

Glass frogs (Centrolenidae) of Yanayacu Biological Station, Ecuador, with the description of a new species and comments on centrolenid systematics

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We describe *Centrolene bacatum*, *C. buckleyi*, *Cochranella posadae*, and a new species of *Cochranella* from Yanayacu Biological Station on the Amazonian slopes of the Ecuadorian Andes. The new species differs from other species in Centrolenidae by a combination of characters, including reduced webbing between Fingers III and IV, and kidneys covered with white peritoneum. We summarize the current generic and infrageneric classification in Centrolenidae and discuss some of its problems. A phylogenetic analysis of morphological and behavioural data shows that the genera *Centrolene* and *Cochranella* might not be monophyletic; the genus *Hyalinobatrachium* and, in particular, the group *H. fleischmanni* seem to be monophyletic. However, an analysis with many more characters is needed to resolve the relationships of glass frogs. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, 147, 489–513.

ADDITIONAL KEYWORDS: Andes – *Centrolene* – *Cochranella* – *Hyalinobatrachium*.

INTRODUCTION

The anuran family Centrolenidae was proposed by Taylor (1951) and currently contains 136 recognized species distributed throughout the Neotropics (southern Mexico to Bolivia, north-eastern Argentina and south-eastern Brazil; Frost, 2004). Glass frogs are nocturnal, epiphyllous and arboreal. In all species for which the reproductive biology is known, eggs are laid out of the water on vegetation (leaves or branches) overhanging streams, or on rocks above the stream (Savage, 2002). Contributions by several authors (Ruiz-Carranza & Lynch, 1991a, 1995a, 1998; Bolívar, Grant & Osorio 1999; Señaris, 2001; Duellman & Señaris, 2003) have increased our knowledge of characters and their distribution in Centrolenidae

(hypothesis of relationships summarized in Fig. 1). A merit of this hypothesis (Fig. 1) is that it includes morphological and behavioural characters, some of which seem to be synapomorphies (e.g. presence of humeral spines in males, venter-to-venter combat, red heart visible in life, bulbous liver); however, the generic and infrageneric relationships are poorly supported (see Fig. 1 and Discussion).

At present, 31 species of centrolenids have been reported from Ecuador (Coloma & Quiguango-Ubillús, 2002–04). Although several studies have focused on the glass frogs of Ecuador (e.g. Lynch & Duellman, 1973; Duellman, 1980, 1981; Flores, 1985; Flores & McDiarmid, 1989; Wild, 1994; Guayasamin & Bonaccorso, 2004), our knowledge of their ecology and natural history is still limited. Herein, we present morphological, ecological and behavioural information on the centrolenid frogs of Yanayacu Biological Station and describe a new species of

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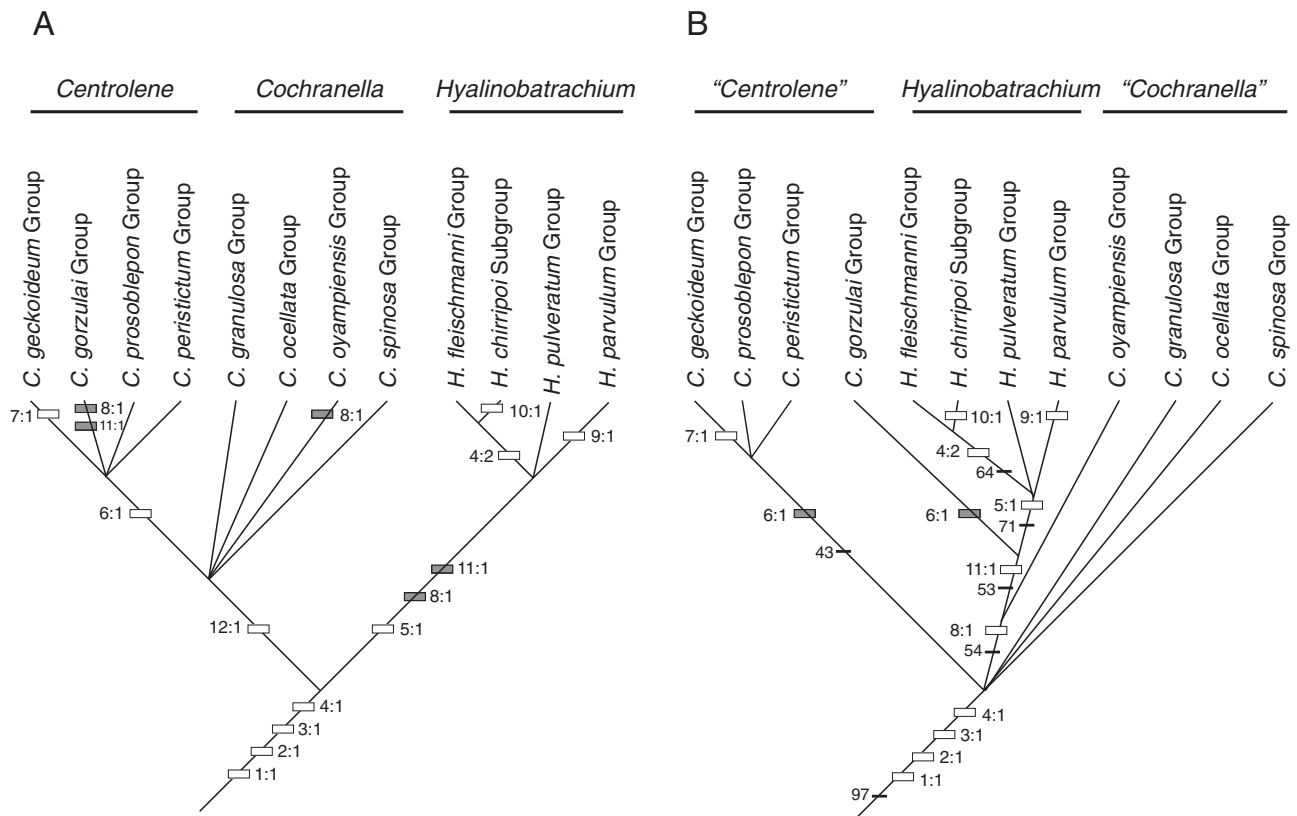


Figure 1. Phylogenetic relationships among genera and species groups within Centrolenidae. A, tree topology suggested by Ruiz-Carranza & Lynch (1991a, b, c, 1996, 1998) and modified by Bolívar *et al.* (1999), Señaris (2001) and Duellman & Señaris (2003). B, single, most-parsimonious tree of the phylogenetic relationships of Centrolenidae (tree length = 13, CI = 0.923, RI = 0.9474, RC = 0.8745). Numbers refer to the following characters: (1) tibiale and fibulare, 0 = not fused, 1 = partially or completely fused; *(2) T-shaped terminal phalanges, 0 = absent, 1 = present; (3) dilated medial process on Metacarpal III, 0 = absent, 1 = present; (4) eggs deposition site, 0 = deposited in water, 1 = not deposited in water, 2 = deposited on underside of leaves; (5) shape of liver, 0 = liver lobed, 1 = liver bulbous; (6) humeral spine in males, 0 = absent, 1 = present; (7) relative size of disc of Finger III, 0 = disc small (< 80% of eye diameter), 1 = disc large (> 80% of eye diameter); (8) coloration of hepatic peritoneum, 0 = clear, 1 = white; (9) coloration of peritoneum covering urinary bladder, 0 = clear, 1 = white; (10) red heart visible in ventral view, 0 = heart not visible, 1 = red heart visible; (11) coloration of parietal peritoneum, 0 = white, 1 = clear. Character 12 (venter-to-venter fight behaviour) was hypothesized to be a synapomorphy shared by Centrolene and Cochranella (Bolívar *et al.*, 1999); however, the distribution of this behaviour has been reported in only nine species (Guayasamin & Barrio-Amorós, 2005) and we did not include in B. Numbers next to tick marks represent bootstrap support values. Grey boxes denote characters that appear more than once in the tree. *T-shaped terminal phalanges are also present in *Allophryne ruthveni*.

Cochranella. Additionally, we summarize the generic and infrageneric classification of taxa included in Centrolenidae.

MATERIAL AND METHODS

We examined alcohol-preserved specimens from the herpetological collections at the Museo de Zoología of the Pontificia Universidad Católica del Ecuador (QCAZ), The University of Kansas Natural History Museum (KU) and Museo de Historia Natural La Salle (MHNLS). In addition to the type series of the

new species, specimens examined are listed in Appendix 1; if specimens were not available for direct comparison, we relied on descriptions in the literature.

Measurements were taken as described by Guayasamin & Bonaccorso (2004) and are as follows: (1) snout-vent length (SVL); (2) tibia length; (3) foot length; (4) head length; (5) head width; (6) interorbital distance; (7) upper eyelid width; (8) internarial distance; (9) eye-to-nostril distance; (10) snout-to-eye distance; (11) eye diameter; (12) tympanum diameter; (13) eye-to-tympanum distance; (14) radioulna length;

(15) hand length; (16) Finger I length; (17) disc diameter of Finger III. In order to provide an objective description of the relative size of Fingers I and II, we measured both fingers (as the distance between the distal margin of the palmar tubercle and the tip of the finger) and provide a quantitative value (see Diagnosis). Sexual maturity was determined by the presence of vocal slits and nuptial pads in males and by the presence of eggs or convoluted oviducts in females. For ease of comparison, the numerical diagnosis parallels that of Lynch & Duellman (1973) as modified by Ruiz-Carranza & Lynch (1991a) and Noonan & Bonett (2003). Terminology for webbing was modified from that described by Savage & Heyer (1967; Fig. 2). Credits for photographs are as follows: MRB = Martin R. Bustamante, WCF = W. Chris Funk; when credits are not shown, photographs were taken by Juan M. Guayasamin. Acoustic terminology follows Duellman & Trueb (1994). For the generic placement of the new species, we follow the classification proposed by Ruiz-Carranza & Lynch (1991a).

PHYLOGENETIC ANALYSIS

Characters were obtained from the literature (Ruiz-Carranza & Lynch, 1991a, 1998; Señaris, 2001; Duellman & Señaris, 2003) and are as follows: (1) tibiale and fibulare, 0 = not fused, 1 = partially or completely fused; (2) T-shaped terminal phalanges, 0 = absent, 1 = present; (3) dilated medial process on Metacarpal III, 0 = absent, 1 = present; (4) egg deposition site, 0 = deposited in water, 1 = not deposited in water, 2 = deposited on underside of leaves; (5) shape of liver, 0 = liver lobed, 1 = liver bulbous; (6) humeral spine in males, 0 = absent, 1 = present; (7) relative size of disc of Finger III, 0 = disc small (< 80% of eye diameter), 1 = disc large (> 80% of eye diameter); (8) coloration of hepatic peritoneum, 0 = clear, 1 = white; (9) coloration of peritoneum covering urinary bladder, 0 = clear, 1 = white; (10) red heart visible in ventral view, 0 = heart not visible, 1 = red heart visible; (11) coloration of parietal peritoneum, 0 = white, 1 = clear. We performed a parsimony analysis with PAUP* 4.0b10

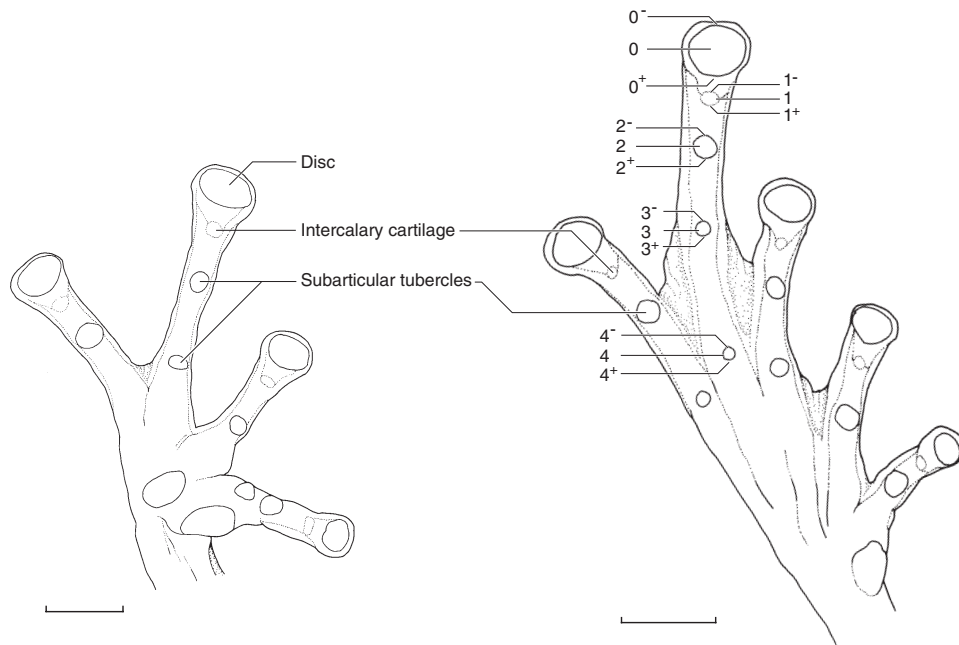


Figure 2. Terminology (modified from Savage & Heyer, 1967) used for webbing formula in hands and feet. Roman numerals represent fingers or toes; Arabic numerals represent the number of phalanges completely or partially free of webbing. We use 0⁻ to indicate that the web reaches the distal margin of the disc; 0 indicates that the web reaches the middle of the disc; 0⁺ indicates that the web reaches the proximal margin of the disc; 1⁻ indicates that the web reaches the distal margin of the intercalary cartilage; 1 indicates that the web reaches the middle of the intercalary cartilage; 1⁺ indicates that the web reaches the proximal margin of the intercalary cartilage; 2⁻ indicates that the web reaches the distal margin of the distal subarticular tubercle; 2 indicates that the web reaches the middle of the distal subarticular tubercle; 2⁺ indicates that the web reaches the proximal margin of the distal subarticular tubercle; the notation for 3 and 4 follow the same pattern described for 2. When, for example, the webbing reaches a midpoint between the intercalary cartilage and the distal subarticular tubercle in Finger IV, and the proximal margin of the disc in Finger V, the appropriate notation between these two fingers would be IV 1^{1/2}-0⁺ V. Scale bar = 2 mm.

(Swofford, 2002) using the accelerated character transformation (ACCTRAN) optimization, and branch-and-bound search. Characters were unordered and equally weighted. As outgroups, we used *Allophryne ruthveni* and *Physalaemus coloradorum*. We used non-parametric bootstrapping (bs, 1000 pseudoreplicates) to assess the stability of internal nodes in the resulting topologies (Felsenstein, 1985).

STUDY SITE

All collections were made in the cloud forests surrounding Yanayacu Biological Station (0°41'S, 77°53'W; 2100 m; Fig. 3) owned by Yanayacu Biological Station (YBS) and the neighbouring Reserva San Isidro (RSI) on the eastern slopes of the Cordillera Oriental de los Andes, Provincia Napo, Ecuador. Fieldwork was conducted over the periods 24 April–15 May 2002, 12–23 August 2002, 3–16 September 2002, 24–30 October 2002, 10–30 April 2003, 5–15 June 2003, 11 August–4 September 2003, 27 November–15 December 2003 and 30 April–01 May 2004. Specimens and tissues were deposited at QCAZ. YBS and RSI comprise approximately 2500–3000 ha of montane

forest, corresponding to Evergreen Lower Montane Forest and Cloud Montane Forest (Bosque Siempreverde Montano Bajo and Bosque de Neblina Montano; Valencia *et al.*, 1999), and including primary and secondary forests and pastures. YBS is located 5 km south-west of Cosanga, a small town on the Quito–Tena Road. Cosanga has a mean annual rainfall of 3159 mm (INHAMI, 2003). YBS and RSI are located in a valley between the slopes of Volcán Antisana to the west and the Cordillera de los Guacamayos to the east. The Río Cosanga, which drains this valley, flows north into the Río Quijos.

SPECIES ACCOUNTS

CENTROLENE BACATUM WILD, 1994

Diagnosis: A species that differs from other species in the family by the following combination of characters: (1) vomerine teeth absent; (2) in life, bones green; (3) in preservative, parietal peritoneum white, pericardium silver white, hepatic peritoneum clear, digestive tract and kidneys cream; (4) in life, dorsum dark green with white warts; in preservative, dorsum lavender with small white spots; (5) no webbing between Fingers I and II; webbing between outer fingers reduced, II 2–3^{1/3} III 2^{1/2}–2^{1/4} IV; (6) webbing formula on foot usually I 1^{1/2}–2⁺ II 1–2 III 1⁺–2^{1/4} IV 2^{1/2}–1⁺V; (7) snout rounded in dorsal aspect, bluntly rounded in lateral profile; (8) dorsal skin finely shagreen with few white warts and tiny spinules; (9) ulnar and inner tarsal folds low or absent; outer tarsal fold absent; (10) humeral spine present; (11) tympanum orientated almost vertically, with slight posterior and lateral inclinations, tympanic annulus visible except for dorsal border, which is covered by supratympanic fold; tympanic membrane pigmented, differentiated from surrounding skin; (12) SVL in males 19.4–21.8 mm (mean = 20.6; *n* = 9); in one female 20.9 mm; (13) prepollical spine not protruding externally; males with large, unpigmented nuptial excrescence (Type I of Flores, 1985); (14) several small, white tubercles immediately posteroventral to vent; pair of large, round tubercles posteroventral to vent (as illustrated by Lynch & Duellman, 1973: fig. 2A); (15) when adpressed, Fingers I and II about equal in length (Finger I 91.3–104.5% of Finger II); (16) liver tetralobed; (17) diameter of eye about twice width of disc of Finger III.

Centrolene bacatum is easily distinguished from other species in YBS by having white tubercles in an area that extends from below the eye to the insertion of the arm (Wild, 1994: fig. 3). Additionally, *Centrolene bacatum* is smaller than *C. buckleyi* [SVL in males, 19.4–21.8 mm (*n* = 9) in *C. bacatum*; 25.0–34.7 mm (*n* = 20) in *C. buckleyi*] and has a snout that is bluntly

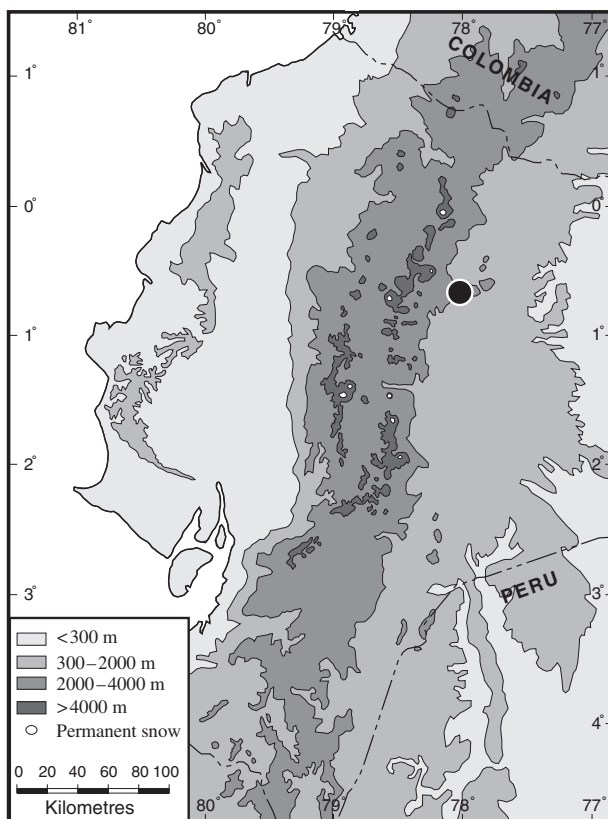


Figure 3. Location of Yanayacu Biological Station (circle) in Ecuador.

rounded in lateral profile (sloping in *C. buckleyi*). Characters differentiating species in the *Centrolene prosoblepon* group are summarized in Table 1.

Colour in life: Dorsum dark green with cream lateral stripe continuing as a series of cream tubercles under eye; throat and ventral surfaces of limbs green; digits pale green; parietal peritoneum white; visceral peritoneum clear; bones green; iris pale bronze with black reticulation (W. E. Duellman field notes 4 March 1984, in Wild, 1994; Fig. 4F).

Colour in preservative: Dorsum of head and body lavender with small, unpigmented spots and white warts; limbs cream lavender with numerous small, unpigmented spots and some white warts; white warts on

lateral surface of head; conspicuous white border on the upper lip, lower lip lacks white pigmentation; tympanum pigmented with purple specks; cloacal region with cream or white warts; iris silvery white with dark purple reticulation. Dorsally, Fingers I and II and Toes I–III unpigmented; some pigmentation visible on Fingers III and IV and Toes IV and V. A male (QCAZ 22386) was dissected to determine coloration of internal organs: white parietal peritoneum covering the anterior half of the belly, silvery-white pericardium, clear hepatic peritoneum, cream visceral peritoneum, and cream kidneys.

Distribution, ecology, and natural history: *Centrolene bacatum* is known from three localities: 11.2 km

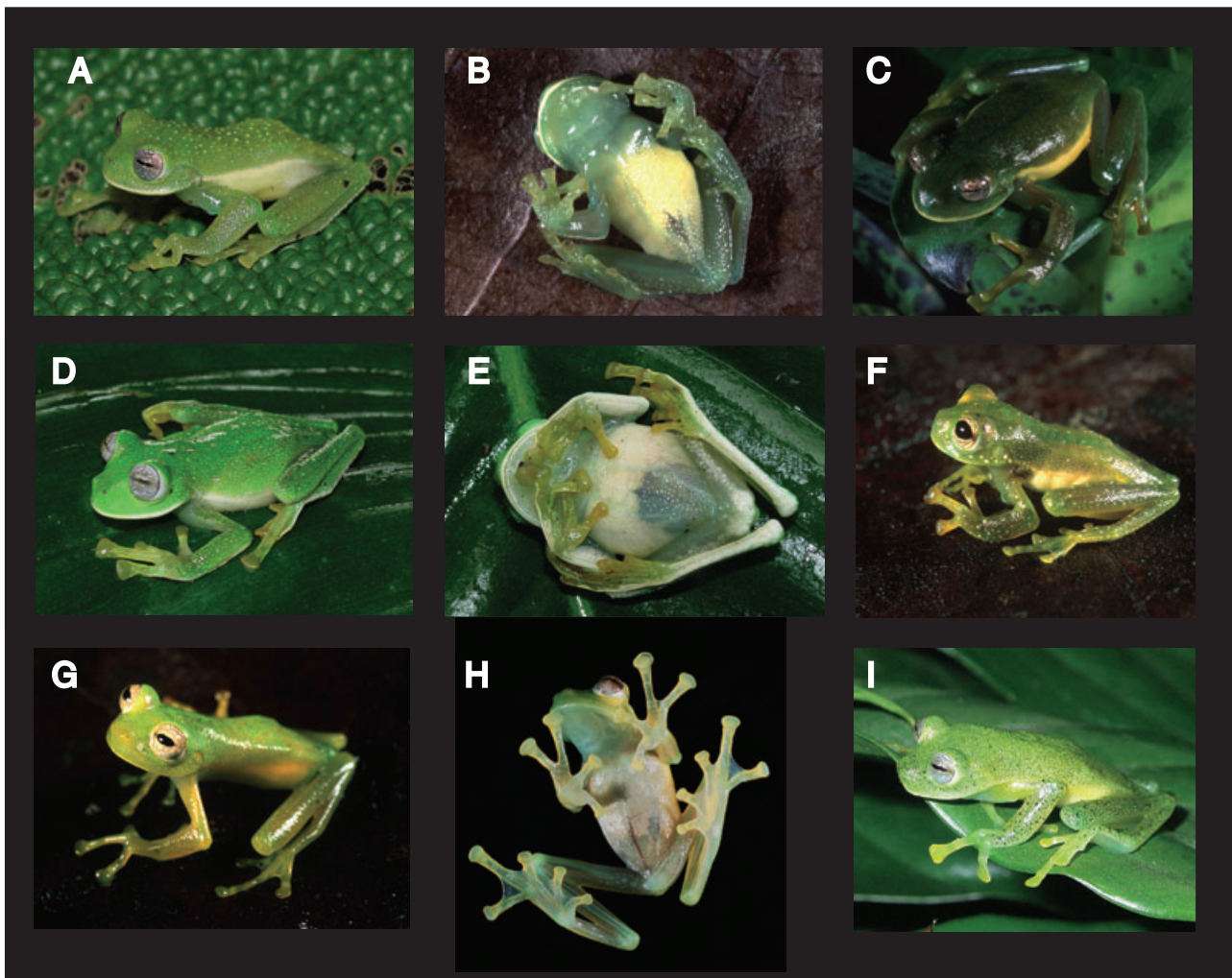


Figure 4. Photographs of glass frogs. A, B, *Centrolene buckleyi* from Yanayacu Biological Station, male, dorsolateral and ventral views, QCAZ 26032 (WCF); C, *Centrolene buckleyi* from Carchi, male, dorsolateral view, MECN 1246 (MRB); D, E, *Cochranella posadae*, male, dorsolateral and ventral views, QCAZ 25090 (WCF); F, *Centrolene bacatum*, dorsolateral view, male, QCAZ 26056 (MRB); G, H, *Cochranella wileyi* sp. nov., males, dorsolateral and ventral views, QCAZ 26029 and 27441, respectively (MRB); I, *Cochranella griffithsi*, dorsolateral view, QCAZ 29525 (JMG).

Table 1. Character state distribution in species of the *Centrolene prosoblepon* group. Spinules are as described by Flores (1985). For simplicity, when coding snout shape in lateral view, the character state 'truncate' contains truncate or subtruncate. The character state 'sloping' means gradually inclined anteroventrally

	Snout (lateral view)	Texture of dorsal skin of males	Dorsal coloration in preservative	Teeth on vomer	Webbing on Finger IV	Webbing on Toe V	SVL in adult males (mm)	Source
<i>C. altitudinale</i>	Round to slightly sloping	Shagreen with small spinules	Lavender with white spots	Absent	Reaching level of distal subarticular tubercle	Reaching level of distal subarticular tubercle	21.5–24.5 (n = 12)	Señaris (2001)
<i>C. andinum</i>	Round to slightly sloping	Shagreen	Lavender to cream lavender with dark purple spots	Present	Reaching level of distal subarticular tubercle	Reaching level of intercalary cartilage	21.5–25.1 (n = 16)	Señaris (2001); this work
<i>C. audax</i>	Truncate	Shagreen with spinules and white warts	Lavender with white warts	Present	Reaching level of distal subarticular tubercle	Reaching level of intercalary cartilage	23.0–23.6 (n = 3)	Lynch & Duellman (1973); this work
<i>C. bacatum</i>	Bluntly rounded	Shagreen with spinules and white warts	Lavender with white warts	Absent	Reaching level of distal subarticular tubercle	Reaching level of intercalary cartilage	19.4–20.7 (n = 8)	Wild (1994); this work
<i>C. ballux</i>	Bluntly rounded	Shagreen	Lavender with small cream flecks	Absent	Reaching level of distal subarticular tubercle	Reaching level between distal subarticular tubercle and intercalary cartilage	19.2–22.2 (n = 25)	Duellman & Burrowes (1989); this work
<i>C. buckleyi</i>	Slightly sloping to sloping	Shagreen with or without small warts and spinules	Lavender with or without whitish warts	Absent	Usually not reaching level of distal subarticular tubercle	Reaching level between distal subarticular tubercle and intercalary cartilage	25.0–34.7 (n = 20)	This work
<i>C. fernandoi</i>	Round	Shagreen with spinules and white warts	Lavender with white warts	Present	Reaching level of distal subarticular tubercle	Reaching level of intercalary cartilage	22.5–26.4 (n = 9)	Duellman & Schulte (1993); this work
<i>C. grandisonae</i>	Round	Pustular	Lavender with yellowish warts	Usually present	Reaching level of distal subarticular tubercle	Reaching level between distal subarticular tubercle and intercalary cartilage	25.1–29.3 (n = 9)	Duellman (1980); this work

<i>C. guanacarium</i>	Round	Shagreen	Pale lavender with white spots	Present	Reaching level of distal subarticular tubercle	Reaching level between distal subarticular tubercle and intercalary cartilage	20.6–22.3 (n = 3)	Ruiz-Carranza & Lynch (1995c)
<i>C. heloderma</i>	Sloping	Pustular	GrEy lavender	Absent	Reaching level of distal subarticular tubercle	Reaching level of intercalary cartilage	26.8–31.5 (n = 17)	Duellman (1981); this work
<i>C. hesperium</i>	Slightly sloping	Shagreen with spinules	Lavender with irregular pigmentless spots and white spinules	Absent	Not reaching level distal subarticular tubercle	Reaching level of between distal subarticular tubercle and intercalary cartilage	23.0–27.3 (n = 54)	Cadle & McDiarmid (1990)
<i>C. huilense</i>	Sloping	Shagreen with spinules	Lavender with cream spinules and purple spots	Absent	Reaching level of distal subarticular tubercle	Reaching or almost reaching level of intercalary cartilage	23.6–26.7 (n = 7)	Ruiz-Carranza & Lynch (1995c); this work
<i>C. hybrida</i>	Round	Shagreen	Pale lavender	Absent	Reaching or almost reaching level of distal subarticular tubercle	Reaching or almost reaching level of intercalary cartilage	20.0–21.9 (n = 18)	Ruiz-Carranza & Lynch (1991b)
<i>C. ilex</i>	Truncate	Shagreen	Lavender	Present	Reaching level of distal subarticular tubercle	Reaching level of intercalary cartilage	27.0 (n = 1)	Savage (1967); this work
<i>C. lemniscatus</i>	Round	Shagreen with spinules	Lavender with unpigmented spinules	Absent	Reaching level of distal subarticular tubercle	Reaching level between distal subarticular tubercle and intercalary cartilage	27.0 (n = 1)	Duellman & Schulte (1993); this work
<i>C. muelleri</i>	Slightly sloping	Finely shagreen with dorsolateral rows of warts	Greyish lavender with black spots and cream warts	Absent	Reaching level of distal subarticular tubercle	Reaching level between distal subarticular tubercle and intercalary cartilage	23.5	Duellman & Schulte (1993); this work
<i>C. notostictum</i>	Truncate	Shagreen with spinules	Pale lavender with white spots	Absent	Reaching or almost reaching level of distal subarticular tubercle	Reaching or almost reaching level of intercalary cartilage	19.4–22.7 (n = 31)	Ruiz-Carranza & Lynch (1991b)

Table 1. *Continued*

	Snout (lateral view)	Texture of dorsal skin of males	Dorsal coloration in preservative	Teeth on vomer	Webbing on Finger IV	Webbing on Toe V	SVL in adult males (mm)	Source
<i>C. pipilatatum</i>	Truncate	Shagreen with spinules and white warts	Lavender with dark purple spots and white warts	Absent	Reaching level of distal subarticular tubercle	Reaching level between distal subarticular tubercle and intercalary cartilage	19.5–22.9 (<i>n</i> = 10)	Lynch & Duellman (1973); this work
<i>C. prosoblepon</i>	Round to truncate	Shagreen	Lavender with dark purple and/ or cream spots	Present	Reaching level between distal subarticular tubercle and intercalary cartilage	Reaching level of intercalary cartilage	21.7–26.6 (<i>n</i> = 5)	Lynch & Duellman (1973); this work
<i>C. quindianum</i>	Round	Shagreen with spinules	Lavender with dark purple spots and white spinules	Absent	Reaching level of distal subarticular tubercle	Reaching or almost reaching level of intercalary cartilage	24.0–26.6 (<i>n</i> = 10)	Ruiz-Carranza & Lynch (1995c)
<i>C. robledoii</i>	Round	Shagreen	Lavender with dark purple spots	Absent	Reaching or almost reaching level of distal subarticular tubercle	Reaching level between distal subarticular tubercle and intercalary cartilage	19.9–24.4 (<i>n</i> = 13)	Ruiz-Carranza & Lynch (1995c)
<i>C. scirtetes</i>	Round	Shagreen with spinules	Lavender with black spots and white spinules	Absent	Reaching level of distal subarticular tubercle	Reaching level of intercalary cartilage	24.4 (<i>n</i> = 1)	Duellman & Burrowes (1989); this work
<i>C. tayrona</i>	Sloping	Shagreen	Pale lavender	Absent	Reaching level of distal subarticular tubercle	Reaching or almost reaching level of intercalary cartilage	28.2–30.8 (<i>n</i> = 13)	Ruiz-Carranza & Lynch (1991b); this work

west-southwest of Plan de Milagro (03°02'S, 78°35'W, 2350 m), Provincia Morona-Santiago, Ecuador; YBS (0°41'S, 77°53'W; 2100 m), Provincia Napo, Ecuador; and 35 km south-east of San Francisco (01°07'S, 76°49'W, 1950 m), Departamento Putumayo, Colombia. Ten individuals of *Centrolene bacatum* were found at YBS during 3 years of inventory work; it is the most abundant centrolenid at Yanayacu. Four adult males were found in primary forest and one adult male was found in secondary forest on leaves approximately 130–200 cm above streams. A male (QCAZ 22728) was found close to two egg clutches that were on the upper side (not on the tip) of different leaves; the male was not in the same leaf as the egg clutches, suggesting that the clutches were not being guarded by the male. Egg clutches (QCAZ 28500-01) had 16 and 20 eggs, respectively; embryos have a whitish coloration. Males call from the upper side of leaves.

Remarks: Wild (1994) described *Centrolene bacatum* and placed it in the *Centrolene prosoblepon* group; however, there is little support for the monophyly of the group (see Discussion) and we consider this placement as tentative until a well-supported phylogeny is available. *Centrolene bacatum* was known only from males (Wild, 1994); during our fieldwork, we found one female (QCAZ 17807; SVL = 20.9 mm), which matches the description provided by Wild (1994), except that it has a smooth dorsum (dorsum shagreen with minute spinules in males) and the following foot webbing: I $1^{1/2}$ -2⁺ II 1-2^{1/3} III 1⁺-2⁺ IV 2^{1/2}-1 V. In males, nuptial pads are more reduced than the Type I described by Flores (1985).

CENTROLENE BUCKLEYI (BOULENGER, 1882)

Diagnosis: *Centrolene buckleyi* differs from other species in the family by the following combination of characters: (1) vomerine teeth absent; (2) in life, bones green; (3) in preservative, parietal peritoneum and pericardium white, hepatic peritoneum clear, visceral peritoneum cream, peritoneum around kidneys cream; (4) in life, dorsum uniform green with or without spinules and scattered, whitish warts; in preservative, dorsum lavender with or without whitish warts; (5) webbing absent between Fingers I and II, basal webbing between Fingers II and III; webbing between outer fingers usually III (2^{1/2}-3⁻)-(2^{1/3}-2^{2/3}) IV; (6) webbing formula on foot usually I (1^{1/2}-2⁻)-(2±2^{1/4}) II (1-1⁺)-(2^{1/4}-2^{1/2}) III (1±1^{1/2})-(2^{1/3}-2^{2/3}) IV (2^{2/3}-3⁻)-1^{2/3} V; (7) snout round in dorsal aspect, slightly sloping to sloping in lateral profile (Fig. 5A, B); (8) dorsal skin finely shagreen, with or without spinules; (9) ulnar and tarsal tubercles absent; outer ulnar and tarsal folds low or absent; (10) humeral spine present; (11) tympanum orientated almost vertically, with slight

lateral and posterior inclinations, tympanic annulus visible except for its dorsal border, which is covered by a low supratympanic fold; tympanic membrane not differentiated from skin around tympanum; (12) SVL in males 27.9–30.5 mm (mean = 28.9; $n = 20$); in females 29.8–34.4 mm (mean = 31.7; $n = 5$); (13) prepollical spine not protruding externally; nuptial pad large (Type I of Flores, 1985); nuptial excrescences cream, finely granular; (14) pair of large, round tubercles posteroventral to vent (as illustrated by Lynch & Duellman, 1973: fig. 2A); (15) when adpressed, Finger II longer than Finger I (Fig. 6A); (16) liver with four lobes; (17) diameter of eye almost twice width of disc of Finger III.

Centrolene buckleyi is in the *Centrolene prosoblepon* species group based on the possession of humeral spines, green bones, eye larger than disc of Finger III, and white pericardium and parietal peritoneum (but see Remarks). Most species in the *Centrolene prosoblepon* group differ from those in the *Centrolene peristictum* group by lacking white pigment on the digestive tract (white pigment present in the *Centrolene peristictum* group) and from species in the *Centrolene geckoideum* group by having an eye that is larger than the disc of Finger III (diameter of eye < disc of Finger III in the *Centrolene geckoideum* group).

Centrolene buckleyi is easily distinguished from other species in the region by having a humeral spine (in males), white upper lip, a moderate size (SVL in males 27.9–30.5 mm; in females 29.8–34.4 mm) and a sloping snout in lateral profile. Additional characters distinguishing species in the *Centrolene prosoblepon* group (as defined by Ruiz-Carranza & Lynch, 1991a) are presented in Table 1.

Colour in life: Dorsal surfaces bright to dark green, sharply demarcated laterally from white lower flanks; throat and most of venter pale green; parietal peritoneum yellowish white; heart not visible; edge of upper lip, outer edge of tarsus and cloacal stripe white; bones green; iris pale copper flecked with black (Lynch & Duellman, 1973; Fig. 4A–C). Additionally, specimens from YBS have white warts on dorsum (Fig. 4A).

Colour in preservative: Dorsum of head and body lavender with or without small, unpigmented spots; limbs cream with slight lavender tonality; conspicuous white border on the upper lip, lower lip lacks white pigmentation; dorsally, all fingers, Toes I–III and most of Toe IV unpigmented; outer edge of forearm faintly marked with white pigment; cloacal region mostly unpigmented, except for few minute white spots. Males with cream nuptial pad on Finger I. Ulnar and tarsal folds whitish; venter cream. Two males (QCAZ 26031 and 32) were dissected to observe coloration of internal organs: parietal peritoneum white covering the anterior two-thirds to three-quarters of the belly,

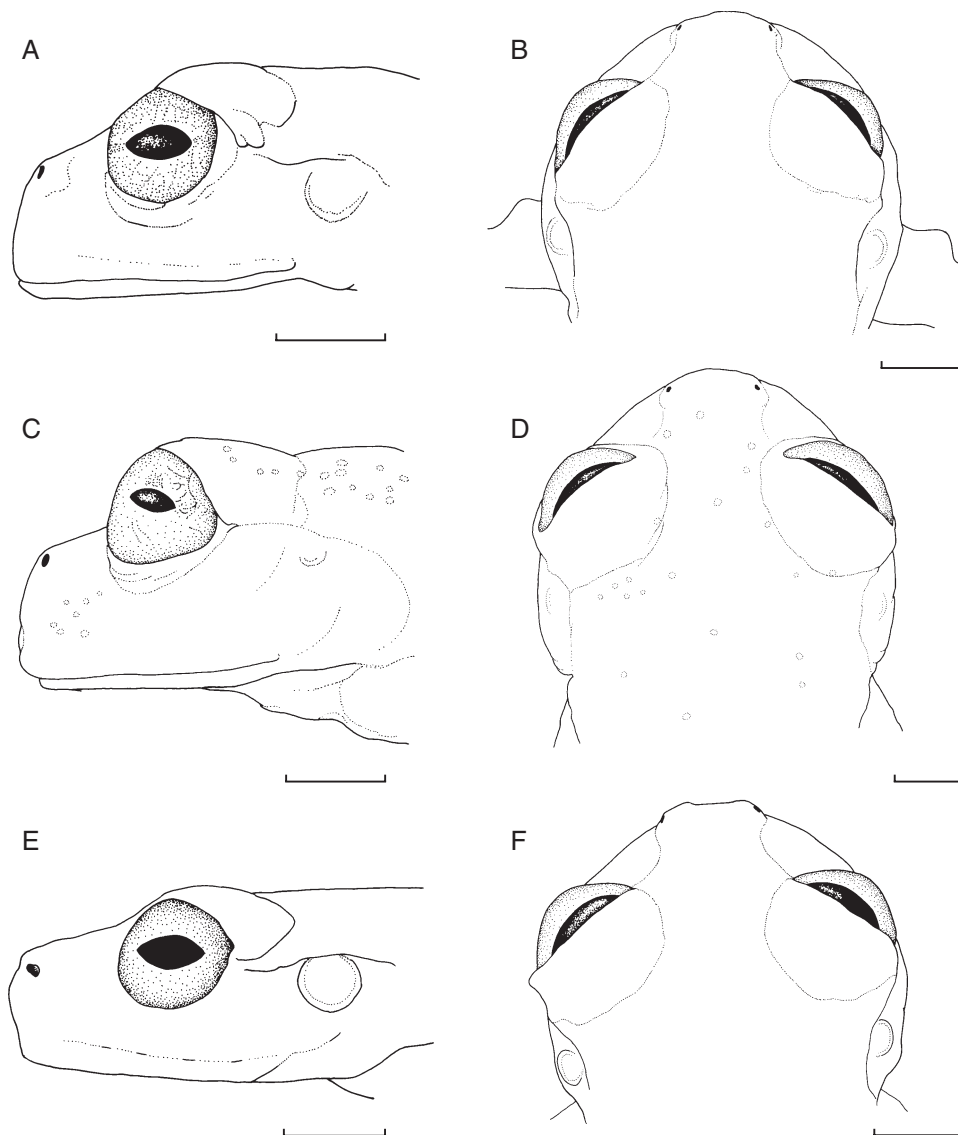


Figure 5. Lateral and dorsal views of heads. A, B, *Centrolene buckleyi*, male, QCAZ 22388; C, D, *Cochranella posadae*, male, QCAZ 26023; E, *Cochranella wileyi* sp. nov., female, QCAZ 26028; F, *Cochranella wileyi* sp. nov., male, QCAZ 26029. Scale bar = 2 mm.

pericardium white, hepatic peritoneum transparent, visceral peritoneum cream, kidneys cream.

Measurements (in mm): Measurements of the specimens collected at YBS are shown in Table 2.

Distribution, ecology, and natural history: *Centrolene buckleyi* is found between 2100 and 3300 m in the Andes of Venezuela through Colombia to southern Ecuador (Frost, 2004) and northern Peru (Duellman & Wild, 1993). Although we have inventoried Yanayacu intensively for 3 years, only three individuals of *C. buckleyi* have been found, suggesting that this species is quite rare. One male (QCAZ 22388) was found on a leaf approximately 160 cm above a stream in

secondary cloud forest at night. This male was found close to a clutch of eggs. A second male (QCAZ 26031) was found calling from a bamboo leaf 300 cm above a stream in primary forest, also at night.

Call: We recorded nine calls of one male *Centrolene buckleyi* (QCAZ 26032; SVL = 25.9 mm) in the laboratory of QCAZ (air temperature = 22.7 °C; cassette number QCAZ-CC-154). The male began calling from a cooler, escaped the cooler, and then continued calling in a dark room. Each call consisted of 1–5 notes, each note with two distinct metallic, high-pitched pulses (Fig. 7). These calls presumably represent advertisement calls, although recordings of other males in the field will be

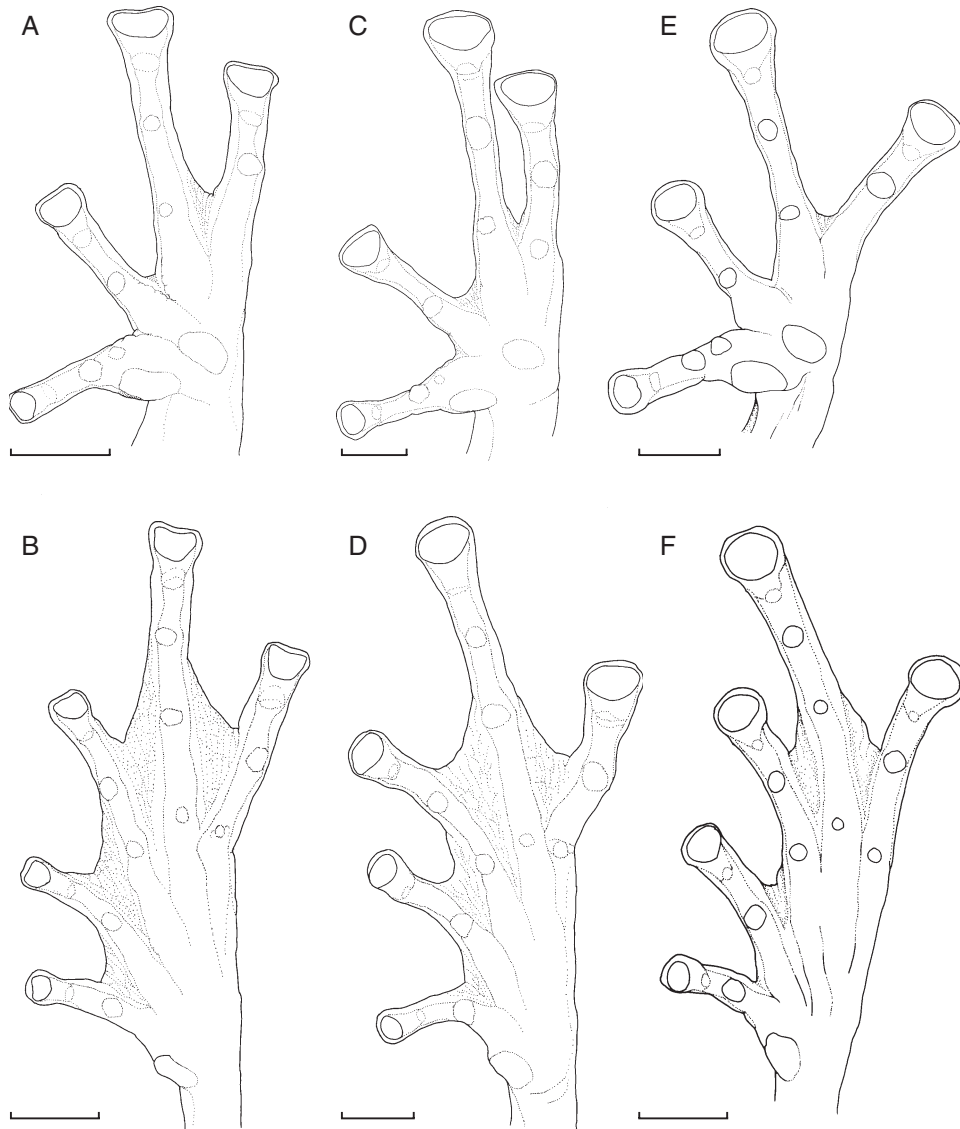


Figure 6. Ventral view of hands and feet. A, B, *Centrolene buckleyi*, male, QCAZ 22388; C, D, *Cochranella posadae*, males, QCAZ 25090 and 26023, respectively; E, F, *Cochranella wileyi* sp. nov., female, QCAZ 26028. Scale bar = 2 mm.

necessary to confirm this presumption. A detailed summary of call parameters is given in Table 3. The call of the specimen collected at YBS differs remarkably from previous reports. According to Bolívar *et al.* (1999), the fundamental frequency of a *C. buckleyi* in Colombia ($4^{\circ}44'39''\text{N}$, $76^{\circ}18'16''\text{W}$; 2220 m) was 5200 Hz (highest frequency in the YBS specimen = 4139 Hz; Table 3). The differences between these calls may represent geographical variation within a single species, different type of call and/or measurement errors, but it is also possible that the two populations represent distinct lineages (discussed below).

Remarks: The validity of the *Centrolene prosoblepon* group as a monophyletic group remains to be tested; it

is important to emphasize that phenetic groups (if not supported by unambiguous synapomorphies) are convenient only for some taxonomic activities such as identifying and naming species. Specimens of *Centrolene buckleyi* collected in YBS (QCAZ 22388, 26031 and 32) differ from the description presented by Lynch & Duellman (1973) in the following (characters in parentheses are from Lynch & Duellman, 1973): (1) dorsum with scattered whitish warts (no warts); (2) when addressed, Finger II longer than Finger I (first and second fingers equal in length); (3) outer edge of forearm with lightly white dermal ridge (ulnar ridge absent); (4) inner edge of tarsus with low fold (tarsal fold absent); and (5) SVL in males, 25.3–26.5 mm (28.4–29.5 mm). Examination of a larger series of

C. buckleyi (Appendix 1) reveals that most of the differences mentioned above are artefacts of a small sample size or mistaken observations. Additionally, Lynch & Renjifo (2001) mentioned that males of *C. buckleyi* have tubercles in the reproductive season. Myers & Donnelly (1997) elevated the Venezuelan populations of *Centrolene buckleyi* (*Centrolenella buckleyi venezuelensis* Rivero, 1968) to the species level, *Centrolene venezuelense* (Rivero, 1968), but they did not provide evidence supporting this taxonomic change. Although it is possible that the populations in Venezuela form a distinct lineage (Señaris, 2001), taxonomic changes need to be justified with studies across the distribution range of '*Centrolene buckleyi*'.

Table 2. Measurements (in mm) of *Centrolene buckleyi* from Yanayacu Biological Station

	QCAZ 22388	QCAZ 26031	QCAZ 26032
Sex	Male	Male	Male
SVL	25.3	26.5	25.9
Tibia	14.7	14.9	14.7
Foot	12.6	12.2	12.8
Head length	7.3	8.0	7.8
Head width	8.7	9.0	8.7
Interorbital distance	2.9	2.9	3.1
Upper eyelid width	2.1	2.3	2.1
Internarial distance	1.9	2.2	2.0
Eye-to-nostril distance	1.5	1.6	1.6
Snout-to-eye-distance	2.9	3.1	3.2
Eye diameter	2.9	3.2	2.8
Tympanum diameter	0.9	1.0	1.0
Eye-to-tympanum distance	1.1	1.2	1.3
Radioulna length	6.2	5.9	6.1
Hand length	8.5	8.6	8.4
Finger I length	5.4	5.3	5.1
Disc of Finger III	1.5	1.7	1.6

Table 3. Call parameters of a single male *Centrolene buckleyi* (QCAZ 26032). All calls consist of at least one note with two distinct pulses (Fig. 7). Calls were recorded in the laboratory at 22.7 °C. *N* refers to the number of samples for the given call parameter

Call parameter	Mean	Range	SD	<i>N</i>
Number of notes per call	2	1–5	1.6	9
Call duration (ms)	1005	258–3364	1168.6	9
Note duration (ms)	277.9	243–333	21.8	18
First pulse duration (ms)	143.6	127–172	12.4	18
Second pulse duration (ms)	135.8	106–177	22.7	18
Interval between calls (s)	112.8	41–203	53.3	8
Fund. freq. of first pulse (Hz)	3658.8	3520–3868	126.7	18
Fund. freq. of second pulse (Hz)	4014.4	3856–4139	86.1	18

COCHRANELLA POSADAE RUIZ-CARRANZA
& LYNCH, 1995

Diagnosis: *Cochranella posadae* differs from other species in the family by the following combination of characters: (1) vomers lacking teeth; (2) colour of bones in life light green; (3) in preservative, parietal peritoneum and pericardium white, hepatic peritoneum clear, visceral peritoneum cream, peritoneum around kidneys transparent (overall coloration of kidneys cream, but blood vessels are visible, giving a

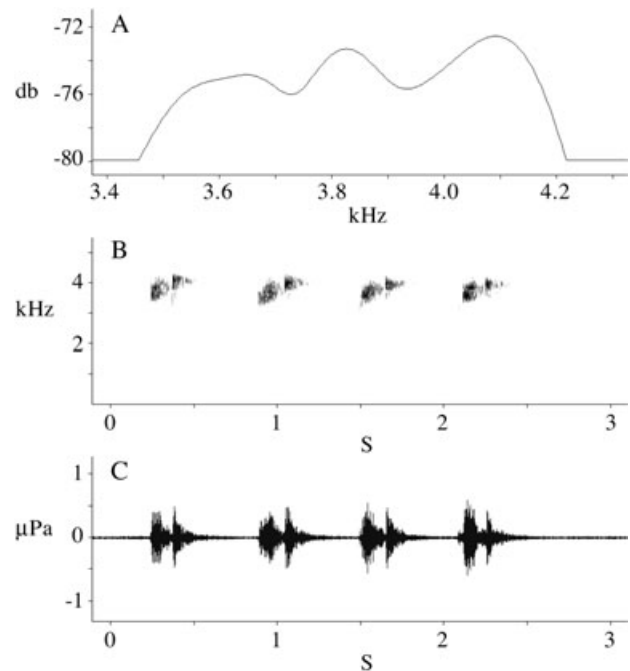


Figure 7. A, power spectrum; B, sonagram; and C, oscillogram of the advertisement call of *Centrolene buckleyi* (QCAZ 26032). The call shown here consists of four notes, each note with two distinct pulses. The power spectrum was measured along the duration of the first note.

brown tonality); (4) in life, dorsum green with small greenish-white warts, ventrolateral border of arm, Finger IV, tarsus and Toe V white; in preservative, dorsum of head, body and limbs lavender with numerous small bluish white warts, ventrolateral border of arm, Finger IV, tarsus and Toe V white; venter cream; cloacal region with white warts; iris whitish lavender with dark purple reticulation; (5) webbing absent between Fingers I and II, basal between Fingers II and III; webbing between outer fingers reduced, III $2^{3/4}$ – $2^{1/2}$ IV; (6) webbing formula on foot I 2^- – 2^+ II $1^{1/3}$ – $2^{1/3}$ III $1^{1/2}$ – $2^{2/3}$ IV 3–2 V (Table 6); (7) snout truncate to round in dorsal aspect, and truncate to slightly sloping in lateral profile; (8) dorsal skin covered with numerous small warts and some scattered larger warts; no spinules (*sensu* Flores, 1985) visible; (9) ulnar and tarsal folds absent; (10) humeral spine absent; (11) tympanum almost vertical, with slight posterior and lateral inclinations, tympanic annulus visible only ventrally; tympanic membrane not differentiated from surrounding skin; (12) SVL in males 30.7–34.1 mm (mean = 32.3, $n = 6$); in females 30.2–33.3 mm (mean = 31.4, $n = 4$); (13) prepollical spine not protruding externally; nuptial pad large (Type I of Flores, 1985; Fig. 8); nuptial excrescences cream, finely granular; (14) pair of large, round tubercles posteroventral to vent (Lynch & Duellman, 1973: fig. 2A); (15) when adpressed, Finger II longer than Finger I; (16) liver with three or four lobes (condition uncertain because part of liver was removed for molecular studies); (17) diameter of eye almost twice width of disc of Finger III.

Cochranella posadae is part of the *Cochranella ocellata* species group (as defined by Ruiz-Carranza & Lynch, 1991a, 1995a) based on the absence of white pigment in the visceral peritoneum (white visceral peritoneum in the *Cochranella granulosa* group) and the presence of reduced webbing between Fingers III and IV (extensive webbing between Fingers III and IV in the *Cochranella spinosa* group). Characters used to distinguish species in the *Cochranella ocellata* group are presented in Table 4.

Colour in life (based on images shown in Fig. 4D, E): Dorsum of head, body and limbs bright green with small, scattered, greenish-white warts; conspicuous white border on upper lip, thin white border on lower lip; ventrolateral border of arm, Finger IV, tarsus and Toe V white; region located posteroventral to cloaca white; parietal peritoneum white, covering about the anterior half of the belly medially; iris white with dark grey reticulation.

Colour in preservative: Dorsum of head, body and limbs lavender with some of the larger warts being bluish white; conspicuous white border on upper lip,

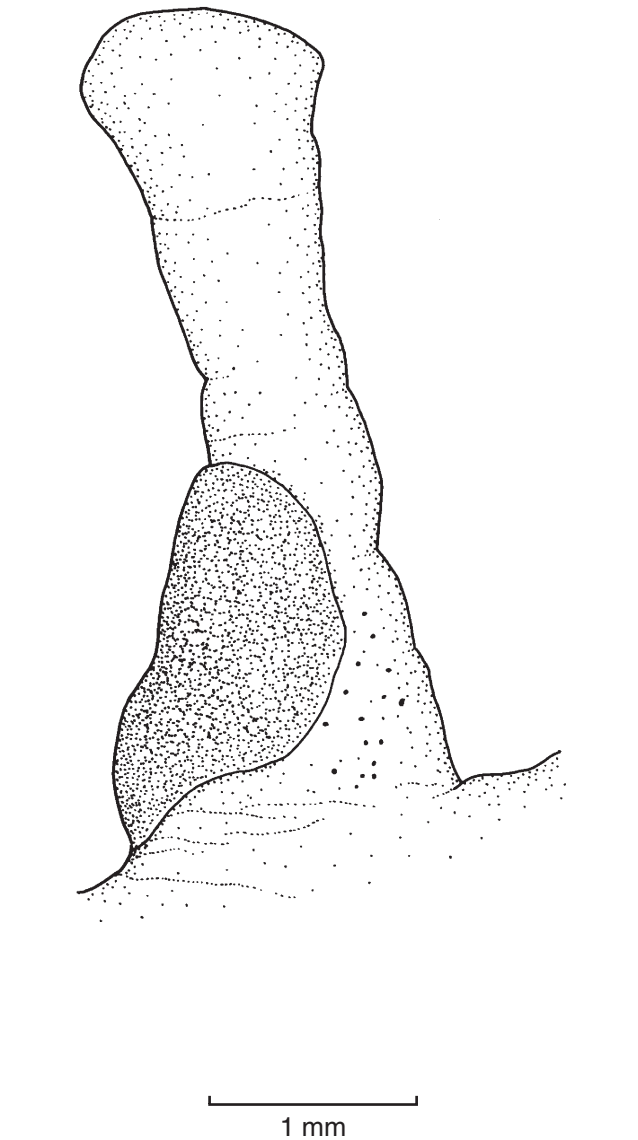


Figure 8. Dorsal view of Finger I of *Cochranella posadae*, male, QCAZ 26023. Scale bar = 1 mm.

thin white border on lower lip (Fig. 9); ventrolateral border of arm, Finger IV, tarsus and Toe V white, but ventral surface of forearm and tarsus completely covered with white pigment in two specimens (QCAZ 25090 and 26022; Figs 4E, 10); dorsally, Fingers I and II and Toes I–III unpigmented; some pigmentation visible on Fingers III and IV and Toes IV and V; cloacal region with several white warts; males with cream nuptial pad on Finger I; parietal peritoneum white, covering approximately anterior two-thirds of belly; pericardium silver-white, hepatic peritoneum clear, digestive tract cream, kidneys creamy brown.

Table 4. Character states of species of the *Cochranella ocellata* group. Nuptial pad, spinules and spicules are as described by Flores (1985). For simplicity, when coding snout shape in dorsal view, the character state 'round' contains snouts that have been described in the literature as round, subovoid or subacuminate. When coding snout shape in lateral view, the character state 'truncate' includes truncate or subtruncate

	Snout (dorsal view; lateral view)	Texture of dorsal skin of males	Dorsal coloration in preservative	Teeth on vomer	SVL in adult males (mm)	Source
<i>C. anomala</i>	Truncate; truncate	Shagreen with spinules and warts corresponding to ocelli	Brown with dark flecks and black ocelli enclosing white spots	Absent	24.1 (<i>n</i> = 1)	Lynch & Duellman (1973)
<i>C. armata</i>	Truncate; truncate	Shagreen with spinules	Pale lavender with scattered darker lavender spots	Absent	23.3–24.8 (<i>n</i> = 12)	Lynch & Ruiz-Carranza (1996)
<i>C. balionota</i>	Truncate; protruding	Shagreen	Cream with reddish brown markings and white spots	Absent	20.5–22.5 (<i>n</i> = 13)	Duellman (1981); this work
<i>C. bejaranoi</i>	Round; truncate	Shagreen with spinules	Dark lavender with minute white spots	Absent	23.6–23.8 (<i>n</i> = 4)	This work
<i>C. cariticommata</i>	Round; truncate	Shagreen	Pale lavender with small white spots	Absent	23.6 (<i>n</i> = 1)	This work
<i>C. chami</i>	Truncate; truncate	Shagreen with numerous subconical tubercles	Pale to dark lavender with white spots	Present	30.5–34.6 (<i>n</i> = 6)	Ruiz-Carranza & Lynch (1995b)
<i>C. chancas</i>	Truncate; truncate	Shagreen with spinules	Dull grey with small cream spots	Absent	24.8 (<i>n</i> = 1)	This work
<i>C. cochranae</i>	Truncate; truncate	Shagreen with spinules	Lavender with dark purple ocelli with cream centres	Present	23.6–26.3 (<i>n</i> = 5)	This work
<i>C. cristinae</i>	Round; truncate	Smooth to finely shagreen	Pale to dark lavender with small black spots	Absent or present	26.0–31.1 (<i>n</i> = 12)	Ruiz-Carranza & Lynch (1995b)
<i>C. garciae</i>	Round; truncate to sloping	Finely shagreen with spiculated tubercles	Pale to dark lavender with dark lavender spots and white tubercles	Absent	25.1–27.7 (<i>n</i> = 15)	Ruiz-Carranza & Lynch (1995a)
<i>C. griffithsi</i>	Truncate; truncate to protruding	Shagreen with or without spinules	Pale to dark lavender with or without dark flecks	Absent	19.9–26.6 (<i>n</i> = 14)	This work
<i>C. ignota</i>	Truncate; truncate	Shagreen with warts	Pale lavender with dark purple ocelli with cream centre	Absent	22.3–25.4 (<i>n</i> = 31)	Lynch (1990)
<i>C. luminosa</i>	Round; truncate	Finely shagreen with small subconical tubercles and small warts	Pale to dark lavender with small white spots	Present	27.8–30.0 (<i>n</i> = 13)	Ruiz-Carranza & Lynch (1995b)
<i>C. luteopunctata</i>	Round; truncate	Smooth with tiny spinules	Lilac with cream spots outlined by dark lilac	Present	33.1 (<i>n</i> = 1)	Ruiz-Carranza & Lynch (1996)

<i>C. megacheira</i>	Truncate; truncate	Covered with warts, spinules, and spicules	Lavender with dark purple spots	Absent	27.1–32.8 (<i>n</i> = 20)	Lynch & Duellman (1973)
<i>C. nephelophila</i>	Truncate; truncate	Smooth with diminutive tubercles	Lavender with black spots	Absent	22.6–24.1 (<i>n</i> = 2)	Ruiz-Carranza & Lynch (1991c)
<i>C. ocellata</i>	Round; round	Shagreen with spinules	Dark lavender with cream ocelli	Absent	21.0–25.1 (<i>n</i> = 3)	Duellman (1976)
<i>C. oreonympha</i>	Round; truncate	With numerous small tubercles	Pale lavender with dark lavender spots	Absent	24.0–26.3 (<i>n</i> = 15)	Ruiz-Carranza & Lynch (1991c)
<i>C. phenax</i>	Truncate; truncate	With numerous small spinules	Lavender with cream spots	Absent	19.7–22.0 (<i>n</i> = 4)	This work
<i>C. pluvialis</i>	Truncate; truncate	With warts and spinules	Lavender with cream spots	Absent	24.9–26.5 (<i>n</i> = 5)	Cannatella & Duellman (1982); this work
<i>C. prasina</i>	Round; truncate	Smooth	Lavender	Absent or Present	32.8–33.9 (<i>n</i> = 3)	This work
<i>C. posadae</i>	Round to truncate; truncate to slightly sloping	With numerous small warts and scattered larger warts	Lavender with whitish warts	Absent	30.7–34.1 (<i>n</i> = 6)	Ruiz-Carranza & Lynch (1995a); this work
<i>C. rosada</i>	Truncate; truncate	Finally shagreen with small pustules	Pale to dark lavender with white spots	Absent	24.1–28.3 (<i>n</i> = 15)	Ruiz-Carranza & Lynch (1997)
<i>C. ruizi</i>	Truncate; truncate	Smooth with or without spinules	Dull olive brown with black spots	Absent	24.3–26.4 (<i>n</i> = 19)	Lynch (1993)
<i>C. siren</i>	Truncate; truncate	Shagreen with spinules	Lavender with small white spots	Absent	19.8–22.0 (<i>n</i> = 14)	Lynch & Duellman (1973); this work
<i>C. spilota</i>	Truncate; truncate	Finally shagreen	Lavender with small white spots	Present	25.3–26.4 (<i>n</i> = 2)	Ruiz-Carranza & Lynch (1997)
<i>C. truebae</i>	Truncate; truncate	Shagreen with warts, spinules, and spinules	Lavender with dark purple and cream spots	Absent	22.6–24.8 (<i>n</i> = 13)	Duellman (1976)
<i>C. vozmedianoi</i>	Truncate; truncate	Shagreen with low warts	Pale green with small emerald warts	Absent	26.2–28.4 (<i>n</i> = 3)	Ayarzagüena & Señaris (1997); this work
<i>C. wileyi</i> sp. nov.	Truncate; truncate to protruding	Shagreen with spinules	Pale lavender	Absent	23.3–26.1 (<i>n</i> = 5)	This work

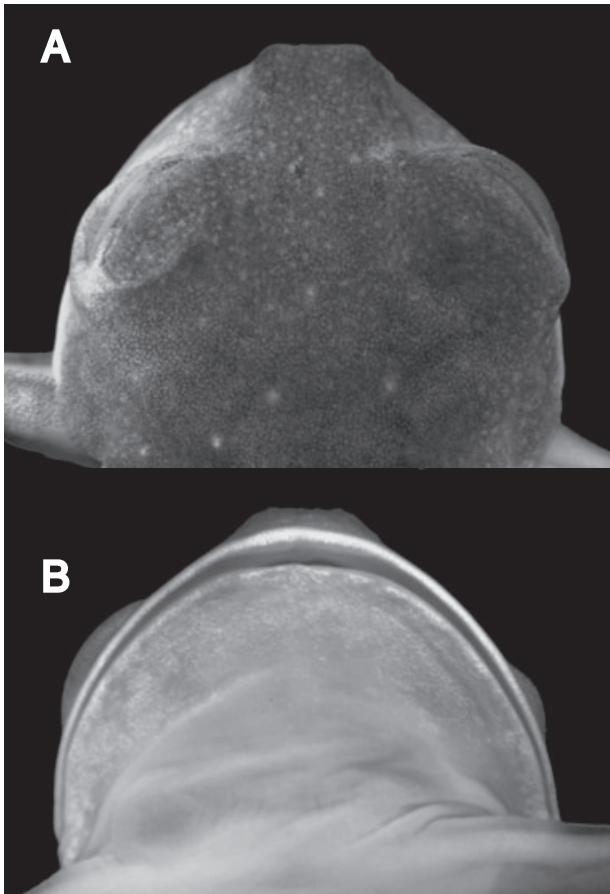


Figure 9. Head of *Cochranella posadae*, male, QCAZ 25090. A, texture of skin in dorsal view; note numerous small warts and scattered, larger warts; B, colour pattern in ventral view; note white pigments on upper and lower lips. Head width = 10.1 mm.

Measurements (in mm): Measurements of the specimens of *Cochranella posadae* collected in YBS are given in Table 5. Males collected in YBS are smaller (SVL = 30.7–31.9, $n = 3$) than Colombian specimens (SVL = 32.7–34.1 mm, $n = 3$; Ruiz-Carranza & Lynch, 1995a).

Distribution, ecology and natural history: *Cochranella posadae* is known from Caldas (Samaná), Cauca (Inza) and Huila (San José Isnos) departments on the eastern flank of the Central Cordillera in Colombia, between 1100 and 2800 m (IUCN, Conservation International & NatureServe, 2004), and from the cloud forests surrounding YBS (0°41'S, 77°53'W; 2100 m) in Ecuador. Three individuals were collected during 3 years of inventory work at Yanayacu. All frogs were found calling on the same night (12 June 2003) on ferns 110–220 cm above a stream.



Figure 10. Ventral view of hand (left) and foot (right) of *Cochranella posadae*, male, QCAZ 25090. Note white pigments covering surface of arm, tarsus and heel. Additional white pigmentation is visible on external border of Finger IV and Toe V. Hand length = 11.0 mm; foot length = 15.6 mm.

COCHRANELLA WILEYI SP. NOV.

Holotype: QCAZ 26028 (Fig. 11), adult female, YBS (0°41'S, 77°53'W; 2100 m), Provincia de Napo, Ecuador, collected by M. R. Bustamante on 5 January 2001.

Paratopotypes: Adult males. QCAZ 26024, collected by D. Almeida-Reinoso on 13 June 2003. QCAZ 26029 and 30, collected by M. R. Bustamante on 11 May 2002. QCAZ 26057, collected by D. Almeida-Reinoso on 14 December 2003. QCAZ 27435, collected by M. R. Bustamante on 30 April 2004.

Diagnosis: *Cochranella wileyi* sp. nov. (Fig. 4G, H) differs from other species in the family by the following combination of characters: (1) vomerine teeth absent; (2) in life, bones pale green; (3) in preservative, dorsum lavender; parietal peritoneum and pericardium white, hepatic peritoneum clear, visceral peritoneum cream, peritoneum around kidneys white with small, unpigmented spots; (4) in life, dorsum uniform pale green; in preservative, dorsum lavender; (5) webbing

Table 5. Measurements (in mm) of *Cochranella posadae* from Yanayacu Biological Station

	QCAZ 25090	QCAZ 26022	QCAZ 26023
Sex	Male	Male	Male
SVL	30.7	31.9	31.0
Tibia	19.5	20.0	20.0
Foot	15.6	15.6	14.6
Head length	9.6	9.7	9.7
Head width	10.1	10.3	10.3
Interorbital distance	2.9	3.1	3.3
Upper eyelid width	2.7	2.5	2.7
Internarial distance	2.5	2.4	2.4
Eye-to-nostril distance	2.2	2.1	2.1
Snout-to-eye distance	4.5	4.4	4.2
Eye diameter	3.9	3.8	3.7
Tympanum diameter	1.1	1.0	–
Eye-to-tympanum distance	1.4	1.6	–
Radioulna length	7.3	7.3	7.2
Hand length	11.0	10.8	10.7
Finger I length	6.3	6.3	6.4
Disc of Finger III	2.1	2.1	2.0

Table 6. Variation in webbing formula on feet of *Cochranella posadae*

Museum no. (QCAZ)	Webbing formula on foot
26023	I 2 ⁻ -2 ⁺ II 1 ^{2/3} -2 ^{1/3} III 1 ^{1/2} -2 ^{2/3} IV 3-2 ⁻ V
25090	I 2 ⁻ -2 ^{1/4} II 1 ⁺ -2 ^{1/2} III 1 ^{1/4} -2 ^{2/3} IV 3-1 ^{4/5} V
26022	I 1 ^{2/3} -2 ⁺ II 1 ^{1/4} -2 ^{1/4} III 1 ^{1/2} -2 ^{1/3} IV 2 ^{2/3} -1 ^{1/2} V

absent between inner fingers; webbing reduced between outer fingers, III 3⁻-2 2/3 IV; (6) webbing formula on foot usually I 2⁻-2^{1/3} II (1^{1/3}-1^{2/3})-(2^{1/2}-3⁻) III (1 ± 1^{2/3})-(2^{2/3}-3⁻) IV (3⁻-3⁺)-(2⁻-2⁺) V; (7) snout truncate in dorsal aspect, truncate to protruding in lateral profile; (8) dorsal skin finely shagreen in males and females, with numerous spinules in males; (9) low and thin ulnar fold; tarsal fold absent; (10) humeral spine absent; (11) tympanum orientated almost vertically, with slight posterior and lateral inclinations, tympanic annulus visible anteroventrally, tympanic membrane clearly differentiated; (12) SVL in males 24.0–26.2 mm (mean = 24.6, *n* = 5); 27.1 mm in one female; (13) prepollical spine not protruding externally; nuptial pad large (Type I of Flores, 1985); nuptial excrescences cream, finely granular; (14) pair of large, round tubercles posteroventral to vent (Lynch & Duellman, 1973: fig. 2A); (15) when adpressed, Finger II slightly

**Figure 11.** Dorsal (top) and ventral (bottom) views of the holotype of *Cochranella wileyi* sp. nov., adult female, SVL = 27.1 mm, QCAZ 26028.

longer than Finger I; (16) liver tetralobed; (17) diameter of eye about twice width of disc of Finger III.

Cochranella wileyi is assigned to the *Cochranella ocellata* species group (as defined by Ruiz-Carranza & Lynch, 1991a, 1995a) based on the absence of white pigment in the visceral peritoneum (white visceral peritoneum in the *Cochranella granulosa* group) and the presence of reduced webbing between Fingers III and IV (extensive webbing between Fingers III and IV in the *Cochranella spinosa* group). Characters used to distinguish among species in the *Cochranella ocellata* group are presented in Table 4. *Cochranella wileyi* is likely to be confused with *C. cariticommata* and *C. griffithsi*, but the kidneys (Fig. 12) in *C. wileyi* are

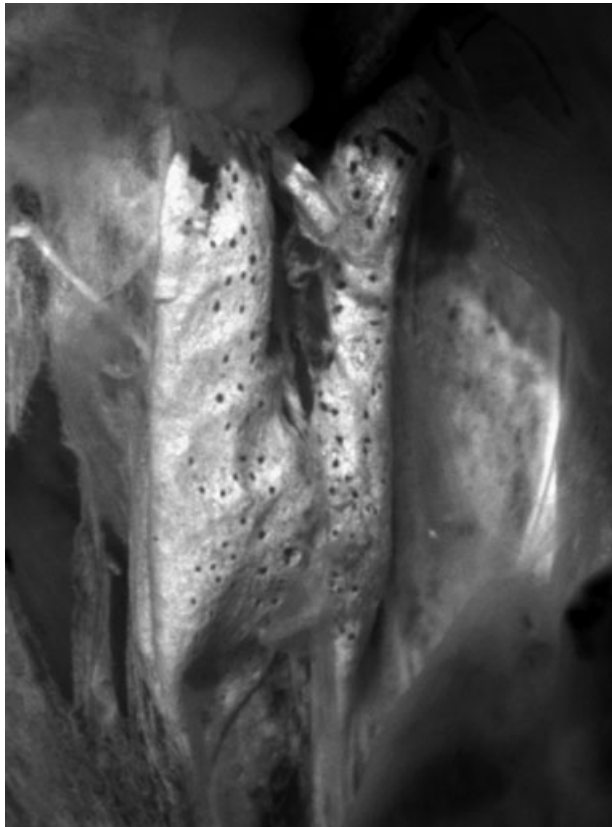


Figure 12. Kidneys of *Cochranella wileyi* sp. nov., male, QCAZ 26030, ventral view. Note that kidneys are covered with a white peritoneum and small, unpigmented spots. Length of kidneys = 4.7 mm.

covered with a white peritoneum (kidneys cream in *C. cariticomata*); additional differences between these two species are summarized in Table 4. Although no discrete characters separate *Cochranella wileyi* and *C. griffithsi* (Table 4), we argue that they represent evolutionary independent lineages. The two species have allopatric distributions: *C. wileyi* is found on the Amazonian slopes of the Ecuadorian Andes, whereas *C. griffithsi* inhabits the Pacific slopes of the Andes in southern Colombia and adjacent Ecuador. Additionally, the two species have differences in the frequencies of at least two characters. In preservative, all the specimens of *C. wileyi* have a thin white border on the upper lip (white border on upper lip absent in 65% of *C. griffithsi*, $n = 60$) and a dorsum without dark flecks (dorsum with dark purple or black flecks in 90% of *C. griffithsi*, $n = 60$). Based on the distribution of the species and the morphological differences mentioned above, and using the evolutionary species concept (Wiley, 1978; modified from Simpson, 1961), we hypothesize that *C. wileyi* and *C. griffithsi* are distinct species.

Description of holotype: Adult female, SVL 27.1 mm (Fig. 11). Head slightly wider than body; head length 88.8% of head width, 29.5% of SVL; snout truncate in dorsal and lateral profiles; canthus weakly defined; loreal region concave; lips slightly flared; nostrils closer to tip of snout than to eye, not protuberant, directed anterolaterally; internarial area barely depressed; eye large, directed anterolaterally; transverse diameter of disc of Finger III 45% of eye diameter; supratympanic fold low, obscuring posterodorsal portion of tympanic annulus; tympanum orientated almost vertically, with slight posterior and lateral inclination; tympanic membrane translucent, with pigments only on its upper half; vomers lacking teeth; choanae large, longitudinally rectangular; tongue ovoid, with ventral posterior fifth not attached to mouth floor and posterior margin notched.

Humeral spine absent; low ulnar fold evident; relative length of fingers: III > IV > II > I; no webbing between inner fingers; webbing formula for outer fingers III 3⁻–2^{2/3} IV (Fig. 6E); fingers with narrow lateral fringes; discs expanded, nearly round; disc pads elliptical; subarticular tubercles round, simple; supernumerary tubercles small; palmar tubercle elliptical, simple. Length of tibia 60.9% of SVL; no tarsal fold evident; webbing formula on foot I 2–2^{1/3} II 1^{2/3}–3⁻ III 2⁻–2^{2/3} IV 3–2⁻ V (Fig. 6F); toes with narrow lateral fringes; discs on toes round; disc on Toe IV narrower than disc on Finger III; disc pads round; inner metatarsal tubercle large, ovoid; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent.

Skin on dorsal surfaces of head, body, and lateral surface of head and flanks shagreen without spinules; throat smooth, cream; belly and lower flanks slightly areolate; cloacal opening directed posteriorly at upper level of thighs, surrounded by low, white tubercles; pair of large, round tubercles posteroventral to vent.

Colour in life: (based on QCAZ 27441, adult male; M. R. Bustamente field notes; Fig. 4G, H). Dorsum pale green; lower flanks and venter transparent; parietal peritoneum white, covering anterior part of abdomen (heart not visible); iris white-copper with black reticulation; bones green.

Colour in preservative: Dorsum of head, body and limbs pale lavender; thin white border on the upper lip; dorsally, all fingers, Toes I–III and most of Toe IV unpigmented; cloacal region mostly unpigmented, except for a few minute white pigmented flecks. Males with cream nuptial pad on Finger I. Two males (QCAZ 26029 and 30) were dissected to observe coloration of internal organs: parietal peritoneum white, pericardium white, hepatic peritoneum clear, visceral peritoneum cream, peritoneum around kidneys white with small, unpigmented spots (Fig. 12).

Table 7. Measurements of holotype and paratypes of *Cochranella wileyi* sp. nov. (in mm)

	QCAZ 26028 Holotype	QCAZ 26024 Paratype	QCAZ 26029 Paratype	QCAZ 26030 Paratype	QCAZ 26057 Paratype	QCAZ 27435 Paratype
Sex	Female	Male	Male	Male	Male	Male
SVL	27.1	26.1	23.6	25.0	24.9	23.3
Tibia	16.5	14.8	14.4	15.0	15.8	13.5
Foot	13.0	12.0	11.9	12.7	12.9	11.5
Head length	8.0	7.8	7.5	7.6	8.0	7.3
Head width	9.0	8.3	8.1	8.3	8.9	8.1
Interorbital distance	2.7	2.5	2.4	2.7	2.7	2.4
Upper eyelid width	2.3	2.4	2.3	2.3	2.3	1.8
Internarial distance	1.9	2.3	1.9	1.9	2.1	1.9
Eye-to-nostril distance	2.2	2.0	1.8	1.8	2.0	1.7
Snout-to-eye distance	3.4	3.3	3.0	3.1	3.0	2.9
Eye diameter	3.4	3.4	2.8	3.1	2.9	2.8
Tympanum diameter	1.0	0.8	1.0	1.0	1.0	0.9
Eye-to-tympanum distance	0.8	1.0	1.3	0.8	1.4	1.1
Radioulna length	6.1	6.1	6.0	6.1	6.2	5.7
Hand length	9.2	7.9	8.2	8.5	8.7	7.8
Finger I length	5.6	5.0	4.9	5.0	5.4	5.0
Disc of Finger III	1.7	1.9	1.7	1.7	1.7	1.5

Measurements (in mm): Measurements of the holotype and paratypes of *Cochranella wileyi* sp. nov. are given in Table 7.

Variation: All males have the following characteristics: (1) dorsal skin shagreen, but with numerous small spinules; (2) long vocal slits, extending posterolaterally from the posterolateral base of tongue to angle of jaws; (3) nuptial pad large, ovoid, granular, extending from ventrolateral base to dorsal surface of Finger I, covering the proximal half of the length of Finger I (Type I of Flores, 1985); and (4) low tarsal fold on the inner edge of foot. In lateral view, head protruding (QCAZ 26030, 26057, 27435). Variation of webbing formula on feet is presented in Table 8.

Etymology: The specific name is a noun in the genitive case and a patronym for E. O. Wiley, one of the most influential persons in the development of phylogenetic systematics and use of the evolutionary species concept.

Distribution, ecology and natural history: *Cochranella wileyi* is known only from the cloud forests surrounding YBS (0°41'S, 77°53'W; 2100 m). Six individuals were collected during 3 years of inventory work at Yanayacu, suggesting that *Cochranella wileyi* is a rare species. Frogs were found in primary forest at night on leaves 120–220 cm above streams (five males) or above the ground (one female). Three males were found near egg clutches, which were on the tip of leaves (Fig. 13); as in *Centrolene bacatum*, males were

Table 8. Variation in webbing formula on feet of *Cochranella wileyi* sp. nov.

Museum no. (QCAZ)	Webbing formula on foot
26028 (Holotype)	I 2–2 ^{1/3} II 1 ^{2/3} –3 [–] III 2 [–] –2 ^{2/3} IV 3–2 [–] V
26024	I 2–2 ^{1/3} II 1 ^{2/3} –3 [–] III 2 [–] –2 ^{2/3} IV 3–2 [–] V
26029	I 2–2 ^{1/3} II 1 ^{1/3} –2 ^{2/3} III 2 [–] –2 ^{2/3} IV 3 [–] –2 [–] V
26030	I 2–2 ^{1/3} II 1 ^{2/3} –2 ^{1/2} III 1 ^{2/3} –2 ^{2/3} IV 3–2 [–] V
26057	I 2–2 ^{1/3} II 1 ^{2/3} –3 [–] III 1 ^{2/3} –3 [–] IV 3–2 [–] V
27435	I 2–2 ^{1/3} II 1 ^{1/3} –2 ^{3/4} III 1 ⁺ –3 [–] IV 3–2 [–] V

never found in the same leaf as the egg clutches, suggesting that males do not guard the eggs. Distance between egg clutches varies, but can be as close as 20 cm; the number of eggs per clutch varies from 19 to 28 (mean = 22, $n = 17$); eggs are whitish as well as embryos in early developmental stages (QCAZ 28497–500). One male (QCAZ 26024) was found guarding two clutches and two other males (QCAZ 26029 and 30) were found together near four clutches (Fig. 13). It is unknown which of the two males was guarding which of these four clutches. Males call from the upper side of leaves.

Remarks: In Ecuador, we are aware of only two species in which egg clutches are deposited on the tip of leaves, *Cochranella griffithsi* and *C. wileyi*.



Figure 13. Egg clutches of *Cochranella wileyi* sp. nov. Note that egg clutches are hanging on the tip of leaves. Each egg mass contains between 19 and 28 eggs.

DISCUSSION

Morphological and behavioural characters that indicate monophyly of Centrolenidae include: (1) partial or complete of tibiale and fibulare; (2) T-shaped terminal phalanges; (3) dilated medial process on Metacarpal III (Fig. 15); and (4) eggs deposited on vegetation or rock faces above streams (Hayes & Starrett, 1980; Ruiz-Carranza & Lynch, 1991a; Fig. 1). A recent phylogenetic analysis based on molecular data (12S and 16S mitochondrial rRNA genes and the intervening tRNA gene for valine) was consistent with the monophyly of Centrolenidae (Darst & Cannatella, 2004), although taxon sampling of Centrolenidae was low (four species).

The most commonly accepted generic classification within Centrolenidae was proposed by Ruiz-Carranza & Lynch (1991a), who recognized three genera: *Centrolene*, *Cochranella* and *Hyalinobatrachium*. Savage (2002: 358) recently included the small-eyed species of *Centrolene* (*sensu* Ruiz-Carranza & Lynch, 1991a) in the genus *Centrolenella*; however, we consider that a generic change based on one character is not justified unless it is an unambiguous synapomorphy. The original definitions of the genera and species groups by Ruiz-Carranza & Lynch (1991a) have been modified by several authors (Ruiz-Carranza & Lynch, 1995a, 1998; Señaris, 2001; Duellman & Señaris, 2003); below (Appendix 2), we summarize the current generic and infrageneric classification of Centrolenidae (also shown in Fig. 1A).

Our phylogenetic analysis shows that the distribution of characters under the parsimony criterion is not congruent with the current generic classification, and we suggest that *Centrolene* and *Cochranella* are not monophyletic (Fig. 1B). However, we are unwilling to make any taxonomic change until a more robust phy-

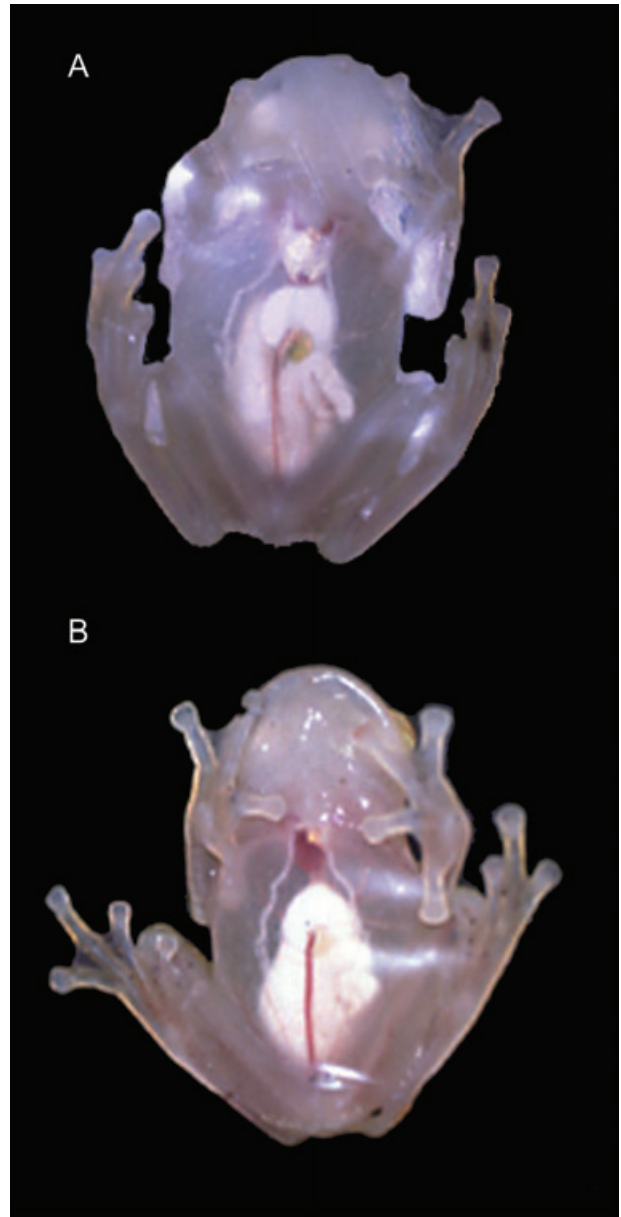


Figure 14. Ventral view of two individuals of *Hyalinobatrachium crurifasciatum* showing intraspecific variation of the pericardium. A, white pericardium, MHNLS 16477; B, mostly clear pericardium, but see upper right corner of the heart, MHNLS 16475.

logeny is available. The monophyly of species groups is also weakly supported; for example, and as mentioned by Noonan & Harvey (2000), the *Centrolene prosoblepon* and *C. peristictum* species groups are practically identical, differing only in the colour of the bones in life (green or white in the *C. prosoblepon* species group, and pale green in the *C. peristictum* species group) and in colour of the peritoneum covering the

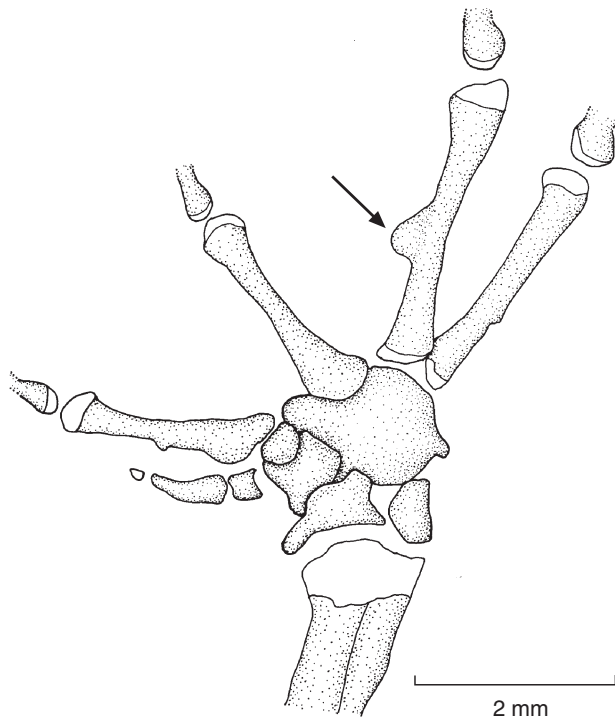


Figure 15. Ventral view of hand of *Cochranella wileyi* sp. nov., QCAZ 26029. Arrow indicates medial process of Metacarpal III, a character present in all centrolenid frogs.

digestive tract (cream in most, but not all, of the species in the *C. prosoblepon* species group, and white in the *C. peristictum* species group). However, the genus *Hyalinobatrachium* and, in particular, the *H. fleischmanni* group are well supported and might be monophyletic (Fig. 1B).

We need a better understanding of the distribution of behavioural and morphological characters in Centrolenidae. We have observed that some characters are more variable than they have been reported to be in the literature; for example, in species in the genus *Centrolene*, the liver may have three, four or five lobes. *Centrolene ballux*, *C. bacatum*, *C. huilense* and *C. grandisonae* have tetralobed livers and *Centrolene buckleyi* is polymorphic with respect to the number of lobes in the liver, having four or five lobes (J. M. Guayasamin, pers. observ.). Additionally, some of the characters that diagnose species groups may vary intraspecifically. As an example, the pericardium of *H. crurifasciatum* is polymorphic and can be silvery white or transparent (J. M. Guayasamin, pers. observ.; Fig. 14). Therefore, *H. crurifasciatum* can be included in or excluded from the *H. chirripoi* subgroup (see definition of the *H. chirripoi* subgroup in Appendix 2 and Fig. 1). We also need to test the prediction that species in the genera *Cochranella* and

Centrolene have a venter-to-venter combat behaviour and that species in the genus *Hyalinobatrachium* have an amplexus-like combat (Bolívar *et al.*, 1999). A phylogenetic analysis, with a combined set of data (morphological, behavioural and molecular) is necessary to test the monophyly of the genera and species groups within Centrolenidae. The tree presented in this work (Fig. 1B) is preliminary, and highlights some of the weaknesses and strengths of the current classification.

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- (paratypes); *C. buckleyi*, KU 118006, 148429–30, 155481, 155483, 155485, 164505, 164509–11, 164513, 164515, QCAZ 22388, 26031–32; *C. fernandoi*, KU 211771–75 (paratypes); *C. grandisonae*, KU 164670–84; *C. heloderma*, KU 164716–19; *C. huilense*, KU 169720–47; *C. ilex*, KU 116464; *C. lemniscatus*, KU 217300 (holotype); *C. lynchi*, KU 164692–99 (paratypes); *C. muelleri*, KU 217301 (holotype); *C. peristictum*, KU 178137–49; *C. pipilatum*, KU 143279–82 (paratypes); *C. prosoblepon*, KU 291165–73; *C. scirtetes*, KU 202720 (holotype); *C. tayrona*, KU 169750–52.
- Cochranella balionota*, KU 164703–11 (paratypes); *C. bejaranoi*, KU 182370–71 (paratypes); *C. cariticomata*, KU 202806 (holotype), 202805 (paratype); *C. chancas*, KU 211778 (holotype); *C. cochranae*, KU 121033–35; *C. griffithsi*, KU 142649, 164519–76, 173116; *C. ignota*, KU 209763–65 (paratypes); *C. megacheira*, KU 143246–70 (paratypes); *C. ocellata*, KU 197030; *C. phenax*, KU 162264, 162266–67 (paratypes); *C. pluvialis*, KU 173225–27 (paratypes); *C. posadae* QCAZ 25090, 26022–23; *C. prasina*, KU 169691–92 (paratypes); *C. siren*, KU 146611–23 (paratypes); *C. truebae*, KU 162269–80 (paratypes); *C. vozmediano*, MHNLS 16427, 16430.

APPENDIX 2

GENERIC AND INFRAGENERIC CLASSIFICATION OF CENTROLENIDAE

Genus *Centrolene*. – Trilobed liver, males with humeral spines (Ruiz-Carranza & Lynch, 1991a), venter-to-venter combat behaviour in males (Bolívar *et al.*, 1999). *Centrolene azulae*, *C. mariae* and *C. puyoense* are only known from females, and their placement in *Centrolene* is tentative; therefore, these species are not included in any infrageneric species group.

– *Centrolene geckoideum* species group: Disc of Finger III large (> 80% of eye diameter); bones green in life; parietal peritoneum and pericardium white; vomerine teeth present (Ruiz-Carranza & Lynch, 1991a). Species composition: *Centrolene acanthidiocephalum*, *C. geckoideum*, *C. medemi*, *C. paezorum* and *C. petrophilum*.

– *Centrolene gorzulai* species group: Large eye (eye diameter > transverse diameter of disc on Finger III); bones green in life; pericardium and hepatic peritoneum white; parietal peritoneum partially white or clear; visceral peritoneum white or clear; vomerine teeth absent (Duellman & Señaris, 2003). Species composition: *Centrolene gorzulai*, *C. lema* and *C. papillahallicum*.

– *Centrolene prosoblepon* species group: Large eye (eye diameter > transverse diameter of disc on Finger

APPENDIX 1

SPECIMENS EXAMINED

Allophryne ruthveni, KU 166713, 167756; *Physalaemus colouradorum*, KU 117791–92. *Centrolene andinum*, MHNLS 16485–92; *C. audax*, KU 143290, 143292 (paratypes); *C. bacatum*, KU 202807–12 (paratypes), QCAZ 16212, 17807, 22386–87, 22728, 26025–27, 26056, 27438; *C. ballux*, KU 164726–32

III); bones green or white in life; parietal peritoneum and pericardium white, some species also have white pigment (= guanophores) on digestive tract; vomerine teeth present or absent (Ruiz-Carranza & Lynch, 1991a). Species composition: *Centrolene altitudinale*, *C. andinum*, *C. audax*, *C. bacatum*, *C. ballux*, *C. buckleyi*, *C. fernandoi*, *C. grandisonae*, *C. guanacarum*, *C. heloderma*, *C. hesperium*, *C. huilensi*, *C. hybrida*, *C. ilex*, *C. lemniscatum*, *C. muelleri*, *C. notostictum*, *C. pipilatum*, *C. prosoblepon*, *C. quindianum*, *C. robledoi*, *C. scirtetes* and *C. tayrona*.

– *Centrolene peristictum* species group: Large eye (eye diameter > transverse diameter of disc on Finger III); bones pale green in life; white pigment on parietal peritoneum and pericardium, and on digestive tract; vomerine teeth absent (Ruiz-Carranza & Lynch, 1991a). Species composition: *Centrolene antioquiense*, *C. gemmatum*, *C. litorale*, *C. lynchi*, *C. peristictum*, and *C. sanchezi*.

Genus *Cochranella*. – Trilobed liver; males lacking humeral spines (Ruiz-Carranza & Lynch, 1991a), venter-to-venter combat behaviour in males (Bolívar *et al.*, 1999).

– *Cochranella granulosa* species group: Large eye (eye diameter > transverse diameter of disc on Finger III); bones pale green in life; parietal peritoneum and pericardium white; digestive tract white; vomerine teeth present (Ruiz-Carranza & Lynch, 1991a). Species composition: *Cochranella daidalea*, *C. euknemos*, *C. granulosa*, *C. mache*, *C. ramirezi*, *C. resplendens*, *C. savagei* and *C. solitaria*.

– *Cochranella ocellata* species group: Large eye (eye diameter > transverse diameter of disc on Finger III); bones green to white in life; pericardium white, parietal peritoneum white or clear; vomerine teeth present or absent (Ruiz-Carranza & Lynch, 1991a); reduced webbing between Fingers III and IV (Ruiz-Carranza & Lynch, 1995a). Harvey (1996) incorrectly assigned *Cochranella nola* to the *C. ocellata* group; *Cochranella nola* has extensive webbing between Fingers III and IV (Harvey, 1996; Fig. 4) and should be placed in the *Cochranella spinosa* group (*sensu* Ruiz-Carranza & Lynch, 1995a; see below). Species composition: *Cochranella anomala*, *C. armata*, *C. balionota*, *C. bejaranoi*, *C. cariticomata*, *C. chami*, *C. chancas*, *C. cochranae*, *C. cristinae*, *C. garciae*, *C. griffithsi*, *C. ignota*, *C. luminosa*, *C. luteopunctata*, *C. megacheira*, *C. nephelophila*, *C. ocellata*, *C. oreonympha*, *C. phenax*, *C. pluviialis*, *C. posadae*, *C. prasina*, *C. rosada*, *C. ruizi*, *C. siren*, *C. spilota*, *C. truebae*, *C. vozmedianoi* and *C. wileyi* sp. nov.

– *Cochranella oyampiensis* species group: Large eye (eye diameter > transverse diameter of disc on Finger III); bones green or pale green in life; parietal peritoneum and pericardium white, digestive tract white,

hepatic peritoneum with white pigment; vomerine teeth present or absent (Señaris, 2001). Species composition: *Cochranella castroviejoi*, *C. helenae* and *C. oyampiensis*.

– *Cochranella spinosa* species group: Large eye (eye diameter > transverse diameter of disc on Finger III); bones green to white in life; pericardium white, parietal peritoneum white or clear; vomerine teeth present or absent (Ruiz-Carranza & Lynch, 1991a); extensive webbing between Fingers III and IV (Ruiz-Carranza & Lynch, 1995a). Species composition: *Cochranella adiazeta*, *C. albomaculata*, *C. ametarsia*, *C. croceopodes*, *C. duidaeana*, *C. euhystrix*, *C. flavopunctata*, *C. geijskesi*, *C. megistra*, *C. midas*, *C. nola*, *C. ocellifera*, *C. orejuela*, *C. punctulata*, *C. ritae*, *C. riveroi*, *C. saxiscandens*, *C. spiculata*, *C. spinosa*, *C. susatamai*, *C. tangarana* and *C. xanthocheridia*.

Genus *Hyalinobatrachium*: White, bulbous liver; males lacking humeral spines, clear parietal peritoneum (Ruiz-Carranza & Lynch, 1991a; Noonan & Harvey, 2000); amplexus-like combat behaviour in males (Bolívar *et al.*, 1999).

– *Hyalinobatrachium fleischmanni* species group: Large eye (eye diameter > transverse diameter of disc on Finger III), bones white in life, digestive tract white, pericardium white in most species, vomerine teeth absent (Ruiz-Carranza & Lynch, 1991a), and eggs deposited in one layer (Ruiz-Carranza & Lynch, 1998). Species composition: *Hyalinobatrachium aureoguttatum*, *H. bergeri*, *H. cardiacalyptum*, *H. chirripoi*, *H. colymbiphyllum*, *H. crurifasciatum* (but see Discussion), *H. crybetes*, *H. duranti*, *H. eccentricum*, *H. esmeralda*, *H. fleischmanni*, *H. fragile*, *H. iaspidiense*, *H. ibama*, *H. ignioculus*, *H. lemur*, *H. loreocarinatum*, *H. mondolfii*, *H. munozorum*, *H. nouraguensis*, *H. orientale*, *H. ostracodermoides*, *H. pallidum*, *H. pellucidum*, *H. petersi*, *H. revocatum*, *H. ruedai*, *H. talamancae*, *H. taylori*, *H. valerioi* and *H. vireovittatum*.

A subgroup of species (*Hyalinobatrachium chirripoi*) is recognized within the *H. fleischmanni* species group (Ruiz-Carranza & Lynch, 1998). Species in the *H. chirripoi* subgroup have a clear parietal peritoneum and a clear pericardium (in life, red heart visible) and include: *H. bergeri*, *H. cardiacalyptum*, *H. chirripoi*, *H. colymbiphyllum*, *H. crybetes*, *H. fragile*, *H. iaspidiense*, *H. lemur*, *H. munozorum*, *H. orientale*, *H. pallidum*, *H. pellucidum*, *H. petersi*, *H. talamancae* and *H. vireovittatum*.

– *Hyalinobatrachium pulveratum* species group: Large eye (eye diameter > transverse diameter of disc on Finger III); bones pale green in life; pericardium and digestive tract white; vomerine teeth present (Ruiz-Carranza & Lynch, 1991a). Species composition: *Hyalinobatrachium antisthenesi* and *H. pulveratum*.

– *Hyalinobatrachium parvulum* species group: present or absent (Ruiz-Carranza & Lynch, 1991a).
 Large eye (eye diameter > transverse diameter of disc on Finger III); bones green or white in life; pericardium and urinary bladder white; vomerine teeth
 Species composition: *Hyalinobatrachium eurygnathum*, *H. parvulum* and *H. uranoscopum*.

APPENDIX 3

Data matrix for phylogenetic analysis

	1	2	3	4	5	6	7	8	9	10	11
<i>Physalaemus colouradorum</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Allophryne ruthveni</i>	0	1	0	0	0	0	0	0	0	0	0
<i>Centrolene geckoideum</i> group	1	1	1	1	0	1	1	0	0	0	0
<i>C. gorzulai</i> group	1	1	1	1	0	1	0	1	0	0	1
<i>C. prosoblepon</i> group	1	1	1	1	0	1	0	0	0	0	0
<i>C. peristictum</i> group	1	1	1	1	0	1	0	0	0	0	0
<i>Cochranella granulosa</i> group	1	1	1	1	0	0	0	0	0	0	0
<i>C. ocellata</i> group	1	1	1	1	0	0	0	0	0	0	0
<i>C. oyampiensis</i> group	1	1	1	1	0	0	0	1	0	0	0
<i>C. spinosa</i> group	1	1	1	1	0	0	0	0	0	0	0
<i>H. fleischmanni</i> group	1	1	1	2	1	0	0	1	0	0	1
<i>H. chirripoi</i> subgroup	1	1	1	2	1	0	0	1	0	1	1
<i>H. pulveratum</i> group	1	1	1	1	1	0	0	1	0	0	1
<i>H. parvulum</i> group	1	1	1	1	1	0	0	1	1	0	1