

OCCASIONAL PAPERS

**of the
MUSEUM OF NATURAL HISTORY
The University of Kansas
Lawrence, Kansas**

NUMBER 155. PAGES 1-33

11 MARCH 1993

**NEW SPECIES OF CENTROLENID FROGS
FROM NORTHERN PERU**

WILLIAM E. DUELLMAN AND RAINER SCHULTE

Museum of Natural History and Department of Systematics and Ecology, The University of Kansas, Lawrence, Kansas 66045-2454, USA (WED); Proyecto de Investigación de la Biología de las Cordilleras Orientales, Apartado 258, Tarapoto, Peru (RS)

ABSTRACT Eight new species of centrolenid frogs are described from the eastern slopes of the Cordillera Central and ridges extending eastward and southward from the main cordillera of the Andes in Departamento San Martín in northern Peru. Three of these species are described in the genus *Centrolene*; they have dark dorsal pigmentation in preservative, and the males have humeral spines. Four species are placed in the genus *Cochranella*; they have dark dorsal pigmentation in preservative, but males lack humeral spines. One of the species of *Cochranella* is known only from females. One species is white in preservative and is a member of the genus *Hyalinobatrachium*. Three species recognized in the genus *Cochranella* by Ruiz-Carranza and Lynch (1991) are placed in the genus *Centrolene*.

Key words: Anura, Centrolenidae, New species, Peru.

RESUMEN Ocho especies nuevas de ranas centrolénidas se describen de las laderas orientales de la Cordillera Central y de las montañas que se extienden al este y al sur de la cordillera principal de los Andes en el Departamento de San Martín en el norte de Perú. Tres de estas especies se describen en el género *Centrolene*; tienen pigmentación oscura en el dorso en preservativo, y los machos tienen espinas humerales. Tres especies se ponen en el género *Cochranella*; tienen pigmentación oscura en el dorso en preservativo, pero los machos no tienen espinas humerales. Sólo las hembras se conocen de una de las especies de *Cochranella*. Una especie es blanca en preservativo y es un miembro del género *Hyalinobatrachium*. Tres especies reconocidas en el género *Cochranella* por Ruiz-Carranza and Lynch (1991) se ponen en el género *Centrolene*.

Palabras claves: Anura, Centrolenidae, Especies nuevas, Perú.

In recent years, six species of frogs have been named in the genus *Centrolenella* from the cloud forests on the eastern slopes of the Andes or isolated mountain ranges in central and southern Amazonian Peru—*C. spiculata* and *C. truebae* from Departamento Ayacucho (Duellman, 1976), *C. mariae* from Departamento Huánuco (Duellman and Toft, 1979), *C. phenax* and *C. pluvialis* from Departamento Cuzco (Cannatella and Duellman, 1982), and *C. azulae* from Departamento Huánuco (Flores and McDiarmid, 1989). Even with the descriptions of these new species (all except the holotype of *C. azulae* were collected for the first time in the 1970s), it seemed reasonable that many additional species would be discovered as new areas were explored, especially in northern Peru. This supposition was verified with the discovery of *C. euhystrix* and *C. hesperia* on the Pacific versant of the Andes in northern Peru in 1987 (Cadle and McDiarmid, 1990) and by our discovery of eight undescribed species on the eastern Andean slopes in Departamento San Martín in northern Peru in 1989.

In the Departamento San Martín, a complex series of ridges reaching elevations of more than 1000 m extend eastward and southward from the Cordillera Central of the Andes. These steep, rocky ridges support lower montane rainforest and cloud forest, whereas the intervening valleys, most of which are extensively cultivated, contain remnants of dry tropical forest. Many small streams cascade down these slopes; major drainage systems flow south (e.g., Río Mayo) or east (e.g., Río Cainarache) into the Río Huallaga, which separates the Cordillera Central from the Cordillera Oriental. In northern Peru, the Cordillera Oriental terminates in a series of ridges with elevations of 1000–1200 m. The Río Huallaga cuts a canyon through these front ranges between Shapaja and Chazuta, to the south of which is the northern end of the Cordillera Azul (Fig. 1).

Adult centrolenids were collected on the eastern slopes of the Cordillera Central and on two associated ridges. One site is on the west slope of a pass, Abra Tangarana, to the west of the valley of the Río Mayo. The other sites are on a ridge north of Tarapoto and east of the Río Mayo.

METHODS AND MATERIALS

In the following descriptions, species are assigned to genera and species groups according to the definitions provided by Ruíz-Carranza and Lynch (1991), and the numbered characters in the diagnoses follow the standard established by Lynch and Duellman (1973) as modified by Cannatella and Duellman (1982) and Flores (1985). None of the species of centrolenids in Central America, Chococoan South America, Venezuela, and southeastern Brazil is shared with the upper Amazon Basin and the Amazonian slopes of the Andes. Consequently, comparisons of the new taxa are made only with

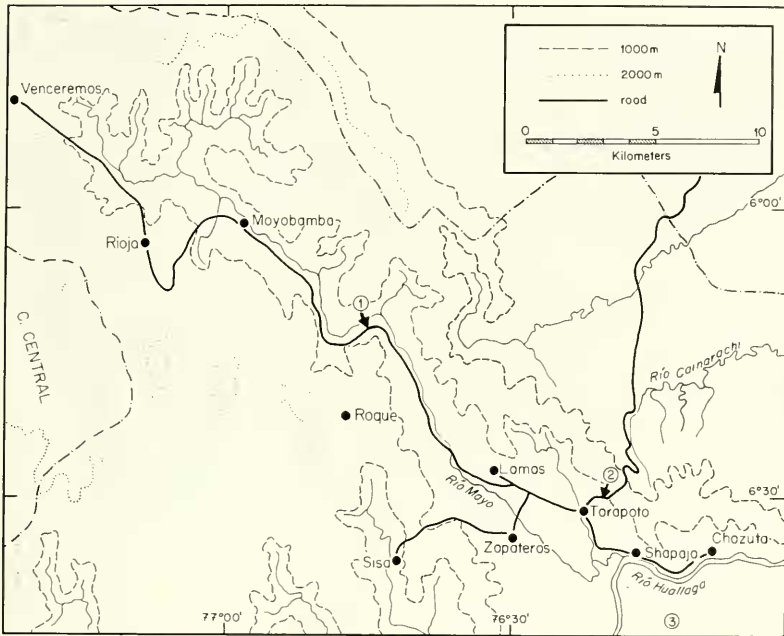


Fig. 1. Map of part of Departamento San Martín, Perú, showing localities mentioned in text; circled numbers are: 1 = Abra Tangarana, 2 = Cataratas Ahuashiyacu, 3 = northern end of Cordillera Azul. Based on Mapa Físico Político Departamento de San Martín, Ed. 2, 1985, Instituto Geográfico Nacional, Lima, Perú.

those species from the upper Amazon Basin and the Amazonian slopes of the Andes.

All measurements were taken to the nearest 0.1 mm with dial calipers. Abbreviations used in the descriptions are: ED (eye diameter) = greatest length of eye visible externally; EW (eyelid width) = greatest diagonal width of upper eyelid; FL (foot length) = distance from proximal base of inner metatarsal tubercle to tip of fourth toe; HL (head length) = distance between tip of snout and posterior edge of angle of jaws; HnL (hand length) = distance between proximal base of palmar tubercle and tip of third finger; HW (head width) = greatest width of head at lateral margins of jaws; IOD (interorbital distance) = width of top of head between nearest medial margins of upper eyelids; SL (snout length) = distance from tip of snout to anterior corner of orbit; SVL (snout-vent length) = distance from tip of snout to posterior end of body; T-E (tympanum-eye) = distance between anterior border of tympanic annulus and posterior corner of eyelid; TL (tibia length) = distance from knee to heel; TYM (tympanum) = horizontal

length of tympanum including annulus. Relative lengths of digits were determined by adpressing adjacent digits. Webbing formulae follow the scheme of Savage and Heyer (1967) as modified by Myers and Duellman (1982). Nuptial pad terminology follows Flores (1985).

Museum collections are abbreviated as follows: KU = Museum of Natural History, The University of Kansas; LSUMZ = Museum of Zoology, Louisiana State University; MHNSM = Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru. Comparisons of the new taxa were made with KU specimens of the other species.

DESCRIPTIONS OF NEW SPECIES

Centrolene fernandoi new species

Figure 2

Holotype.—KU 211770, an adult male, from the west slope of Abra Tangarana, 7 km (by road) northeast of San Juan de Pacaysapa (06°12'S, 76°44'W, 1080 m), Provincia Lamas, Departamento San Martín, Perú, one of a series collected on 5 February 1989 by William E. Duellman and Rainer Schulte.

Paratopotypes.—KU 211771–75 and MHNSM 6176–78; same date and collectors.

Diagnosis.—A species in the *Centrolene prosoblepon* group characterized by: (1) vomerine teeth present; (2) bones green; (3) parietal peritoneum white; visceral peritoneum clear; (4) color in life, lime-green with bluish white flecks dorsally; in preservative, pale lavender; (5) modal webbing between outer fingers III 2—2 IV; (6) modal webbing on foot I 1—1+II 1—2 III 1—2 IV 2—1 V; (7) snout rounded in dorsal view, bluntly rounded in profile; (8) dorsal skin shagreened with scattered minute spicules; (9) arms and legs lacking tubercles and dermal folds; (10) humeral spine present; (11) tympanum distinct, oriented posterolaterally with slight dorsal inclination; (12) prepollex enlarged; unpigmented nuptial excrescences (Type I) present; prepollical spine absent; (13) pair of enlarged tubercles below vent; (14) first finger longer than second.

Of the other *Centrolene* in the region with vomerine teeth, *C. andax* differs from *C. fernandoi* (characters in parentheses) by having the snout truncate in profile (bluntly rounded), skin on dorsum shagreened without spicules (shagreened with scattered small spicules), and in life, golden (bluish-white) flecks on dorsum, digits pale yellow (pale green), and iris pale bronze (silvery-green) with black reticulations. *Centrolene mariaae* differs by having large, pale spots on the dorsum, truncate snout in profile, and only basal webbing between Fingers III and IV; *C. azulae* and *C. puyoensis* differ by having ulnar folds, snout truncate in profile in *C. azulae*



Fig. 2. Upper left—paratype of *Cochranella croceopodes*, KU 211804, female, 24.7 mm SVL. Upper right.—holotype of *Centrolene fernandoi*, KU 211770, male, 24.0 mm SVL. Middle left—holotype of *Centrolene lemniscatum*, KU 217300, male, 27.0 mm SVL. Middle right—holotype of *Hyalinobatrachium lemur*, KU 211768, male, 20.4 mm SVL. Lower left—holotype of *Cochranella saxiscandens*, KU 211779, male, 21.7 mm SVL. Lower right—holotype of *Cochranella tangarana*, KU 211776, male, 23.3 mm SVL.

and truncate in dorsal view in *C. puyoensis*, and less extensive webbing between Fingers III and IV in *C. puyoensis*.

Description.—Nine adult males; SVL 22.5–26.4 mm. Body slender, elongate. Head distinct, about as wide as long, round in outline as viewed from below; HW 31.3–38.1% (\bar{x} = 33.2) of SVL; HL 30.0–36.0% (\bar{x} = 33.7) of SVL; snout rounded in dorsal view, bluntly rounded with slight anteroventral inclination in profile; SL 34.2–41.0% (\bar{x} = 37.3) of HL; canthus rostralis straight, indistinct, round in section; loreal region concave; lips barely flared anterior to orbit (Fig. 3C). Nostril ovoid, directed anteriorly on protuberance; internarial area slightly depressed. Eye large, ED 34.3–41.1% (\bar{x} = 37.3) of HL, directed anterolaterally at 37–40° (\bar{x} = 39.2) from midline; greatest diagonal EW 57.1–67.0% (\bar{x} = 60.0) of IOD. Tympanum distinct, lower four-fifths visible, oriented posterolaterally with slight dorsal inclination, separated from eye by distance 1.64–1.90 (\bar{x} = 1.71) times TYM, which is 31.2–41.4% (\bar{x} = 35.7) of ED; tympanic annulus slightly elevated anteriorly and ventrally; supratympanic fold moderate, obscuring tympanic annulus dorsally.

Skin on dorsal surfaces of head, body, and limbs shagreened with small spicules on side of head ventral and posterior to orbit and on dorsolateral surfaces of body. Flanks smooth dorsally, granular ventrally. Skin on belly and proximal four fifths of ventral surfaces of thighs coarsely granular; other ventral surfaces smooth. Vent directed posteroventrally at upper level of thighs; cloacal sheath short, unmodified; para- and subcloacal folds absent; one pair of large, round, flat tubercles on ventral surfaces of thighs below vent.

Breadth of upper arm about one half that of forearm; humeral spine present; ulnar fold and tubercles absent; hand moderately large; HnL 88.0–95.2% (\bar{x} = 91.0) of HL; digits broad, bearing narrow lateral fringes, including outer edge of Finger IV but not inner edge of Finger I; length of digits II < I < IV < III; webbing basal between Fingers I and II; webbing formula for other fingers II 2—2 III 2—(1-1/2) IV (Fig. 5C). Terminal discs elliptical; width of disc on Finger III about 1.3 times TYM; width of disc on Finger I 64.3–69.2% (\bar{x} = 66.7) of that on Finger III. Subarticular tubercles as wide as digits, round, elevated; penultimate tubercle on Finger IV largest; supernumerary tubercles present on proximal segments (absent on Fingers III and IV in some specimens); palmar tubercle large, broadly ovoid with diagonal orientation, elevated, its length 15.5–20.5% (\bar{x} = 17.7) of HnL. Thenar tubercle elliptical, diffuse proximally, barely elevated, about as long as palmar tubercle; prepollex slightly enlarged; Type I nuptial excrescence present; prepollical spine absent.

Hind limbs long, slender; TL 54.3–59.2% (\bar{x} = 56.7) of SVL; FL 43.0–48.2% (\bar{x} = 45.2) of SVL; dermal fringes, tarsal tubercles, and tarsal fold absent; inner metatarsal tubercle elongately elliptical, barely elevated, not

visible from above; outer metatarsal tubercle absent; toes moderately slender, bearing lateral fringes, including outer edge of Toe V and inner edge of Toe I; length of toes I < II < III < V < IV; toes about three-fourths webbed; webbing formula I 1—2 II (1—1½)—(2⁻—2⁺) III (1—1½)—2 IV 2—(1—1½) V. Terminal discs subtruncate; width of digit on Toe I 45.5–55.5% (\bar{x} = 50.3) of that on Toe IV, which is 69.2–73.3% (\bar{x} = 71.3) of that on Finger III; subarticular tubercles not as wide as digits, round, elevated.

Dentigerous processes of vomers ovoid, between nearly quadrangular choanae, narrowly separated medially, each bearing 2–5 (\bar{x} = 3.3) teeth. Tongue nearly round, barely free posteriorly. Vocal slit elongate, extending from posterolateral margin of tongue toward angle of jaw; vocal sac single, median, subgular.

Color in life: Dorsum lime-green with small bluish-white flecks; digits pale green; parietal peritoneum white; visceral peritoneum clear; heart not visible; bones green; iris pale silvery-green with fine black reticulations.

Color in preservative: General appearance lavender with small, elevated, cream flecks dorsally, cream ventrally. Under 25× magnification, dense melanophores in skin of dorsal surfaces of head and body with scattered, small, unpigmented elevations; equally dense melanophores in loreal region; less dense melanophores on upper lip, in tympanic region, and on dorsal surfaces of forelimbs, hind limbs, third and fourth fingers, tarsi, and fourth and fifth toes. Edge of upper eyelid pigmented. Flanks, anterior and posterior surfaces of thighs, inner two fingers and inner three toes, and all ventral surfaces cream with no melanophores.

Measurements (mm with means in parentheses): SVL 22.5–26.4 (23.7), TL 12.9–14.3 (13.4), FL 10.2–11.5 (10.7), HW 7.3–8.9 (7.9), HL 7.6–8.4 (8.0), SL 2.8–3.2 (3.0), ED 2.8–3.2 (3.0), IOD 2.8–3.1 (3.0), T–E 1.7–1.9 (1.8), TYM 1.0–1.2 (1.1), HnL 7.2–7.4 (7.3).

Distribution and ecology.—All individuals were on the upper surfaces of leaves of trees 1.5–2.0 m above a small stream in a narrow ravine at night. Although centrolenids were calling, no call was associated with this species. The type locality is on the road between Moyobamba and Tarapoto. The stream flows southward at a point about 0.5 km above (northeast of) Somos Libres (a road maintenance camp) and about 1 km below (southwest of) the crest of the ridge.

Etymology.—The specific name is a patronym for Fernando M. Cuadros V. of the Universidad Nacional Mayor de San Marcos in Lima in recognition of his cheerful companionship and dedication to collecting frogs in northern Peru in 1989.

Remarks.—The most similar species to *C. fernandoi* is *C. audax*, which is known from elevations of 1660–1700 m on the Amazonian slopes of the Andes in northern Ecuador.

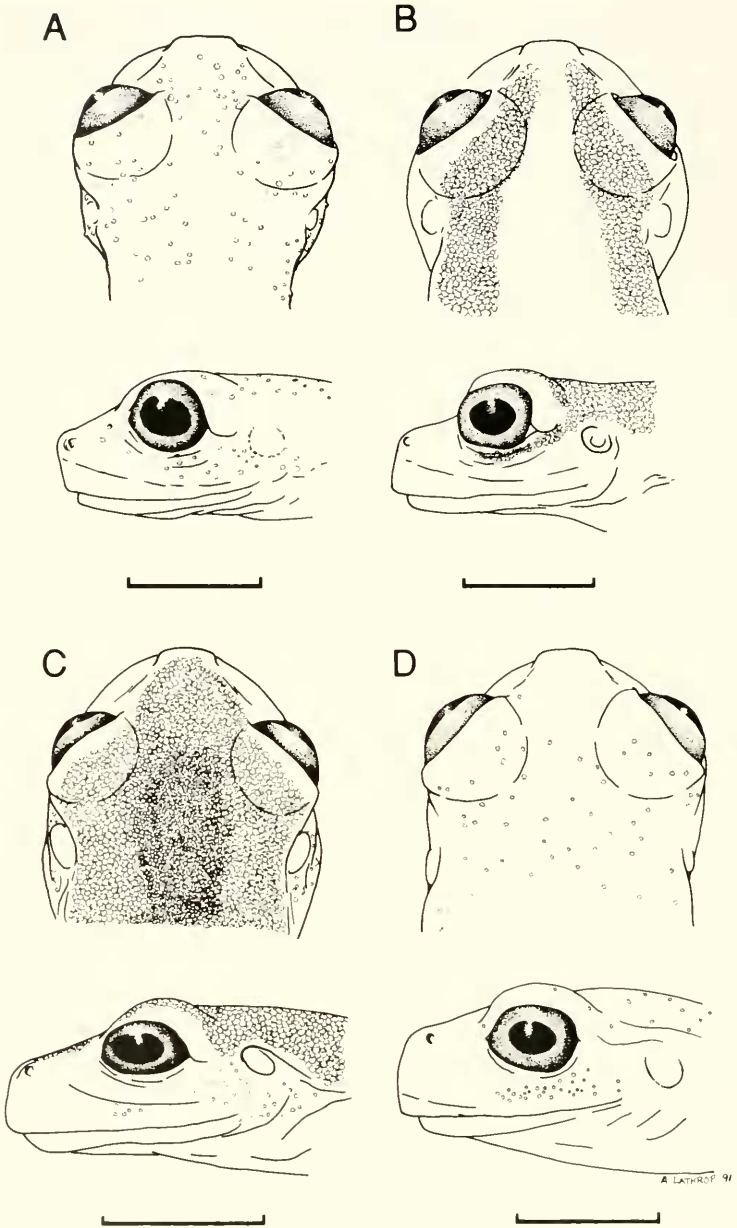


Fig. 3. Heads of centrolenids: A. *Cochranella chancas*, KU 211778. B. *Cochranella croceopodes*, KU 211804. C. *Centrolene fernandoi*, KU 211770. D. *Centrolene lemmiscatum*, KU 217300. Scale = 5 mm.

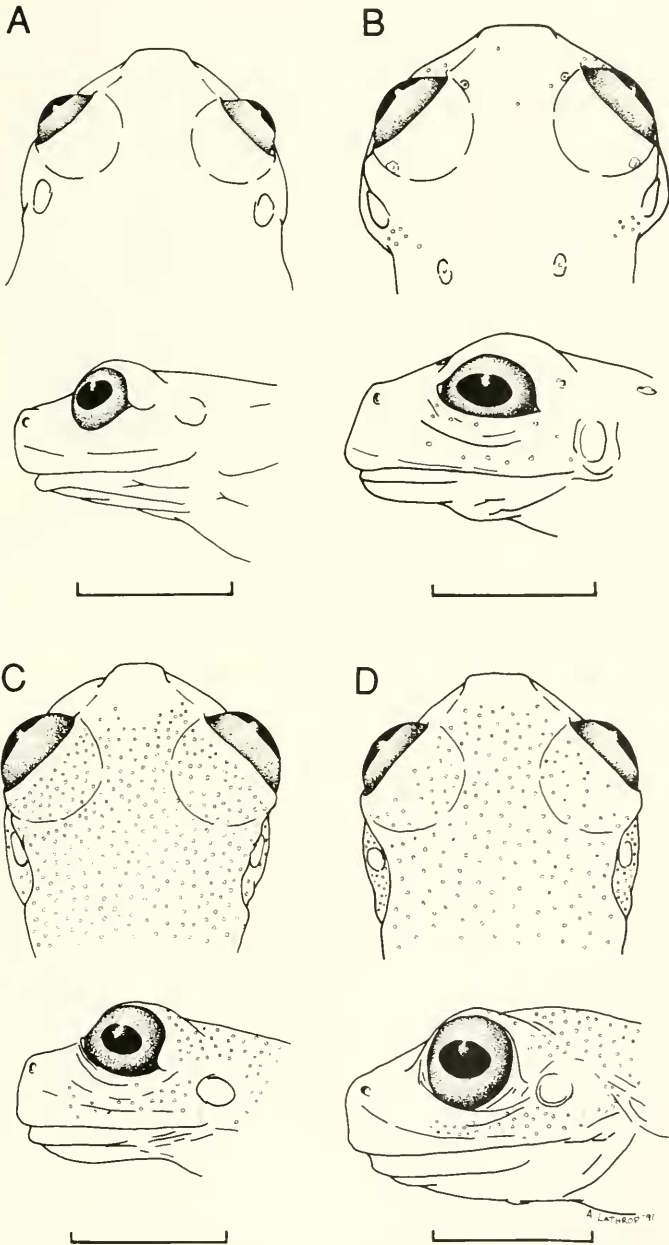


Fig. 4. Heads of centrolenids: A. *Hyalinobatrachium lemur*, KU 211768. B. *Centrolene muelleri*, KU 217301. C. *Cochranella saxiscandens*, KU 211779. D. *Cochranella tangarana*, KU 211777. Scale = 5 mm.

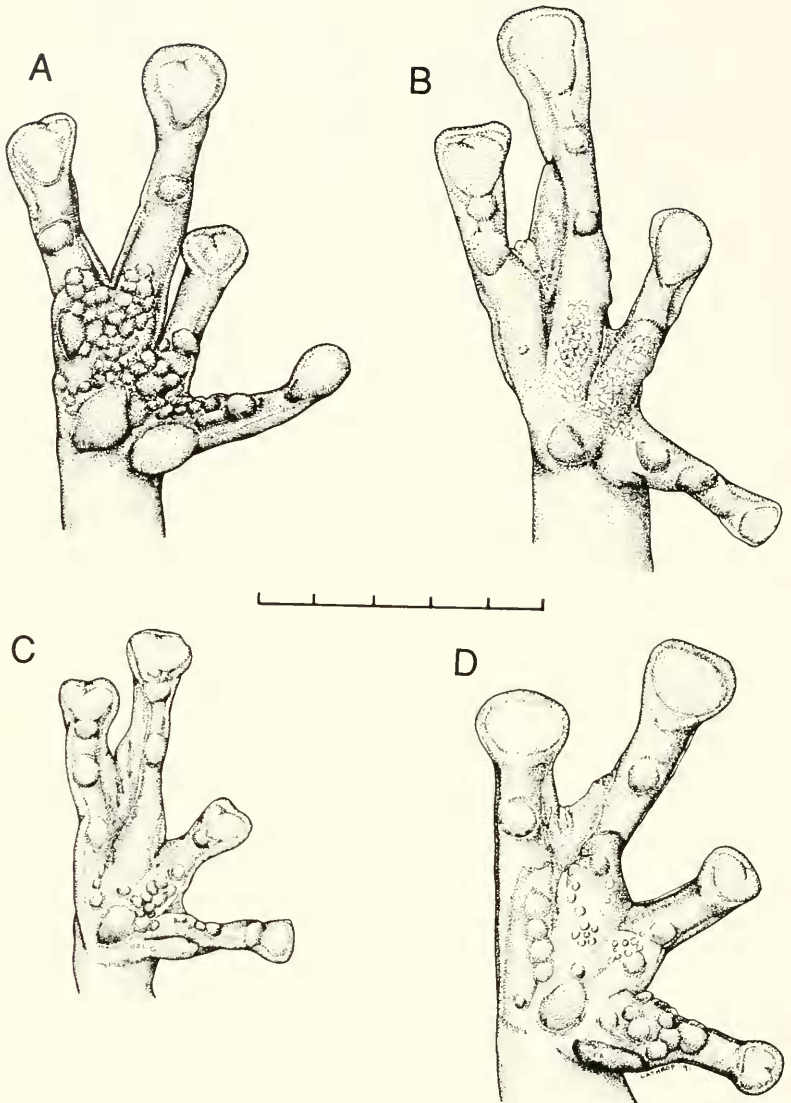


Fig. 5. Hands of centrolenids: A. *Cochranella chancas*, KU 211778. B. *Cochranella croceopodes*, KU 211804. C. *Centrolene fernandoi*, KU 211770. D. *Centrolene lemmiscatum*, KU 217300. Scale = 5 mm.

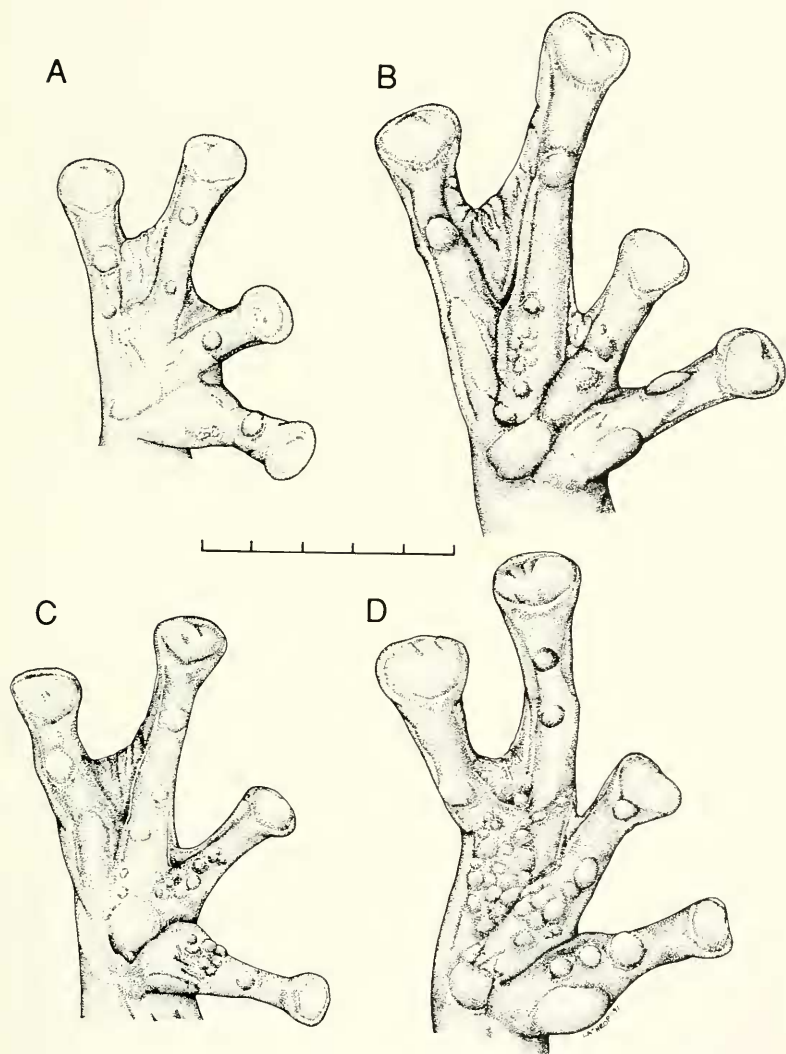


Fig. 6. Hands of centrolenids: A. *Hyalinobatrachium lemur*, KU 211768. B. *Centrolene muelleri*, KU 217301. C. *Cochranella saxiscandens*, KU 211779. D. *Cochranella tangarana*, KU 211777. Scale = 5 mm.

Centrolene lemniscatum new species

Figure 2

Holotype.—KU 217300, an adult male, from 14 km (by road) west of Venceremos (05°44'S, 77°32'W, 2000 m), Provincia Rioja, Departamento San Martín, Perú, obtained on 9 July 1989 by Rainer Schulte.

Diagnosis.—A species in the *Centrolene prosoblepon* group characterized by: (1) vomerine teeth absent; (2) bones green; (3) parietal peritoneum white; visceral peritoneum clear; (4) color in life, dorsum pale green with white labial stripe continuous with broad lateral stripe on body; in preservative, pale lavender with white lateral stripe; (5) webbing between outer fingers III 2½—2½ IV; (6) webbing on foot I 1½—2+II 1—2+III 1+—2½ IV 2½—2·V; (7) snout bluntly rounded in dorsal view and in profile; (8) dorsal skin spiculate; (9) arms and legs lacking tubercles and dermal folds; (10) humeral spine present; (11) tympanum indistinct, oriented posterolaterally; (12) prepollex enlarged; nuptial excrescence absent; prepollical spine absent; (13) two pairs of enlarged tubercles below vent; (14) first finger shorter than second.

Two other species in the region have white labial stripes. Of these, *Cochranella croceopodes* differs by having a diffuse yellow line on the flanks, first finger longer than the second, vomerine teeth, a distinct tympanum, more webbing on the hand, and presumably no humeral spines in males. *Centrolene lemniscatum* is like *C. hesperium* in having a distinct lateral white stripe that is continuous with the labial stripe, no vomerine teeth, and humeral spines. *Centrolene lemniscatum* differs from *C. hesperium* (characters in parentheses) by having the snout rounded in profile (sloping anteroventrally), and an indistinct tympanum (concealed), and in lacking dermal folds on the limbs (present).

Description.—One adult male; SVL 27.0 mm. Body robust. Head distinct, about as wide as long, round in outline as viewed from below; HW 30.3% of SVL; HL 30.7% of SVL; snout rounded with upper margin truncate in dorsal view; bluntly rounded in profile; SL 41.0% of HL; canthus rostralis straight, barely evident, round in section; loreal region slightly concave; lips slightly flared anterior to orbit (Fig. 3D). Nostril ovoid, directed anterolaterally on protuberance; internarial area barely depressed. Eye moderately large, ED 34.9% of HL, directed anterolaterally at 42° from midline; greatest diagonal EW 70.0% of IOD. Tympanum indistinct, oriented laterally with slight posterior inclination; tympanic annulus not evident; supratympanic fold moderately heavy, obscuring upper part of tympanum.

Skin on dorsal surfaces of head and body spiculate, with numerous small spicules below orbit; skin on limbs smooth. Flanks smooth dorsally,

granular ventrally. Skin on belly and ventral surfaces of thighs coarsely granular; other ventral surfaces smooth. Vent directed posteroventrally at upper level of thighs; cloacal sheath short, unmodified; para- and subcloacal folds absent; two pairs of moderately large, round, elevated tubercles on ventral surfaces of thighs below vent.

Breadth of upper arm about one half that of forearm; humeral spine present; ulnar fold and tubercles absent; hand large; HnL 106% of HL; digits broad, bearing narrow lateral fringes, including outer edge of Finger IV and inner edge of Finger I; length of digits $I < II < IV < III$; webbing absent between Fingers I, II, and III; webbing formula for other fingers $III\ 2-2\frac{1}{2}\ IV$ (Fig. 5D). Terminal discs subtruncate; width of disc on Finger III 65.5% of ED; width of disc on Finger I 57.9% of that on Finger III. Subarticular tubercles nearly as wide as digits, round, elevated; distal tubercle on Finger IV largest; supernumerary tubercles prominent on proximal segments; palmar tubercle moderately large, ovoid with diagonal orientation, elevated, its length 13.6% of HnL. Thenar tubercle ovoid, diffuse proximally, barely elevated, much longer than palmar tubercle; prepollex slightly enlarged; Type I nuptial excrescence present; prepollical spine absent.

Hind limbs long, slender; TL 56.3% of SVL; FL 51.9% of SVL; dermal fringes, tarsal tubercles, and tarsal fold absent; inner metatarsal tubercle elongately elliptical, elevated, visible from above; outer metatarsal tubercle absent; toes moderately slender, bearing lateral fringes, including outer edge of Toe V and inner edge of Toe I; length of toes $I < II < III < V < IV$; toes about three-fifths webbed; webbing formula $I\ 1\frac{1}{2}-2+II\ 1-2+III\ 1+-2\frac{1}{2}\ IV\ 2\frac{1}{2}-2\ V$. Terminal discs subtruncate; width of digit on Toe I 56% of that on Toe IV, which is 93.1% of that on Finger III; subarticular tubercles as wide as digits, round, elevated.

Vomerine teeth absent; choanae widely separated, quadrangular. Tongue shallowly cordiform, free posteriorly for about one third of its length. Vocal slit elongate, extending from posterolateral margin of tongue toward angle of jaw; vocal sac single, median, subgular.

Color in life: Dorsum medium green with irregular patches of yellowish-green; white labial stripe continuous with distinct lateral white stripe above insertion of arm extending to groin; flanks below lateral stripe cream; narrow white stripe on outer edge of forearm and foot; digits pale yellowish-green; parietal peritoneum white; visceral peritoneum clear; heart not visible; bones green; iris silvery-bronze with black flecks.

Color in preservative: General appearance grayish lavender on dorsal surfaces of head and body, cream on limbs and venter; white lateral stripe distinct. Under 25 \times magnification, dense melanophores in skin of dorsal surfaces of head and body; tips of spicules unpigmented; less dense melanophores in loreal and tympanic regions and on dorsal surfaces of

forelimbs, thighs, shanks, tarsi, and fourth and fifth toes. Edge of upper eyelid pigmented. Edge of upper lip and lateral stripe white; flanks, anterior and posterior surfaces of thighs, fingers and inner three toes, and all ventral surfaces cream with no melanophores.

Measurements (in mm): SVL 27.0, TL 15.2, FL 14.0, HW 8.2, HL 8.3, SL 3.4, E-N 1.8, ED 2.9, EW 2.1, IOD 3.0, HnL 8.8.

Distribution and ecology.—The holotype was on a bush in a stream in cloud forest at night. The type locality is on the road between Pomacochas (= Florida) and Rioja; Veneceremos is 89 km (by road) northwest of Rioja.

Etymology.—The specific name is a Latin adjective meaning adorned with ribbons; it alludes to the distinctive pale dorsolateral stripes.

Remarks.—*Centrolenella lemmiscatum* exhibits only slight differences from *C. hesperium*, which is known only from forested slopes at elevations of 1500–1800 m on the Pacific versant in northern Peru (Cadle and McDiarmid, 1990). Conceivably, the single specimen of *C. lemmiscatum* represents geographic variation in *C. hesperium*, but no species of frog is known to occur in the vicinity of the type locality of *C. hesperium* on the Pacific slopes of Peru and on the eastern slopes of the Cordillera Central in Peru.

Centrolene muelleri new species

Figure 7

Holotype.—KU 217301, an adult male from 14 km (by road) west of Venceremos (05°44'S, 77°32'W, 2000 m), Provincia Rioja, Departamento San Martín, Perú, obtained on 9 July 1989 by Rainer Schulte.

Diagnosis.—A species in the *Centrolene prosoblepon* group characterized by: (1) vomerine teeth absent; (2) bones green; (3) parietal peritoneum white; visceral peritoneum clear; (4) color in life, green with dark greenish-black spots and pale yellow tubercles; in preservative, brown with black spots and cream tubercles; (5) webbing on outer fingers III 2⁺—2⁺ IV; (6) webbing on foot I 1½—2 II 1⁺—2 III 2—2½ IV 2½—1½ V; (7) snout truncate in dorsal view, inclined anteroventrally in profile; (8) dorsal skin smooth with dorsolateral rows of tubercles; (9) low, scalloped dermal fold on outer edge of forearm and tarsus; (10) humeral spine present; (11) tympanum distinct, oriented posterolaterally with slight dorsal inclination; (12) prepollex enlarged; unpigmented nuptial excrescences (Type 1) present; prepollical spine absent; (13) pair of enlarged tubercles below vent; (14) first finger longer than second.

Centrolene muelleri differs from all other members of the genus by having large, conical tubercles on the dorsal surfaces of the head, body, and limbs. Other species that have dermal fringes on the limbs include *C. gemmatum* and *C. hesperium*, both of which have the first finger shorter

than the second (first longer than second in *C. muelleri*), and *C. pipilatum*, which has minute black flecks instead of large dark spots on the dorsum.

Description.—One adult male; SVL 23.5 mm. Body slender, elongate. Head distinct, slightly wider than long, round in outline as viewed from below; HW 32.3% of SVL; HL 31.1% of SVL; snout slightly protruding, truncate in dorsal view; slightly inclined anteroventrally in profile; SL 37.0% of HL; canthus rostralis straight, indistinct, round in section; loreal region concave; lips not flared anterior to orbit (Fig. 4B). Nostril ovoid, directed dorsolaterally on protuberance; internarial area depressed. Eye moderately large, ED 35.6% of HL, directed anterolaterally at 42° from midline; greatest diagonal EW 46.7% of IOD. Tympanum distinct, completely visible, oriented posterolaterally with slight dorsal inclination, separated from eye by distance 1.20 times TYM, which is 42.3% of ED; tympanic annulus slightly elevated; supratympanic fold weak, barely obscuring tympanic annulus dorsally.

Skin on dorsal surfaces of head, body, and limbs smooth with dorsolateral row of tubercles extending from occiput to insertion of hind limb; row of small tubercles on upper lip; one tubercle on each side of head at anterior corner of orbit and one medial to posterior corner of orbit; tubercles on dorsal surfaces of forelimbs, thighs, shanks, and tarsi. Flanks smooth dorsally, granular ventrally. Skin on belly and ventral surfaces of thighs coarsely granular; other ventral surfaces smooth. Vent directed posteroventrally at upper level of thighs; cloacal sheath short; tubercular para- and subcloacal folds present; one pair of large, subconical tubercles on ventral surfaces of thighs below vent.

Breadth of upper arm about one half that of forearm; humeral spine present; scalloped dermal folds on inner and outer edges of forearm; hand large; HnL 105% of HL; digits broad, bearing broad lateral fringes, including outer edge of Finger IV and inner edge of Finger I; length of digits $II < I < IV < III$; webbing basal between Fingers I and II; webbing formula for other fingers $II 2^+ - 3 III 2^+ - 2^+ IV$ (Fig. 6B). Terminal discs broadly elliptical; width of disc on Finger III 1.45 times TYM; width of disc on Finger I 50% of that on Finger III. Subarticular tubercles as wide as digits, round, elevated; distal tubercle on Finger I conical; all tubercles about same size; supernumerary tubercles present on proximal segments; palmar tubercle moderately large, broadly ovoid with diagonal orientation, elevated, its length 14.3% of HnL. Thenar tubercle ovoid, elevated, slightly longer than palmar tubercle; prepollex enlarged; Type I nuptial excrescence present; prepollical spine absent.

Hind limbs long, slender; TL 61.2% of SVL; FL 44.4% of SVL; pair of flaplike tubercles on heel; scalloped dermal fold on outer edge of tarsus; inner tarsal fold absent; inner metatarsal tubercle elongate, elliptical, barely elevated, visible from above; outer metatarsal tubercle absent; toes

moderately slender, bearing lateral fringes, including outer edge of Toe V and inner edge of Toe I; length of toes I < II < III < V < IV; toes about three-fourths webbed; webbing formula I 1½—2 II 1+—2 III 2—2½ IV 2½—1½ V. Terminal discs subtruncate; width of digit on Toe I 53.8% of that on Toe IV, which is 81.3% that on Finger III; subarticular tubercles about as wide as digits, round, subconical.

Vomerine teeth absent; choanae round, widely separated. Tongue narrowly cordiform, barely free posteriorly. Vocal slit elongate, extending from posterolateral margin of tongue toward angle of jaw; vocal sac single, median, subgular.

Color in life: Dorsum green with small black spots and cream tubercles; parietal peritoneum white; visceral peritoneum clear; heart not visible; bones green.

Color in preservative: General appearance grayish brown with small dark spots and cream spots corresponding to tubercles on head, body, and limbs dorsally; cream ventrally. Under 25× magnification, dark spots on head and body formed by aggregations of melanophores; elsewhere on body melanophores not so dense; narrow band of melanophores on dorsal surfaces of thighs and upper arms; melanophores present on outer two toes, absent on fingers. Edge of upper eyelid pigmented. Flanks, anterior and posterior surfaces of thighs, fingers, inner three toes, and all ventral surfaces cream without melanophores.

Measurements (in mm): SVL 23.5, TL 14.4, FL 10.4, HW 7.6, HL 7.3, SL 2.7, ED 2.6, EW 1.4, IOD 3.0, T-E 1.2, TYM 1.1, HnL 7.7.

Distribution and ecology.—The holotype was on a low bush at the edge of a stream in cloud forest at night. See the account of *Centrolene lemniscatum* for a description of the type locality.

Etymology.—The specific name is a patronym for Paul S. Müller, of the Universität des Saarlandes, who originally supported Schulte's field studies in Peru.

Remarks.—The holotype is slightly desiccated; however, all of the characters are readily discernable.

Cochranella chancas new species

Figure 8

Holotype.—KU 211778, an adult male, from the west slope of Abra Tangarana, 7 km (by road) northeast of San Juan de Pacaysapa (06°12'S, 76°44'W, 1080 m), Provincia Lamas, Departamento San Martín, Perú, obtained on 5 February 1989 by William E. Duellman.

Diagnosis.—A species in the *Cochranella ocellata* group characterized by: (1) vomerine teeth absent; (2) bones green; (3) parietal peritoneum white; visceral peritoneum clear; (4) color in life, dull yellowish-green with

minute yellow flecks; in preservative, dull gray with cream flecks; (5) webbing basal between outer fingers; (6) webbing on foot I 2⁺—3 II 2⁺—3 III 2—3 IV 3—2 V; (7) snout bluntly rounded in dorsal view, truncate in profile; (8) dorsal skin smooth with minute spicules on head and in thoracic region; (9) arms and legs lacking tubercles and dermal folds; (10) humeral spine absent in males; (11) tympanum weakly defined, oriented posterolaterally with slight dorsal inclination; (12) prepollex not enlarged. Type I nuptial excrescence present; prepollical spine absent; (13) one pair of large tubercles below vent; (14) first and second fingers equal in length.

Cochranella chancas is compared with other species having a white parietal peritoneum (heart not visible) and green bones that lack vomerine teeth and humeral spines. Of these species, *C. megacheira* and *C. truebae* differ from *C. chancas* by having dark dorsal markings (black spots in *C. megacheira* and many black flecks in *C. truebae*). *Cochranella cochranae* and *C. ocellata* differ from *C. chancas* by having well-defined ocelli on the dorsum. *Cochranella phenax*, *C. pluvialis*, *C. siren*, and *C. euhystrix* have spicules over the entire dorsum, whereas in *C. chancas* the dorsum is smooth except for minute spicules on the head and in the thoracic region. Moreover, *C. phenax* (male SVL 20.2–22.1 mm) and *C. siren* (male SVL 19.8–22.0 mm) are smaller than *C. chancas* (male SVL 24.9 mm) and have proportionately shorter snouts that are truncate in dorsal view (bluntly rounded in *C. chancas*), whereas *C. euhystrix* (male SVL 28.5–31.3 mm) is larger. Two other species are similar to *C. chancas*: *C. bejaranoi* is like *C. chancas* in coloration and in having most of Finger IV free of webbing, but it differs by having spicules over the entire dorsum of the head and body, in having the first finger shorter than the second, and in lacking enlarged tubercles below the vent; *C. flavopunctata* also is like *C. chancas* in coloration, but it differs by having all skin on the dorsum smooth to shagreened without spicules, only 1½ phalanges of Finger IV free of webbing, and first finger longer than second. Some individuals of *C. flavopunctata* and *C. siren* have vomerine teeth.

Description.—One adult male; SVL 24.9 mm. Body slender, elongate. Head distinct, about as wide as long, round in outline as viewed from below; HW 29.7% of SVL; HL 30.5% of SVL; snout slightly protruding with upper margin truncate in dorsal view, truncate in profile; SL 36.8% of HL; canthus rostralis straight, indistinct, round in section; loreal region concave; lips noticeably flared anterior to orbit (Fig. 3A). Nostril ovoid, directed anterolaterally on protuberance; internarial area depressed. Eye large, ED 42.1% of HL, directed anterolaterally at 35° from midline; greatest diagonal EW 88.9% of IOD. Tympanum barely distinct, completely visible, oriented posterolaterally with slight dorsal inclination, separated from eye by distance 1.36 times TYM, which is 34.4% of ED; tympanic annulus slightly elevated anteriorly and ventrally; supratympanic fold weak.

barely obscuring tympanic annulus dorsally.

Skin on dorsal surfaces of head, body, and limbs smooth except for small, round elevations corresponding to pale flecks and small spicules on head and in thoracic region. Flanks smooth dorsally, finely granular ventrally. Skin on belly and proximal three fourths of ventral surfaces of thighs coarsely granular; other ventral surfaces smooth. Vent directed posteroventrally at upper level of thighs; cloacal sheath short, unmodified; para- and subcloacal folds absent; one pair of large, round, flat tubercles on ventral surfaces of thighs below vent.

Breadth of upper arm about one half that of forearm; humeral spine absent; ulnar fold and tubercles absent; hand moderately large; HnL 90.8% of HL; digits broad, bearing narrow lateral fringes, including outer edge of Finger IV and inner edge of Finger I; length of digits I = II < IV < III; webbing basal between Fingers III and IV, absent between other fingers (Fig. 5A). Terminal discs elliptical; width of disc on Finger III equals TYM; width of disc on Finger I 68% of that on Finger III. Subarticular tubercles about as wide as digits, round, elevated; distal tubercle on Finger IV largest; supernumerary tubercles low, diffuse, present only on proximal segments; palmar tubercle large, nearly rectangular with diagonal orientation, elevated, its length 18.8% of HnL. Thenar tubercle elliptical, diffuse distally, barely elevated, nearly as long as palmar tubercle; prepollex not enlarged; Type I nuptial excrescence present; prepollical spine absent.

Hind limbs long, slender; TL 59.0% of SVL; FL 43.4% of SVL; dermal fringes, tarsal tubercles, and tarsal fold absent; inner metatarsal tubercle ovoid, elevated, visible from above; outer metatarsal tubercle absent; toes moderately slender, bearing lateral fringes, including outer edge of Toe V and inner edge of Toe I; length of toes I < II < III < V < IV; toes about three-fifths webbed; webbing formula I 2⁺—3 II 2⁺—3 III 2—3 IV 3—2 V. Terminal discs subtruncate; width of digit on Toe I 73% of that on Toe IV, which equals that on Finger III; subarticular tubercles not as wide as digits, round, elevated.

Vomerine teeth absent; choanae widely separated, subtriangular with apex anteromedially and rounded posterolaterally. Tongue shallowly cordiform, barely free posteriorly. Vocal slit elongate, extending from posterolateral margin of tongue toward angle of jaw; vocal sac single, median, subgular.

Color in life: Dorsum dull yellowish-green with minute yellow flecks (elevated); parietal peritoneum white; visceral peritoneum clear; heart not visible; bones green; iris pale yellowish-bronze.

Color in preservative: General appearance grayish-brown with minute cream flecks dorsally, cream ventrally. Under 25× magnification, dense melanophores in skin of dorsal surfaces of head, body, forearms, and shanks with scattered, small, unpigmented elevations; equally dense

melanophores in loreal and tympanic regions; less dense melanophores on dorsal surfaces of fourth fingers, thighs, tarsi, and fourth and fifth toes. Edge of upper eyelid unpigmented. Upper lip, flanks, upper arms, anterior and posterior surfaces of thighs, inner three fingers and toes, and all ventral surfaces, except chest, cream with no melanophores; chest white.

Measurements (in mm): SVL 24.9, TL 14.7, FL 10.8, HW 7.4, HL 7.6, SL 2.8, ED 3.2, EW 2.4, IOD 2.7, T-E 1.5, TYM 1.1, HnL 6.9.

Distribution and ecology.—The only known specimen was perched on a leaf over a stream in a narrow ravine at night. See the account of *Centrolene fernandoi* for a description of the type locality, the only site from which this species is known.

Etymology.—The specific name is a noun in apposition and is the name of the local indigenous people, Chancas, who were nearly exterminated by the Incas; the survivors are centered in the town of Lamas.

Remarks.—Loathful though we are to describe a new species on the basis of a single individual, the holotype of *C. chancas* has a combination of characters unknown in any other member of the genus.

Cochranella croceopodes new species

Figure 2

Holotype.—KU 211804, an adult female, from 23.2 km (by road) northeast of Tarapoto (06°27'S, 76°48'W, 800 m), Provincia San Martín, Departamento San Martín, Perú, obtained on 15 February 1989 by William E. Duellman.

Paratype.—KU 211799, an adult female, from Cataratas Ahuashiyacu, 730 m, 14 km (by road) northeast of Tarapoto, Provincia San Martín, Departamento San Martín, Perú, obtained on 11 February 1989 by John J. Wiens.

Diagnosis.—A species in the *Cochranella granulosa* group characterized by: (1) vomerine teeth present; (2) bones green; (3) parietal and visceral peritonea white; (4) color in life, uniform dull green dorsally with white margin of upper lip, diffuse yellow line on flanks, and digits yellow; in preservative, dark lavender; (5) modal webbing between outer fingers III 2—1+IV; (6) modal webbing on foot I 1—1+II 1+—2 III 1+—2 IV 2—1 V; (7) snout bluntly rounded in dorsal view and nearly truncate in profile; (8) dorsal skin shagreened; (9) arms and legs lacking tubercles and dermal folds; (10) state of humeral spine unknown; (11) tympanum distinct, oriented laterally with slight dorsal inclination; (12) prepollex not enlarged; prepollical spine absent; state of nuptial excrescences unknown; (13) pair of enlarged tubercles below vent; (14) first finger longer than second.

Cochranella croceopodes is compared with other species having lateral stripes—*Centrolene hesperium* and *C. lemniscatum*. Both of these species



Fig. 7. Holotype of *Centrolene muelleri*, KU 217301, male, 23.5 mm SVL.

lack vomerine teeth, have broader and more distinct lateral stripes, and the first finger is shorter than the second. Furthermore, the males have humeral spines.

Description.—Two adult females; SVL 24.7–24.8 mm. Body robust. Head distinct, about as wide as long, round in outline as viewed from below; HW 33.9–34.0% of SVL; HL 33.9–34.8% of SVL; snout slightly protruding, bluntly rounded in dorsal view and nearly truncate with slight anteroventral inclination in profile; SL 38.1% of HL; canthus rostralis straight, indistinct, round in section; loreal region barely concave; lips not flared anterior to orbit (Fig. 3B). Nostril ovoid, directed anterolaterally on protuberance; internarial area depressed. Eye moderately large, ED 38.1% of HL, directed anterolaterally at 45° from midline; greatest diagonal EW 67.7–71.0% of IOD. Tympanum distinct, almost entirely visible, oriented dorsolaterally with slight posterior inclination, separated from eye by distance 1.38–1.58 times TYM, which is 37.5–40.6% of ED; tympanic annulus slightly elevated anteriorly, posteriorly, and ventrally; supratympanic fold moderately heavy, obscuring tympanic annulus dorsally.

Skin on dorsal surfaces of head, body, and limbs shagreened. Flanks smooth dorsally, finely granular ventrally. Skin on belly and ventral surfaces of thighs coarsely granular; other ventral surfaces smooth. Vent directed posteroventrally at upper level of thighs; cloacal sheath short, unmodified;

para- and subcloacal folds absent; one pair of large, round, slightly elevated tubercles on ventral surfaces of thighs below vent.

Breadth of upper arm about one half that of forearm; humeral spine absent (males unknown); ulnar fold and tubercles absent; hand moderately large; HnL 88.4–90.5% of HL; digits broad, bearing narrow lateral fringes, including outer edge of Finger IV but excluding inner edge of Finger I; length of digits $II < I < IV < III$; webbing absent between Fingers I and II; webbing formula for other fingers $II\ 2^-3\ III\ 2-1^+IV$ (Fig. 5B). Terminal discs elliptical; that on fourth finger slightly indented medially; width of disc on Finger III 1.33–1.38 times TYM; width of disc on Finger I 62.5–66.7% of that on Finger III. Subarticular tubercles round, subconical; penultimate tubercle on Finger IV largest, as wide as digit; supernumerary tubercles low, present on proximal segments of Fingers I–III; palmar tubercle large, broadly ovoid with diagonal orientation, elevated with median depression, its length 17.1–19.0% of HnL. Thenar tubercle elongately elliptical, diffuse proximally, barely elevated, longer than palmar tubercle; prepollex not enlarged. Condition of nuptial excrescence and prepollical spine unknown.

Hind limbs long, slender; TL 53.8–59.7% of SVL; FL 43.7–50.8% of SVL; dermal fringes, tarsal tubercles, and tarsal fold absent; inner metatarsal tubercle elliptical, elevated distally, visible from above; outer metatarsal tubercle absent; toes moderately slender, bearing lateral fringes, including outer edge of Toe V and inner edge of Toe I; length of toes $I < II < III < V < IV$; toes about three-fourths webbed; webbing formula $I\ 1-(1^+-2^-)\ II\ 1^+-2^-III\ (1^+-1\frac{1}{2}^-)-2\ IV\ (2^-2^-)-1\ V$. Terminal discs elliptical; width of digit on Toe I 61.5% of that on Toe IV, which equals that on Finger III; subarticular tubercles as wide as digits, round, elevated.

Dentigerous processes of vomers elliptical, slightly inclined posteromedially, narrowly separated medially, each with four or five ($\bar{x} = 4.8$) teeth; choanae widely separated, subtriangular with anteromedial apex and lateral rounded base. Tongue slightly longer than wide, barely free posteriorly. Condition of vocal slit and sac unknown.

Color in life: Dorsum dull green; margin of upper lip white; diffuse yellow line on flanks from axilla to groin; fingers and toes yellow; throat and ventral surfaces of limbs pale green; parietal and visceral peritonea white; heart not visible; bones green; iris dull bronze with back flecks and brownish suffusion anteriorly and posteriorly.

Color in preservative: General appearance dark lavender dorsally, cream ventrally. Under 25× magnification, lavender with underlying melanophores in skin of dorsal surfaces of head and body, and in loreal and tympanic regions; less dense melanophores on dorsal surfaces of limbs, third and fourth fingers, and fourth and fifth toes. Edge of upper eyelid pigmented. Edge of upper eyelid pigmented. Upper lip, lower one half of

tympanum, flanks, posterior surfaces of thighs, inner two fingers, inner three toes, and all ventral surfaces cream with no melanophores.

Measurements (in mm; holotype followed by paratype): SVL 24.7, 24.8; TL 13.3, 14.8; FL 10.8, 12.6; HW 8.4, 8.4; HL 8.6, 8.4; SL 3.2, 3.2; ED 3.2, 3.2; EW 2.1, 2.2; IOD 3.1, 3.1; T-E 1.9, 1.8; TYM 1.2, 1.3; HnL 7.6, 7.9.

Distribution and ecology.—The species is known only from two localities on a northwest–southeast ridge north of Tarapoto. The type locality is on the north slope and in the drainage of the Río Cainarachi. The locality is at the edge of the Tarapoto–Yurimaguas road, 3.2 km north of the tunnel through the upper part of the ridge. The second locality is on the south slope of the same ridge (for description see account of *Cochranella saxiscandens*). The holotype was found at night on the upper surface of an aroid on a vertical rock face about 3 m above the ground in an area of dripping water. The paratype was on a low herb next to a cascading stream at night.

Etymology.—The specific name is an adjective derived from the Greek *croceos* meaning yellow-orange and the Greek *podos* meaning foot; the name refers to the bright yellow hands and feet.

Remarks.—The definitive placement of this species in *Cochranella* must await the discovery of males in order to determine the presence or absence of humeral spines.

Cochranella saxiscandens new species

Figure 2

Holotype.—KU 211779, an adult male, from Cataratas Ahaushiyacu (06°30'S, 76°20'W, 730 m), 14 km (by road) northeast of Tarapoto, Provincia San Martín, Departamento San Martín, Perú, one of a series collected on 8 February 1989 by William E. Duellman, Rainer Schulte, and John J. Wiens.

Paratypes.—KU 211780–88 and MHNSM 6166–71 collected with the holotype; KU 211789–98, 211800–01 from the type locality collected on 11 February 1989 by John J. Wiens; KU 211802–03 from 15 km northeast of Tarapoto, 800 m, collected on 11 February 1989 by Rainer Schulte; KU 217299 from the type locality obtained on 3 June 1989 by Rainer Schulte.

Diagnosis.—A species in the *Cochranella ocellata* group characterized by: (1) vomerine teeth present; (2) bones green; (3) parietal peritoneum white; visceral peritoneum clear; (4) color in life, dull dark green to black dorsally and paler green laterally; in preservative, dark olive-brown to black; (5) modal webbing between outer fingers III 2—2 IV; (6) modal webbing on foot I 1+—1½ II 1—2 III 1—2 IV 2—1 V; (7) snout bluntly rounded in dorsal view and in profile; (8) dorsal skin spiculate; (9) arms



Fig. 8. Holotype of *Cochranella chancas*. KU 211778, male, 24.9 mm SVL.

and legs lacking tubercles and dermal folds; inner tarsal fold present; (10) humeral spine absent; (11) tympanum distinct, oriented dorsolaterally with slight posterior inclination; (12) prepollex enlarged; unpigmented nuptial excrescences (Type I) present; prepollical spine absent; (13) no enlarged tubercles below vent; (14) first finger longer than second.

Of the nine other species of *Cochranella* in the region, *C. resplendens* differs from *C. saxiscandens* by having dermal folds on the limbs (as do *Centrolene azulae* and *pyvoensis*); *C. ametarsia* and *C. ritae* differ by having black flecks on the dorsum. Four of the other species (*C. cochranae*, *flavopunctata*, *midas*, and *siren*) differ from *C. saxiscandens* by having pale spots or flecks on the dorsum. Only *C. spiculata* and *C. tangarana* are like *C. saxiscandens* in having a uniformly darkly pigmented dorsum that is finely spiculate; both of these species differ from *C. saxiscandens* (characters in parentheses) by having a lavender dorsum (dark gray to black) in preservative, melanophores absent on the ventral surfaces of shanks and tarsi (present), and inner tarsal fold absent (present).

Description.—Thirty adult males; SVL 20.8–23.2 mm (\bar{x} = 22.0). Body moderately robust. Head distinct, about as wide as long, round in outline as viewed from below; HW 31.2–37.3% (\bar{x} = 35.1) of SVL; HL 32.0–36.2% (\bar{x} = 34.3) of SVL; snout rounded with upper margin truncate in dorsal view; bluntly rounded in profile; SL 34.1–43.8% (\bar{x} = 38.6) of HL; canthus rostralis slightly curved, indistinct, round in section; loreal region barely concave; lips not flared anterior to orbit (Fig. 4C). Nostril round, directed dorsolaterally on slight protuberance; internarial area not depressed. Eye

moderately large, ED 32.4–45.6% (\bar{x} = 37.2) of HL, directed anterolaterally at 40–42° from midline; greatest diagonal EW 55.4–63.8% (\bar{x} = 57.7) of IOD. Tympanum distinct, lower four-fifths visible, oriented dorsolaterally with slight posterior inclination, separated from eye by distance 1.20–1.43 (\bar{x} = 1.33) times TYM, which is 26.4–43.7% (\bar{x} = 35.3) of ED; tympanic annulus slightly elevated; supratympanic fold heavy, obscuring dorsal part of tympanum.

Skin on dorsal surfaces of head and body finely spiculate; spicules also present on upper lip and in tympanic region. Dorsal surfaces of limbs smooth except for a few low spicules on proximal part of forearm in some specimens. Flanks smooth. Skin on belly and ventral surfaces of thighs coarsely granular; other ventral surfaces smooth. Vent directed posteroventrally at upper level of thighs; cloacal sheath short, unmodified; para- and subcloacal folds absent; no conspicuous tubercles on ventral surfaces of thighs below vent.

Breadth of upper arm about one half that of forearm; humeral spine absent; ulnar fold and tubercles absent; hand large; HnL 92–111% (\bar{x} = 101) of HL; digits broad, bearing narrow lateral fringes, including outer edge of Finger IV but not inner edge of Finger I; length of digits II < I < IV < III; webbing basal between Fingers I and II; webbing formula for other fingers II (1½–2⁻)—(2–3) III (2–2)—(2–2⁺) IV (Fig. 6C). Terminal discs subtruncate; width of disc on Finger III about twice TYM; width of disc on Finger I 62.5–81.3% (\bar{x} = 72.4) of that on Finger III. Subarticular tubercles not as wide as digits, round, elevated; all tubercles about same size, except distal tubercle on Finger IV largest; small supernumerary tubercles variously evident on proximal segments; palmar tubercle large, ovoid with diagonal orientation, elevated, its length 15.8–18.8% (\bar{x} = 16.9) of HnL. Thenar tubercle elliptical, elevated, much longer than palmar tubercle; prepollex slightly enlarged; Type I nuptial excrescence present; prepollical spine absent.

Hind limbs long, slender; TL 56.2–61.1% (\bar{x} = 58.4) of SVL; FL 46.4–52.8% (\bar{x} = 49.3) of SVL; dermal fringes and tarsal tubercles absent; inner tarsal fold present; inner metatarsal tubercle elliptical, slightly elevated, barely visible from above; outer metatarsal tubercle absent; toes moderately slender, bearing lateral fringes, including outer edge of Toe V and inner edge of Toe I; length of toes I < II < III < V < IV; toes about three-fourths webbed; webbing formula I (1–1)—(1–1⁺) II (1–1⁺)—I III 1—(2–2) IV (2–2)—(1–1⁺) V. Terminal discs subtruncate; width of digit on Toe I 53.8–61.5% (\bar{x} = 58.7) of that on Toe IV, which is 75.0–92.8% (\bar{x} = 83.2) that on Finger III; subarticular tubercles not as wide as digits, round, elevated.

Vomerine tooth rows transverse to slightly inclined posteromedially, narrowly separated medially, between ovoid choanae, each with one to five (\bar{x} = 2.9) teeth. Tongue broadly cordiform, barely free posteriorly. Vocal

slit elongate, extending from posterolateral margin of tongue toward angle of jaw; vocal sac single, median, subgular.

Color in life: Dorsum dull dark green to black; flanks paler green; tinge of yellow on digits; parietal peritoneum white; visceral peritoneum clear; heart not visible; bones green; iris dull gray with black reticulations, tinge of red dorsally.

Color in preservative: General appearance dark olive-brown to black dorsally, cream ventrally. Under 25× magnification, dense melanophores in skin of dorsal surfaces of head and body; less dense melanophores on dorsal surfaces of limbs, including digits and webbing. Edge of upper eyelid pigmented. Venter cream with melanophores on margin of chin and on ventral surfaces of forearms, shanks, and tarsi.

Measurements (in mm: mean and 1 SD in parentheses): SVL 20.8–23.2 (22.0 ± 1.1), TL 12.3–13.7 (12.9 ± 0.4), FL 9.9–11.5 (10.9 ± 0.4), HW 6.9–8.4 (7.7 ± 0.4), HL 6.9–8.0 (7.5 ± 0.3), SL 2.5–3.4 (2.9 ± 0.2), ED 2.4–3.3 (2.8 ± 0.2), EW 1.5–2.3 (1.9 ± 0.2), IOD 2.3–3.1 (2.6 ± 0.2), T–E 1.1–1.4 (1.2 ± 1.1), TYM 0.9–1.2 (1.0 ± 0.1), HnL 6.8–8.4 (7.6 ± 0.4).

Distribution and ecology.—The species is known from only two sites on the south slope of the northwest–southeast range of mountains immediately to the north of Tarapoto. Both sites are on the road between Tarapoto and Yurimaguas. The type locality is a rocky gorge into which two streams plunge. The sides of the gorge are nearly vertical rocky walls, and the floor of the gorge is littered with huge boulders. About 50 m beyond the bases of the waterfalls, the two streams merge, and the resulting wider stream flows over, under, and around these boulders, many of which support a thin layer of moss. Small ferns and herbs also grow on some of the boulders. Small trees, ferns, and a variety of herbs grow in patches of soil on the floor of the gorge.

A few of the frogs were perched on ferns on boulders, but most were on the boulders within 10 cm of the waterline at night. Several individuals were on the bare, wet undersides of boulders over the stream. When disturbed, the frogs ran rapidly across the boulders instead of leaping away. The call is a soft chirp.

Etymology.—The specific name is an adjective derived from the Latin *saxum* meaning rock and the Latin *scandens* meaning climbing; the name alludes to the habit of these frogs of scampering across bare rocks.

Remarks.—Most centrolenids are active on vegetation above streams at night. However, some species are known to inhabit rocks in streams. *Cochranella orejuela* were found at night on rocks along a steep stream bank or on rocks within the stream (Duellman and Burrowes, 1989). *Centrolene medemi* were found on rock cliffs in the spray zone of waterfalls (WED, pers. observ.), as were *Cochranella euhystrix* (Cadle and McDiarmid (1990). *Centrolene geckoideum* and *C. paezorum* inhabit

similar rocky areas and apparently do not perch on vegetation (Lynch et al., 1983; Ruíz-Carranza et al., 1986; WED, pers. observ.).

Cochranella tangarana new species

Figure 2

Holotype.—KU 211776, an adult male, from the west slope of Abra Tangarana, 7 km (by road) northeast of San Juan de Pacaysapa (06°12'S, 76°44'W, 1080 m), Provincia Lamas, Departamento San Martín, Perú, one of a series collected on 5 February 1989 by William E. Duellman, Rainer Schulte, and John J. Wiens.

Paratopotypes.—KU 211777 (male) and MHNSM 6179 (female); same date and collectors.

Diagnosis.—A species in the *Cochranella ocellata* group characterized by: (1) vomerine teeth present; (2) bones green; (3) parietal peritoneum white; visceral peritoneum clear; (4) color in life, uniform dark green dorsally; in preservative, dark lavender; (5) modal webbing on outer fingers III 2—1½ V; (6) modal webbing on foot I 1—1½ II 1—2 III 1—2 VI 2—1 V; (7) snout truncate in dorsal view and in profile; (8) dorsal skin finely spiculate; (9) arms and legs lacking tubercles and dermal folds; (10) humeral spine absent; (11) tympanum distinct, oriented dorsolaterally with slight posterior inclination; (12) prepollex enlarged; nuptial excrescences (Type I) present; prepollical spine absent; (13) pair of enlarged tubercles below vent; (14) first finger equal to, or barely longer than, second.

Of the nine other species of *Cochranella* in the region, *C. resplendens* differs from *C. tangarana* by having dermal folds on the limbs (as do *Centrolene azulae* and *pyoensis*); *C. ametarsia* and *C. ritae* differ by having black flecks on the dorsum. Four of the other species (*C. cochranae*, *flavopunctata*, *midas*, and *siren*) differ from *C. tangarana* by having pale spots or flecks on the dorsum. Only *C. saxiscandens* and *C. spiculata* resemble *C. tangarana* in having a uniformly darkly pigmented dorsum that is finely spiculate. *Centrolenella tangarana* differs from *C. saxiscandens* (characters in parentheses) by having a lavender dorsum (dark gray to black) in preservative, melanophores absent on ventral surfaces of shanks and tarsi (present), and inner tarsal fold absent (present). *Centrolenella tangarana* is most similar to *C. spiculata* which differs by having a shorter snout that is round in profile, more conspicuous tympanum, more conspicuous spicules on the head and body, and spicules on the dorsal surfaces of the forearms and shanks.

Description.—Two adult males and one adult female; SVL 23.3, 22.5, and 22.5 mm, respectively. Body moderately robust. Head distinct, about as wide as long, round in outline as viewed from below; HW 31.5–35.5% (\bar{x} = 33.3) of SVL; HL 33.5–36.0% (\bar{x} = 34.4) of SVL; snout truncate in

dorsal view and in profile; SL 37.0–40.7% (\bar{x} = 38.7) of HL; canthus rostralis curved, indistinct, round in section; loreal region concave; lips slightly flared anterior to orbit (Fig. 4D). Nostril ovoid, directed dorsolaterally on protuberance; internarial area depressed. Eye moderately large, ED 30.7–35.5% (\bar{x} = 33.6) of HL, directed anterolaterally at 37–38° from midline; greatest diagonal EW 63.3–65.5% (\bar{x} = 64.7) of IOD. Tympanum distinct, completely visible, oriented dorsolaterally with slight posterior inclination, separated from eye by distance 1.7–1.9 (\bar{x} = 1.8) times TYM, which is 37.0–45.8% (\bar{x} = 40.7) of ED; tympanic annulus slightly elevated; supratympanic fold weak, barely obscuring tympanic annulus dorsally.

Skin on dorsal surfaces of head and body finely spiculate (less so in female); dorsal surfaces of limbs smooth; small spicules on side of head below orbit and in tympanic region. Flanks smooth. Skin on belly and ventral surfaces of thighs coarsely granular; other ventral surfaces smooth. Vent directed posteroventrally at upper level of thighs; cloacal sheath short, unmodified; para- and subcloacal folds absent; one pair of large, round, slightly elevated tubercles on ventral surfaces of thighs below vent.

Breadth of upper arm about one half that of forearm; humeral spine absent; ulnar fold and tubercles absent; hand moderately large; HnL 95–101% (\bar{x} = 97.3) of HL; digits broad, bearing narrow lateral fringes, including outer edge of Finger IV but not inner edge of Finger I; length of digits I > II < IV < III; webbing basal between Fingers I and II; webbing formula for other fingers II (1–2)–3 III (2–2)–(1+–2) IV (Fig. 6D). Terminal discs subtruncate; width of disc on Finger III about 1.5 TYM; width of disc on Finger I 71.4–78.5% (\bar{x} = 75.6) of that on Finger III. Subarticular tubercles as wide as digits, round, elevated; all tubercles about same size; supernumerary tubercles present on proximal segments; palmar tubercle large, nearly quadrangular with diagonal orientation, elevated, its length 15.8–16.4% (\bar{x} = 16.2) of HnL. Thenar tubercle broadly elliptical, barely elevated, longer than palmar tubercle; prepollex enlarged; Type I nuptial excrescence present; prepollical spine absent.

Hind limbs long, slender; TL 57.1–59.6% (\bar{x} = 58.6) of SVL; FL 46.7–48.9% (\bar{x} = 47.7) of SVL; dermal fringes, tarsal tubercles, and tarsal fold absent; inner metatarsal tubercle elliptical, slightly elevated, barely visible from above; outer metatarsal tubercle absent; toes moderately slender, bearing lateral fringes, including outer edge of Toe V and inner edge of Toe I; length of toes I < II < III < V < IV; toes about three-fourths webbed; webbing formula I (1–1+)–(1½–2) II (1–1+)–2 III 1–(2–2) IV (2–2)–1 V. Terminal discs subtruncate; width of digit on Toe I 61.5–66.7% (\bar{x} = 63.9) of that on Toe IV, which is 84.6–92.9% (\bar{x} = 87.7) of that on Finger III; subarticular tubercles as wide as digits, round, elevated.

Vomerine tooth rows elongate, posteromedially inclined, narrowly separated medially, between ovoid choanae, each with two to five ($\bar{x} = 3.5$) teeth. Tongue narrowly cordiform, barely free posteriorly. Vocal slit elongate, extending from posterolateral margin of tongue toward angle of jaw; vocal sac single, median, subgular.

Color in life: Dorsum uniform dark green; anterior and posterior surfaces of thighs pale green; digits pale yellow; vocal sac pale green; parietal peritoneum white; visceral peritoneum clear; heart not visible; bones green; iris bronze with black reticulations.

Color in preservative: General appearance dark lavender dorsally, cream ventrally. Under 25 \times magnification, dorsal surfaces of head and body dark lavender except for tips of spicules, which are unpigmented; moderately dense melanophores in loreal, labial, and tympanic regions, and on dorsal surfaces of limbs; less dense melanophores on flanks, dorsal surfaces of Fingers III and IV and Toes III–V, and anterior and posterior surfaces of thighs. Edge of upper eyelid pigmented. Venter cream; scattered melanophores apically and posterolaterally on chin in one male (KU 211777).

Measurements (in mm: male holotype and male paratype, followed by female paratype): SVL 23.3, 22.5, 22.5; TL 13.3, 13.4, 13.3; FL 11.1, 10.5, 11.0; HW 7.6, 7.4, 8.0; HL 7.8, 7.6, 8.1; SL 3.0, 3.1, 3.0; ED 2.4, 2.7, 2.8; EW 1.7, 1.9, 1.9; IOD 2.6, 3.0, 2.9; T–E 1.2, 1.0, 1.1; TYM 1.1, 1.0, 1.1; HnL 7.9, 7.3, 7.6.

Distribution and ecology.—The species is known only from the type locality and another ravine about 0.5 km to the northeast. See the account of *Centrolene fernandoi* for a description of the type locality.

All individuals were found at night perched on the dorsal surfaces of ferns, leaves of trees, aroids, and other herbaceous plants at the edge of, or overhanging, a small cascading stream in a narrow rocky ravine. All were less than 2 m above the ground or water. The call is a harsh, high-pitched “tzeet.”

Etymology.—The specific name is a noun in apposition and refers to the type locality. Tangarana is the local name for the tree, *Triplaris poeppigiana* (Polygonaceae), colonized by small red ants that have a painful sting.

Remarks.—A male 22.0 mm SVL (LSUMZ 37104) from the Cordillera Colón, Departamento Amazonas, Perú, superficially is like *Cochranella tangarana*, but it lacks vomerine teeth and has large pale spots on the dorsum.

Hyalinobatrachium lemur new species

Figure 2

Holotype.—KU 211768, an adult male, from the west slope of Abra Tangarana, 7 km (by road) northeast of San Juan de Pacaysapa (06°12'S,

76°44'W, 1080 m), Provincia Lamas, Departamento San Martín, Perú, obtained on 5 February 1989 by William E. Duellman.

Paratopotype.—KU 211769, collected with the holotype.

Diagnosis.—A species in the *Hyalinobatrachium fleischmanni* group characterized by: (1) vomerine teeth absent; (2) bones white; (3) parietal peritoneum clear; visceral peritoneum white; (4) color in life, pale green with diffuse, dull yellow spots; in preservative, creamy white with scattered melanophores; (5) modal webbing on outer fingers III 2—1 IV; (6) modal webbing on foot I 1—1½ II 1—2 III 1—2 IV 2—1 V; (7) snout truncate in dorsal view and in profile; (8) dorsal skin smooth; (9) arms and legs lacking tubercles and dermal folds; (10) humeral spine absent; (11) tympanum indistinct; (12) prepollex not enlarged; nuptial excrescences absent; prepollical spine absent; (13) no enlarged tubercles below vent; (14) first finger longer than second.

Hyalinobatrachium lemur differs from *H. bergeri* and *H. pellucidum* by having smooth, instead of shagreened, skin on the dorsum and by having more extensive webbing on Finger IV (1 free phalanx in *H. lemur*, as opposed to 2 free phalanges in the others). *Hyalinobatrachium munozorum* is like *H. lemur* in having smooth skin on the dorsum, but it differs by having a round, instead of truncate, snout in profile, less webbing on Finger IV (2 phalanges free), and smaller terminal discs on the fingers.

Description.—One adult male and one adult female; SVL 20.4 and 21.3 mm, respectively. Body robust. Head not distinct from body, wider than long, round in outline as viewed from below; HW 39.2, 37.1% of SVL; HL 30.9, 29.6% of SVL; snout slightly protruding, rounded with upper margin truncate in dorsal view; truncate in profile; SL 44.4% of HL; canthus rostralis slightly curved, indistinct, round in section; loreal region concave; lips not flared anterior to orbit (Fig. 4A). Nostril ovoid, directed laterally on low protuberance; internarial area barely depressed. Eye moderately large, ED 36.5% of HL, directed anterolaterally at 35, 36° from midline; greatest diagonal EW 60.0, 66.7% of IOD. Tympanum indistinct, oriented dorsolaterally, separated from eye by distance 1.1, 1.3 times TYM, which is 30.4% of ED; tympanic annulus slightly elevated; supratympanic fold weak, barely obscuring upper part of tympanum.

Skin on dorsal surfaces of head, body, and limbs smooth. Flanks smooth dorsally, finely granular ventrally. Skin on belly and ventral surfaces of thighs granular; other ventral surfaces smooth. Vent directed posteriorly at upper level of thighs; cloacal sheath short, unmodified; para- and subcloacal folds absent; one pair of elongate, elevated tubercles on ventral surfaces of thighs below vent.

Breadth of upper arm about one half that of forearm; humeral spine absent; ulnar fold and tubercles absent; hand large; HnL 96.8, 96.4% of HL; digits broad, bearing broad lateral fringes; fringes narrow on outer edge of Finger IV and inner edge of Finger I; length of digits II < I < IV <

III; fingers about one-half webbed; webbing formula I 2—(2-3) II (1½-2*)—3 III (2-2)—(1-1) IV (Fig. 6A). Terminal discs round; width of disc on Finger III equals twice TYM; width of disc on Finger I 80.8, 84.6% of that on Finger III. Subarticular tubercles not as wide as digits, round, barely elevated; all tubercles about same size; supernumerary tubercles absent; palmar tubercle moderately large, round, indistinct, its length 13.2, 12.7% of HnL. Thenar tubercle elliptical, diffuse, barely elevated, longer than palmar tubercle; prepollex not enlarged; nuptial excrescence and prepollical spine absent.

Hind limbs long, slender: TL 53.4, 49.5% of SVL; FL 53.5, 46.5% of SVL; dermal fringes, tarsal tubercles, and tarsal fold absent; inner metatarsal tubercle elliptical, barely elevated, visible from above; outer metatarsal tubercle absent; toes moderately slender, bearing lateral fringes, including outer edge of Toe V and inner edge of Toe I; length of toes I < II < III < V < IV; toes about three-fourths webbed; webbing formula I (1-1*)—(1½-2) II (1-1*)—(2-2) III 1-2 IV 2—(1-1*) V. Terminal discs round; width of digit on Toe I 88.9, 77.8% of that on Toe IV, which is 64.3, 69.2% of that on Finger III; subarticular tubercles not as wide as digits, round, barely elevated.

Vomerine teeth absent; choanae widely separated, ovoid. Tongue broadly cordiform, barely free posteriorly. Vocal slit elongate, extending from posterolateral margin of tongue toward angle of jaw; vocal sac single, median, subgular, extending onto chest.

Color in life: Dorsum pale green with small, diffuse yellow spots; digits pale yellow; parietal peritoneum clear; visceral peritoneum white; heart visible; bones white; iris cream below, yellow above.

Color in preservative: General appearance white dorsally and cream ventrally. Under 25× magnification, with exception of unpigmented areas corresponding to yellow spots in life, scattered melanophores in skin of dorsal surfaces of head, body, forelimbs, thighs, shanks, tarsi, fourth fingers, and fourth and fifth toes. Other surfaces cream with no melanophores.

Measurements (in mm; holotype followed by paratype): SVL 20.4, 21.3; TL 10.9, 11.4; FL 10.1, 9.9; HW 8.0, 7.9; HL 6.3, 6.3; SL 2.8, 2.8; ED 2.3, 2.3; EW 1.5, 1.5; IOD 2.3, 2.5; T-E 0.9, 0.6; TYM 0.7, 0.7; HnL 6.1, 6.6.

Distribution and ecology.—At the type locality, both individuals were on the upper surfaces of leaves of trees 1.5–2.0 m above a stream in a narrow ravine at night. The call is a soft “peep.” See the account of *Centrolene fernandoi* for a description of the type locality.

Etymology.—The specific name is a Latin noun in apposition meaning ghost of the departed. The name refers to the characteristic loss of color in preserved specimens of members of the genus *Hyalinobatrachium*.

Remarks.—The paratype contains numerous, large, unpigmented ova. Three specimens of *Hyalinobatrachium* (KU 217295–97 from Cataratas Ahuashiyacu, 730 m, 14 km [by road] north of Tarapoto, Departamento San Martín, Perú) are poorly preserved males, 21.5, 20.3, and 19.9 mm SVL. They appear to have rounded snouts in profile, smooth dorsal skin, two phalanges on Finger IV free of webbing, and comparatively small terminal discs on the fingers. Thus, they are referred to *H. munozorum*, a species that is widely distributed in the Amazonian lowlands and on the lower slopes of the Andes from southern Colombia to central Peru.

DISCUSSION

Cadle and McDiarmid (1990) emphasized the frustrations of understanding relationships among centrolenid frogs: this dilemma was resolved partially by Ruíz-Carranza and Lynch (1991), who defined three genera. According to their classification, frogs of the genus *Centrolene* share the derived character state of a humeral spine in males. Those of the genus *Hyalinobatrachium* are united by a single synapomorphy—a bulbous, instead of the usual trilobate, liver. Centrolenids having the plesiomorphic states of the absence of humeral spines in males and a trilobate liver were relegated to the genus *Cochranella*.

The generic assignment of species known only from females can be a problem. For example, Ruíz-Carranza and Lynch (1991) placed three species known to them only from females—*azulae*, *mariae*, and *puyoensis*—in *Cochranella*. Males of *mariae* have humeral spines (Martin Hensel, pers. comm.); thus, the proper name for the species is *Centrolene mariae*. Flores and McDiarmid (1989) considered *azulae* and *puyoensis* to be closely related to *mariae*; if their suppositions are correct, those two species also should be placed in *Centrolene*.

According to the classification of Ruíz-Carranza and Lynch (1991), as amended herein, the centrolenid fauna of Peru consists of six species of *Centrolene* (*azulae*, *fernandoi*, *hesperium*, *lemniscatum*, *mariae*, and *muelleri*), 10 species of *Cochranella* (*chancas*, *croceopedes*, *euhystrix*, *ocellata*, *phenax*, *pluvialis*, *saxiscandens*, *spiculata*, *tangarana*, and *truebae*), and three species of *Hyalinobatrachium* (*bergeri*, *lemur*, and *munozorum*).

All but three of the 19 currently recognized species of centrolenids in Peru have been named in the past decade; one of us (WED) has seen specimens of at least four additional unnamed species. As more biological exploration is undertaken on the humid eastern slopes of the Andes and extra-Andean ridges rising from the Amazonian lowlands, we expect many more species of centrolenids to be discovered.

Acknowledgments: Duellman's research on patterns of speciation and biogeography of Andean anurans is supported by a grant (BSR 8805920) from the National Science Foundation. We are grateful to our field companions—Fernando M. Cuadros V., Michael E. Morrison, and John J. Wiens—for enduring many wet nights in the quest for frogs. We are grateful to Roy W. McDiarmid and John D. Lynch for helpful suggestions and to the latter for providing us with a copy of the manuscript defining the genera of centrolenid frogs. The illustrations were executed by Amy Lathrop, and the photographic prints were made by John E. Simmons from color slides. Erik R. Wild took most of the morphometric data. Permits for collecting and exportation of specimens were provided by Ing. Gonzalo Bravo Mejía Muñoz and Biol. José Purisaca of the Dirección General Forestal y de Fauna, Ministerio de Agricultura, Lima, Perú. We are grateful to Gerardo Lamas and his staff at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, for many courtesies, and to B. Anthony Luscombe, Asociación de Ecología y Conservación, in Lima, Perú, for logistic aid.

LITERATURE CITED

- CADLE, J. E., AND R. W. MCDIARMID. 1990. Two new species of *Centrolenella* (Anura: Centrolenidae) from northwestern Peru. *Proc. Biol. Soc. Washington* 103:746–768.
- CANNATELLA, D. C., AND W. E. DUELLMAN. 1982. Two new species of *Centrolenella*, with a brief review of the genus in Perú and Bolivia. *Herpetologica* 38:380–388.
- CANNATELLA, D. C., AND W. W. LAMAR. 1986. Synonymy and distribution of *Centrolenella orientalis* with notes on its life history (Anura: Centrolenidae). *J. Herpetol.* 20:307–317.
- DUELLMAN, W. E. 1976. Centrolenid frogs from Peru. *Univ. Kansas Mus. Nat. Hist. Occas. Pap.* 52:1–11.
- DUELLMAN, W. E., AND P. A. BURROWES. 1989. New species of frogs, *Centrolenella*, from the Pacific versant of Ecuador and southern Colombia. *Univ. Kansas Mus. Nat. Hist. Occas. Pap.* 132:1–14.
- DUELLMAN, W. E., AND C. A. TOFT. 1979. Anurans from the Serranía de Sira, Amazonian Perú: Taxonomy and biogeography. *Herpetologica* 35:60–70.
- FLORES, G. 1985. A new *Centrolenella* (Anura) from Ecuador, with comments on nuptial pads and prepollical spines in *Centrolenella*. *J. Herpetol.* 19:313–320.
- FLORES, G., AND R. W. MCDIARMID. 1989. Two new species of South American *Centrolenella* (Anura: Centrolenidae) related to *C. mariae*. *Herpetologica* 45:401–411.
- LYNCH, J. D., AND W. E. DUELLMAN. 1973. A review of the centrolenid frogs of Ecuador, with descriptions of new species. *Univ. Kansas Mus. Nat. Hist. Occas. Pap.* 16:1–66.
- LYNCH, J. D., P. M. RUIZ, AND J. V. RUEDA. 1983. Notes on the distribution and reproductive biology of *Centrolene geckoideum* Jiménez de la Espada in Colombia and Ecuador (Amphibia: Centrolenidae). *Stud. Neotrop. Fauna Environ.* 18:230–243.

- MYERS, C. W., AND W. E. DUELLMAN. 1982. A new species of *Hyla* from Cerro Colorado, and other treefrog records and geographical notes from western Panama. Amer. Mus. Nat. Hist. Novit. 2752:1-32.
- RUIZ-CARRANZA, P. M., J. HERNÁNDEZ-CAMACHO, AND C. ARDILA-ROBAYO. 1986. Una nueva especie Colombiano del género *Centrolene* Jiménez de la Espada 1872 (Amphibia: Anura) y redefinición del género. Caldasia 15(71-75):431-444.
- RUIZ-CARRANZA, P. M., AND J. D. LYNCH. 1991. Ranas Centrolenidae de Colombia I. Propuesta de una nueva clasificación genérica. Lozania 57:1-30.
- SAVAGE, J. M., AND W. R. HEYER. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. Beitr. Neotrop. Fauna 5(2):111-131.