a tendinous insertion. The base of the bony pars media plectri is expanded to form the stapedial footplate that is attached to a thick disc of pliable, alcian blue-negative tissue in the anterior portion of the fenestra ovalis. We assume that the pars externa plectri is absent, although without developmental data we cannot rule out the possibility that it is fully ossified and fused with the pars media plectri. The stapes is not suspended in an air-filled middle ear cavity and does not reach the space between the squamosal and m. depressor mandibulae. Rather, the stapes is in close contact with the skull along its entire length, lying medial to the m. depressor mandibulae and the elongate tendon of the m. petrohyoideus and projecting anteroventrolaterad from the fenestra ovalis along the cartilaginous otic capsule in the area between the hyale and the ossified prootic and onto the palatoquadrate and posterior face of the ventral ramus of the squamosal in the ventral portion of the squamosal embayment (Fig. 4B). Although the stapes is bound to the otic capsule, palatoquadrate, and squamosal by a thin sheet of transparent connective tissue attached to the palatoquadrate, prootic, and squamosal, it moves freely and seems to lack any direct ligamentous attachments. The distal portion of the stapes varies from a simple, slightly expanded terminus (e.g., CD 869) to an expanded, bony blade (Fig. 4B).

Color in preservative.—Dorsal surfaces brown with pale and dark brown markings of variable shapes and sizes, often bordered with darker brown, almost black lines. Parotoid macroglands same color as adjacent area. Flanks below oblique lateral row of tubercles dark brown (e.g., ICN 28799) to pale, yellowish brown with scattered dark brown tubercles (e.g., ICN 28816). Tubercles of oblique lateral ridge pale brown on dorsal surface, dark brown on ventral surface. Rostrum brown with tan or cream area below eye, forming either an indistinct blotch or well-defined vertical stripe. Cream or tan spots or vertical stripes often present along upper lip. Venter tan or cream with irregular brown reticulation, spots, and blotches, often more concentrated on the throat. Arm dorsally brown or dark brown, lacking conspicuous bands or bars; Fingers II and III cream, Fingers IV and V brown or dark brown (matching dorsal surface of arm). Exposed surfaces of hind limb (thigh, shank, and foot) uniform brown or brown with dark brown bars that align when limb flexed. Concealed surfaces of hind limb (posterior surface of thigh, inner surface of shank, and inner two or three toes) cream with variable brown spots and blotches.

Color in life.—Description based on TG's field notes for UV-C 12953–56, 12995–99, and 14864 and photographs of UV-C 14864, 14888, 14911, 14910–11, 14918–19 and 14921. As exemplified by the specimens in Fig. 1, dorsal coloration was extremely variable, generally consisting of varying shades of brown (tan to almost black), either uniform or with irregular wavy lines and blotches, often with a red or orange tinge, at least laterally, and yellow, brown, and black lines. Many individuals possessed a black interorbital bar and X-shaped mark between the shoulders. The flank below the oblique lateral row of tubercles was reddish orange. The rostrum, side of head, and parotoid macrogland were brown or dark brown with one or more pale brown, dull orange, cream, or yellow infraorbital vertical stripes. The iris was pale brown, bronze, gold, or yellow, with black reticulation in field notes; the pupil ring was solid orange or gold. The throat was dark brown with red or reddish-orange marbling and scattered white spots. The belly was orange with dark brown mottling and white dots or gray with red marbling. The inner fingers (II–III) and toes (I–III) were orange dorsally, whereas the outer fingers (IV–V) and toes (IV–V) were dark brown with orange above each articulation. Plantar surfaces were orange with dark brown blotches. The ventral surfaces of the legs were dark brown with white mottling and spots.

Distribution and natural history.—Rhinella paraguas is known from two areas of the Pacific versant of the Cordillera Occidental: (1) Several localities in the Serranía de los Paraguas, including numerous points near El Boquerón (ca. 4°44′N, 76°18′W), adjacent to the town of El Cairo (4°47.170′N, 76°13.791′W) and Paso de Galápagos (ca. 4°53′N, 76°16′W), and (2) approximately 150 km SW along the Cordillera Occidental at Hacienda San Pedro, 3°29′N, 76°42′W. These localities share numerous species (Grant et al., 1997; Grant and Castro, 1998; Lynch, 1998), and the absence of *R. paraguas* from the intervening area is probably a collecting artifact. Localities for *R. paraguas* range in elevation from 1800 to 2500 m above sea level and are all found in mature cloud forest.

Rhinella paraguas is nocturnal and semiarboreal, climbing to perch on leaves and branches usually 50–200 cm (maximum 300 cm) above the ground. During the day, individuals conceal themselves in leaf litter (e.g., UV-C 12994 and UV-C 14888–89, collected when disturbed in leaf litter). Most specimens for which detailed collection data are available were taken on vegetation, but UV-C 12995–99, from Hacienda San Pedro, were active on the ground at 2115–0200 h, as was one of the specimens in the series UV-C 12953–56, from El Boquerón, between 2200–0300 h. *Rhinella paraguas* is a forest species not associated with streams or other water bodies. Observations at El Boquerón suggest that the species has a patchy distribution, presumably governed by habitat characteristics. Specimens were common along a trail that arches down the ridge from near the summit of the road at El Boquerón, which we consistently found to be even wetter than the adjacent forest. In contrast, this species was collected only rarely along the trails at other points in the forest or in leaf litter beside the road.

Although we have collected adults and juveniles of both sexes, we have not observed any reproductive behavior. The few, large, pale orange ovarian ova (e.g., CD 2843: 41.9 mm SVL, 61 mature ova total; mean diameter of 18 mature ova = 2.24 ± 0.23 mm) and the distance of all specimens from water suggest either direct development or endotrophic, nidicolous larvae.

Although *R. paraguas* has a greatly reduced middle ear and adult males lack vocal slits, the species is capable of vocalizing. The call is a soft, short trill; a single recorded call of an undetermined specimen consisted of 13 notes in 0.44 s (recording quality inadequate to score additional parameters). We have observed calling behavior in *R. paraguas* only while being handled or in a collecting bag with other individuals, so we assume this is a release call and not an advertisement call.

Etymology.—The specific epithet is a noun in apposition used in reference to the Serranía de los Paraguas, where the holotype and most of the paratypes were collected.

Discussion

A comment on Rhinella lindae.—Rivero and Castaño (1990:4) reported "the fusion of stomach and abdominal wall" in *R. lindae*, which would be an additional difference between it and *R. paraguas*. However, this apparent "fusion" occurs in many of the soft-tissue structures in the type specimens of *R. lindae* (e.g., between oviducts and abdominal muscles) and seems to be an artifact of preservation, given that both the holotype and paratype are desiccated in a manner consistent with fixation in a high concentration of formalin. Similarly, Rivero and Castaño (1990:4) reported that "a cartilaginous omosternum seems to be present," but our examination of the holotype and paratype showed the omosternum to be absent. We confirm the bicondylar articulation of the sacrum and urostyle and presence of a complete middle ear reported by Rivero and Castaño (1990).

Phylogenetic relationships.—The phylogenetic relationships among the 10 species of the *R. acrolopha* group are largely unknown. To date, phylogenetic analyses have included at most three species, with *R. festae* from the eastern slopes of the Andes in Ecuador placed as sister to *R. macrorhina* and *R. rostrata* from the western slopes of the Cordillera Central and Occidental, respectively, in Antioquia, Colombia (Van Bocxlaer et al., 2010; Pyron and Wiens, 2011).

More progress has been made in understanding the relationships between the *R. acrolopha* group and other bufonids, although questions still remain. Trueb (1971) noted the external similarity between the *R. margaritifera* and *R. acrolopha* groups, and recent phylogenetic analyses have supported a close relationship between them (e.g., Frost et al., 2006). However, molecular evidence indicates an even closer relationship between the *R. acrolopha* group and certain species of the *R. veraguensis* group, specifically *R. chavin*, *R. manu*, *R. nesiotes*, and *R. yanachaga* (Pramuk, 2006; Chaparro et al., 2007; Pramuk et al., 2008; Van Bocxlaer et al., 2010; Pyron and Wiens, 2011; Peloso et al., 2012; Moravec et al., 2014). Furthermore, the results of those analyses of DNA sequences are consistent with the distribution of several putative morphological synapomorphies, including: (1) occurrence of few, large, unpigmented eggs in the *R. acrolopha* group and *R. chavin*, *R. justinianoi*, *R. manu*, *R. multiverrucosa*, *R. nesiotes*, and *R. yanachaga* of the *R. veraguensis* group (Duellman and Toft, 1979; Lehr et al., 2001, 2005, 2007; Chaparro et al., 2007); (2) m. levator mandibulae externus undivided with trigeminal nerve passing medial (deep) to the muscle in *R. paraguas* (reported herein) and all other species of the *R. acrolopha* group (TG, personal observation) and at least *R. manu* (Chaparro et al., 2007) and *R. quechua* (TG, personal observation) of the *R. veraguensis* group; and (3) absence of the m. adductor longus in the *R. acrolopha* group (Trueb, 1971; TG, personal observation) and *R. manu* (Chaparro et al., 2007). In contrast, species of the *R. margaritifera* group possess many small, pigmented eggs, a divided m. levator mandibulae externus with V_3 passing between the two slips, and usually (for an exception, see Vélez-Rodríguez and Ruiz-Carranza, 2002) the m. adductor longus (Trueb, 1971; Frost et al., 2006). As such, available evidence suggests the existence of a clade of montane toads that extends from Cerro Tacarcuna near the Colombo-Panamanian border south along the Andes to southeastern Peru.

Although it is apparent that the *R. acrolopha* group is most closely related to certain species of the *R. veraguensis* group, other species of the *R. veraguensis* group (including *R. veraguensis*, in which the m. levator mandibulae externus is divided into two distinct slips with V_3 passing between them; TG, personal observation) fall outside the inclusive *R. margaritifera* group + *R. acrolopha* group clade, and data are too sparse to determine the contents and internal relationships of this clade and alter the taxonomy. Moravec et al. (2014) found *R. festae* to be nested between *R. nesiotes* and *R. chavin* + *R. yanachaga* and proposed the *R. festae* group for those species and *R. macrorhina* and *R. rostrata* (not included in their analysis). DNA sequences are available for only 3 of the 10 *R. acrolopha* group species and 6 of the 19 *R. veraguensis* group species, however, and Moravec et al. (2014) did not address any species of the *R. acrolopha* group or *R. veraguensis* group that have not been sequenced. Pramuk (2006), Chaparro et al. (2007), and Van Bocxlaer et al. (2010) found the nearest relatives of the *R. acrolopha* group to form a grade, whereas Pyron and Wiens (2011) found them to form a clade. Further, morphological observations are limited (e.g., information on musculature for the *R. veraguensis* group only exists for *R. quechua*, *R. manu*, and *R. veraguensis*) and several key characters that vary within the *R. acrolopha* group (e.g., occurrence of tympana, vocal slits, nuptial pads) also vary within the *R. veraguensis* group, suggesting that some *R. acrolopha* group species might be more closely related to species of the *R. veraguensis* group than to other species of the *R. acrolopha* group.

Middle ear and hearing.—The most striking anatomical characteristic of *R. paraguas* is its middle ear. Most anurans possess a tympanic middle ear composed of (1) a tympanic membrane formed by modified skin that is thinner and less glandular than adjacent skin, (2) a cartilaginous annulus tympanicus, (3) a stapes composed of a cartilaginous pars externa plectri, an ossified pars media plectri, and a cartilaginous pars interna plectri, and (4) a cartilaginous operculum (Wever, 1985; Mason, 2006). Reduction of the middle ear has been described for numerous species, including the loss of the tympanic membrane, tympanic annulus, stapes, and operculum (Jaslow et al., 1988; Mason, 2006), and the tympanic membrane, tympanic annulus, and stapes are entirely absent in most species of the *R. acrolopha* group. *Rhinella paraguas* lacks a tympanic membrane and annulus and only the stapes and operculum remain. Further, instead of being suspended in an air-filled middle ear chamber (which is absent), the stapes extends along, and is in close contact with, the cartilaginous otic capsule and palatoquadrate and the ventral ramus of the squamosal. As such, we assume that sound vibrations are received by the suspensorium and transferred to the stapes and, ultimately, the auditory papilla.

To our knowledge, *R. paraguas* is the first anuran reported in which the stapes articulates with the suspensorium, but a similar morphology occurs in most salamanders. All salamanders lack a tympanic membrane and middle ear chamber. The stapes is absent in sirenids and salamandrids (Trueb, 1993), but in salamanders that possess one, it almost invariably bears a stylus that either articulates (directly or via a ligamentous attachment) or fuses with the suspensorium (Kingsbury and Reed, 1909; Wever, 1985). Following metamorphosis, the stapes of most salamanders fuses with the otic capsule and seems to have no acoustic function, but the mobile stapes probably functions as an inertial element that generates stimulatory waves in the inner ear fluids when acoustic vibrations penetrate the head (Lombard and Hetherington, 1993). This system is thought to function well in aquatic and fossorial species, but the stapes loses its acoustic function in terrestrial organisms that possess limbs and do not maintain the head in contact with the substrate. Indeed, Wever (1985:422) concluded that when in the aerial medium, these salamanders "must be practically deaf." Given that *R. paraguas* seems to be entirely terrestrial or semiarboreal and is not closely related to any aquatic species, it is unlikely that its middle ear morphology is related to aquatic hearing. The middle ear might be more effective when the toads are concealed in leaf litter during the day and the lower jaw presumably contacts the substrate, but more research is required to understand the auditory mechanism in this species.

Amphibian declines in the Serranía de los Paraguas.—At the same time that knowledge of the diversity of amphibians is increasing, so too is the undeniable decline of many of amphibian species around the world (Köhler et al., 2005). Lynch and Grant (1998) reported dead and dying frogs at El Boquerón in the Serranía de los Paraguas, one of the localities of *R. paraguas* and a site that has been the subject of numerous batrachological studies (Lynch, 1992, 1996, 1998; Lynch and Ruiz-Carranza, 1996a, 1996b; Grant et al., 1997; Ruiz-Carranza et al., 1997; Bolívar-G. et al., 1999; Lynch and Ardila-Robayo, 1999). This alarming observation coincided with an El Niño-induced drought in this otherwise rain-soaked region, which Lynch and Grant (1998) hypothesized to be the cause of the die-off. More recently, Velásquez-E. et al. (2008) reported that several of the specimens collected during the die-off tested positive for *Batrachochytrium dendrobatidis* (Bd), which causes chytridiomycosis and amphibian mortality (Berger et al., 1998). The association of both unusual weather and Bd with this die-off suggests that a combination of extreme environmental disturbances and disease might be responsible (Rohr and Raffel, 2010).

After a hiatus of several years, we returned to this locality in 2004 to assess the status of the amphibians. Although our time in the Serranía de los Paraguas was limited (only 3 days and nights of collecting) and our sampling effort was inadequate to quantify diversity, the amphibian community clearly differed from that that we observed previously (see also Velásquez-E. et al., 2008). The most compelling evidence of decline is the apparent absence of all the dendrobatoids known to occur at this locality (Grant et al., 1997). *Anomaloglossus atopoglossus* and *Hyloxalus lehmanni* (both reported as *Colostethus*; see Grant et al., 2006) were common previously, and their frequent vocalizations and diurnal activity made them conspicuous. The third species, *Colostethus agilis*, was less common, but its diurnal vocalizations also were conspicuous. Despite the absence of those species, *R. paraguas* was abundant in 2004, as it was when Lynch and Grant (1998) observed dead and dying individuals of other anuran species, suggesting that it is resistant to whatever caused the decline in sympatric species. Vaughan and Mendelson (2007) also reported that three montane species of the Central American bufonid genus *Incilius* (reported as *Crepidophryne*; see Mendelson et al., 2011) persist despite massive amphibian declines throughout the region. Vaughan and Mendelson (2007) suggested that the persistence might be due to those species' apparent dissociation from free-flowing water and consequent isolation from chytrid-infected stream habitats, which might explain the persistence of *R. paraguas* as well.

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Appendix

Specimens Examined

Rhinella acrolopha.—COLOMBIA: Chocó: Parque Nacional Natural de los Katios, ICN 31525, 31527, 31529. PANAMA: Darién: Cerro Mali, LACM 54337–38, KU 76944–46, KU 76962–64, KU 76969.

Rhinella festae.—ECUADOR: Pastaza: Arajuno, KU 124950; Morona-Santiago: W slope Cordillera de Cutucu, Camp 2, "Yapitya", KU 209647.

Rhinella lindae.—COLOMBIA: Antioquia: Mpio. Frontino, Murri (60°43′N, 76°20′W), carretera Nutibara–La Blanquita, ca. 1600–1800 m, CSJ 1880 (holotype), 1881.

Rhinella macrorhina.—COLOMBIA: Antioquia: Santa Rita, 1930 m, LACM 44394; Santa Rita, 1890–1910 m, LACM 44395 (holotype); Santa Rita Creek, 14 miles north of the village of Mesopotamia, American Museum of Natural History (AMNH) 1384; Mpio. Guatapé, Vda. Santa Rita, Finca Montepinar, 6°18.16′N, 75°08.06′W, 1840–1890 m, ICN 41558–85, MHUA 0094, 0101–102, 0127–129, 0151, 0179–80.

Rhinella nicefori.—COLOMBIA: Antioquia: Mpio. Yarumal, 3.5 km al N de los Llanos Cuiba, ICN 10063–65; Mpio. Yarumal, Los Llanos de Cuibá, 1–2 km on road La Apartado–San José de la Montaña, 6°48.583′N, 75°30.053′W, 2640 m, ICN 41541–57.

Rhinella quechua.—BOLIVIA: La Paz: Río Zongo, 1200 m, MZUSP A-60763.

Rhinella rostrata.—COLOMBIA: Antioquia: Santa Rita Creek, 14 miles north of the village of Mesopotamia, AMNH 1359 (holotype).

Rhinella ruizi.—COLOMBIA: Antioquia: Mpio. Bello, 6.6–8.1 km WSW de la Inspección de Policía San Félix, Serranía de las Baldías, 2820–3100 m, ICN 4119, 4160, 4241, 4266–68, 4601, 4603, 8374, 9817, 9818 (holotype), 9819–30, 13944–46, 33720–21, 33722–24; "Medellín" (probably the type locality), ICN 4114; Mpio. Sonsón, km 149–150 carretera La Dorada–Sonsón, 2530 m ICN 4172–75, 4177; Mpio. Sonsón, 8 km E por carretera de Sonsón, 2780 m, ICN 9832; Mpio. Sonsón, 12.5 km E por carretera de Sonsón, 2540 m, ICN 9833; 1.4 km S por carretera de la unión de las carreteras Sonsón–La Dorada y Argelia, 2330 m, ICN 9834.

Rhinella tenrec.—COLOMBIA: Antioquia: Mpio. Dabeiba, near Campamento Ingeominas (ca. 6°42′N, 76°27′W), near the headwaters of Rio Amparrado, 805 m, ICN 8315–16, 10574–76, 10839, 10844, 13839, 13840 (holotype), 13841–42.

Rhinella truebae.—ICN 14780 (holotype), without locality data, probably from southern Depto. Antioquia, Colombia.

Rhinella veraguensis.—PERU: Puno: Oceneque, MZUSP A-096183 (previously British Museum [BM] 1904.5.7.31).