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A New Species of *Craugastor* (Anura: Craugastoridae) from the Magdalena River Valley, Colombia, with Evaluation of the Characters used to Identify Species of the *Craugastor fitzingeri* Group

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Abstract. The *Craugastor fitzingeri* group is composed of eight species, four of which occur in sympatry in Colombia: *C. crassidigitus, C. fitzingeri, C. longirostris,* and *C. raniformis*. These four species frequently are confused due to their external similarity and extensive intraspecific variation, particularly between the species with disjunct populations in the middle and upper Magdalena River Valley, Colombia. Here we present the results of a revision of the variation in the morphological characters used to distinguish these four species. We confirm that the color patterns on the rear of the thigh and the degree of foot webbing are useful for distinguishing among these species; however, the color pattern on the throat was found to present extensive intraspecific variation. We show that *C. fitzingeri* and *C. longirostris* are restricted to the Pacific lowlands and upper basins of the Cauca River Valley in Colombia and that populations in the Magdalena River Valley previously identified as those species correspond a new species, which we describe herein. This new species and *C. raniformis* are the only species of *C. fitzingeri* group that reach the Magdalena River Valley. Finally, we provide a dichotomous key to identify the species of the *Craugastor fitzingeri* group.

Keywords. Brachycephaloidea; Morphology; New species; South America; Systematics; Taxonomy; Terrarana.

Resumen. Actualmente el grupo de especies *Craugastor fitzingeri* incluye ocho especies, cuatro de las cuales tienen distribución en Colombia: *C. crassidigitus, C. fitzingeri, C. longirostris* y *C. raniformis*. Estas cuatro especies además de ser muy similares morfológicamente, también presentan un alto grado de variación en los caracteres tradicionalmente usados para su identificación. En este articulo presentamos una revisión de la variación asociada a tres caracteres usados en la sistemática de este grupo, incrementando también el muestreo de las poblaciones aisladas del medio y alto Valle del Río Magdalena, Colombia. En los resultados de este revisión se confirmo que los patrones de coloración sobre las superficies posteriores de los muslos, así como también la extensión de la membrana entre los dedos pediales son caracteres útiles para reconocer especies dentro del grupo. También se encontró que los patrones de coloración sobre la garganta son muy variables y por lo tanto se recomienda no usar este carácter para identificar especies dentro del grupo. Como consecuencia de estos resultados se redefine la distribución de *C. fitzingeri* y *C. longirostris,* las cuales quedan restringidas a las tierras bajas del pacífico y al alto Valle del Río Cauca. Por otro lado las poblaciones previamente identificadas como *C. fitzingeri* y *C. longirostris* del Valle del Río Magdalena son propuestas como una nueva especie para el grupo, la cual es descrita en este articulo. La nueva especie junto con *C. raniformis* son las únicas especies del grupo que tienen distribución en el Valle del Río Magdalena. Finalmente proponemos una clave dicotómica para identificar especies dentro del grupo de especies *Craugastor fitzingeri.*

INTRODUCTION

Among the amphibians most commonly encountered in the lowland forests of the Chocó and Magdalena Valley of northern South America are the frogs of the *Craugastor fitzingeri* group. The group is composed of seven species, all of which are morphologically similar except *C. tabasarae,* which is strikingly different from the others. Even though the *C. fitzingeri* group is one of the best studied assemblages of terraranas (Savage, 1976; Lynch, 1976; Lynch and Myers, 1983; Miyamoto, 1986; Savage et al., 2004; Hedges et al., 2008), the similar external morphology and the extensive intraspecific variation hinder species identification.

Lynch and Myers (1983) contributed most to resolving problems in the identification of species from northwestern South America; however, their study focused primarily on populations from the lowland forests of the Chocó, with only limited sampling of the disjunct populations of *Craugastor fitzingeri* (Schmidt, 1857), *C. longirostris* (Boulenger, 1898), and *C. raniformis* (Boulenger, 1896) in the Magdalena River Valley in Colombia. In the present study, we examined a greatly expanded sample of these disjunct populations to assess variation of the three characters used to distinguish among the Colombian species of the *C. fitzingeri* group: color pattern on the throat, color pattern on posterior surfaces of the thighs, and degree of toe webbing. Based on our findings, we propose redefined

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species limits and distribution patterns for the frogs currently assigned to the *C. fitzingeri* group in Colombia and describe a new species from the Magdalena River Valley.

MATERIALS AND METHODS

The detailed analysis of variation included 407 specimens of the *Craugastor fitzingeri* group deposited in the amphibian collection of the Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Museo de Historia Natural (ICN). Localities extend across the entire distribution of the group in Colombia, including three departments (10 municipalities) for *Craugastor fitzingeri;* four departments (10 municipalities) for *C. longirostris,* and eight departments (23 municipalities) for *Craugastor raniformis* (see Appendix 1). Terminology used to describe the characteristics of the frog and the 14 statements summarizing the taxonomically informative characters of the species follows Lynch and Duellman (1997) and Duellman and Lehr (2009). The degree of toe webbing was measured following the proposed of Savage and Heyer (1997).

Characters used to identify species in the *Craugastor fitzingeri* group

The revision of the *Craugastor fitzingeri* group by Lynch and Myers (1983) focused on structural characters of external morphology, colors patterns, and vocalizations. In that revision, Lynch and Myers (1983) demonstrated that toe webbing and color pattern are the least variable diagnostic characters. Considering the results obtained by Lynch and Myers (1983), we focused analyses of variation on three characters: 1) color pattern on posterior thigh surfaces, 2) color pattern on throat, and 3) degree of webbing on outer (postaxial) side of Toe III. First, we defined the character states for each character based on the range of variation observed in each species and the information reported by Lynch and Myers (1983) for these characters. Next, each frog was scored and the frequencies of each character state in each species were calculated for each geographic distribution. These frequencies were compared to the variation for each species (sensu Lynch and Myers, 1983) in order to identify consistent discontinuities in variation that allow species limits to be identified.

Advertisement call

The vocalizations of *Craugastor fitzingeri, C. metriosistus,* and *C. raniformis* were analyzed. Calls of *C. fitzingeri* and *C. raniformis* were obtained from the American Museum of Natural History (AMNH) and the zoological collections of Universidad del Valle, Cali, Colombia, respectively (UV-CD). The advertisement call of *C. fitzingeri* was recorded by Charles Myers in April 1967 (AMNH reel 235), near the Río Jaque, 1.5 km above Río Imamadó, 50 m above sea level (asl), Darién Province, extreme eastern Panamá; air temperature at calling site 23°C. The voucher is deposited in the University of Kansas, Museum of Natural History, Division of Herpetology, Lawrence, Kansas (KU 114498). The advertisement call of *C. raniformis* was recorded by Wilmar Bolívar-G. in April 2011, Isla Palma, 7 m asl, Buenaventura Municipality, Valle del Cauca Department, Colombia, 25°C air temperature. The voucher is deposited in the Zoological collections of Universidad del Valle, Cali, Colombia (UV-CD 711). The advertisement call of *C. metriosistus* was recorded by Mauricio Rivera from Sonsón Municipality, Vereda Parcelas, Corregimiento San Miguel, Quebrada San Antonio, Antioquia Department, Colombia; air temperature at calling site 26°C. The voucher is deposited in the Museum of Herpetology Universidad de Antioquia (MHUA-A 8403).

All recordings were edited with Audition CS6 for MacOS X and analyzed with the software Raven Pro 1.5 for MacOS X from the Cornell Laboratory of Ornithology (Bioacoustics Research Program). Measured parameters included number of notes per call, note duration, number of pulses per note, call length, fundamental frequency, and dominant frequency. The terms and definitions for the acoustic analyses follow Márquez et al. (1995). Call voucher numbers are given in Table 1.

Table 1. Parameters of the advertisement call of *Craugastor fitzingeri, C. metriosistus* and *C. raniformis*. The best spectogram segments of the advertisement call of *Craugastor fitzingeri* include a superimposed call of other species. Most parameters can be evaluated without ambiguity (with the exception of the number of pulses per note).

Parameter	*Craugastor fitzingeri* KU 114498	*Craugastor metriosistus* sp. nov. MHUA-A 8403	*Craugastor raniformis* UV-CD-711
Call	1	15	5
Notes	21	15	95
Notes/Call	21	1–2	16–21 (19.2 ± 2.5)
Note duration (ms)	17–32 (23.6 ± 4.3)	58–82 (73.5 ± 7.1)	42–56 (49.3 ± 2.5)
Pulses	—	16–24 (20.2 ± 2.3)	10–16 (14.0 ± 1.0)
Call length (ms)	3071	58–82 (73.5 ± 7.1)	1064–1446 (1301 ± 190)
Fundamental frequency (Hz)	1859.8–4339.5	1973.7–4512.2	2791.2–3684.1
Dominant frequency (Hz)	1859.8–4339.5	1973.7–4512.2	2791.2–3684.1

RESULTS

Color pattern on posterior surfaces of thighs

Lynch and Myers (1983) showed that in some species of the *Craugastor fitzingeri* group the posterior surfaces of the thighs are uniform brown or gray, whereas in others the posterior surfaces of the thighs possess pale marks (tan or yellowish). *Craugastor crassidigitus* (Taylor, 1952), *C. chingopetaca* (Köhler and Sunyer, 2006), *C. longirostris* and *C. talamancae* (Dunn, 1931) have uniform thigh coloration (Lynch and Myers, 1983; Savage, 2002; Köhler and Sunyer, 2006), whereas *C. fitzingeri, C. raniformis,* and *C. tabasarae* (Savage et al., 2004) have pale marks on a dark ground color (Lynch and Myers, 1983; Savage et al., 2004). Savage et al. (2004) reported that in *C. tabasarae* the color pattern on the posterior surfaces of thighs have vertical dark bars on light ground color. Such characterization is unique within the *C. fitzingeri* group and can therefore be regarded as apomorphic.

Additionally, Lynch and Myers (1983) mention that the shape and size of thigh spotting aid in distinguishing *Craugastor fitzingeri* from *C. raniformis.* However, *C. raniformis* has a wide range of pale markings, so for the purposes of this study the presence of pale spotting on posterior thigh surfaces (independent of the shape and size) was utilized as the single character state. The following set of color patterns on the posterior surface of the thigh correspond to each state: State 1: Ground color of posterior thigh surface dark to reddish brown with conspicuous, small, pale spots with well-defined borders (Fig. 1A–B). State 2: Ground color of posterior thigh surface reddish brown with diffuse cream blotches lacking well-defined borders (Fig. 1C–D).

Color pattern on throat

According to Lynch and Myers (1983), the throat is white or yellow, like the chest, with a weak to strong

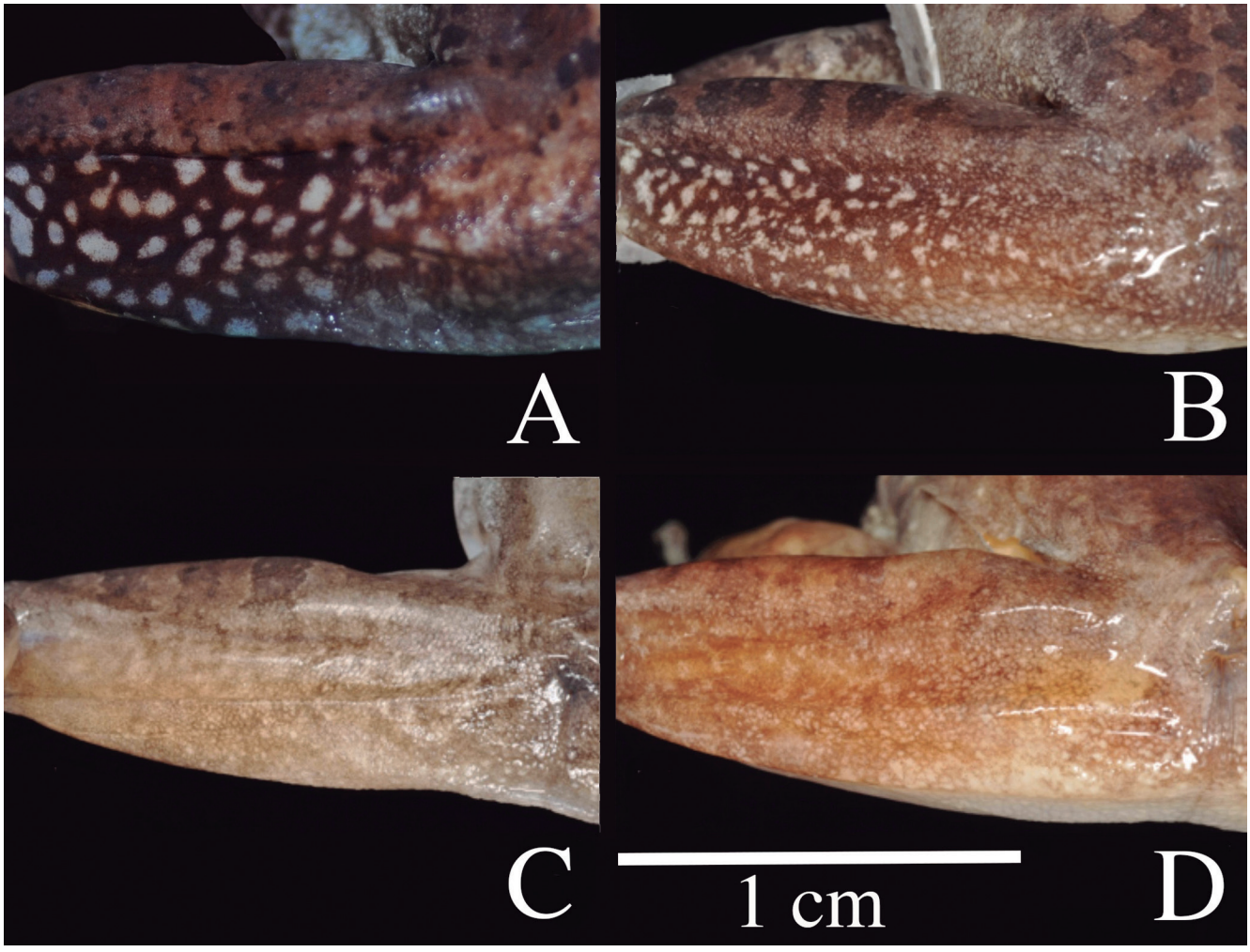

Figure 1. Color on posterior surfaces of thighs in the *Craugastor fitzingeri* group. **(A)** *C. fitzingeri* (ICN 12510), **(B)** *C. raniformis* (ICN 41276), **(C–D)** *C. metriosistus* (ICN 55567, 52846).

suffusion of melanophores that is either uniformly distributed or arranged in definite patterns. The throat of *Craugastor fitzingeri* is sparsely to heavily flecked with brown with a narrow to broad white sagittal stripe. Usually, *C. longirostris* has a definite pattern in which the melanophores are faintly to heavily clumped to form a spotted pattern that often includes a closely spaced pair of spots or short lines slightly anterior to a more widely spaced pair of markings on the anterior portion of the chest. However, some individuals of *C. longirostris* exhibit nearly uniform pigmentation on the throat. In contrast, the throats of *C. chingopetaca, C. crassidigitus, C. raniformis, C. tabasarae,* and *C. talamancae* are white to cream and finely to heavily peppered with melanophores across the entire surface (Savage, 2002; Savage et al., 2004; Köhler and Sunyer, 2006). Lynch and Myers (1983) also note that a faint indication of a white gular stripe similar to that observed in *C. fitzingeri* is rarely present in *C. longirostris* and *C. raniformis*. The following set of color patterns for the throat corresponds to each state: State 1: Ground cream, finely peppered with melanophores (Fig. 2A–B). State 2: Ground cream with melanophores clumped to form small or large spots (Fig. 2C–D). State 3: Median white gular stripe with heavy concentration of melanophores distributed on either side (Fig. 2E–F).

Webbing on outer side of Toe III

According to Lynch and Myers (1983), Savage (2002), and Köhler and Sunyer (2006), *Craugastor chingopetaca, C. crassidigitus, C. fitzingeri, C. longirostris, C. raniformis,* and *C. talamancae* have moderate toe webbing, whereas *C. tabasarae* has basal toe webbing (Savage et al., 2004). We reevaluated variation in this character in *C. fitzingeri, C. longirostris, C. raniformis* and the Magdalena River Valley samples and found discrete variation in the degree of webbing on the outer (postaxial) margin of Toe III. The following set of webbing patterns on the outer side of Toe III corresponds to each state: State 1: Webbing reaches midway between basal and distal subarticular tubercle in outer side of Toe III (3^{-}, $2^{⅔}$ or $2^{½}$ sensu

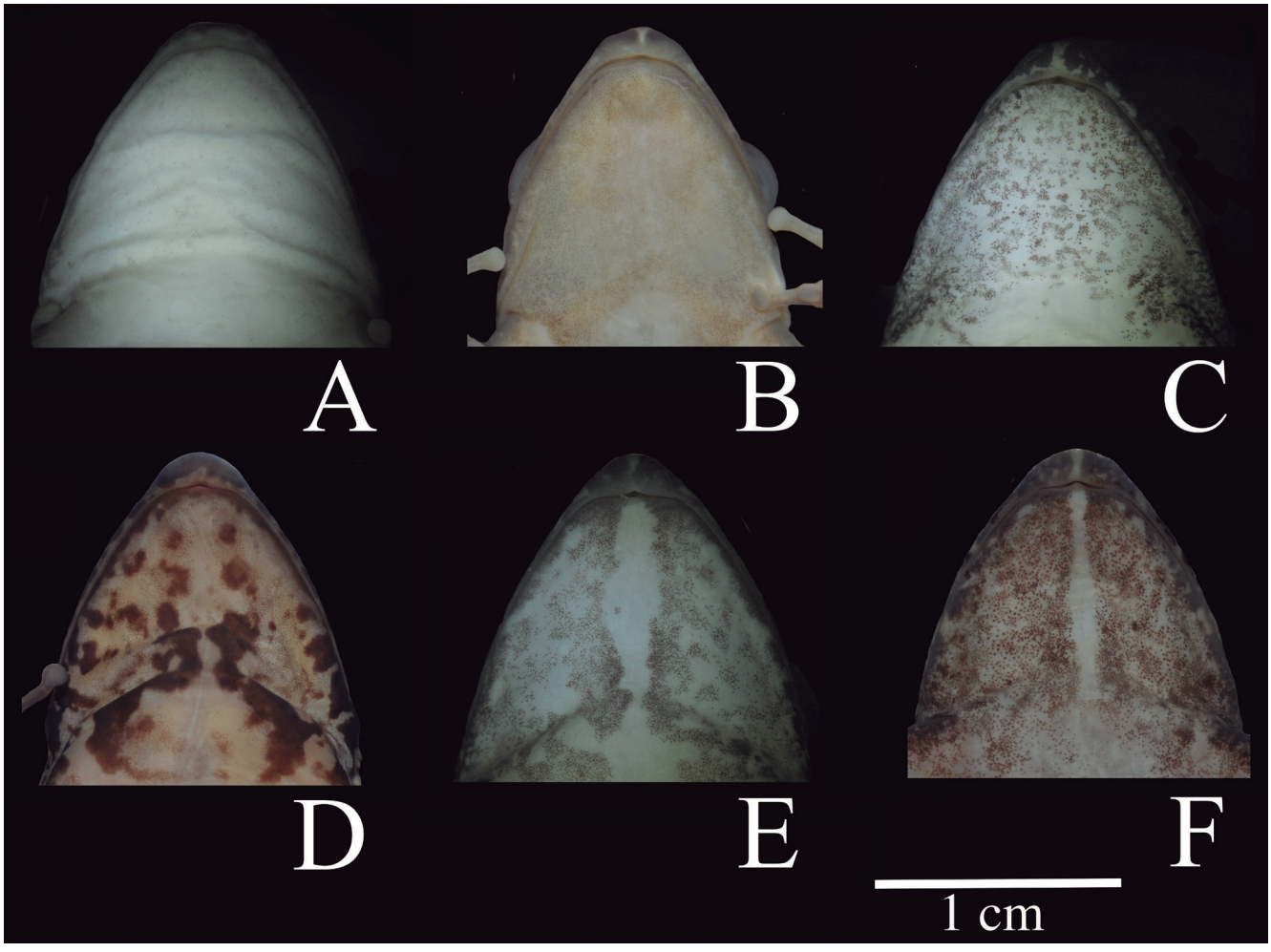

Figure 2. Color on the throat in the *Craugastor fitzingeri* group. **(A)** *C. raniformis* (ICN 4932), **(B)** *C. longirostris* (ICN 10767), **(C)** *C. raniformis* (ICN 38653), **(D)** *C. longirostris* (ICN 38986), **(E)** *C. metriosistus* (ICN 43540), **(F)** *C. fitzingeri* (ICN 10775).

Savage and Heyer, 1997; Fig. 3A–B). State 2: Webbing reaches proximal portion of distal subarticular tubercle in outer side of Toe III (2⅛, 2⁺ or 2 sensu Savage and Heyer, 1997; Fig. 3C–D).

The *Craugastor fitzingeri* group in the Magdalena River Valley

The populations of the *Craugastor fitzingeri* group (sensu Lynch, 1994; Lynch and Duellman, 1997; Hedges et al. 2008) distributed in the Magdalena River Valley agree with the characteristics found in other species of the group: vocal slits and nuptial pads present in males (nuptial pads absent in *C. tabasarae*); lacking cranial crests; tympanic membrane and prominent annulus; discs on all fingers and toes; Finger I > Finger II; subarticular tubercles present; supernumerary tubercles (accessory tubercles) low and restricted to the proximal segments of fingers (present only on base of Finger I and II in *C. chingopetaca*); absents on palm. An inner tarsal fold is present in all (except *C. talamancae*) and Toe III is longer than Toe V when both are pressed against Toe IV. However, some of these populations are distinct from all previously recognized members of the *C. fitzingeri* group in having a unique combination of features that leads us to describe them as:

Figure 3. Degree of webbing on outer side of Toe III in the *Craugastor fitzingeri* group. **(A)** *C. longirostris* (ICN 10766); **(B)** *C. raniformis* (ICN 32580), **(C)** *C. metriosistus* (ICN 55567); **(D)** *C. fitzingeri* (ICN 9358).

Craugastor metriosistus, sp. nov.
Figs. 1CD, 2E, 3C, 4C, 5A, and 6

Holotype

ICN 55561, adult female, collected 30 September 2011 by Jhon Jairo Ospina-Sarria, Teddy Angarita-Sierra, Raúl Pedroza and John D. Lynch at Quebrada Caño la Batea (07°59'N, 73°24'W, 340–350 m asl), Finca el Cobre, Vereda Vega del Oso, Municipality San Martin, Department of Cesar, Colombia.

Paratypes

ICN 55562, 55569–70, adults females; ICN 55563, 55566, 55568, 55571, subadults females; ICN 55565, juvenile female; ICN 55567, subadult male; ICN 55564, juvenile; data as holotype. ICN 55555, adult female, ICN 55556, 55573, subadult females, ICN 55558, juvenile female; ICN 55554, 55557, 55560, 55572, adults males; ICN 55559, subadult male; ICN 55574–75, juveniles; Quebrada La Colorada, 1.7 km south of the urban area (07°58'N, 73°30'W, 115 m asl), Municipality San Martin, Department of Cesar, Colombia.

Diagnosis

Craugastor metriosistus sp. nov. is diagnosed by the following combination of characteristics: (1) smooth dorsal skin with occasional low warts, not forming ridges on shoulder; smooth ventral skin; discoidal fold present; dorsolateral folds absent; (2) tympanic membrane differentiated, its length compared to eye length is 61.5–68.6% in males and 58.0–66.6% in females; tympanic annulus prominent; supratympanic fold well defined, black, extending from the posterior corner of the orbit along the upper edge of the temporal region toward the insertion of the arm; (3) subacuminate snout in dorsal profile, rounded to nearly truncate in lateral profile; sharp canthus rostralis; (4) upper eyelid has nonpungent tubercles; wider than interorbital distance; cranial crest absent; (5) choanae slightly smaller or equal to the dentigerous process; triangular dentigerous processes of vomers, positioned posteriorly to level of choanae and separated medially by a distance less than the width of the visible dentigerous processes, each process with 5–7 teeth; (6) males with vocal slits and with subgular vocal sac not evident externally; nuptial pads on thumb present; (7) Finger I longer than Finger II, discs present on all fingers; finger

discs I–II round; finger discs III–IV truncate; (8) fingers with lateral fringes; palmar tubercle partially divided distally; thenar tubercle oval and equal in size of palmar tubercle; supernumerary tubercles low and restricted to the proximal segments of the digits, in Finger I and IV larger than on Fingers II–III; subarticular tubercles larger than supernumerary tubercles, round and projecting; (9) ulnar tubercles present, subconical and not forming a distinct fold; (10) heel lacking tubercles; outer edge of tarsus lacking tubercle, inner tarsal fold present along distal two-thirds; (11) elongate inner metatarsal tubercle, its length 2–3 times its width; low, round outer metatarsal tubercle, one–fourth size of inner; no supernumerary plantar tubercles; subconical and projecting subarticular tubercles; (12) toes with broad lateral fringes; moderately extensive webbing; webbing formula I ($1^{½}$ – 2^{-}) – (2 – 2^{+}) II ($1^{½}$ – $1^{⅔}$) – ($2^{⅔}$ – 3) III ($2^{⅓}$ – 2) – $3^{⅔}$ IV ($3^{⅔}$ – 4) – (2 – $2^{½}$) V; Toe V shorter than Toe III; Toe V reaching the base of the penultimate subarticular tubercle of Toe IV; Toe III extending to distal border of penultimate subarticular tubercle of Toe IV; discs of toes equal to or larger than discs on outer fingers; (13) color in life: body and limbs brown to orange brown, few small dorsolateral and post–tympanic black spots regularly paired (two or three); yellow flecks on surfaces of dorsum and limbs; occasionally, specimens include an interocular bar, a W-shaped scapular mark and a contrasting broad middorsal white or cream stripe; throat white with some melanophores giving a mottled dusky appearance, throat sometimes with a faint median white stripe; venter pale yellow; weak vertical bars on lips, black supratympanic and canthal stripe; loreal region with black facemask; interorbital blotch absent; brown dorsal surfaces of limbs with oblique gray bars; posterior thighs surfaces uniformly brown to reddish lacking blotches or with diffuse cream blotches uniformly distributed without clearly defined borders (Fig. 1C–D); groin and anterior thighs surfaces reddish orange; iris bicolored, upper edge light brown, lower edge reddish brown with black reticulum; (14) males are smaller than females; snout-vent length (SVL) in adult males 35.7–37.6 mm (n = 4; X = 36.9 ± 0.9); in adult females 51.5–60.7 mm (n = 5; X = 57.6 ± 3.5).

Comparisons with other species

Craugastor metriosistus differs from all other species in the group by having the combination of moderate

Figure 4. Colombian species of the *Craugastor fizingeri* group in life. **(A)** *C. fitzingeri* (Buenaventura, Valle del Cauca), **(B)** *C. longirostris* (Buenaventura, Valle del Cauca), **(C)** *C. metriosistus* (San Martin, Cesar, ICN 55569), **(D)** *C. raniformis* (Buenaventura, Valle del Cauca).

toe webbing on the outer side of Toe III (webbing reaches proximal portion of distal subarticular tubercle in outer side of Toe III), color uniformly reddish brown on the posterior surfaces of the thighs, Toe III > Toe V, supernumerary tubercles low and restricted to the proximal segments of all fingers, and supratympanic ridge distinctly curved downwards. It is morphological most similar to *C. chingopetaca* and *C. raniformis;* however, *C. metriosistus* has Toe III > Toe V, supernumerary tubercles restricted to the proximal segments of all fingers, a supratympanic ridge distinctly curved downwards (*C. chingopetaca* with supernumerary tubercles present only on base of Fingers I and II, Toe III and Toe V of equal length, and supratympanic ridge only slightly curved downward), and uniformly reddish brown to brown on the posterior surfaces of the thighs (*C. raniformis* has the posterior surfaces of the thighs with pale markings on a dark ground color). It differs of *C. longirostris* and *C. talamancae* by having more webbing on the outer side of Toe III (*C. longirostris* and *C. talamancae* have basal toe webbing) and an inner tarsal fold (absent in *C. talamancae*), and is distinguished from *C. tabasarae* by the uniform coloration reddish brown posterior thighs surfaces (*C. tabasarae* has the posterior surfaces of thighs with vertical dark bars on light ground color). It differs from *C. crassidigitus* by having less webbing extension of outer side of Toe III and inner side of Toe IV (Fig. 3; Lynch and Myers, 1983: fig. 18B). *Craugastor metriosistus* is also larger (SVL in adult males 35.7–37.6 mm, in adult females 51.5–60.7 mm) than *C. crassidigitus* (SVL in adult males 20.2–30.2 mm, in adult females 34.3–44.7 mm). *Craugastor metriosistus* differs from *C. fitzingeri* by having uniform reddish brown coloration on the posterior surfaces of the thighs (*C. fitzingeri* has the posterior surfaces of the thighs with pale markings on a dark ground color Fig. 1A–D) and the presence of a black facemask on the loreal region (black facemask absent in *C. fitzingeri,* Fig. 4A, C). Vocalizations also differentiate *C. metriosistus* from *C. fitzingeri* and the sympatric *C. raniformis*. In *C. metriosistus* the advertisement call consists of one or sometimes two notes per call, with note duration of 0.058–0.082 s (X = 0.073 s). In contrast, in *C. fitzingeri* and *C. raniformis* the advertisement call comprises 21 notes per call with note duration of 0.017–0.032 s (X = 0.023 s) s and 16–21 (19.2 ± 2.5) notes per call with note duration of 0.042–0.056 s (X = 0.049 s), respectively (Table 1, Fig. 5).

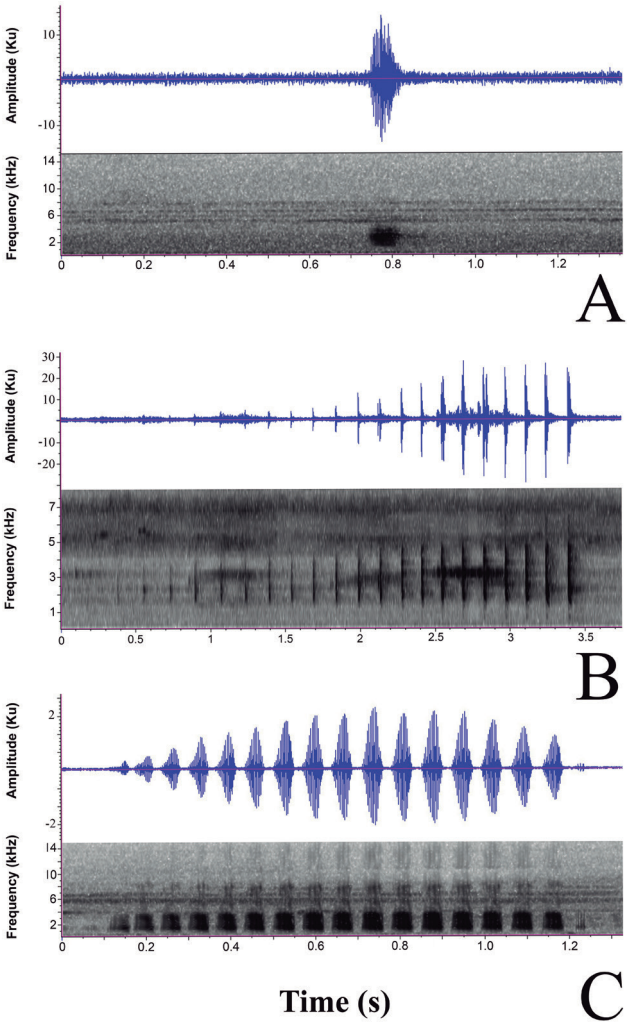

Figure 5. Spectrograms and oscillograms of the advertisement call of **(A)** *Craugastor metriosistus,* **(B)** *C. fitzingeri,* **(C)** *C. raniformis.*

Description of the holotype (Fig. 6A–B)

An adult female of 60.7 mm SVL. Head as wide as body, head width 37.5% of SVL; slightly wider than long, head length 36.4% of SVL. Snout subacuminate in dorsal profile, round in lateral profile; canthus rostralis slightly concave; loreal region concave with small tubercles (under magnification), sloping abruptly to lips; lips not flared; nostrils protuberant, directed laterally; internarial distance 70.3% of eye to nostril distance; eye to nostril distance 117.3% of eye length.

Upper eyelid wider than interorbital distance, 135% of the interorbital distance; upper eyelid has nonpungent tubercles; cranial crests absent. Tympanic membrane evident, its length 57.9% of eye diameter; tympanic annulus prominent; supratympanic ridge originating at the corner of eye, encroaching the top edge of the tympanic membrane and before curving downward toward the angle of the jaw; postrictal tubercles conical, four on each side of head, no other enlarged tubercles on head. Choanae ⅓ size of dentigerous process, not concealed by palatal shelf of maxillary arch. Dentigerous process with six teeth in a nearly tranverse row along posterior border. Tongue as long as wide, its posterior border notched, posterior third not free. Skin on dorsum, flanks, and both sides of head and upper surfaces of limbs smooth, lacking of warts or ridges. Skin of throat, venter and undersides of limbs

smooth. Discoidal fold prominent and complete posterior and laterally; cloacal opening not extended in sheath. Forearm with low ulnar tubercles. Palmar tubercle bifid, equal or slightly larger than oval thenar tubercle. Supernumerary tubercles low and restricted to the proximal segments of the digits, in Finger I and IV larger than on Fingers II–III; subarticular tubercles subconical, projecting, basal ones larger on Fingers I–II than Fingers III–IV. Fingers with weak lateral fringes and expanded, retuse (indented) disk covers. Discs of inner two fingers slightly wider than digit below disc, those on outer two fingers twice as wide as digit below disc. Finger I > Finger II, relative finger lengths (adpressed) III > I > IV > II. No tubercles on heel or tarsus; inner edge of tarsus bearing low fold along distal ½. Inner metatarsal tubercle elongate, its length 2–3 times its width; outer metatarsal tubercle round or slightly elongated, ¼ the size of inner. No supernumerary plantar tubercles. Subarticular tubercles subconical, projecting, basal ones larger on Toes I–IV than Toe V. Relative length of adpressed Toes IV > III > V > II > I; tip of Toe V extending to penultimate subarticular tubercle of Toe IV; tip of Toe III extending to distal edge of penultimate subarticular tubercle of Toe IV. Toes with moderate webbing, the web encompassing all the basal subarticular tubercles of all toes (on the outer side of Toe III, the web/webbing reaches the proximal portion of the distal subarticular tubercle). Dark brown above with two darker flecking behind the annulus tympanic, weak interorbital

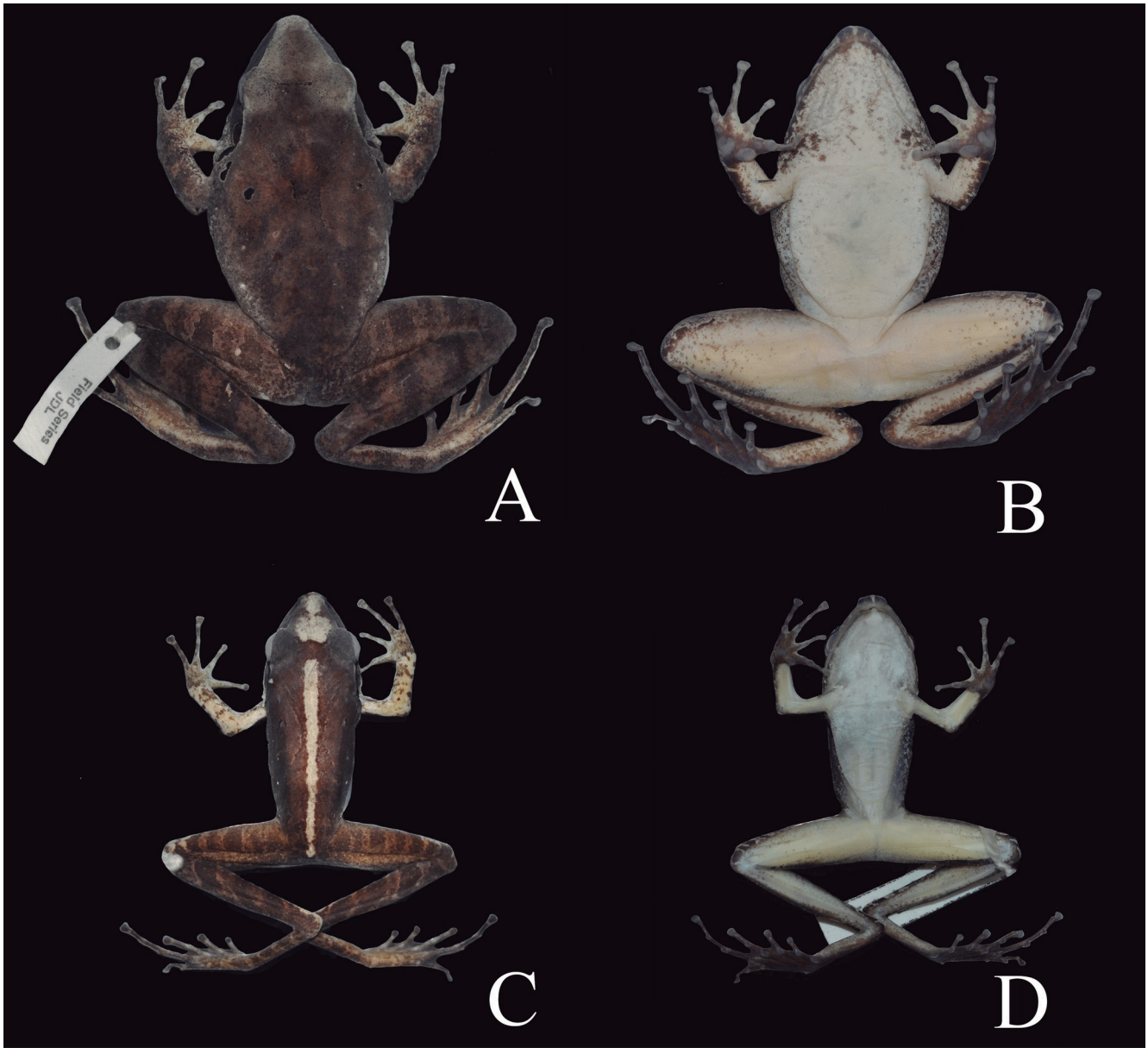

Figure 6. Variation in dorsal and ventral color of *Craugastor metriosistus.* **(A–B)** Adult female (Holotype, ICN 55561); **(C–D)** juvenile female (paratype, ICN 55558).

Table 2. Measurements and proportions (in percentages) of the type series of *Craugastor metriosistus* sp. nov. Mean and standard deviation in parentheses follow ranges for males and females adults.

	Females (*n* = 5)	**Males (*n* = 4)**
Snout–vent length	51.5–60.7 (57.6 ± 3.5)	35.7–37.7 (36.9 ± 0.9)
Head width	21.0–22.8 (22.4 ± 0.8)	13.8–14.8 (14.3 ± 0.4)
Head length	19.6–22.1 (20.9 ± 0.8)	13.0–14.4 (13.7 ± 0.6)
Interorbital distance	3.9–5.4 (4.6 ± 0.5)	2.4–2.9 (2.6 ± 0.2)
Upper eyelid width	4.8–6.1 (5.6 ± 0.5)	3.8–4.2 (3.9 ± 0.1)
Eye diameter	6.2–7.2 (6.6 ± 0.4)	5.1–5.4 (5.2 ± 0.1)
Eye–nostril distance	7.2–8.1 (7.8 ± 0.3)	4.7–4.9 (4.8 ± 0.1)
Internarial distance	4.9–5.7 (5.3 ± 0.3)	3.2–3.9 (3.5 ± 0.3)
Tympanum diameter	4.0–4.2 (4.1 ± 0.1)	3.2–3.6 (3.4 ± 0.2)
Tibia length	33.4–38.5 (36.5 ± 1.9)	22.5–24.2 (23.4 ± 0.7)
Foot length	32.0–39.8 (34.2 ± 3.3)	18.7–21.1 (19.8 ± 1.0)
Head width/head length	103.1–107.5	102.7–106.1
Head width/Snout–vent length	37.5–40.7	37.6–39.4
Eye–nostril distance/Head width	33.9–35.5	33.1–34.0
Interorbital distance/Head width	18.5–23.0	16.8–20.1
Internarial distance/Interorbital distance	101.8–126.6	110.3–148.0
Tympanum diameter/Eye diameter	57.9–66.6	61.5–68.6
Tibia length/Snout–vent length	60.8–64.8	59.6–66.1
Foot length/Snout–vent length	54.2–77.2	49.6–59.1

bar present. A black canthal stripe originating from the tip of the snout or at the level of the nostrils extending to the orbit, and forming a facemask with the postorbital stripes. Supratympanic stripe present and four labial bars evident. Hind limbs moderate, tibia length 63.4% of SVL; foot length 57.6% of SVL. Limbs with gray bars, posterior thighs surfaces brown with diffuse cream blotches uniformly distributed without clearly defined borders. Venter and undersides of limbs cream with some melanophores, throat cream with melanophores arranged in small spots distributed uniformly on throat.

Measurements of holotype (mm)

SVL = 60.7; Head length = 22.1; Head width = 22.8; Internarial distance = 5.7; Eye–nostril distance = 8.1; Eye diameter = 6.9; Upper eyelid width = 6.1; Interorbital distance = 4.5; Tympanum diameter = 4.0; Tibia length = 38.5; Foot length = 35.0.

Color of holotype

In life, body and limbs brown to orange brown with darker brown or blackish brown markings on dorsum, including a faint dark hourglass mark; with two post–tympanic black spots and a weak interocular bar. Throat with melanophores giving a mottled, dusky appearance, weak vertical bars on lips, black supratympanic and canthal stripe; loreal region with black facemask; brown dorsal surfaces of limbs with oblique gray bars; posterior thighs surfaces reddish with diffuse cream blotches uniformly distributed without clearly defined borders; groin and anterior thighs surfaces reddish orange; iris bicolored, upper edge light brown, lower edge reddish brown with black reticulum. In preservative, dorsal surfaces brown, dark brown, or grayish brown with darker brown or blackish brown markings, including a faint dark hourglass mark. Supratympanic and canthal stripes dark brown. Labial bars gray. Loreal region with black or grey facemask. Limbs brown with dark oblique bars; posterior thighs surfaces brown with diffuse cream blotches uniformly distributed without clearly defined borders. Venter and undersides of limbs cream with some melanophores, groin and throat cream, with melanophores arranged in small spots giving a mottled and dusky appearance (Fig. 6A–B).

Variation

Males are smaller than females (Table 2). The coloration on the dorsum, belly, and throat of *Craugastor metriosistus* present variation. Most specimens exhibit brown coloration on dorsal surfaces, dark brown or grayish brown with darker brown or blackish brown markings, some with a faint dark hourglass mark, while the coloration on the throat is cream with melanophores giving a mottled dusky appearance (Fig. 6A–B). Two females, one juvenile (ICN 55558) and one adult (ICN 55573), have a contrasting broad white or cream vertebral stripe and a faint white median gular stripe (Fig. 6C–D). In those two specimens, the arms have cream blotches.

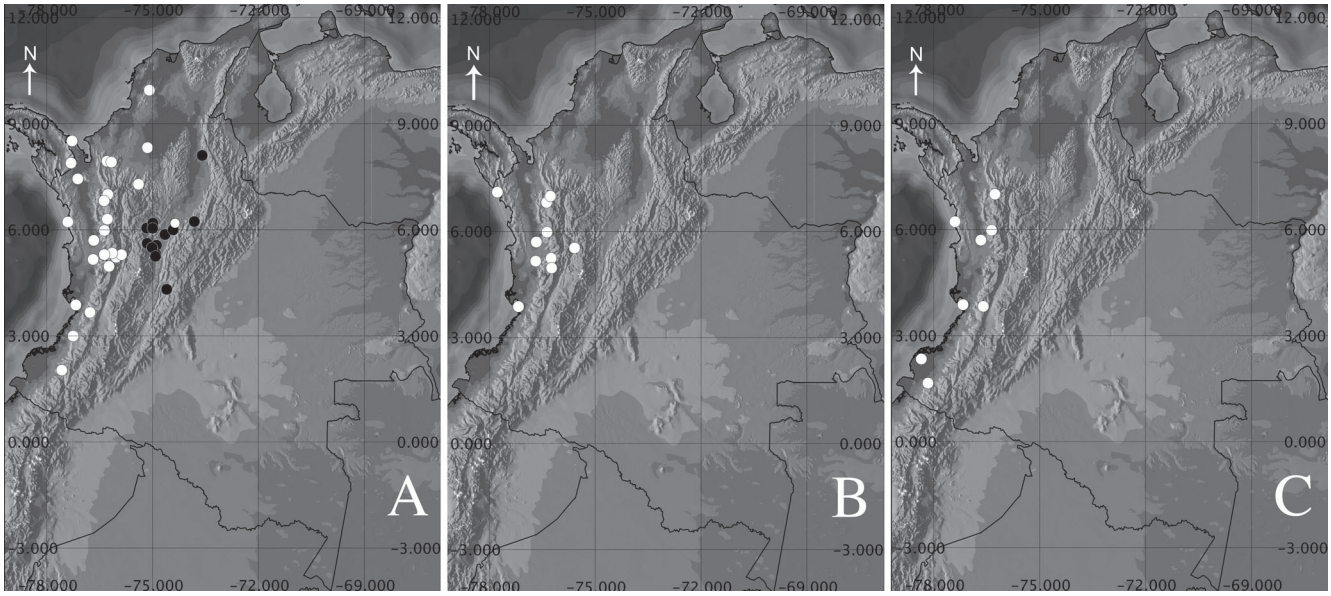

Figure 7. Map showing distribution of the *Craugastor fitzingeri* group in Colombia. **(A)** *C. metriosistus* (black circle) and *C. raniformis* (white circle); **(B)** *Craugastor fitzingeri;* **(C)** *C. longirostris.*

Advertisement call

The call of *Craugastor metriosistus* (Fig. 5A, Table 1) is composed of a short single or sometimes double note emitted at sporadic intervals, 0.058–0.082 s duration (X = 0.073 ± 0.007 s). The call did not show separation of harmonics. The number of pulses per note was 16–24 pulses (X = 20.2 ± 2.3 pulses). The fundamental and dominant frequencies are the same, 1973.7–4512.2 Hz.

Etymology

The specific epithet is a noun, being a compound of the Greek *metrios* (moderate) + *istos* (web), in reference to the moderate webbing on the outer side of Toe III.

Distribution

Craugastor metriosistus is distributed on the middle and upper portions of the Magdalena River Valley, Colombia (Fig. 7A). Department of Antioquia: Municipalities of Puerto Triunfo (425–500 m asl), San Carlos (970 m asl), San Luis (320–470 m asl), and Sonsón (1150 m asl). Department of Boyacá: Municipality of Puerto Boyacá (300–600 m asl). Department of Caldas: Municipalities of La Victoria (510 m asl), Norcasia (560 m), and Samaná (520–720 m asl). Department of Cesar: Municipality of San Martin (115–350 m). Department of Santander: Municipality of Landazuri (450–680 m asl). Department of Tolima: Municipality Mariquita (340 m asl).

Natural history

Craugastor metriosistus was found on rocks within and along of the stream. The males were calling and the females were gravid with both mature and immature unpigmented oocytes (cream color). This species was also found sitting on the ground or dead vegetation to heights of at least 1.5 m above ground. *Craugastor metriosistus* was found in sympatry with *Hyalinobatrachium fleischmanni, Dendrobates truncatus,* and *Rheobates palmatus*.

Summary of the variation in characters used to identify species in the *Craugastor fitzingeri* group

Color patterns on posterior thigh surfaces (Fig. 8)

All the specimens of *Craugastor fitzingeri* and *C. raniformis* have the State I (ground color of posterior thigh surface dark to reddish brown with conspicuous, small, pale spots with well-defined borders), whereas the specimens of *C. longirostris* and *C. metriosistus* the State II (ground color of posterior thigh surface reddish brown with diffuse cream blotches lacking well-defined borders) (Fig. 8). That is, the color patterns on the rear of the thighs only show interspecific variation and thereby confirm the taxonomic utility proposed by Lynch and Myers (1983).

Color patterns on throat (Fig. 9)

Both *Craugastor longirostris* as *C. raniformis* show States II–I (ground cream finely peppered with melanophores and ground cream with melanophores clumped to

form small or large spots). In *C. metriosistus* some specimens show the State III (median white gular stripe with heavy concentration of melanophores distributed to either side) and others the State II. On the other hand, all the specimens of *Craugastor fitzingeri* have the State III (Fig. 9). These findings are consistent with the reports of Lynch and Myers (1983). However, the presence of State III within of *C. metriosistus* increases the distribution of this state character in the *Craugastor fitzingeri* group.

Extension of webbing on outer side of Toe III (Fig. 10)

Both *Craugastor fitzingeri* as *C. metriosistus* have State II (webbing reaches proximal portion of distal subarticular tubercle in outer side of Toe III), whereas in *C. longirostris* and *C. raniformis* the State I (webbing reaches midway between basal and distal subarticular tubercle in outer side of Toe III). These findings demonstrate that the extension of webbing on outer side of Toe III can be also utilized as a diagnostic character within the *Craugastor fitzingeri* group.

DISCUSSION

The distribution of the evaluated character states in the *Craugastor fitzingeri* group shows that the color on the posterior surfaces of the thighs and the degree of webbing on the outer side of Toe III are diagnostically useful to identify species. The color of the throat is considered problematic, since two of the three states were found within *C. longirostris, C. metriosistus,* and *C. raniformis*. The only exception was *C. fitzingeri,* in which all specimens presented State 3; however, this state was also shared with some individuals of *C. metriosistus*. Lynch and Myers (1983) reported the presence of a white gular stripe (State III) in some individuals of *C. longirostris* and *C. raniformis,* although this was not corroborated in our evaluation. We suggest not to use the color on the throat to identify species of the *Craugastor fitzingeri* group and propose restructuring the homology between its states, since these imply at least two characters: (1) presence/absence of melanophores and (2) presence/absence of a white median gular stripe when melanophores are present. Considering this new approach and re-analyzing the results shows that the coloration on the throat is a polymorphic character in the *Craugastor fitzingeri* group.

On the other hand, we demonstrated that the disjunct populations from the Magdalena River Valley identified previously as *Craugastor fitzingeri, C. longirostris,* and some *C. raniformis* correspond to the new species *C. metriosistus*. Consequently, the distribution of

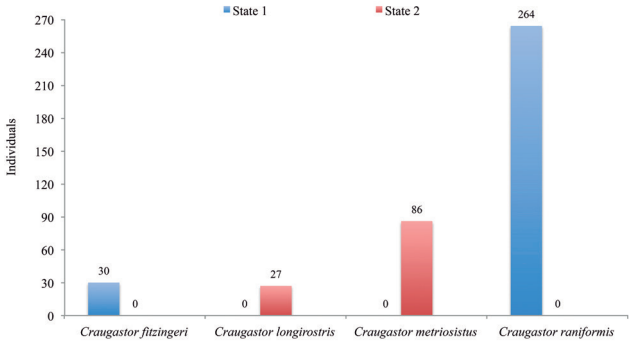

Figure 8. Histogram illustrating the frequency of the color patterns on posterior surfaces of thighs in Colombian species of the *Craugastor fitzingeri* group. State 1: Ground color of posterior thigh surface dark to reddish brown with conspicuous, small, pale spots with well-defined borders. State 2: Ground color of posterior thigh surface reddish brown with diffuse cream blotches lacking well-defined borders.

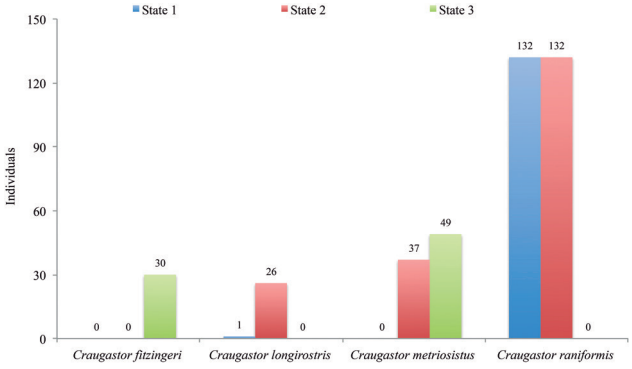

Figure 9. Histogram illustrating the frequency of the color patterns on throat in Colombian species of the *Craugastor fitzingeri* group. State 1: Ground cream, finely peppered with melanophores. State 2: Ground cream with melanophores clumped to form small or large spots. State 3: Median white gular stripe with heavy concentration of melanophores distributed on either side.

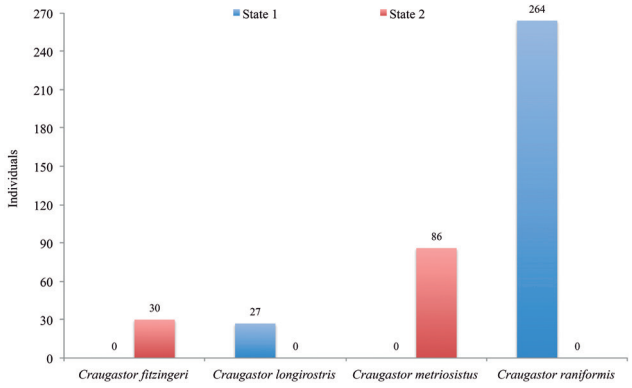

Figure 10. Histogram illustrating the frequency of the degree of webbing on the outer (postaxial) side of Toe III in Colombian species of the *Craugastor fitzingeri* group. State 1: Webbing reaches midway between basal and distal subarticular tubercle in outer side of Toe III (3^-, $2^{⅘}$ or $2^{½}$ sensu Savage and Heyer, 1997). State 2: Webbing reaches proximal portion of distal subarticular tubercle in outer side of Toe III ($2^{⅘}$, 2^+ or 2 sensu Savage and Heyer, 1997).

C. fitzingeri and *C. longirostris* is restricted to the Pacific lowlands and upper basins of the Cauca River Valley in Colombia, with only *C. raniformis* being sympatric with *C. metriosistus* in the northern Magdalena River Valley (Fig. 7). Additionally, we emphasize the need to study the bioacoustics of the *C. fitzingeri* group in order to increase evidence to diagnose those species, given that advertisement calls have been described for only four of the eight species. The call of *C. metriosistus* is more similar to that described for *C. crassidigitus,* since in *C. fitzingeri* vocalizations are like the "tic" or "click" sound a person produces with the tongue and the roof of the mouth, and in *C. raniformis* the call is goat-like (Lynch and Myers, 1983).

Finally we provided a dichotomous key to identify species within of the *Craugastor fitzingeri* group (see Appendix 2) and transfer *Craugastor taurus* from the *C. fitzingeri* group (sensu Padial et al., 2014) to the previous *C. punctariolus* species series, since it was referred to the *C. fitzingeri* in error (J.M. Padial, personal communication).

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APPENDIX 1

Specimens examined

All specimens are from Colombia.

Craugastor fitzingeri (*n* = 30): **Antioquia:** Caramanta: ICN 572; Dabeida: ICN 9350–54, 9356–61, 10755, 10759, 10765, 10770, 10775, 10777, 12510–11; Frontino: ICN 19240, 19243, 19246. **Chocó:** El Carmen: ICN 14324; Istmina: ICN 4952; Jurado: ICN 52804; Tado: ICN 27497; Quibdo: ICN 52056; San Jose del Palmar: ICN 41290. **Valle del Cauca:** Buenvaentura: ICN 42789.

Craugastor longirostris (*n* = 27): **Antioquia:** Dabeiba: ICN 10753, 10757, 10766–67, 10774, 10776, 13856. **Chocó:** Bahía Solano: ICN 12095; El Carmen: ICN 14338; Quibdo: ICN 52057. **Nariño:** Barbacoas: ICN 53581, 53653; Olaya Herrera: ICN 38986, 38988–90. **Valle del Cauca:** Buenventura: ICN 42786–87; Restrepo: ICN 13210–11, 13214–18, 13223, 13225.

Craugastor metriosistus (*n* = 64): **Antioquia:** Cocorná: ICN 15805; Puerto Triunfo: ICN 39386–88, 39390–91; San Carlos: ICN 39395–97, 42419; San Luis: ICN 15810, 15693, 39393-94; Sonsón: ICN 39392. **Boyacá:** Puerto Boyacá: ICN 38614, 38617, 38633, 38635-36, 38645, 38651–52, 38655, 44565–67, 44721–22, 45402, 45406. **Caldas:** La Victoria: ICN 43540–42; Norcasia: ICN 43539, 52835–43, 52856–57; Samaná: ICN 34988, 52844–55. **Cundinamarca:** Nilo: ICN 1253. **Santander:** Landazuri: ICN 10182, 16877. **Tolima:** Mariquita: ICN 43931–32.

Craugastor raniformis (*n* = 264): **Antioquia:** Dabeiba: ICN 9357, 10756; Frontino: ICN 14321, 18880–84, 18886; Urrao: ICN 18850–60, 18862–79; Valdivia: ICN 9214. **Bolivar:** San Juan Nepomuceno: ICN 42273. **Boyacá:** Puerto Boyacá: ICN 38576–79, 38582, 38586–38602, 38605–13, 38615–16, 38618–32, 38634, 38640, 38643, 38646, 38649, 38653–54, 44564, 45407, 45412–17, 45419–20, 45422, 45424. **Cauca:** López de Micay: ICN 4932, 6402. **Chocó:** Acandí: ICN 1589; Bahía Solano: ICN 12099; Carmen de Atrato: ICN 17042, 17166, 17731–32, 17734; Itsmina: ICN 40383; Quibdó: ICN 584, 52058-60; Riosucio: ICN 47133, 47135–39, 47141–45, 47147, 47149, 47151–53, 47155, 47157–59; San José del Palmar: ICN 41269, 41271–72, 41275–84, 41286; Tadó, ICN 27480. **Córboda:** Ayapel: ICN 48907; Tierralta: ICN 8589, 39350–52, 39354–56, 39358–64, 41318, 43344–47, 43349, 52293–97, 52299–52302, 52304, 52306, 52309–13, 52315–18. **Risaralda:** Mistrató: ICN 30470–75, 30477–92, 31816–18, 31820–22, 31824–35; Pueblo Rico ICN 17163–64, 17720, 17725, 27487; Santa Cecilia, ICN 1624. **Valle del Cauca:** Buenaventura: ICN 11460; Dagua: ICN 32565–70, 32574–76, 32579–86, 32589, 38940.

APPENDIX 2

Dichotomous key to identify species of the *Craugastor fitzingeri* group

1. Ground color of posterior thigh surface dark to reddish brown with conspicuous, small, pale spots with well-defined borders...2
   Ground color of posterior thigh surface reddish brown with diffuse cream blotches, lacking well-defined borders borders ...4
2. Webbing reaching proximal portion of distal subarticular tubercle on outer (postaxial) side of Toe III ($2^{⅓}$, 2^{+}, 2 sensu Savage and Heyer, 1997) ..... *Craugastor fitzingeri*
   Webbing reaching midway between basal and distal subarticular tubercle on outer (postaxial) side of Toe III (3^{-}, $2^{⅔}$, $2^{½}$ sensu Savage and Heyer, 1997) 3
3. Skin of venter smooth..... *C. raniformis*
   Skin of venter granulate..... *C. tabasarae*
4. Inner tarsal fold absent.....*C. talamancae*
   Inner tarsal fold present 5
5. Webbing reaching midway between basal and distal subarticular tubercle on outer (postaxial) side of Toe III (3^{-}, $2^{⅔}$, $2^{½}$ sensu Savage and Heyer, 1997) .....*C. longirostris*
   Webbing reaching proximal portion of distal subarticular tubercle on outer (postaxial) side of Toe III ($2^{⅓}$, 2^{+} or 2 sensu Savage and Heyer, 1997).....6
6. Supernumerary tubercles low, restricted to proximal segments of Fingers I and II, supratympanic ridge only slightly curved downward ..... *C. chingopetaca*
   Supernumerary tubercles low, present on proximal segments of all fingers, and a supratympanic ridge distinctly curved downwards.....7
7. Adult males 35.7–37.6 mm snout–vent lengths (SVL), adult females 51.5–60.7 mm SVL..... *C. metriosistus*
   Adult males 20.2–30.2 mm SVL, adult females 34.3–44.7 mm SVL..... *C. crassidigitus*