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A new species of Glassfrog (Anura: Centrolenidae) from the lowlands of northwestern Ecuador, with comments on centrolenid osteology

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Abstract

A new species of Glassfrog is described from the lowlands of northwestern Ecuador. The species is placed in the genus *Centrolene* and differs from the genera, *Cochranella* and *Hyalinobatrachium,* by having humeral spines in males. It differs from congenerics by having a uniformly green dorsal coloration, conspicuous humeral spine, and white iris with clearly defined black reticulations. Detailed cranial and postcranial osteological descriptions are provided, and some of osteological features that seem to be peculiar to centrolenids are discussed. A new suite of traits to characterize Glassfrogs and simplify comparisons among species is proposed.

Key words: Centrolenidae, *Centrolene,* Ecuador, New species, Osteology

Resumen

Describimos una nueva especie de centrolénido de las tierras bajas del noroccidente del Ecuador. La especie nueva difiere de las especies en los géneros *Cochranella* y *Hyalinobatrachium* porque los machos tienen espinas humerales. Se diferencia de especies del género *Centrolene* por tener una coloración dorsal verde uniforme, espina humeral conspicua y un iris blanco brillante con evidente reticulación negra. Presentamos una descripción osteológica detallada de la especie nueva y discutimos algunas características osteológicas que parecen ser únicas a las ranas de cristal. Finalmente, proponemos un nuevo set de atributos para caracterizar especies de centrolénidos y así facilitar su comparación.

Palabras claves: Centrolenidae, *Centrolene,* Ecuador, especie nueva, osteología

Introduction

The anuran family Centrolenidae contains 139 recognized species (Amphibiaweb, 2006) distributed throughout the Neotropics. The monophyly of the family is supported by morphological (Taylor 1951, Hayes & Starrett 1980), behavioral (Ruíz-Carranza & Lynch 1991), and molecular characters (Darst & Cannatella 2004, Faivovich *et al.* 2005, Wiens *et al.* 2005, Frost *et al.* 2006, Grant *et al.* 2006). Recent publications (Cisneros-Heredia & McDiarmid 2006, Guayasamin *et al.* 2006) provide a review of the generic and infrageneric classification of Glassfrogs. A particularly useful morphological characteristic to distinguish these frogs from other anurans (except rhacophorids, hyperoliids, and some species of the genus *Litoria;* Tyler & Davies 1978, Liem

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1970) is the presence of a dilated medial process on Metacarpal IV (Hayes & Starrett 1980). This character is present in all Glassfrogs examined thus far (71 species; Appendix 1; JMG pers. observ.).

Currently, three genera are recognized in Centrolenidae—*Centrolene*, *Cochranella*, and *Hyalinobatrachium* (Ruíz-Carranza & Lynch 1991). *Centrolene* is characterized by the presence of humeral spines in adult males, and *Hyalinobatrachium* has a bulbous liver (Ruíz-Carranza & Lynch 1991). *Cochranella* is defined by two plesiomorphic characters, the absence of both bulbous liver and humeral spines. The monophyly of each of the three genera has not been tested, and recent studies (Frost *et al.* 2006, Guayasamin *et al.* 2006) suggest that these genera represent artificial (i.e., non-monophyletic) groups. However, until a new hypothesis of relationships is available, we follow the classification proposed by Ruíz-Carranza & Lynch (1991).

In this paper, we describe a new species of Glassfrog from the lowlands of northwestern Ecuador and provide a detailed description of its osteology. We also propose a set of key characters to simplify comparisons among centrolenid species.

Material and methods

We examined alcohol-preserved specimens from the herpetological collections at ICN, QCAZ, KU, MCZ, MHNLS, and UCR; museum abbreviations are as in Frost (2006). In addition to the type series of the new species, specimens examined are listed in Appendices 1 and 2; if specimens were not available for direct comparison, we relied on reports in the literature. Morphological measurements were taken with digital calipers to the nearest 0.1 mm, as follow: (1) snout–vent length (SVL) = distance from tip of snout to posterior margin of vent; (2) tibia length = length of flexed leg from knee to heel; (3) foot length = distance from proximal margin of outer metatarsal tubercle to tip of Toe IV; (4) head length = distance from tip of snout to posterior angle of jaw articulation; (5) head width = width of head measured at level of jaw articulations; (6) interorbital distance = distance between upper eyelids, representing the width of the underlying frontoparietals; (7) upper eyelid width = greatest transverse width of upper eyelid; (8) internarial distance = distance between nostrils; (9) eye-nostril distance = distance from posterior margin of nostril to anterior margin of eye; (10) snout-eye distance = distance from tip of snout to anterior margin of eye; (11) eye diameter = distance between anterior and posterior borders of eye; (12) tympanum diameter = distance between anterior and posterior margins of tympanic annulus; (13) eye-tympanum distance = distance from posterior border of eye to anterior margin of tympanic annulus; (14) radioulna length = length of flexed forearm from elbow to proximal border of palmar tubercle; (15) hand length = distance from the proximal margin of palmar tubercle to tip of Finger IV; (16) Finger-II length = distance from outer margin of palmar tubercle to tip of Finger II; (17) Finger-III length = distance from outer margin of palmar tubercle to tip of Finger III; (18) disc of Finger IV = greatest width of disc of Finger IV; and (19) Finger-IV width = width of Finger IV measured at the level of distal subarticular tubercle, including lateral fringes and excluding webbing.

Sexual maturity was determined by the presence of vocal slits in males and by the presence of eggs and/or convoluted oviducts in females. Terminology for webbing is that described by Savage and Heyer (1967), as modified by Guayasamin *et al.* (2006). Fingers are numbered preaxially to postaxially from II–V, in consistency with the hypothesis that Digit I was lost in anurans (Alberch & Gale 1985, Shubin & Alberch 1986, Fabrezi & Alberch 1996); the reader is cautioned that the accounts of other authors, fingers are numbered from I to IV. Because of the increasing diversity of Glassfrogs and our better understanding of key taxonomic traits, we include a *Characterization* section, which is intended to simplify comparisons among species in the family.

Frost *et al.* (2006) redefined the family Centrolenidae, proposing that it contains two subfamilies—Allophryninae for *Allophryne ruthveni*, and Centroleninae for Glassfrogs. The close relationship between *A. ruthveni* and Glassfrogs has been recognized by several authors (Noble 1931, Duellman 2001, Austin *et al.*

2002, Burton 2004, Faivovich *et al.* 2005, Wiens *et al.*, 2005). Therefore, we consider the taxonomic rearrangement proposed by Frost *et al.* (2006) to be unnecessary, because it joins two perfectly distinctive groups (i.e., Centrolenidae and Allophrynidae) into one family, thereby contributing to nomenclatural instability. We think that a much more appropriate solution would have been to create a new, unranked clade that contains the two families (Guayasamin *et al.*, in prep). Throughout this work, we use the name Centrolenidae to refer only to Glassfrogs (exclusive of Allophrynidae).

Centrolene callistommum **Guayasamin & Trueb, new species**

(Figs. 1–6)

Holotype.—QCAZ 25832, adult male, from stream affluent of Río Bogotá (1°05'13.8" N, 78°41'25.8" W, 83 m), nearby San Francisco de Bogotá, Provincia de Esmeraldas, Ecuador; obtained on 01 November 2000 by Italo G. Tapia and Néstor Acosta-Buenaño.

Paratopotypes.—QCAZ 27776–8, 28558, adult females, 28555–56, 28557 (C&S), adult males, same data as holotype.

Paratypes.—QCAZ 28803, adult male, stream affluent of Río Bogotá (1°05'9.06" N, 78°41'8.7" W, 77 m) located 2 km E San Francisco de Bogotá on the San Francisco–Durango Road, Provincia de Esmeraldas, Ecuador; obtained on November 2001 by Italo G. Tapia and Néstor Acosta-Buenaño. QCAZ 27744–45, adult males, and 27768, adult female, from Río La Carolina (0°42'16.16" N, 78°12'4.14" W, 500 m), on the Ibarra–Lita Road, nearby Jijón y Caamaño, Provincia de Carchi, Ecuador; obtained on 02 October 2001 by Italo G. Tapia and Fernando Ayala-V.

Diagnosis.—Centrolene callistommum is easily distinguished from species in the other two centrolenid genera by having a white ventral parietal peritoneum (transparent in *Hyalinobatrachium*) and possessing conspicuous humeral spines in males (spines absent in *Hyalinobatrachium* and *Cochranella*). It differs from other species in the genus *Centrolene* by its large size (in 6 males, SVL 26.7–29.6 mm; in 5 females, SVL 30.3–31.8 mm), uniform green dorsal coloration (Table 1), and its brilliant white iris that bears black reticulations (Fig. 1). *Centrolene callistommum* most closely resembles *C. ilex* (Savage, 1967), *C. prosoblepon* (Boettger, 1892), and *C. andinum* (Rivero, 1968). Adult males of *Centrolene callistommum* can be clearly differentiated from adult males of *C. ilex* by having conspicuous humeral spines (adult males of *C. ilex* with small humeral spine embedded in the arm musculature; Fig. 2). However, we are not aware of any character state that would allow differentiating females of these two species. *Centrolene callistommum* differs from both *C. prosoblepon* and *C. andinum* by having a uniform green dorsal coloration (dorsum green with spots in *C. andinum* and *C. prosoblepon*), slightly larger body size (in *C. callistommum*, SVL = 26.7–31.8 mm; in *C. andinum*, SVL = 21.5–27.6 mm; in *C. prosoblepon*, SVL = 21.7–27.2; Lynch and Duellman, 1973; Señaris and Ayarzagüena, 2005), and a white iris with black reticulations (in *C. prosoblepon*, iris gray or golden gray with black reticulations; in *C. andinum*, iris gray or dark gray with black reticulations; Lynch and Duellman, 1973; Señaris and Ayarzagüena, 2005). Furthermore, *C. callistommum* and *C. andinum* are allopatric, with the latter species being endemic of the Colombian and Venezuelan Andes.

Characterization.—(1) Humeral spines present in males; (2) liver tetralobed, covered by clear peritoneum; (3) white chromatophores (guanophores) in the anterior two thirds of the ventral parietal peritoneum; white pericardium; translucent peritoneum covering intestines, stomach, testes, gall bladder, kidneys, and urinary bladder; (4) in life, dorsum uniform yellowish green, iris brilliant white with black reticulations (Fig. 1); bones green; (5) in preservative, dorsum lavender (Fig. 3); (6) dorsal surfaces of males and females shagreen, but minute spinules evident in males (only visible under ×100 magnification); (7) snout truncate in dorsal and lateral profiles (Fig. 4); (8) tympanum small (tympanum diameter 20–30.8% eye diameter), oriented vertically, with lateral inclination; tympanic annulus visible except for dorsal border, which is covered by supratympanic fold; tympanic membrane partially pigmented, differentiated from surrounding skin; (9) no webbing between Fingers II and III, webbing between Fingers III and IV reduced, webbing between Fingers IV and V extensive (Fig. 5), webbing formula: **III**$(1^{2/3}-2)–(3^{+}-3^{1/4})$**IV**$1^{2/3}–(1-1^{1/2})$**V**; (10) prepollex not separated from Finger II; in males, nuptial pad Type I (Fig. 6); (11) Finger II slightly longer than Finger III (Finger III 93.3–100% length of Finger II); (12) ulnar and inner tarsal folds low; outer tarsal fold absent; (13) webbing on foot extensive (Fig. 5), webbing formula: **I**$(0^{+}-1)–(2-2^{+})$**II**$(0^{+}-1)–(2-2^{+})$**III**$(0^{+}-1)$–2–**IV**$(2-2^{1/3})–(1-1^{+})$**V**; (14) skin below vent with paired enlarged tubercles (Fig. 6); (15) disc of Finger IV of moderate size, about 28.6–34.1% eye diameter; (16) vomerine teeth present, each vomer with 2–7 teeth; (17) males call from upper sides of leaves; fighting behavior unknown; females deposit eggs on upper sides of leaves; (18) in males, SVL 26.7–29.6 mm ($\bar{x}$ = 27.9 ± 0.999; *n* = 6); in females, SVL 30.3–31.8 mm ($\bar{x}$ = 31.2 ± 0.581; *n* = 5).

TABLE 1. Character states in species in the genus *Centrolene* distributed in the lowlands (<1000 m; LWA) and cloud forest (1000–3000 m; CWA) on the western slope of the Cordillera Occidental de los Andes. SVL (in mm) refers only to adult males; range is followed by mean and sample size. For details on distribution, see sources and IUCN *et al.* (2004).

Taxon	SVL (males)	Snout in profile	Humeral spine (males)	Vomerine teeth
C. callistommum	26.7–29.6 (27.9, *n = 6*)	Truncate	Evident	Present
C. ballux	19.2–22.2 (20.6, *n = 25*)	Bluntly rounded to truncate	Evident	Absent
C. geckoideum	70.7–77.0 (74.5, *n = 8*)	Truncate	Evident	Present
C. gemmatum	23.3–24.2 (23.6, *n = 5*)	Truncate	Evident	Absent
C. grandisonae	25.1–29.3 (27.2, *n = 44*)	Truncate	Evident	Absent or present
C. guanacarum	20.6–22.3 (n = 3)	Rounded to truncate	Evident	Present
C. heloderma	26.8–31.5 (29.0, *n = 17*)	Sloping	Evident	Absent
C. hesperium	23.0–27.3	Sloping	Evident	Absent
C. ilex	26.3–30.3 (27.7, *n = 12*)	Truncate	Present, but hidden	Present
C. litorale	20.0	Truncate	Evident	Absent
C. lynchi	23.5–26.4 (24.7, *n = 19*)	Truncate	Evident	Absent
C. peristictum	18.7–20.6 (n = 2)	Truncate	Evident	Absent
C. prosoblepon	21.7–25.6 (24.1, *n = 5*)	Rounded to truncate	Evident	Present
C. quindianum	24.0–26.6 (25.6, *n = 10*)	Rounded to truncate	Evident	Absent
C. robledoi	19.9–24.4 (23.1, *n = 13*)	Truncate to sloping	Evident	Absent
C. scirtetes	24.4 (27.2, *n = 44*)	Bluntly rounded to truncate	Evident	Absent

continued.

Taxon	Dorsal coloration in life	Distribution	Source
C. callistommum	Uniform green	LWA	This work
C. ballux	Green, with golden yellow flecks	CWA	Duellman and Burrowes (1989); this work
C. geckoideum	Olive-green with cream spinules	CWA	Lynch *et al.* (1983); this work
C. gemmatum	Green, with minute, yellowish-white and black flecks	CWA	Flores (1985); this work
C. grandisonae	Green, with small, red spots	CWA	Duellman (1980); this work
C. guanacarum	Green, with cream spots	CWA	Ruíz-Carranza & Lynch (1995); this work
C. heloderma	Green, with numerous bluish-white tubercles	CWA	Duellman (1981); this work
C. hesperium	Green, with green spicules	CWA	Cadle and McDiarmid (1990)
C. ilex	Uniform green	LWA, CWA	This work
C. litorale	Green, with dark gray spots	LWA	This work
C. lynchi	Green, with minute yellowish-white and black flecks	CWA	Duellman (1980); Flores (1985)
C. peristictum	Green, with dark green spots and yellowish-white flecks	CWA	Lynch and Duellman (1973); this work
C. prosoblepon	Green, with small, black or yellow spots, or black and yellow spots	LWA, CWA	Lynch and Duellman (1973); this work
C. quindianum	Green with numerous black spots	CWA	Ruíz-Carranza & Lynch (1995); this work
C. robledoi	Green with dark green flecks	LWA, CWA	Ruíz-Carranza & Lynch (1995)
C. scirtetes	Green with small black spots	CWA	Duellman and Burrowes (1989); this work

Description of holotype.—Adult male, SVL 29.6 mm. Head as wide as long; head length 33% SVL; snout truncate in dorsal and lateral profiles; canthus rostralis indistinct, straight; loreal region slightly concave; lips slightly flared; nostril protuberant, closer to tip of snout than to eye, directed dorsolaterally; internarial area barely depressed. Eye large, directed anterolaterally at an angle of 45°; transverse diameter of disc of Finger IV 46% eye diameter. Supratympanic fold conspicuous, obscuring dorsal portion of tympanic annulus; tympanum oriented mostly vertically, but with slight posterolateral inclination; tympanic membrane translucent, partially pigmented and differentiated from surrounding skin. Dentigerous processes of vomer low, situated transversely between choanae, each bearing two to five teeth; choanae large, longitudinally rectangular; tongue ovoid, with ventral posterior fourth not attached to mouth floor and posterior margin notched; vocal slits extending posterolaterally from the posterolateral base of tongue to angle of jaws.

Humeral spine present and visible externally (Fig. 2); low ulnar fold evident; relative lengths of fingers: IV > V > II ≈ III; webbing between Fingers II and III absent, webbing formula for outer fingers: **III**2–$3^{1/4}$ **IV**2^{-}–1^{+} **V**; discs expanded, nearly round; disc pads triangular; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle elliptical, simple; nuptial pad large (Type I of Flores, 1985), ovoid, granular, extending from ventrolateral base to dorsal surface of Finger II, covering the proximal half of Finger II.

Length of tibia 54% SVL; low inner tarsal fold evident; outer tarsal fold absent; feet about fully webbed; webbing formula of foot: **I**1–2^{-}**II**0^{+}–2**III**1^{-}–2^{-}**IV**2–1**V**; discs on toes round; disc on Toe IV narrower that disc on Finger IV; disc pads triangular; inner metatarsal tubercle large, ovoid; outer metatarsal tubercle round, barely evident; subarticular tubercles small, round; supernumerary tubercles absent.

FIGURE 1. *Centrolene callistommum* in life, QCAZ 32055, adult male. Photos by Martín R. Bustamante. Slides catalogued in the QCAZ photographic collection (2343, 2344).

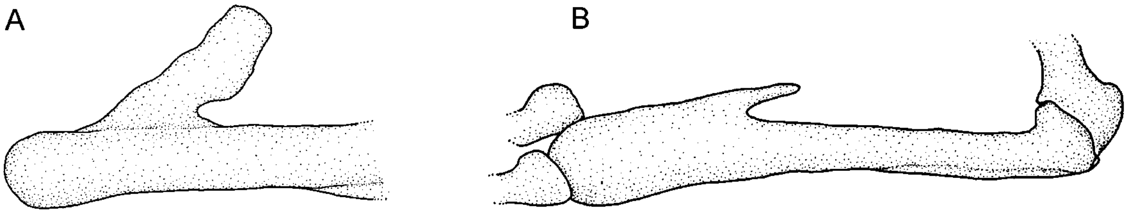

FIGURE 2. Humeral spines of (A) *Centrolene callistommum* (QCAZ 28803, paratype; adult male; SVL = 28.2 mm) and (B) *Centrolene ilex* (ICN 10630, adult male; SVL = 28.4 mm).

FIGURE 3. Holotype of *Centrolene callistommum* in alcohol (QCAZ 25832, adult male; SVL = 29.6 mm).

Skin on dorsal surfaces of head, body, and lateral surface of head and flanks shagreen with numerous minute spinules; throat smooth; belly and lower flanks areolate; cloacal opening directed posteriorly at upper level of thighs, bordered laterally by fleshy, tuberculate, ∩–shaped fold; cloacal tubercles small, fleshy, located immediately posterior to cloacal slit. Pair of large subcloacal tubercles evident in ventral aspect (Fig. 6B).

Color in life.—Based on the color slides shown in Figure 1. Dorsum uniform yellowish green; upper lip with whitish-cream coloration; iris brilliant white with black reticulations; flanks white; parietal peritoneum white, covering anterior two thirds of abdomen (heart not visible); bones green; humeral spine bluish green.

Color in preservative.—Dorsum of head, body, and limbs uniform lavender (Fig. 3); upper lip cream; iris white with dark lavender reticulations; nuptial pad on Finger II cream; dorsally, Fingers II and III and Toes I–III unpigmented; venter cream.

Measurements.—The morphometric data for the holotype (male, QCAZ 25832) are: SVL = 29.6; tibia length = 16.1; foot length = 12.9; head length = 9.7; head width = 9.8; interorbital distance = 3.1; upper eyelid width = 2.8; internarial distance = 2.2; eye-to-nostril distance = 2.2; snout-eye distance = 3.9; eye diameter = 4.1; tympanum diameter = 0.9; eye-tympanum distance = 2.1; radioulna length = 6.4; hand length = 8.8; Finger-II length = 5.7; Finger-III length = 5.4; and disc of Finger IV = 1.9. Measurements of the paratypes are presented in Table 2.

TABLE 2. Measurements (in mm) of the paratypes of *Centrolene callistommum.*

	QCAZ 27744	QCAZ 27745	QCAZ 28555	QCAZ 28556	QCAZ 28803	QCAZ 27768	QCAZ 27776	QCAZ 27777	QCAZ 27778	QCAZ 28558
Sex	Male	Male	Male	Male	Male	Female	Female	Female	Female	Female
SVL	27.7	26.7	27.2	28.1	28.2	30.9	31.3	30.3	31.8	31.5
Tibia length	16.1	15.5	16.2	16.6	16.1	17.6	17.4	17.3	18.8	19.5
Foot length	—	12.5	—	—	12.8	—	13.8	13.8	13.6	—
Head length	8.8	9.2	9.1	9.4	9.7	10.5	10.3	10.1	10.8	10.9
Head width	9.1	9.2	9.1	9.4	10.1	10.6	10.5	10.5	10.8	11.5
Interorbital distance	2.6	2.8	2.8	2.8	3.2	3.0	2.8	2.9	3.1	3.7
Upper eyelid width	—	2.5	2.5	2.6	2.9	2.8	2.6	—	2.6	2.6
Internarial distance	2.0	2.1	2.2	2.0	2.1	2.0	2.2	2.1	2.4	2.3
Eye-nostril distance	2.0	2.1	2.2	2.2	2.2	2.7	2.2	2.6	2.5	2.6
Snout-eye distance	3.3	3.4	3.5	3.4	3.7	3.9	3.8	4.1	3.9	4.1
Eye diameter	3.7	3.5	3.8	4.0	3.9	3.8	3.9	4.1	3.9	4.6
Tympanum diameter	0.9	0.7	0.9	0.8	0.8	0.9	1.0	1.0	1.2	1.1
Eye-tympanum distance	1.6	1.8	1.7	1.8	2.2	2.2	2.1	1.9	2.0	2.1
Radioulna length	6.5	6.2	6.1	—	6.5	7.0	6.6	7.0	6.9	7.1
Hand length	8.2	8.9	—	—	—	—	9.2	9.0	9.7	—
Finger-II length	5.6	5.7	—	—	—	—	6.1	5.9	6.3	—
Finger-III length	5.6	5.5	—	—	—	—	5.7	5.8	6.2	—
Disc of Finger IV	1.6	1.5	—	1.4	1.8	1.8	2.0	1.8	1.8	1.6

Variation.—Females differ from the holotype and other males by lacking spinules on the dorsum and a humeral spine on the arm. One female (QCAZ 27778) has numerous small, dark spots on the dorsum.

Etymology.—The specific name *callistommum* is derived from the Greek *kallistos*–, meaning "most beautiful" and *omma*, meaning "eye."

Distribution and ecology.—*Centrolene callistommum* is known from tributaries of the Río Bogotá (1°05'13.8" N, 78°41'25.8" W, 83 m; 1°05'9.06" N, 78°41'8.7" W, 77 m), Provincia de Esmeraldas, and from the Río La Carolina (0°42'16.16" N, 78°12'4.14" W, 500 m), on the Ibarra–Lita Road, nearby Jijón y Caamaño, Provincia de Carchi, Ecuador (Fig. 7). These localities are in the Evergreen Lowland Forest (*Bosque Siempreverde de Tierras Bajas*) formation as defined by Cerón *et al.* (1999) in northwestern Ecuador. *Centrolene callistommum* is active during the night and has been found on leaves along streams. Males call from the upper sides of leaves, and females deposit pigmented eggs on the upper sides of leaves (QCAZ database).

Relationships.—In general morphology, *Centrolene callistommum* resembles *C. ilex;* however, there are marked differences between the humeral spines in the two species (Fig. 2). Molecular data (JMG, unpubl.) indicate that *C. callistommum* is most closely related to *Centrolene prosoblepon* and *C. andinum*.

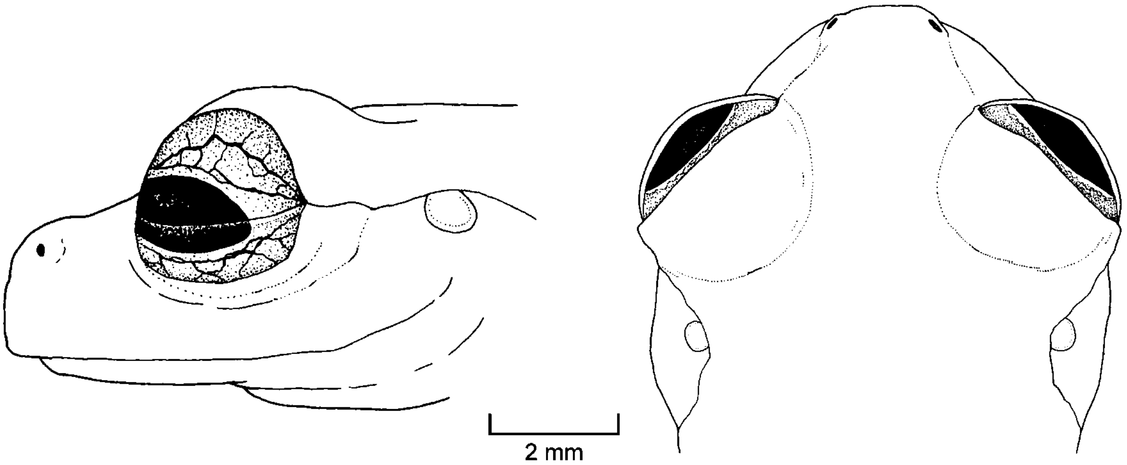

FIGURE 4. Lateral (left) and dorsal (right) aspects of the head of *Centrolene callistommum*, (QCAZ 28803, paratype; adult male; SVL = 28.2 mm).

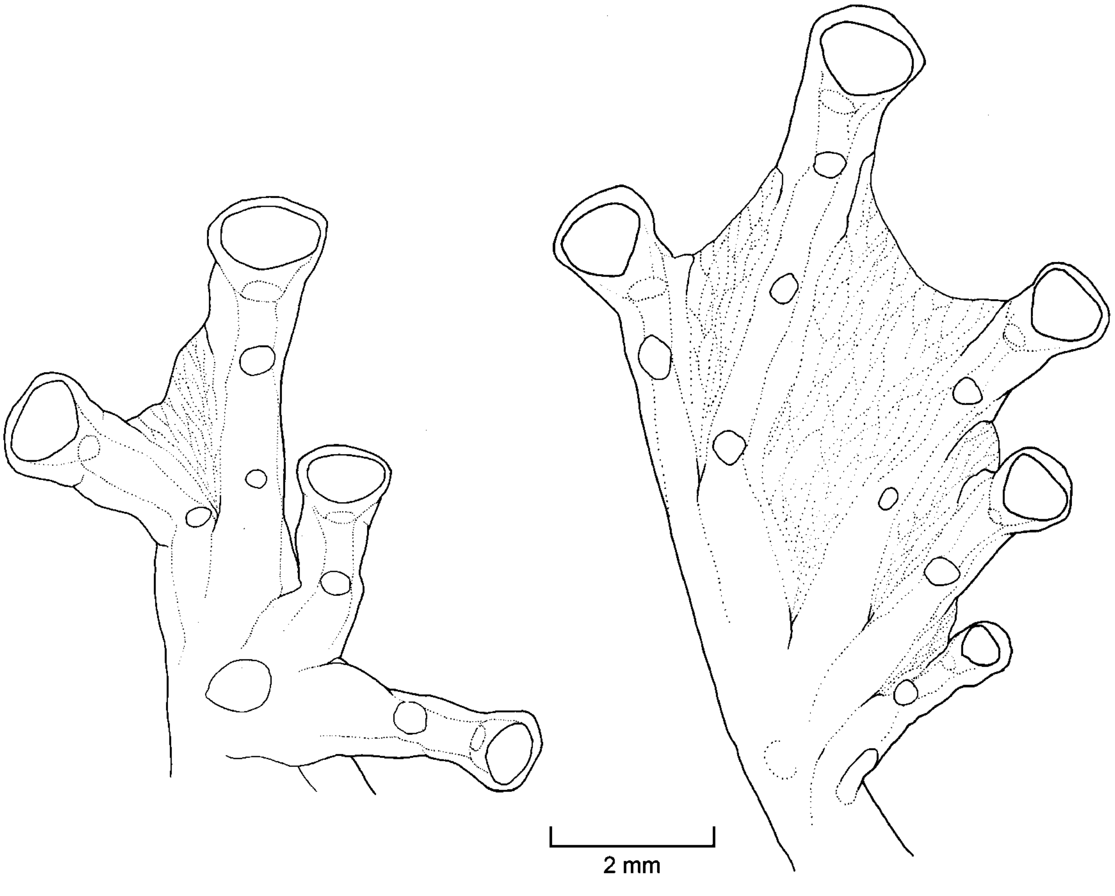

FIGURE 5. Hand and foot of *Centrolene callistommum* (QCAZ 28803, paratype; adult male; SVL = 28.2 mm).

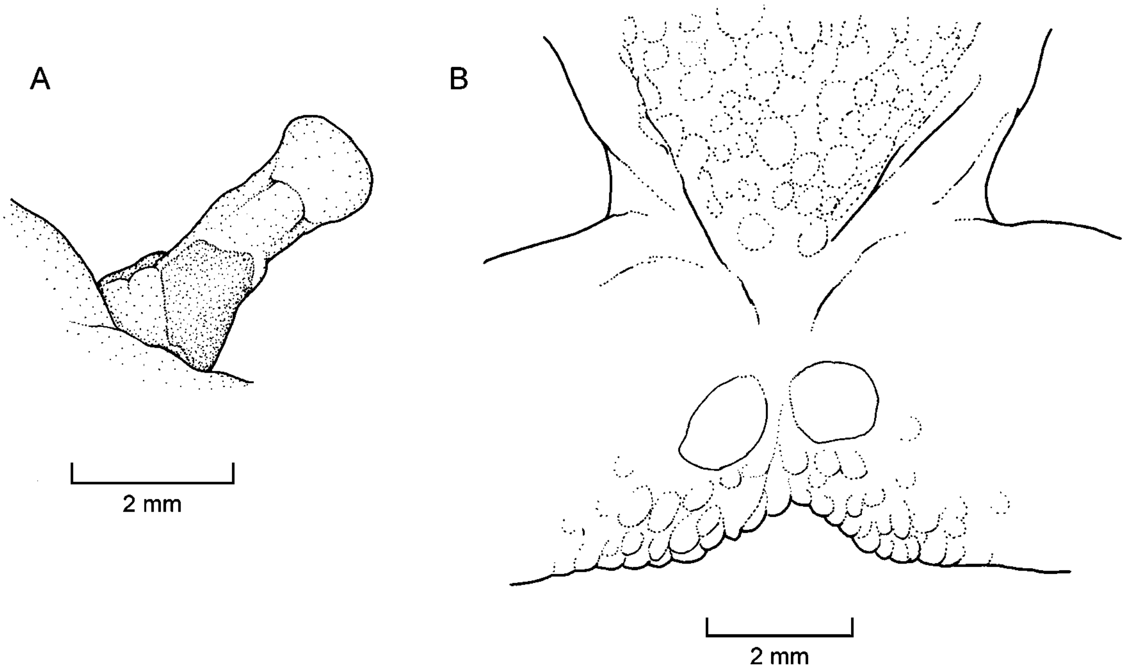

FIGURE 6. (A) Nuptial pad on Finger II and (B) enlarged subcloacal tubercles in *Centrolene callistommum* (QCAZ 25832, holotype; adult male; SVL = 29.6 mm).

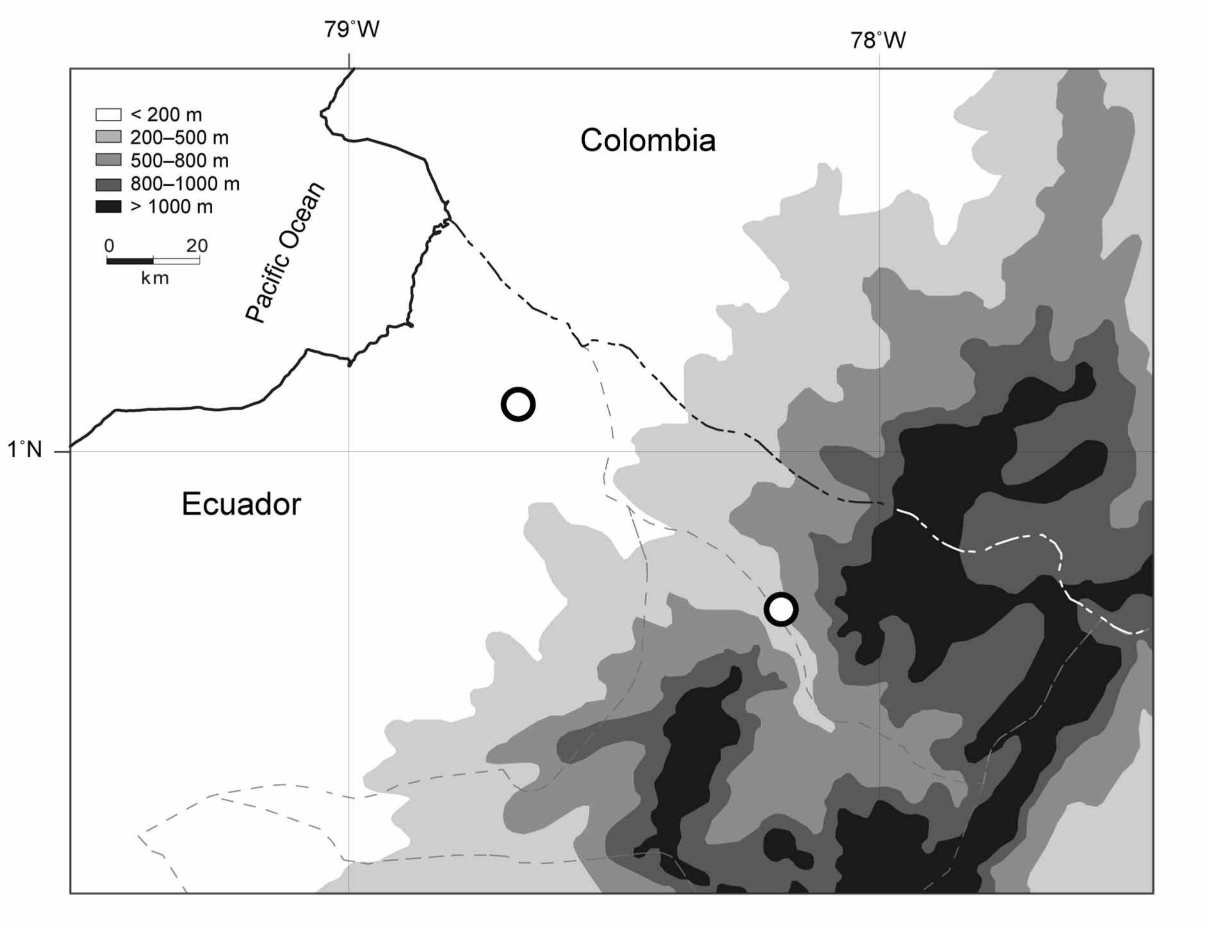

FIGURE 7. Distribution of *Centrolene callistommum* in Ecuador.

Osteology

The following osteological description of *Centrolene callistommum* is based on a cleared-and-double stained adult male (QCAZ 28557, SLV = 27.7 mm).

Cranium

Shape and proportions.—The skull is widest posterior to the orbit at the level of the articulation of the maxilla with the quadratojugal (Fig. 8A, B), where the skull is about 11% wider than long (medially). The rostrum is short, accounting for less than a quarter of the medial length of the skull. The braincase is moderately broad; at the level of the midorbit, the width of the braincase is about 28% of the greatest width of the skull and 31% of the medial skull length. The angle of the jaw lies laterally adjacent to the fenestra ovalis and ventral to the lateral part of the tympanic annulus in dorsal/ventral views.

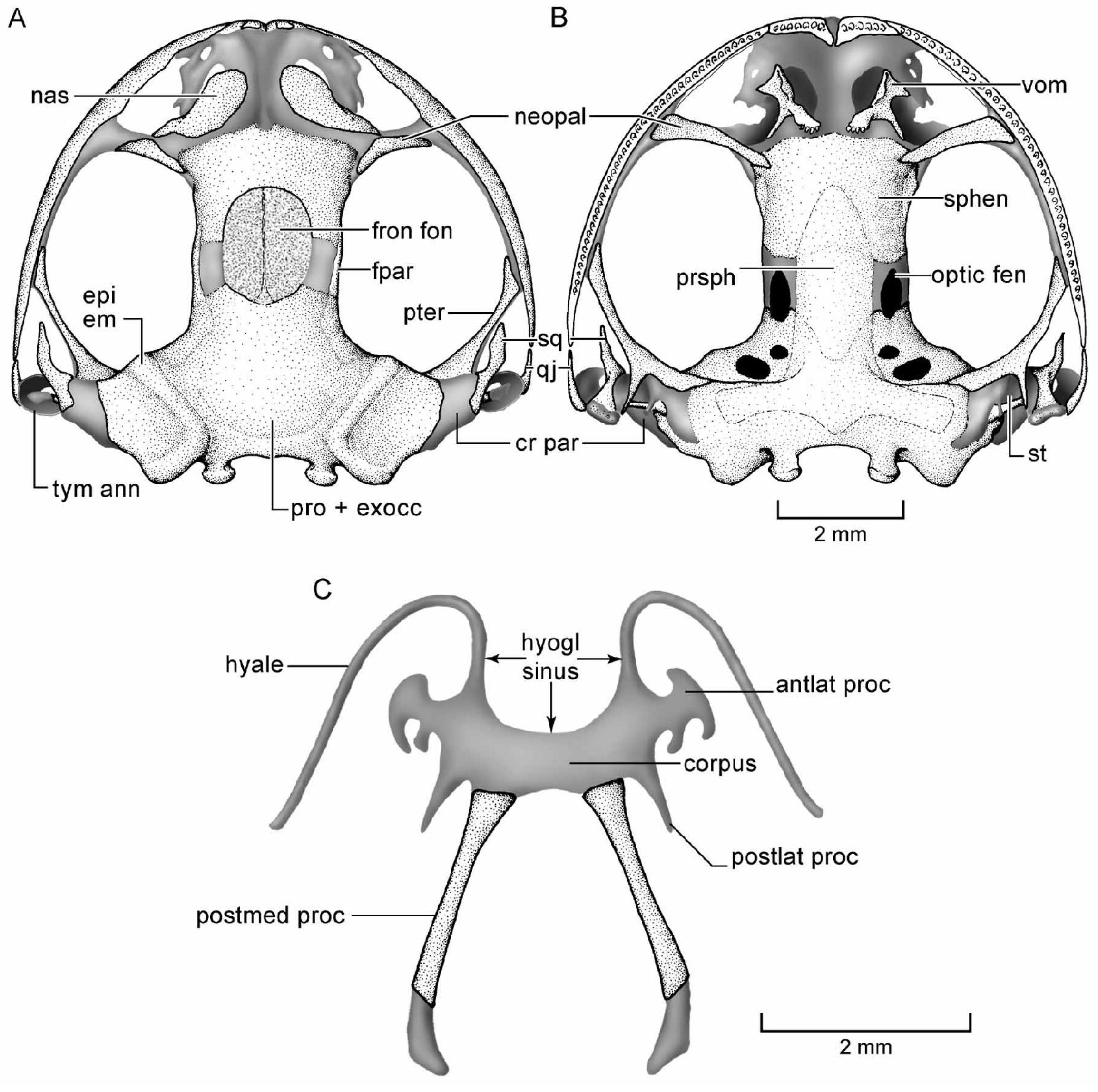

FIGURE 8. Cranium and hyoid of *Centrolene callistommum* (QCAZ 28557, adult male; SVL = 27.7 mm). Cranium in dorsal (A) and ventral (B) aspects. (C) Ventral aspect of hyoid of same specimen. Black and white stippled areas are bone; cartilage shown in gray. Abbreviations: antlat proc = anterolateral process; cr par = crista parotica; epi em = epiotic eminence; fen = fenestra; fpar = frontoparietal; fron fon = frontal fontanelle; hyogl = hyoglossal; nas = nasal; neopal = neopalatine; postlat proc = posterolateral process; postmed proc = posteromedial process; pro + exocc = fused prootic and exoccipital; prsph = parasphenoid; pter = pterygoid; qj = quadratojugal; sq = squamosal; st = stapes (columella); tym ann = tympanic annulus; vom = vomer.

Neurocranium.—The anterior neurocranium comprises large olfactory capsules and the anterior part of the braincase, and is predominantly cartilaginous. The medial walls of the nasal capsules are narrowly separated, with the internasal septum apparently being composed of a thin plate of cartilage between the capsule walls (Fig. 8A); an anteromedial prenasal process is absent. A minute septomaxilla is present but obscured by the staining of the anterior nasal capsule cartilages.

The cartilaginous planum antorbitale has a slight anterolateral orientation in dorsal/ventral aspects. Ventrally, the planum is invested by a simple, unadorned neopalatine, which wraps around the planum to its dorsomedial surface, such that the bone is evident in a dorsal view of the skull. The broad distal end of the neopalatine is narrowly separated from the maxilla; the acuminate medial end articulates with the margin of the sphenethmoid (Fig. 8B).

The braincase and otic capsules are ossified extensively. The anterior margin of the bony sphenethmoid lies at the level of the plana antorbitale, and the posterior margin at about the midlevel of the orbit. There is a moderately broad separation between the sphenethmoid and prootic, within which the optic fenestra lies (Fig. 8B). Most of the fenestra lies in cartilage; however, its posterior margin is formed by the prootic bone. The sphenethmoid is complete dorso- and ventromedially. The exoccipitals are completely fused to one another to form a complete bony margin at the foramen magnum, and fused to the prootics. The contralateral prootics are completely united dorso- and ventromedially; thus, the tectum synoticum (roof) of the posterior braincase is expanded anteriorly and complete (Fig. 8A) over the area in which parietal fontanelles occur in some other centrolenid taxa; the expansion has incorporated the taniae tecti medialis and transversalis into the tectum. As a consequence, the frontoparietal fontanelle is limited to a moderate-sized, subcircular fontanelle that we here term a "frontal fontanelle"; the fontanelle is divided longitudinally by a slender, medial bar of connective tissue, and its posterior border formed by the taenia tecti transversalis that is fused to the tectum synoticum.

The otic capsule is well ossified in the region of the inner ear, and bears a moderately broad, cartilaginous crista parotica that bridges the tympanic cavity from the prootic to the short otic ramus of the squamosal. The epiotic eminences are prominent; the anterior eminence is slightly longer than the posterior and the angle between the two arms is approximately 90°. Ventrally, the lateral wall of the otic capsule is formed in cartilage. The cartilaginous operculum lies posteriorly adjacent to the pars interna plectri of the stapes in the fenestra ovalis, which is formed entirely in cartilage. The pars media plectri is a long, slender, ossified element that extends anterolaterally beneath the crista parotica and behind the palatoquadrate and ventral ramus of the squamosal to terminate in the club-shaped cartilaginous pars externa plectri located in the middle of the incomplete tympanic annulus.

Dorsal investing bones.—Dorsal investing bones are poorly developed. The nasals are thin and widely separated from one another; they only cover the posterior half of the nasal capsules dorsally and afford no lateral protection. The frontoparietals are extraordinarily difficult to discern. Anteriorly, along the orbital margin of the braincase, the bones are exceedingly slender (Fig. 8A). Posteriorly, the frontoparietals seem to be fused with the prootics adjacent the anterior epiotic eminences, because their borders are impossible to discern. The frontoparietal seems to lack a lamina perpendicularis, the vertical component forming the dorsolateral edge of the braincase over the taenia tecti marginalis; however, this part of the bone may be obscured by fusion with the prootic.

Ventral investing and palatal bones.—Owing to the thinness of the bone, the margins of the parasphenoid are difficult to determine accurately. The broad cultriform process (ca. half the width of the braincase) extends anteriorly from the anterior edges of the otic capsule to about the midlength of the sphenethmoid (Fig. 8B). The anterior end of the process is tapered and terminates well posterior to the level of the orbitonasal foramina; the parasphenoid is broadly separated from the neopalatines. The lateral margins of the process are approximately parallel, but they converge gradually toward one another ventral to the sphenethmoid. The parasphenoid alae are moderately long (about equal to the width of the cultriform process), posterolaterally oriented, and distally truncate beneath the midwidth of the otic capsules. A posteromedial process is present, but distinctly separated from the margin of the foramen magnum.

The moderate-sized vomers are broadly separated from one another medially. Each is composed of an arcuate bone bordering anterior and medial margins of the choana. The prechoanal ramus is expanded medially and anteriorly, and bears a ventral flange along its medial edge. The postchoanal process is slender and acuminate. Slender dentigerous processes extend ventromedially from the union of the pre- and postchoanal processes. Each dentigerous process bears four teeth and is broadly separated from its counterpart medially.

The neopalatines are robust and underlie the plana antorbitalae, covering the posterior surfaces and dorsomedial surfaces of these structures (Fig. 8A, B). The bones are unornamented, arcuate, and articulate with the lateral margin of the sphenethmoid just anterior to the orbitonasal foramen. Each bone is narrowly separated from the maxilla; the truncate lateral end is about three times the width of the acuminate medial end.

Maxillary arcade.—The maxillary arcade bears teeth on the premaxillae and maxillae. Although the arcade is complete, the maxillae have a tenuous connection with the slender quadratojugals. The partes palatinae of the maxillae and premaxillae are so narrow that they scarcely are evident. The premaxilla bears a slender acuminate palatine process that configures a V-shape with its contralateral element. There is a simple, juxtaposed articulation between the anterior end of the maxilla and the premaxilla. The pars facialis of the maxilla is low and poorly developed. A preorbital process is absent; thus, the planum antorbitale, along with the entire lateral aspect of the olfactory capsule is entirely exposed.

Suspensory apparatus.—The triradiate pterygoid bears a curved anterior ramus that is oriented anterolaterally toward the maxilla, with which it articulates at approximately the midlength of the orbit. The pterygoid is clearly separated from the maxilla by the pterygoid cartilage, which lies along the medial margin of the maxilla in the orbital region. The medial and posterior rami of the pterygoid are about equal in length; however, the medial ramus is more robust than the posterior. The medial ramus overlaps the cartilaginous anterolateral corner of the ventral margin of the otic capsule, with the margin of the medial ramus being in contact with the edge of the ossified lateral margin of the prootic.

The squamosal is T-shaped; the zygomatic ramus is slightly longer than the otic ramus. The otic ramus overlaps the anterolateral corner and the lateral margin of the crista parotica slightly. The ventral ramus invests the lateral surface of the palatoquadrate, but does not articulate with the quadratojugal.

Hyoid

The width of the cartilaginous hyoid corpus is much greater than its medial length, which is about 27% of the width; Fig. 8C). The anterolateral processes are moderate sized; each has two posterior lobes and a broad, short basal connection to the hyoid corpus. The posterolateral processes are moderately short, broad based, and acuminate distally. The bony posteromedial processes are slightly expanded proximally and widely separated from one another. The hyoglossal sinus is broadly U-shaped and at its greatest width, 64% the width of the hyoid corpus. The hyalia are simple, lacking any processes.

Postcranium

Vertebral column (Fig. 9).—There are eight presacral vertebrae. Presacrals I and II are notably shorter than the posterior presacrals, with the lengths of these anterior vertebrae being only about 30% of their width. Presacrals III and IV are relatively longer and narrower; the length of each is about 58% the width. The lengths of the remaining presacrals are about 76% of the widths. All of the presacrals are non-imbricate except the first, which is partially imbricate. The neural arch of Presacral II bears a rounded, medial process on its anterior and posterior margins; the anterior process articulates with the neural arch of Presacral I.

The transverse processes of Presacrals II–IV are slender, but slightly more robust than those on the posterior presacrals. The vertebral profile in decreasing order of overall width of bony parts is: sacrum > III > II > IV > VIII > VI ≅ VII > V > I. The orientations of the transverse processes of Presacrals II, III, VII, and VIII are lateral to slightly anterolateral, whereas those of the remaining presacrals (IV–VI) are posterolateral. The bony sacral diapophysis is not broadly expanded, and it has a slender base that is less than a third the width of the distal margin. The leading edge of the diapophyses is straight and approximately perpendicular to the longitudinal axis of the body, whereas the posterior margin is concave, smooth, and oriented posterolaterally. The urostyle is long, slender, and equal to or slightly longer than the length of the presacral portion of the vertebral column. The bone has a bicondylar articulation with the sacrum, and bears a low dorsal crest throughout most of its length.

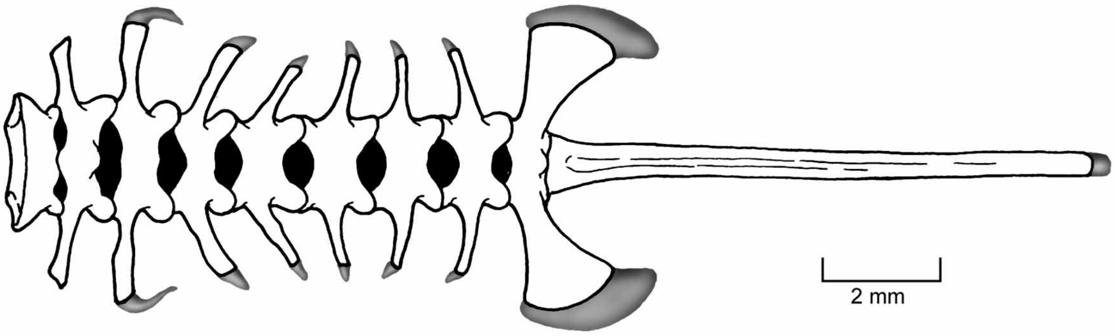

FIGURE 9. Vertebral column of *Centrolene callistommum* (QCAZ 28557, adult male; SVL = 27.7 mm) in dorsal view. Bone shown in white and cartilage in gray.

Pectoral girdle (Fig. 10).—Prezonal elements are absent. The zonal portion of the pectoral girdle is moderately long, with the medial length being about a third the width of the girdle between the glenoid fossae. The clavicles are oriented anteromedially, with the medial tips distinctly separated from one another and located at about the same level of the anterolateral end of the clavicle that articulates with the scapula. The coracoid is stout, with the glenoidal and sternal ends about equally expanded. The midshaft width is about 15% the length of the coracoid, and about 35% the width of the expansion of the sternal end of the bone. The pectoral fenestra is oval and about two and one-half times as wide as it is deep. The scapula is long with a prominent pars acromialis that is distinctly separated from the pars glenoidalis that is about half the length of the anterior head. The bone is about twice the length of the clavicle. The suprascapula is about three-quarters ossified, with the cleithrum apparent as a slender bone along the leading edge of the suprascapular blade. The cartilaginous sternum is about twice as broad as it is long and has a smooth margin.

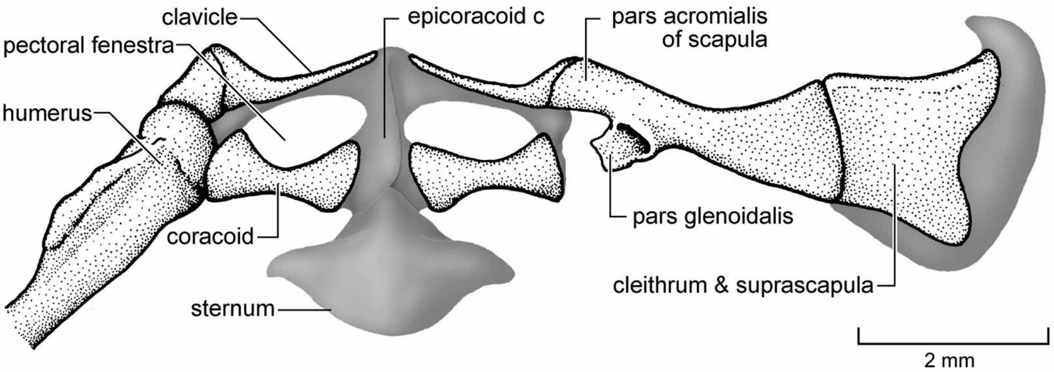

FIGURE 10. Pectoral girdle of *Centrolene callistommum* (QCAZ 28557, adult male; SVL = 27.7 mm) in ventral view. The left scapula and suprascapula have been deflected into the ventral plane for the purposes of illustration. Black and white stippled areas are bone; cartilage shown in gray. Abbreviation: c = cartilage.

Pelvic girdle.—The long, slender ilial shafts lack dorsolateral crests. The overall length of the girdle is about two and one-half times the width between the anterior ends of the ilial shafts. The ilial prominence is broad and low and pubes cartilaginous. The preacetabular angle is approximately 90°. The round acetabulum is formed in cartilage.

Manus and pes (Fig. 11).—The phalangeal formulae for the hand and foot are standard—2-2-3-3 and 2-2-3-4-3, respectively. In increasing order of length, the order of the digits on the hand is: III-II-V-IV, and that of the foot is: I-II-V-III-IV. The carpus is composed of a radiale, ulnare, Element Y, Carpal 1, and a large postaxial element assumed to represent a fusion of Carpals 2–4. Element Y is two and one-half to three times the size of Carpal 1, and the prepollex is composed of one small, proximal bone and an acuminate distal cartilage. The terminal phalanges are T-shaped. The tarsus is composed of two tarsal elements, presumably Tarsal 2 + 3 and Tarsal 1. The prehallux is represented by a bony, rounded basal element associated with a distal block of cartilage.

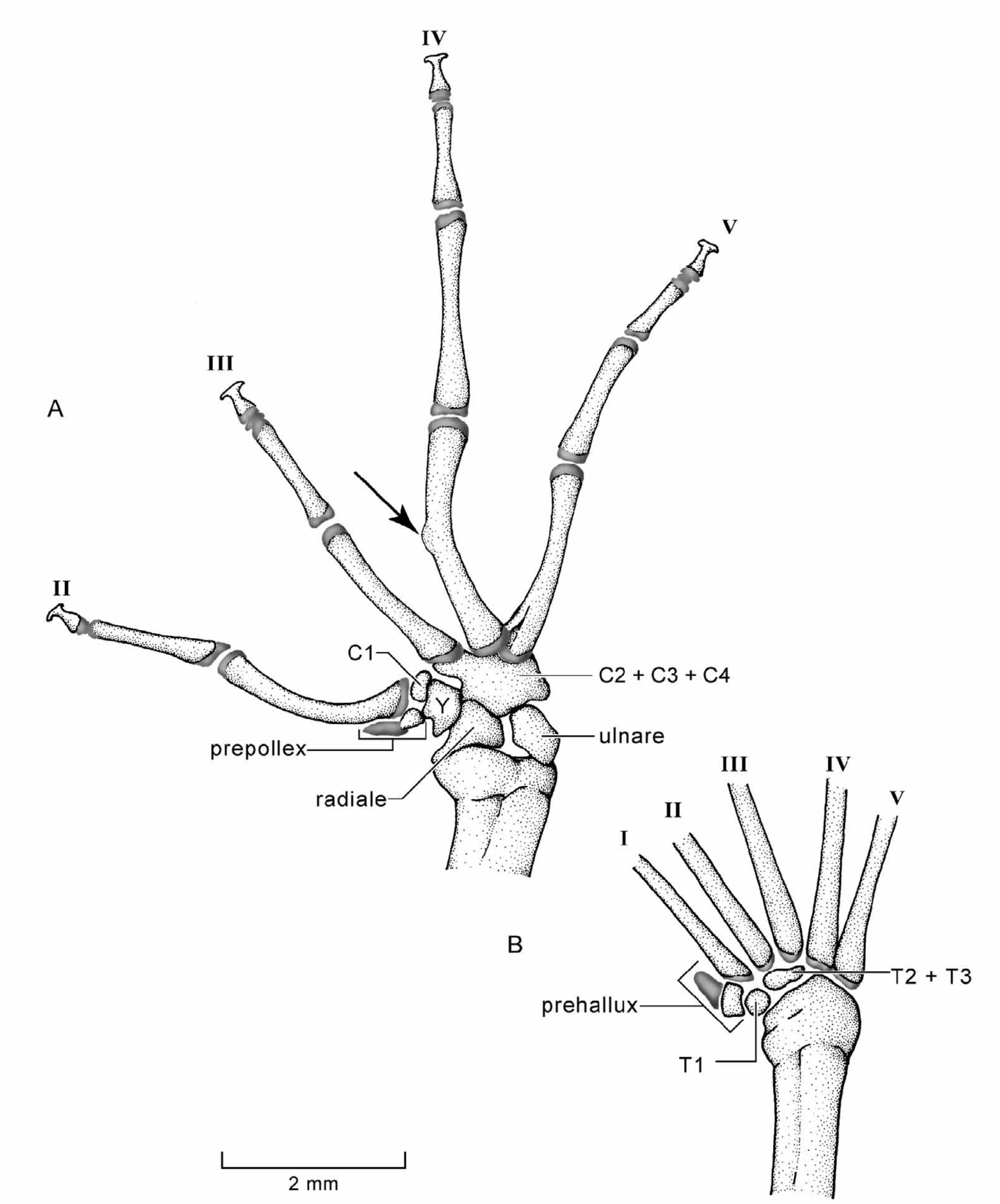

FIGURE 11. Manus (A) and pes (B) of *Centrolene callistommum* (QCAZ 28557, adult male; SVL = 27.7 mm) in dorsal view. Roman numerals denote number of digit, and the arrow designates the medial process of Metacarpal IV, a character present in all centrolenid frogs (Appendix 1). Black and white stippled areas are bone; cartilage shown in gray. Abbreviations: C1–C4 = Carpals 1–4; T1–T3 = Tarsals 1–3; Y = Element Y.

Discussion

Several authors have contributed to our knowledge of the osteology of centrolenids. A significant early contribution was made by Eaton (1958), who described the cranial and postcranial features of *Centrolene prosoblepon,* based on examination of dry skeletal material. Rueda-Almonacid (1994) described the osteology of *C. geckoideum* on the basis of cleared and single-stained specimens. Barrera-Rodríguez (1999) provided osteological descriptions and illustrations of four species of *Hyalinobatrachium* that were cleared and double-stained for cartilage and bone. Finally, in a recent contribution Señaris & Ayarzagüena (2005) described the osteology of 15 Venezuelan centrolenids based on single-stained specimens.

To date, the osteological features that have elicited the most interest are the humeral spines and the partial or complete fusion of the tibiale and fibulare (Jiménez de la Espada 1872, Taylor 1951, Ruíz-Carranza & Lynch 1991, Sanchiz & de La Riva 1993, Cisneros-Heredia & McDiarmid 2006). We have endeavored to provide a baseline osteological description of *Centrolene callistommum* because we think that there are several other features of evolutionary interest. For example, in their study of miniaturization and the anuran skull, Trueb & Alberch (1985) noted that the centrolenids that they examined form a distinct group among anurans because most are small and have well-ossified braincases with a minimal elaboration of dermal investing bones. The shape of the skull (wide braincase) is reminiscent of the proportions of the larval chondrocranium; this, together with the minimal development of dermal investing bones, led Trueb & Alberch (1985) to postulate a premature truncation of cranial development in these anurans.

Although developmental truncation may be reflected in the minimal development of intramembranous bones such as the nasals and frontoparietals in centrolenids, it does not follow that the cranium is poorly ossified. To the contrary, the endocranium of *C. callistommum* like that of other centrolenids, is hyperossified. This is evidenced by the complete medial fusion of the contralateral prootics and exoccipitals; sutures between the paired prootics and exoccipitals are visible in most anurans, but are absent in Glassfrogs. The posterior part of the frontoparietal fontanelle either is obliterated (as it is in *C. callistommum*) or represented in many taxa by a pair of parietal fontanelles separated medially by the ossified taenia tecti medialis and separated from the frontal fontanelle anteriorly by the taenia tecti transversalis. Although the frontoparietal bones are slender, their posterior portions frequently are synostotically incorporated into the underlying prootic. Similarly, the parasphenoid may be independent, or fused partially or wholly with the overlying endocranium (sphenethmoid anteriorly, prootics posteriorly). The otic capsules always are well ossified, but only in the giant *C. geckoideum* are well-developed cristae paroticae present. Neopalatines and pterygoids seem to be invariably present; while the neopalatine always is well developed, the pterygoid is variable.

More attention should be directed to the postcranial skeleton of centrolenids. Perusal of the literature reveals significant variation in the structure of the pectoral girdle with respect to the length of the zonal portion of the girdle and the characteristics of the major bones (clavicles, coracoids, and scapulae) and the sternum. The vertebral column seems relatively conservative, retaining eight procoelous presacrals in most taxa, but the relative sizes of these presacrals vary, as do the nature of the transverse processes and the sacral diapophyses. There is documented variation in the shapes of the terminal phalanges and features of the metacarpals, but little attention has been directed to variation in the carpus and tarsus.

Some of these features described above seem to be peculiar to centrolenids and thus, potentially informative to their phylogenetic relationships. In order to understand many of these features and their variants, we need to survey many more taxa and learn much more about the larvae and their development through metamorphosis and postmetamorphosis—an area that has yet to be addressed.

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Appendix 1. Species with a Dilated Medial Process on Metacarpal IV

Centrolene acanthidiocephalum, C. altitudinale, C. andinum, C. audax, C. bacatum, C. ballux, C. buckleyi, C. callistommum, C. fernandoi, C. hesperium, C. geckoideum, C. grandisonae, C. guanacarum, C. heloderma, C. huilense, C. hybrida, C. lynchi, C. mariaelenae, C. medemi, C. notostictum, C. peristictum, C. pipilatum, C. prosoblepon, C. tayrona, C. venezuelense.

Cochranella adiazeta, C. albomaculata, C. balionota, C. castroviejoi, C. cochranae, C. daidalea, C. euhystrix, C. euknemos, C. flavopunctata, C. granulosa, C. griffithsi, C. helenae, C. ignota, C. mache, C. megacheira, C. mixomaculata, C. oyampiensis, C. pluvialis, C. revocata, C. resplendens, C. ruizi, C. saxiscandens, C. siren, C. spinosa, C. truebae, C. vozmedianoi, C. wileyi.

Hyalinobatrachium antisthenesi, H. aureoguttatum, H. bergeri, H. colymbiphyllum, H. crurifasciatum, H. duranti, H. esmeralda, H. eurygnathum, H. fleischmanni, H. fragile, H. guairarepanensis, H. iaspidiense, H. mondolfii, H. munozorum, H. orientale, H. pallidum, H. taylori, H. uranoscopum, H. valerioi.

Appendix 2. Specimens Examined

Centrolene ballux: ECUADOR: PROVINCIA DE PICHINCHA: 14 km W Chiriboga, 1960 m, KU 164725–27. *Centrolene geckoideum:* ECUADOR: PROVINCIA DE PICHINCHA: 5 km ESE Chiriboga, 2010 m, KU 164492. *Centrolene gemmatum:* ECUADOR: PROVINCIA DE COTOPAXI: San Francisco de Las Pampas, ca. 1800 m, MCZ A-104074, A-104077. *Centrolene grandisonae:* ECUADOR: PROVINCIA DE PICHINCHA: 3.5 km NE Mindo, 1340 m, KU 164686–690. *Centrolene guanacarum:* COLOMBIA: DEPARTAMENTO DEL CAUCA: Municipio de Inzá: Km 84 Popayán–Inza Road, Río Guanacas, 1800–1900 m, ICN 11685. *Centrolene heloderma:* ECUADOR: PROVINCIA DE PICHINCHA: 5 km ESE Chiriboga, 2010 m, KU 164714–15. *Centrolene ilex:* COLOMBIA: DEPARTAMENTO DE ANTIOQUIA: Dabeiba, Río Amparradó, Quebrada Iotó, 805 m, ICN 10625–29, 10630 (C&S), 10631–32. COSTA RICA: PROVINCIA DE LIMÓN: Costa Rican Amphibian Research Center, UCR 16861. PANAMA: COMARCA SAN BLAS: Camp Summit, 400 m, KU 116464. *Centrolene litorale:* COLOMBIA: DEPARTAMENTO DE NARIÑO: Municipio de Tumaco: La Guayacana, 100 m, ICN 13821. *Centrolene peristictum:* ECUADOR: PROVINCIA DE PICHINCHA: Tandapi, 1520 m, KU 118051–52. *Centrolene prosoblepon:* ECUADOR: PROVINCIA DE ESMERALDAS: Reserva Biológica Bilsa, 520 m, KU 291165–75. *Centrolene quindianum:* COLOMBIA: DEPARTAMENTO DE QUINDÍO: Municipio de Filandia: vereda El Roble, Reserva Forestal Bremen, quebradas Las Cruces y La Popa, 2000–2050 m, ICN 24920. *Centrolene scirtetes:* ECUADOR: PROVINCIA DE PICHINCHA : 1.4 km SW Tandayapa, 1920 m, KU 202720.