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Accepted: 22 July 1999

Associate Editor: John Wiens

Herpetologica, 56(3), 2000, 294-302
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A NEW SPECIES OF GLASS FROG (ANURA: CENTROLENIDAE) FROM THE HIGHLANDS OF GUYANA

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ABSTRACT: We describe a new species of *Centrolene* from the highlands of western Guyana. The only other described *Centrolene* known from the Guianan Shield is *C. gorzulai* which differs from the new species in jaw shape, texture of the skin, peritoneal coloration, condition of the prepollex, and presence of an inner metatarsal tubercle. The only centrolenid genus previously recorded from Guyana is *Hyalinobatrachium*. Other than members of the genus *Hyalinobatrachium*, this new *Centrolene* is the only described centrolenid to have a white hepatic peritoneum. The new species is unique among all members of the genus *Centrolene* in the absence of guanophores (white pigment) in the parietal peritoneum. The new species does not conform to any of the currently recognized species groups of the genus *Centrolene*.

Key words: Amphibia; Anura; Centrolenidae; *Centrolene papillahallicum* new species; Guyana

CENTROLENIDS are a diverse component of the Neotropical herpetofauna. Between 1985 and 1993, herpetological exploration in the Andes of Colombia, Venezuela, Ecuador, and Peru resulted in the description of no less than 50 new centrolenids (Duellman, 1993). The size of this family continues to grow as additional centrolenids are discovered in some understudied areas like Honduras (McCranie and Wilson, 1997), Bolivia (Harvey, 1996), and Colombia (Ruiz-Carranza and Lynch, 1995a,b,c, 1996).

Surprisingly few centrolenids are known

from the northeastern coast of South America, and most species from that region occur in the highlands of the Guianan Shield. Only a handful of named species have been reported from French Guiana (two species, *Cochranella oyampiensis* and *Hyalinobatrachium taylori*; Lescure, 1975), Suriname (three species, *Cochranella geijskesi*, *Hyalinobatrachium fleischmanni*, and *H. taylori*; Goin, 1971) and Guyana (one species, *H. taylori*; Goin, 1968, 1971). Reports of *H. fleischmanni* from the Guianas (Goin, 1964) may be based on specimens of *Hyalinobatrachium*

revocatum, as is the case for reports of *H. fleischmanni* from Venezuela (Myers and Donnelly, 1997). However, *H. revocatum* is most likely restricted to the highlands of coastal Venezuela where it was originally described using some of the same material that Goin (1964) referred to *H. fleischmanni* (Rivero, 1985). We suspect that all frogs from the Guianas that have been referred to *H. fleischmanni* are a separate species and that Ldith de Jude's (1904) *Hylella cappellei* may be a valid name for this species.

Rivero (1961) seems to be the first author to report a centrolenid from the Guianan Shield of Venezuela; he reported an undescribed *Cochranella* from Mt. Marahuaca, a species which remains undescribed. From Cerro Duida, he (Rivero, 1968) later described *Centrolenella pulidoi*. Thereafter, Cannatella and Lamar (1986) first reported *Hyalinobatrachium orientale* from localities in the Gran Sabana region of Venezuela, although the identity of these frogs has recently been questioned by Myers and Donnelly (1997, see also Duellman, 1997) who suspect that the various populations referred to this species represent a complex of similar species. Ayarzagüena (1992) described five species from the Guianan Shield of Venezuela, redescribed *Hyalinobatrachium taylori* based on new material collected in Bolívar state, Venezuela, and reported on additional specimens of *H. orientale* from eastern Venezuela. Shortly thereafter, Señaris and Ayarzagüena (1993) described *Centrolenella auyantepuiana* from Auyantepui. Duellman (1997) reported three centrolenids from the Escalera region in southeastern Venezuela including an undescribed species of *Centrolene*, only the second species of the genus confirmed from a locality east of the Orinoco River after *C. gorzulai*. Finally, Myers and Donnelly (1997) described *H. crurifasciatum* from Cerro Tamacuari and provided a synopsis of the centrolenid frogs of Venezuela.

The Guianan Shield extends through portions of Colombia, Venezuela, Guyana, Suriname, French Guiana, and Brazil. These highlands are remnants of the Ro-

raima sandstone formation and are mainly located in Venezuela and Guyana (Hoogmoed, 1979). The fragmented nature of these remnants and the lowland forest and/or savanna which isolate them has resulted in a relatively high degree of endemism. Not surprisingly, the Guianan Shield is home to a number of "highland" endemics (e.g., *Tepuihyla*, *Oreophrynella*). Herpetologically, these highlands have been surveyed in Venezuela (Ayarzagüena, 1992; McDiarmid and Gorzula, 1989; Myers and Donnelly, 1997) and in Suriname (Hoogmoed, 1973), but the highlands of Guyana remain largely unexplored (Duellman and Yoshida, 1996).

During a recent herpetological survey of highland areas in western Guyana, a distinctive new species of *Centrolene* was discovered. Herein, we describe this new species and comment on some of its unusual morphological characteristics.

MATERIALS AND METHODS

Specimens were fixed in 10% formalin and preserved in 70% ethanol. Measurements were taken to the nearest 0.1 mm using dial calipers. Coloration of peritonea was determined from color photographs and dissection of preserved specimens. Webbing formulae are those of Savage and Heyer (1967) as modified by Myers and Duellman (1982). The numbered diagnosis follows the format of Lynch and Duellman (1973) as modified by Ruiz-Carranza and Lynch (1991b). We compared specimens of our new species to published descriptions of related species and to specimens in the UTA Collection of Vertebrates and the Museum of Natural History, University of Kansas.

SYSTEMATICS

Centrolene papillahalicum sp. nov.

Holotype.—University of Guyana, Centre for the Study of Biodiversity HA 721 (Fig. 1), field number BPN 290, an adult male, collected 23 June 1997 by Brice P. Noonan and Daniel W. Carpenter from a small stream on Peters Mountain 3.6 km N of Imbaimadai in the Pacaraima Mountains, 600 m, Administrative Region 7, Guyana; 05° 44' N, 60° 18' W (Fig. 2).



FIG. 1.—Holotype of *Centrolene papillahallicum* (UG/CSB HA 721); Snout-vent length = 18.3 mm.

Paratopotypes.—UTA 52229–30, 52236, 19 June 1997; UTA 52231–35, 52237–47, 23 June 1997; all collected by Brice P. Noonan and Daniel W. Carpenter. UTA 52231–32 to be deaccessioned and deposited in the collection of the University of Guyana, Centre for the Study of Biodiversity.

Diagnosis.—The new species is referred to the genus *Centrolene* because it possesses a humeral spine, the single synapomorphy of *Centrolene* as defined by Ruiz-Carranza and Lynch (1991a). The following combination of features serve to distinguish *Centrolene papillahallicum* from all other centrolenids: (1) vomerine dentigerous processes absent; (2) bones green in life; (3) visceral, pericardial, and hepatic peritonea white; parietal peritoneum clear; (4) dorsum uniform dark green in life; lavender in preservative; (5)

webbing between outer fingers **III**(1–2)—(1–1.5)**IV**; (6) webbing on foot **I**(1–1.5)—(2–2.5)**II**(1–1.5)—(2–2+)**III**(1–1.5)—(2–2+)**IV**(2–2+)—(1–1.5)**V**; (7) snout subtruncate in dorsal view, truncate in profile; (8) dorsal skin shagreen (sensu Lynch and Duellman, 1973); (9) ulnar and tarsal folds absent; broad fringe present on postaxial edge of Toe V; (10) humeral spine present in males; (11) tympanum distinct, directed dorsolaterally with a slight posterior inclination, its diameter one half that of disc of Finger III; (12) average snout-vent length of males is 19.3 mm ($n = 19$), females unknown; (13) prepollex enlarged, round, unpigmented; prepollical spine not protruding externally; nuptial excrescence white, Type I; (14) anal ornamentation consisting of small enameled tubercles ventral to vent; (15) when adpressed, Finger I equal in length to Finger II; (16) liv-

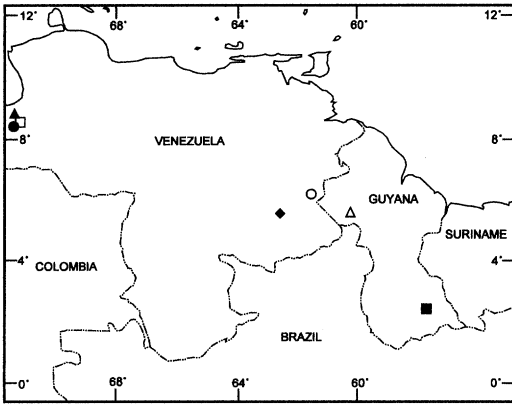


FIG. 2.—Map of Guyana showing the distribution of the genus *Centrolene* in the Guianan Shield. *Centrolene papillahallicum* (open triangle); *C. gorzulai* (closed diamond); the La Escalera specimen (open circle); *C. altitudinale* (open square); *C. andinum* (closed circle); *C. venezuelense* (closed triangle); and the type locality of the only other known Guyanan centrolenid, *Hyalinobatrachium taylori* (closed square).

er trilobed; (17) eye diameter roughly equal to width of disc of Finger III.

This new species can be readily distinguished from all other centrolenids by the unique combination of a white hepatic peritoneum, a clear parietal peritoneum, and the presence of a humeral spine in males. The presence of a humeral spine is the sole synapomorphy uniting the members of the genus *Centrolene*, all but one of which are known to have a white parietal peritoneum and a clear hepatic peritoneum (see discussion of *C. gorzulai* below). Thus the new species is unique in that it possesses two characters found previously only within *Hyalinobatrachium* (white hepatic peritoneum, and a clear parietal peritoneum). Though it would seem more parsimonious to include the new species in the genus *Hyalinobatrachium* based on these two characters rather than placing it in *Centrolene* based on one other (presence of a humeral spine), all members of *Hyalinobatrachium* are defined by the presence of a bulbous liver, and *Centrolene* by the presence of a humeral spine. Thus the new species is placed in the genus *Centrolene* as it possesses the sole synapomorphy of the genus and lacks that of the genus *Hyalinobatrachium*. The

absence of pigmentation in the parietal peritoneum, though previously found only in the genus *Hyalinobatrachium*, was not considered a suitable character for supraspecific classification by Ruiz-Carranza and Lynch (1991a) due to the variability of this character within species. The presence of pigmentation in the hepatic peritoneum must be either a retained ancestral characteristic (as white hepatic peritonea are common in hylids and other families contrary to Ruiz-Carranza and Lynch's (1991a) statement that this is unique to *Hyalinobatrachium*) or a reversal. In the absence of a rigorous phylogenetic hypothesis for this family, we feel more confident placing our new species in the genus *Centrolene* as it possesses the diagnostic feature of the genus as defined by Ruiz-Carranza and Lynch (1991a). While it is currently unclear what makes one character diagnostic (shape of the liver) and one not (hepatic peritoneal coloration) under Ruiz-Carranza and Lynch's (1991a) system, it is hoped that a phylogenetic analysis of the Centrolenidae will elucidate the placement of this species.

The only other named species of *Centrolene* from the Guianan region is *C. gorzulai* which differs from *C. papillahallicum* in the following characters (character states for *C. papillahallicum* in parentheses): notch in lower lip (sensu Ayarzagüena, 1992, his Fig. 1) absent (present); dorsal skin smooth (shagreen); pericardium clear (white); visceral peritoneum clear (white); hepatic peritoneum clear (white); prepollical spine protruding externally (not protruding externally); metatarsal tubercle absent (present); postaxial edge of fifth toe without fringe (fringe present). In addition, the diameter of the eye of *C. gorzulai* is 44% of the head length compared to 36% in the new species. It should be noted that the peritoneal coloration of the only known specimen of *C. gorzulai* is questionable due to the state of preservation (Ayarzagüena, 1992). Duellman (1997) reported an undescribed *Centrolene* (KU 181128) from the Escalera region of Venezuela, which is similar to the new species. This specimen differs from the new species in the following characters (character

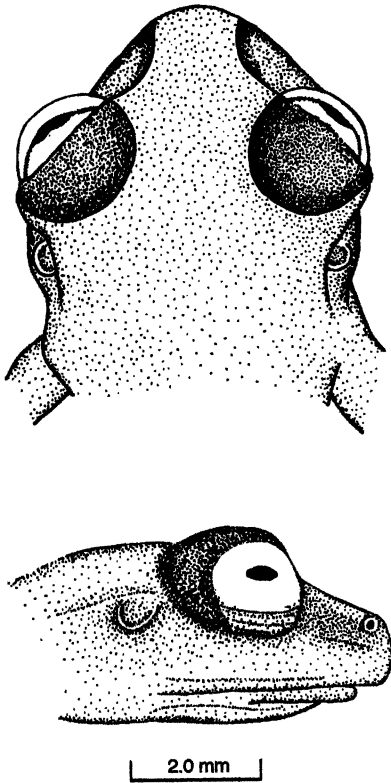


FIG. 3.—(Above) Dorsal and (below) lateral views of the head of *Centrolene papillahallicum* (UTA 52234).

states for *C. papillahallicum* in parentheses): visceral peritoneum clear (white), parietal peritoneum white (clear), anal decoration in the form of paired large tubercles (small scattered tubercles), Finger I longer than Finger II (roughly equal), enameled warts on dorsum absent (present), dorsal lavender color uniform and not attributable to melanophores (under magnification, distinct melanophores visible), pointed projection absent from Toe I (present). It should be noted that the color of the visceral peritoneum is taken from the published report of Duellman (1997); when the specimen was examined, the viscera were missing.

Description of holotype.—Adult male, snout-vent length (SVL) 18.3 mm. Head distinct, wider than body (Fig. 3); head length (measured as distance from angle of jaw to tip of snout) 82% of head width (measured as distance between angles of

jaws); head length 36% of SVL; snout (distance from anterior border of orbit to tip of snout) short, 36% of head length; snout subtruncate in dorsal view, truncate in lateral view, sloping anteroventrally in profile; canthus round; loreal region concave; lips flared below anterior portion of eye to angles of jaws; nostrils slightly protuberant; internarial region depressed. Eyes moderately large, diameter of eye 36% of head length; angle of eyes to midline about 45°; snout length roughly equal to eye diameter (96%); tympanum distinct, directed dorsolaterally with slight posterior inclination, diameter one half that of disc of third finger; tympanic annulus distinct, unpigmented, concealed anterodorsally by supratympanic fold. Vomerine dentigerous processes and teeth absent; choanae moderately sized, round, near margin of mouth; tongue not notched posteriorly; vocal slits paired, extending from lateral base of tongue to angle of jaw.

Humeral spine present; ulnar fold and tubercles absent; forearm larger (in diameter) than upper arm; Finger I equal in length to Finger II (Fig. 4); webbing absent between Fingers I and II, and basal between Fingers II and III; webbing extensive between Finger III and Finger IV (III1.5—2IV); relative lengths of fingers I = II < IV < III; discs broad, truncate; discs on Fingers II–IV about one-fifth larger than those on toes. Subarticular tubercles low and round, as wide as digits; low, round supernumerary tubercles present on palm; palmar tubercle ovoid; prepollex enlarged, spine not protruding; Type I nuptial pad (Flores, 1985; Lynch and Ruiz-Carranza, 1996) raised, elliptical and on dorsal surface of Finger I; nuptial excrescence cream-colored in preservative.

Hind limbs slender, length of tibia 62% of SVL; dermal fringes and tarsal tubercles absent on limbs, fringe present on postaxial edge of Toe V (Fig. 4); inner metatarsal tubercle elliptical, elevated, and visible from above; outer metatarsal tubercle absent; subarticular tubercles large, round, about as wide as digits; low, round supernumerary tubercles present on sole; relative lengths of toes I < V < II < III < IV; toes extensively webbed; webbing formula II—

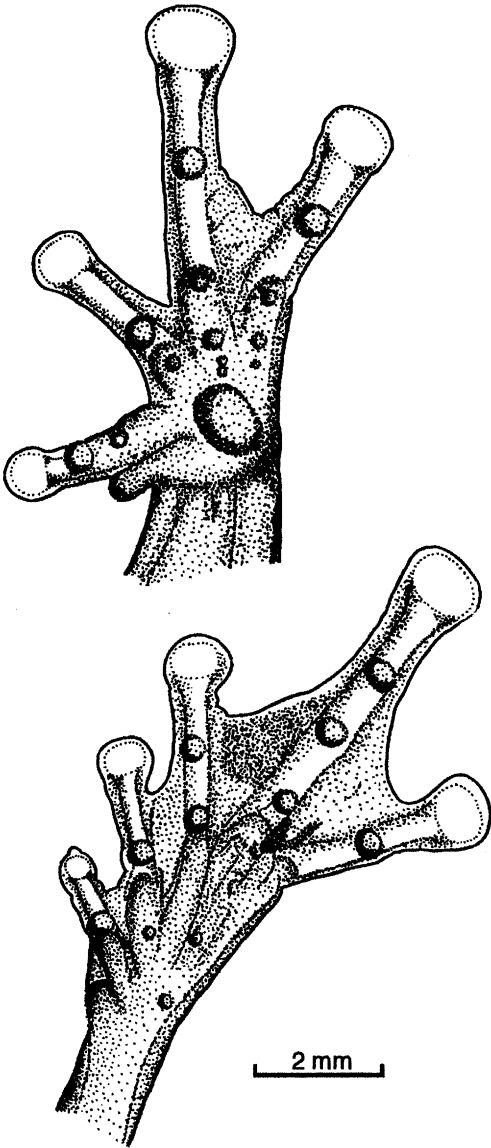


FIG. 4.—Palmar and plantar view of the left hand and foot of *Centrolene papillahalicum* (UTA 52234).

2III—2III—2IV 2—1V; discs on Toes II—IV ovoid, rounded with distinct pointed projection on Toe I; width of disc on Toe IV approximately equal to that of disc on Finger III.

Skin on dorsum shagreen with scattered flat, enameled (white) warts, appearing as pale spots on dorsum. Vent high, above midlevel of thighs, directed posteriorly, concealed by dermal fold; scattered enam-

eled warts below vent extending onto thighs.

Color in life.—Dorsal surfaces dark green; upper lip yellow; hands and feet yellow-green; bones green; iris metallic copper with brown reticulations; yellow ring around pupil incomplete laterally; ventral surfaces cream; parietal peritoneum clear; visceral peritoneum white; hepatic peritoneum white; pericardium white.

Color in preservative.—Dorsum lavender with small, white, enameled warts visible under magnification; eyelids dark lavender; melanophores covering dorsal surfaces of arms and legs; distribution of melanophores on digits highly variable (see Variation section); flanks, shoulder, upper lip, and all ventral surfaces cream; parietal peritoneum clear; visceral peritoneum white (peritoneum covering central $\frac{1}{3}$ of small intestine unpigmented); hepatic peritoneum white; pericardium white; bones white.

Variation.—Measurements in (mm) of holotype followed by mean and range of paratotypes ($n = 19$) in parentheses: SVL of males (females unknown) 18.3 (19.3, 18.3–21.0); head width 7.9 (7.7, 7.3–7.9); head length 6.5 (6.6, 5.9–6.9); snout length 2.3 (2.4, 2.1–2.6); eye diameter 2.2 (2.4, 2.1–2.6); hand length 6.9 (6.9, 6.3–7.2); tibia length 11.3 (12.0, 11.3–13.0). Color pattern conservative with the exception of distribution of melanophores on digits. Hands have pigment on Finger IV only (UTA 52232) or on all fingers (UTA 52247) and any combination in between (melanophores on Fingers I and II usually restricted to discs). Similarly, pigment may be present on Toes III–V only (UTA 52244), on all five toes (UTA 52229), and any combination in between. Variation in webbing of outer fingers and feet is as follows: outer fingers III(1–2)—(1–1½)IV; feet I(1–1½)—(2–2½)II(1–1¼)—(2–2+)III(1–1¼)—(2–2+)IV(2–2; pl)—(1–1½)V.

Etymology.—The specific epithet is a noun in apposition and is derived from the Latin word *papilla*, meaning bud, and *hallex*, referring to the medial-most digit of the pes. The name refers to the unique projection on the end of Toe I in this species.

Distribution and ecology.—*Centrolene papillahallicum* is known only from the type locality, 3.6 km north of Imbaimadai, Region 7, Guyana (Fig. 2). Peters Mountain is approximately 900 m in elevation, is covered in evergreen sclerophyllous forest, and is situated in the highland savanna of western Guyana. The fast flowing stream where *C. papillahallicum* was found is a tributary of the Mazaruni River and varies in size between 0.1–1.0 m deep and 1.0–2.0 m wide at the type locality. This stream has a smooth rock and/or sandy bottom and its banks are steep and about 3.0–4.0 m high. The creek is heavily shaded by the forest canopy.

Adult males were calling from the upper surfaces of leaves of small trees no more than 2.0 m above the surface of the ground. The call consists of a single high-pitched “peep” given at irregular intervals and was heard most frequently following a heavy rain (call not recorded). Calling males were most often in the forest a short distance from the stream. No egg masses or tadpoles attributable to this species were found.

DISCUSSION

The new species possess three particularly noteworthy morphological characteristics, a pointed projection from the distal tip of the Toe I, a white hepatic peritoneum, and a clear parietal peritoneum. Pointed digital tips are known in other minute anurans such as leptodactylids (Hoogmoed et al., 1994; Lynch, 1986), but they are unknown in centrolenids. We have not observed pointed digital tips in other centrolenids that we have examined (Appendix I), nor have we been able to find any mention of digital projections in descriptions or illustrations of hands or feet of centrolenid frogs. Nonetheless, we wonder if pointed toes in centrolenids have been overlooked previously. Although the hands of centrolenids are almost always illustrated, the feet rarely are (see however Wild, 1994). While other authors have noted that a number of characters related to the integument are merely results of preservation, this feature is distinctly present in all specimens.

Ruiz-Carranza and Lynch (1991a) identified four derived character states within the Centrolenidae: presence of humeral spines in males (*Centrolene*), a bulbous liver covered by a white peritoneum (*Hyalinobatrachium*), a urinary bladder covered by white pigment (*parvulum* species group), and a small eye (*geckoideum* species group; defined as the diameter of the eye being less than the transverse diameter of the disc of the third finger). In their discussion of peritoneal coloration, Ruiz-Carranza and Lynch (1991a) stated that the only centrolenids to have a white hepatic peritoneum are members of the genus *Hyalinobatrachium*. *Centrolene papillahallicum* and the specimen from La Escalera both have white hepatic peritonea, and this characteristic can no longer be considered unique to the genus *Hyalinobatrachium* within the Centrolenidae. Moreover, a bulbous liver and a white hepatic peritoneum are not “manifestations of the same condition” as Ruiz-Carranza and Lynch (1991a) argued; both *Centrolene* with white hepatic peritonea also possess trilobed livers. It should be noted that it is possible that the hepatic peritoneum of *C. gorzulai* may also be white, which would be a synapomorphy of the east Guianan members of the genus *Centrolene*.

The genus *Centrolene* was recognized by Ruiz-Carranza and Lynch (1991a) for the group of centrolenids that have a humeral spine present in males. This genus was subdivided into three species groups, the *geckoideum*, *prosolepon*, and *peristicta* groups. Upon examination of the defining characteristics of these groups presented in Ruiz-Carranza and Lynch (1991a), it immediately becomes apparent that, whereas the *geckoideum* group is distinct in having small eyes, the *prosolepon* and *peristicta* groups are practically identical, the only distinctive difference between the two being the color of the bones, which appear to be quite variable within the *prosolepon* group (Table 1, this paper). It should be noted that the use of bone color as a character is often difficult, as preservation causes green bones to fade to white. While we have not exam-

TABLE 1.—Diagnostic characteristics of *Centrolene* species groups (Ruiz-Carranza and Lynch, 1991) and *C. papillihallicum*.

Characteristic	<i>geckoideum</i>	Species group <i>prosoblepon</i>	<i>peristictum</i>	<i>Centrolene</i> <i>papillihallicum</i>
Teeth	present	present or absent	absent	absent
Eye	small	large	large	large
Bones	green	green or white	pale green	green
Parietal peritoneum	white	white	white	clear
Visceral peritoneum	clear	white or clear	white	white
Hepatic peritoneum	clear	clear	clear	white

ined all members of these groups, it would seem that the basis for these species groups [as defined by Ruiz-Carranza and Lynch (1991a)] is questionable. Duellman (1997) suggested that his specimen from La Escalera belonged to the *C. prosoblepon* group which would seem reasonable according to the species group descriptions of Ruiz-Carranza and Lynch (1991a); hepatic peritoneal coloration is not mentioned in their species group descriptions. The presence of a white hepatic peritoneum, however, distinguishes both the specimen from La Escalera and *C. papillihallicum* from all other members of the genus, as Ruiz-Carranza and Lynch (1991a) stated that within the Centrolenidae, only members of the genus *Hylainobatrachium* possess a white hepatic peritoneum. Thus, while both the specimen from La Escalera and *C. papillihallicum* seem to most closely resemble the members of the *prosoblepon* group based solely on the intensity of green pigmentation in their bones, they cannot be definitively placed in any existing species group at this time.

Acknowledgments.—We give special thanks to M. Tammessar, J. Singh, and D. Nariane of the Centre for the Study of Biodiversity, University of Guyana, Georgetown, for their assistance in obtaining the necessary permits to conduct scientific explorations in Guyana, to the North Texas Herpetological Society for providing partial funding for this expedition, and to W. E. Duellman, J. Simmons, and C. Sheil for their assistance and kindness during the senior authors' visit to the KU collection. Invaluable assistance in the field was provided by D. W. Carpenter. We also thank J. A. Campbell, M. A. Donnelly, J. J. Wiens, E. R. Wild, W. E. Duellman, and D. P. Lawson for critically reviewing the manuscript.

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Accepted: 29 September 1999
Associate Editor: John Wiens

APPENDIX I

Specimens Examined

Centrolene ballux, KU 164725 (holotype); *Centrolene buckleyi*, UTA 4523-24, 12766-69; *Centrolene helodermatum*, KU 202806 (holotype); *Centrolene lynchi*, KU 164691 (holotype); *Centrolene peristicium*, KU 118051 (holotype); *Centrolene pipilatum*, KU 143278 (holotype); *Centrolene savagei*, KU 169753 (holotype); *Centrolene scirtetes*, KU 202720 (holotype); *Centrolene sp.* (La Escalera), KU 181128; *Cochranella bejaranoi*, UTA 43911-31, 43943-46, 47252-56; *Cochranella nola*, UTA 45539-40 (paratopotypes); *Cochranella spiculata*, UTA 47280-84.