

A new species of the genus *Centrolene* (Amphibia: Anura: Centrolenidae) from Ecuador with comments on the taxonomy and biogeography of Glassfrogs

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Abstract

We describe a new species of Glassfrog, *Centrolene mariaelenae* n. sp., from the Contrafuerte de Tzunantza, southeastern Ecuador. The new species is assigned to the *Centrolene gorzulai* species group, a clade previously known only from the Guayana Shield region, because the parietal peritoneum is transparent and the hepatic peritoneum is covered by guanophores. We analyze the diversity patterns of Glassfrogs from eastern Ecuador. The distribution of the new species herein described supports previous hypothesis of a biogeographical connection between the Andes and the Guayana Shield for various groups of plants and animals; particularly a relationship between the Guayana Shield and the sandstone outcrops mountain ranges of southeastern Ecuador and northeastern Peru. We also comment on the infrageneric and generic classification of Glassfrogs, and propose the new combinations *Centrolene balionotum* n. comb., *Cochranella antisthenesi* n. comb., and *Cochranella pulverata* n. comb.

Key words: *Centrolene mariaelenae*, new species; taxonomy; biogeography; Ecuador

Resumen

Una nueva especie del genero *Centrolene* (Amphibia: Anura: Centrolenidae) de Ecuador con comentarios sobre la taxonomía y biogeografía de las Ranas de Cristal. Describimos una nueva especie de Rana de Cristal, *Centrolene mariaelenae* n. sp., del Contrafuerte de Tzunantza, sureste de Ecuador. La nueva especie es asignada al grupo *Centrolene gorzulai*, un clado previamente conocido solo del Escudo Guayanés, por poseer el peritoneo parietal transparente y el peritoneo hepático cubierto por guanóforos. Analizamos los patrones de diversidad de Ranas de Cristal en el este de Ecuador. La particular distribución de la especie aquí descrita soporta hipótesis previas respecto a conexiones biogeográficas entre los Andes y el Escudo Guayanés para varios grupos de

plantas y animales, particularmente una relación entre el Escudo Guyanés y las cordilleras con substratos de areniscas del sureste de Ecuador y noreste de Perú. Analizamos también la clasificación infragenérica y genérica de las Ranas de Cristal y proponemos las nuevas combinaciones *Centrolene balionotum* n. comb., *Cochranella antisthenesi* n. comb. y *Cochranella pulverata* n. comb.

Palabras clave: *Centrolene mariaelena*, nueva especie; taxonomía; biogeografía; Ecuador

Introduction

The family Centrolenidae is a clade of anurans, commonly known as Glassfrogs, endemic to the Neotropical region, occurring from southern Mexico through Central America and into South America mainly through the Cordillera de Los Andes from Venezuela to Bolivia, with species in the Amazonas and Orinoco River basins, the Guayana Shield region, southeastern Brasil, and northern Argentina (Frost 2004). One hundred and thirty nine species of Glassfrogs have been described, and 37 taxa have been reported from the Republic of Ecuador (Coloma 2005–2006; Frost 2004, Frost et al. 2006). However, our recent studies on the Centrolenidae of Ecuador have revealed several undescribed or unreported species of Centrolenid frogs in the country; and it is estimated that the diversity in Ecuador will reach at least 50 species (Cisneros-Heredia & McDiarmid 2003, 2004a, 2004b).

Notions concerning the classification of Glassfrogs have changed over the course of the last years, notably with the works on Colombian species by the late Pedro Ruíz-Carranza and John D. Lynch. Considerable advances in our knowledge of the Centrolenidae have been achieved; but its taxonomy is still problematic, and the natural history, ecology, and conservation status of most species are virtually unknown (Cisneros-Heredia & McDiarmid 2003, 2004a). As part of our research project on the Centrolenidae of Ecuador developed since 2002, we analyzed a small collection of amphibians from the eastern slopes of the Andes of southern Ecuador that included an undescribed taxon of Glassfrog whose relationship appears to be with the species assigned to the *C. gorzulai* species group (*sensu* Duellman & Señaris 2003). Herein, we described this new species and discuss some aspects of the taxonomy and biogeography of the Centrolenidae.

Material and methods

Characters and terminology used herein follow the definitions of Ruíz-Carranza & Lynch (1991a; 1991b). Webbing formulae follow the method of Savage & Heyer (1967), as modified by Myers & Duellman (1982). Eye direction angle was calculated as proposed by Wild (1994), and eye and tympanum diameters were measured following Campbell (1994). We follow the definition of the bulla structure as proposed by Myers & Donnelly

(2001), and the nuptial excrescences classification of Flores (1985). Abbreviations in the text are: SVL, snout-vent length; HW, head width at the corners of the mouth; HL, head length, as the straight line distance from the posterior corner of the mouth to the tip of the snout; ED, horizontal eye diameter; IOD, inter-orbital distance, between eyes as the straight line distance between the anterior margins of the orbits; EN, eye-nostril distance from the anterior margin of the orbit to the center of the nostril; IN, internarial distance between the nostrils; TYD, horizontal tympanum diameter; 3DW, width of disc on the third finger; TL, tibia length; FL, foot length measured from the proximal edge of the inner metatarsal tubercle to the tip of the fourth toe. Measurements (in millimeters) were taken with electronic digital calipers (0.05 mm accuracy and rounded to the nearest 0.1 mm); all measurements were taken at least three times each. Sex was determined by examination of internal (gonads) and external (vocal slits, nuptial pads) characters. Relative digits lengths were determined by adpressing adjacent digits equally. Drawings were made using a stereomicroscope or based on digital photographs. Classification of vegetation formations follows Sierra (1999). Geographic position and elevation of collection localities were determined using collector's field notes and museum records; revised according with the 2000 physical map of the Republic of Ecuador (1:1'000000) distributed by the Instituto Geografico Militar, and NIMA (2003).

Twenty diagnostic characters are used for ease of comparison and follow the format of Lynch & Duellman (1973) as subsequently modified by Flores (1985), Heyer (1985), Cadle & McDiarmid (1990), Ruíz-Carranza & Lynch (1991a; 1991b), Wild (1994), Harvey (1996), and McCranie & Wilson (1997): (1) presence or absence of vomerine teeth; (2) color of bones in life and in preservative; (3) color of parietal, pericardial, hepatic, and visceral peritonea; (4) general color in life and in preservative; (5) webbing on hand; (6) webbing on foot; (7) form of snout in dorsal and lateral views; (8) dorsal skin texture; (9) description of tubercles or fringes on hands, arms, feet, and legs; (10) presence or absence of humeral spine on males; (11) description of tympanum; (12) snout-vent length -SVL- of males and females; (13) nuptial excrescences (nuptial pads and nuptial glands), prepollex, and prepollicall spine; (14) anal ornamentation and skin texture of vent; (15) size of finger I vs. II; (16) description of liver; (17) eye diameter vs. width of disc on finger III; (18) iris color in life and preservative; (19) distribution of melanophores on fingers and toes; (20) description of advertisement call.

Institutional abbreviations used are as follows: AMNH—American Museum of Natural History, New York, USA; DFCH-USFQ—Universidad San Francisco de Quito, Quito, Ecuador; DHMECN—División de Herpetología, Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; EPN—Departamento de Biología, Escuela Politécnica Nacional, Quito, Ecuador; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, USA; QCAZ—Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; USNM—National Museum of Natural History, Washington, D.C., USA.

Species description

The southeastern Andean slopes of Ecuador are poorly studied and many new species are continuously found in recent years (Krabbe et al. 1999, Kizirian et al. 2003). The analysis of internal and external morphological characters demonstrate that a specimen of Glassfrog collected on the eastern slopes of the Andes of southern Ecuador, at the Cordillera de Tzunantza, is well separated from all other Centrolenid frogs currently known and described. Its distinction is most evident by the presence of salient features that are otherwise known just from species of the Guianan Shield. Although only one specimen of this new species has been obtained, it shows remarkable characteristics that clearly differentiate it from other species and it is appropriate to describe it as a new species. Moreover, as frogs of the family Centrolenidae have suffered severe declinations, with over 37% of Glassfrog species threatened by extinction (Stuart *et al.* 2004, Cisneros-Heredia and McDiarmid 2005a), it is urgent to improve the understanding on its systematics, diversity, ecology, and biogeography.

Centrolene mariaelenae Cisneros-Heredia & McDiarmid, new species

(Fig. 1–4)

Holotype

DFCH-USFQ D125, an adult male taken along a small stream, tributary of the Jambue River, ca. 16 km S from Zamora, Podocarpus National Park (ca. 04°15'S, 78°56'W, 1820 m), on the western slope of Contrafuerte de Tzunantza, Cordillera Oriental, eastern slopes of the Andes, Provincia de Zamora-Chinchipec, Republic of Ecuador (Fig. 5), on 03 March 2002 by F. Smith and L. Wesch.

Diagnosis

This new taxon possesses a humeral spine thus it is placed in the genus *Centrolene* (Ruíz-Carranza & Lynch 1991a), and it is assigned to the *gorzulai* species group because the parietal peritoneum is transparent and the hepatic peritoneum is covered by guanophores (Noonan & Harvey 2000; Duellman & Señaris 2003). *Centrolene mariaelenae* is diagnosed from other species of the family by the combination of the following characters: (1) vomerine teeth absent; (2) bones white in preservative (unknown in life); (3) parietal peritoneum clear without guanophores in a bib-like fashion; guanophores covering on the pericardial, hepatic and visceral peritonea, except for the clear gall bladder; (4) color in preservative, dorsal and flank surfaces cream with many small dark lavender punctuations and scattered larger dark flecks; (5) webbing absent between fingers I and II, basal between fingers II and III, outer fingers III $\frac{1}{2}$ -II $\frac{1}{2}$ IV; (6) webbing on feet I $\frac{2}{3}$ -II $\frac{2}{3}$ II $\frac{2}{3}$ -III $\frac{2}{3}$ -IV $\frac{2}{3}$ -V $\frac{1}{3}$; (7) snout bluntly truncate in dorsal view and truncate in profile; notch in lower lip absent; nostrils elevated, indentation between the

nostrils; loreal region concave; (8) dorsal skin shagreen; (9) no dermal folds on hands, forearms, feet, or tarsus; (10) humeral spine present in male holotype; (11) tympanum oriented posterolaterally with light dorsal inclination; tympanic annulus rather indistinct; supratympanic fold weak; (12) snout-vent length in male holotype 19.0 mm; females unknown; (13) prepollical spine not protruding externally; unpigmented nuptial pad Type I; (14) pair of large, round, flat tubercles on ventral surfaces of thighs below vent; other anal ornamentation absent, ventral skin granular and not enameled; (15) first finger longer than second, (16) liver apparently bulbous (but see Discussion); (17) eye diameter larger than width of disc on finger III; (18) iris grey in preservative; (19) melanophores absent on fingers and toes except for a few at the base of Toe V; (20) the advertisement call is unknown for this species.



FIGURE 1. Dorsal view of the holotype of *Centrolene mariaelenae* (DFCH-USFQ D125), SVL = 19.0, adult male. Photo by Sebastián Cruz.



FIGURE 2. Dorsal view of the head of the holotype of *Centrolene mariaelenae* (DFCH-USFQ D125), SVL = 19.0, adult male. Photo by Sebastián Cruz.

Comparisons

Centrolene mariaelenae is the only known Andean centrolenid frog that has a humeral spine, transparent parietal peritoneum, and guanophores covering the pericardial, hepatic and visceral peritonea. These characteristics are currently shared only with members of the *gorzulai* species group (*Centrolene gorzulai* [Ayarzagüena], *C. lema* Duellman & Señaris, and *C. papillahallicum* Noonan & Harvey) endemic to the Guayanan Region of eastern

Venezuela and adjacent Guayana (Table 1 and 2, Fig. 5). All other members of the *gorzulai* species group differ from *C. mariaelenae* by having guanophores on the parietal peritoneum in a bib-like fashion covering only the heart and by its color in preservative. Further, *C. gorzulai* differs from *C. mariaelenae* by its subtruncate snout in dorsal view, glandular nuptial pad, prepollical spine protruding externally, and long snout ($EN > IOD$). *Centrolene lema* is distinguished from *C. mariaelenae* by having more hand webbing, visceral peritoneum clear, tympanum barely evident, and melanophores on toes IV and V. *Centrolene papillahallicum* differs from *C. mariaelenae* by having a subtruncate snout in dorsal view; anal ornamentation consisting of small enameled tubercles below vent; first finger equal in length to second; and scattered melanophores on fingers and toes. The distribution of salient characters among species in the *Centrolene gorzulai* group is presented in Table 1. Members of the genus *Hyalinobatrachium* have a clear parietal peritoneum, white visceral and hepatic peritonea, and a bulbous liver, but differ by lacking humeral spines in males, usually having a cream dorsal coloration in preservative with pale spots or reticulations and no dark flecks, and having a clear pericardium (visible heart) in some species.

Description of the holotype

Adult male, SVL = 19.0 mm (Fig. 1). Body slender. Head distinct, slightly wider than long, and wider than body; $HW/HL = 1.12$, $HW/SVL = 0.40$, $HL/SVL = 0.35$. Snout short, bluntly truncate in dorsal view and truncate in profile, $EN/HL = 0.26$; indentation at internarial region between protuberant nostrils; canthus rostralis rounded, rather indistinct, a shallow platform between the canthus rostralis; concave loreal region; lips slightly flared. Eyes large, $ED/HL = 0.35$, directed anterolaterally at about 39° from midline, eyes can be seen when viewed from below, interorbital area wider than eye diameter, $IOD/ED = 1.39$, $EN/ED = 0.74$, $EN/IOD = 0.53$. Tympanum oriented posterolaterally with light dorsal inclination, separated from orbit by distance nearly equal to tympanum diameter; tympanic annulus rather indistinct, slightly elevated anteriorly and ventrally; supratympanic fold weak, $TYD/ED = 0.61$ (Fig. 2). Dentigerous processes of vomers absent, choanae small, rather elliptical, widely separated medially; tongue elongately ovoid, not indented posteriorly, free posteriorly and laterally; vocal slits paired, elongated (around $2/3$ of the tongue length), extending from mid-lateral base of tongue to angles of jaws.

Skin of dorsal surfaces of head, body, and limbs shagreen; belly granular, all other ventral surfaces shagreen. Cloacal opening directed posteriorly at upper level of thighs; no distinct cloacal sheath; a pair of large, round, flat tubercles on ventral surfaces of tights below vent, other anal ornamentation absent, ventral skin granular and not enameled.

Upper arm thin, forearm robust, breadth of upper arm about half that of forearm. Humeral spine present (Fig. 3); ulnar fold and tubercles absent. Relative lengths of fingers $II < I < IV < III$; webbing absent between fingers I and II, basal between finger II and III,

TABLE 1. Comparison of characters and geographic distribution of the members of the *Centrolene gorzulai* species group.

Character/Species	<i>C. gorzulai</i>	<i>C. lema</i>	<i>C. mariaelena</i>	<i>C. papillatolicum</i>
Dorsal coloration	White with dense blue chromatophores	blue Lavander	Cream with two-sized lavender flecks	Lavander
Snout	Subtruncate	Truncate	Truncate	Subtruncate
Parietal peritoneum	Bib-like	Bib-like	Clear	Bib-like
Visceral peritoneum	White	Clear	White	White
Prepollical spine	Protruding	Not protruding	Not protruding	Not protruding
Tympanum	Present	Barely evident	Present	Present
Anal ornamentation	Pair of tubercles	Pair of tubercles	Pair of tubercles	Enameled tubercles
Mean SVL	20.9 mm in males (n = 2) Female, 21.4 mm (n = 2)	20.6 mm in male (n = 1) Female, unknown	19.0 mm in male (n = 1) Female, unknown	19.3 mm in males (n = 19) Female, unknown
Distribution	Cerro Auyán-tepui, Venezuela	Bolivar, Sierra de Lema, Venezuela	Contrafuerte de Zamora-Chinchipec, Ecuador	Peters Mountain, Region 7, Guyana
References	Ayazaguena 1992, Duellman and Señaris 2003 and Señaris 2003	Duellman and Señaris 2003	This paper	Noonan and Harvey, 2000



FIGURE 3. Humeral spine of the holotype of *Centrolene mariaelenae* (DFCH-USFQ D125), SVL = 19.0, adult male. Photo by Sebastián Cruz.

III $2\frac{1}{2}$ – $2\frac{1}{2}$ IV; bulla absent in fingers web, lateral fringes present on fingers III and IV; finger discs wide, nearly truncate; disc on third finger slightly larger than those on toes, and shorter than eye diameter, $3DW/ED = 0.61$, $3DW/TYD = 1.0$; subarticular tubercles rounded and elevated; supernumerary tubercles small, rather indistinct; palmar tubercle

large, ovoid, flat, tenar tubercle indistinct. Protruding prepollical spine absent; nuptial excrescences Type I, unpigmented.



FIGURE 4. Internal morphology of the holotype of *Centrolene mariaelenae* (DFCH-USFQ D125), SVL = 19.0, showing the guanophores covering the pericardium, and the hepatic and visceral peritonea. Photo by Sebastián Cruz.

TABLE 2. Comparison of diagnostic characters of the groups defined for the genus *Centrolene*. 1: Eye diameter versus diameter of third finger disc; 2: for species where it is known; 3: dark and light green are coded as green.

Character/group	<i>geckoideum</i> group	<i>gorzulai</i> group	<i>prosolepon</i> group
Vomerine teeth	Present	Absent	Present or absent
Eye ¹	Small	Large	Large
Bones	Green	Green ²	Green ³ or white
Parietal peritoneum	White (guanophores covering one half or more)	White only over the heart (in a bib-like fashion) or completely clear	White (guanophores covering one half or less)
Visceral peritoneum	Clear	White or clear	White or clear
Hepatic peritoneum	Clear	White	Clear
Relative species size	Very large to medium	Small	Small to medium
Eggs deposition site ²	Rocks	Unknown, but probably on leaves	Leaves (upper side)

Hind limbs slender; heels of adpressed limbs perpendicular to body touch but do not overlap; TL/SVL = 0.57, FL/SVL = 0.46. Fringes and tarsal fold absent; inner metatarsal tubercle small, elliptical, rather indistinct, outer metatarsal tubercle absent; subarticular tubercles; supernumerary tubercles small, rather indistinct. Webbing on foot I2–2½II2–3III2–3IV2⅔–1⅔V; lateral fringes distinct on toe IV; disc on toe I round not expanded, all other discs bluntly truncate, pointed projection on disc of toe I absent.

Coloration of holotype

In preservative, all dorsal surfaces cream with many small, dark, lavender punctuations and scattered bigger dark flecks (Fig. 1–2); venter cream. Bones white in preservative but possibly green in life as in other members of the group. Parietal peritoneum clear, without guanophores in a bib-like fashion; pericardial, hepatic, and visceral peritonea, sclera and testes white (covered by guanophores); gall and urinary bladders clear (Fig. 4).

Measurements (in millimeters)

SVL 19.0; HW 7.4; HL 6.6; ED 2.3; IOD 3.2; EN 1.7; TL 10.8; FL 8.7; TYD 1.4; IN 2.0; 3DW 1.4.

Etymology

The specific name of this Glassfrog is a noun in the genitive case and a patronym for María Elena Heredia, D.F. Cisneros-Heredia's mother, who will always be grateful for her permanent support of his work in herpetology, her friendship, field companionship, and infinite love.

Distribution and ecology

Centrolene mariaelenae is known only from a single specimen collected in the province of Zamora-Chinchipe, Ecuador (Fig. 5). The holotype is an adult male found at night on a leaf ca. 2 m above water in the immediate vicinity of a small stream in old secondary-growth Low Montane Evergreen Forest at 1800 m elevation. The small stream is tributary of the Jambue River on the western slope of the Contrafuerte (Cordillera) de Tzunantza, a ridge part of the Cordillera Oriental (Cordillera Real), southeastern Ecuadorian Andes. The Contrafuerte de Tzunantza is separated to the north by the Nangaritza river valley from the Cordillera del C ndor. *Centrolene mariaelenae* may be distributed over the nearby slopes of the Cordillera Oriental or in the mountain ranges of Cordillera del C ndor or Cordillera del Cutuc . It could have even a wider distribution to the south, reaching northern Peru.

Centrolene mariaelenae was collected sympatrically with two other centrolenid frogs, *Cochranella cochranae* Goin and an undescribed species of *Centrolene*. Several areas near the type locality have been surveyed but only *C. cochranae* and *Hyloscirtus phyllognathus* (Melin) were found in riverine areas (Smith and Wesch, unpubl. data, Almeida and Nogales, unpubl. data).

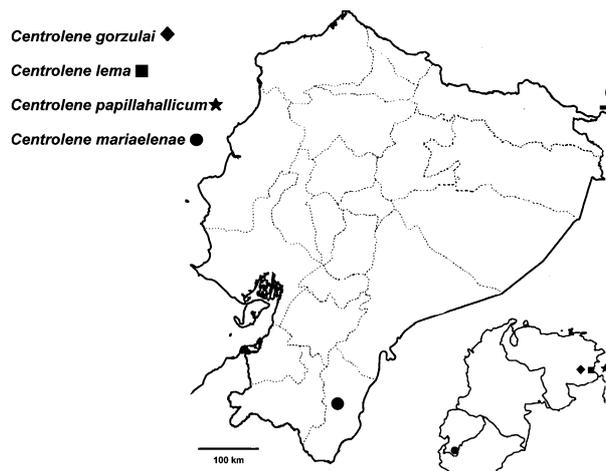


FIGURE 5. Map of Ecuador with the position of the type-locality of *Centrolene mariaelenae*. Lower insert with the northern portion of South America showing the distribution of the taxa of the *Centrolene gorzulai* species group in the Guayana Shield and in southeastern Ecuador.

Discussion*Diversity patterns of Glassfrogs from eastern Ecuador*

The description of *Centrolene mariaelenae* increases the number of described Glassfrogs from eastern Ecuador to 16; yet several taxa remain undescribed or unreported from both lowlands and montane forests, where there are at least 28 species (Tables 3, 4, 5)

(Cisneros-Heredia & McDiarmid 2003, 2004a, 2004b, 2005a). Eastern Ecuador can be divided into two sections: a northern section (above latitude 2° S) that includes the provinces of Sucumbíos, Orellana, Napo, Tungurahua, and northern parts of Pastaza, and a southern section (below latitude 2°) that includes the provinces of Zamora-Chinchipe, Morona-Santiago, and southern parts of Pastaza. A significantly higher number of species occurs in the northern section (23 taxa) than in the southern one (11 taxa), and just six species are shared between the two sections (Table 3 and 4). These data, rather than reflect a real difference on the diversity between the sections, illustrate the paucity of information available, especially from southeastern Ecuador where 36% of the known species are still undescribed (Table 4) (Cisneros-Heredia & McDiardmid 2004a, 2004b). These data illustrates the urgent need to explore areas on this region, including the poorly known mountain ranges of Cutucú and Cóndor.

An analysis of the diversity of Glassfrogs by its distribution along vegetation formations reveals interesting data. Three species have been known from the Amazonian lowlands forests of Ecuador (<600 m above sea level) since Lynch & Duellman (1973): *Cochranella midas* (Lynch and Duellman), *Cochranella resplendens* (Lynch & Duellman), and *Hyalinobatrachium munozorum* (Lynch & Duellman). Until recently, all three species were known in Ecuador just from their type-localities (Lynch & Duellman 1973), but they are much more widespread in Amazonian Ecuador, with *Cochranella midas* apparently distributed along the entire northeastern section of the Amazonian lowlands of Ecuador (Cisneros-Heredia & McDiarmid 2003, 2004a, 2004b, 2005b). Recent surveys have revealed that three additional species also inhabit the Amazonian lowlands of Ecuador; *Hyalinobatrachium ruedai* Ruíz-Carranza & Lynch, *Cochranella ametarsia* (Flores) (both previously known just from Colombia, details will be publish elsewhere), and a new species of *Cochranella* (sp. N1) (M. Bustamante pers. com.) (Table 3 and 4) (Cisneros-Heredia 2003, 2004a, 2004b). Up to four sympatric species of Glassfrogs have been reported on locations at the northern section of the Amazonian lowlands of Ecuador (Table 5) (Duellman 1978; Ron 2001; Cisneros-Heredia 2001–2004; Acosta-Buenaño *et al.* 2003–2004). Only one species is known from the southern section, *Cochranella midas* (reported as *Centrolenella* sp. [EPN 288] Almendáriz 1987). *Hyalinobatrachium munozorum* must be distributed also in southern Amazonian Ecuador as it has been reported from northeastern Peru (Frost 2004).

Most Glassfrogs from the Amazonian lowlands of Ecuador are known from few localities, and are usually reported as rare or infrequent species. This apparent rarity seems an artifact of the collection methodologies combined with the species' habitat and microhabitat specificity. Surveys at the Tiputini Biodiversity Station (Amazonian Ecuador) revealed that at least *Hyalinobatrachium munozorum* and *Cochranella ametarsia* are more common in canopy situations than in stream situations, occupying the later habitats only for small periods of time during the reproductive season. Besides, Amazonian Glassfrogs seem to be highly selective regarding the type of stream used for reproduction.

TABLE 3. Altitudinal distribution of the Glassfrogs known from northeastern Ecuador. Ce = *Centrolene*; Co = *Cochranella*; H = *Hyalinobatrachium*; sp. N1–N2, N7–N8 = undescribed species (see text for explanation). Gray areas indicate altitudinal limits reach in southern Ecuador (see table 4).

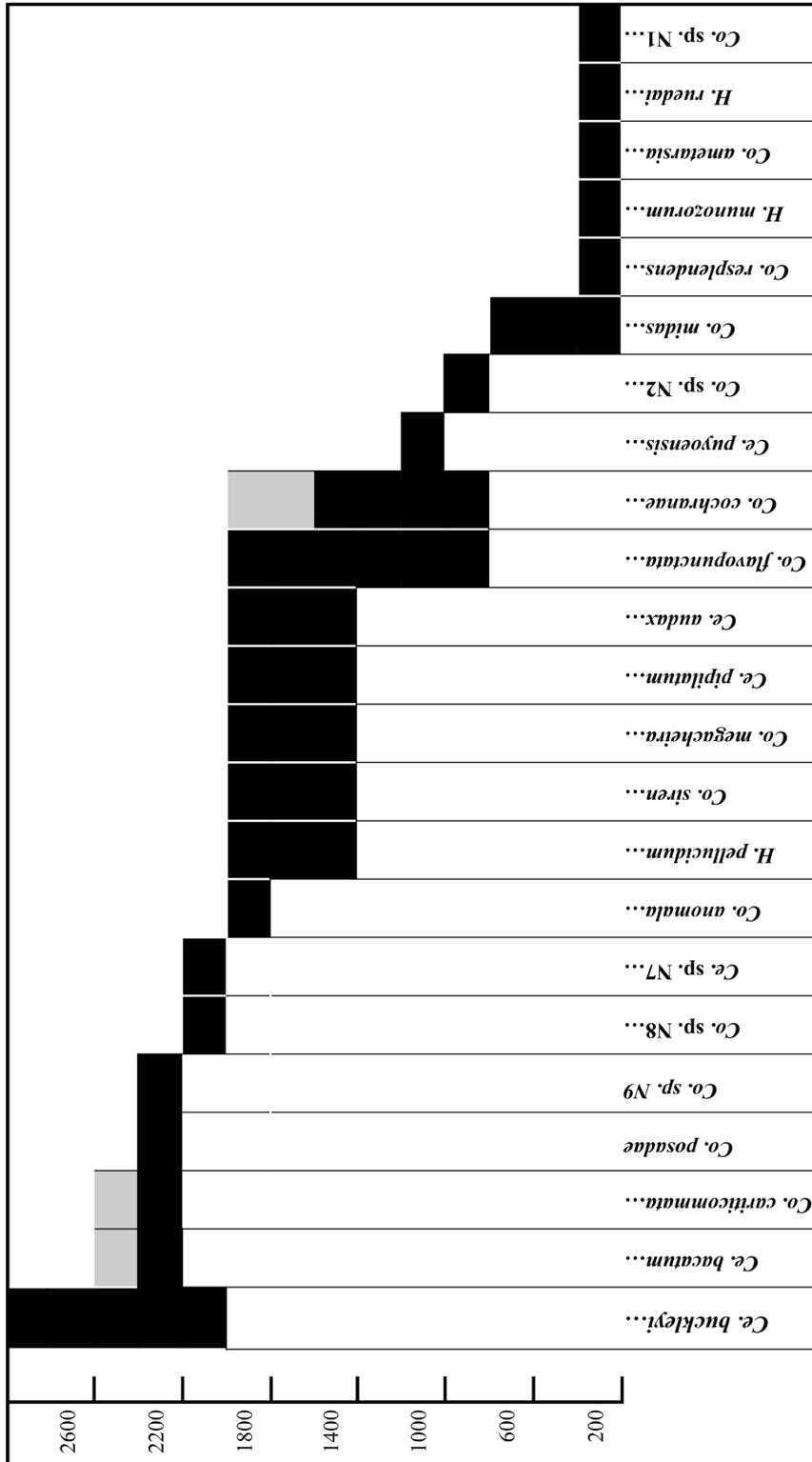
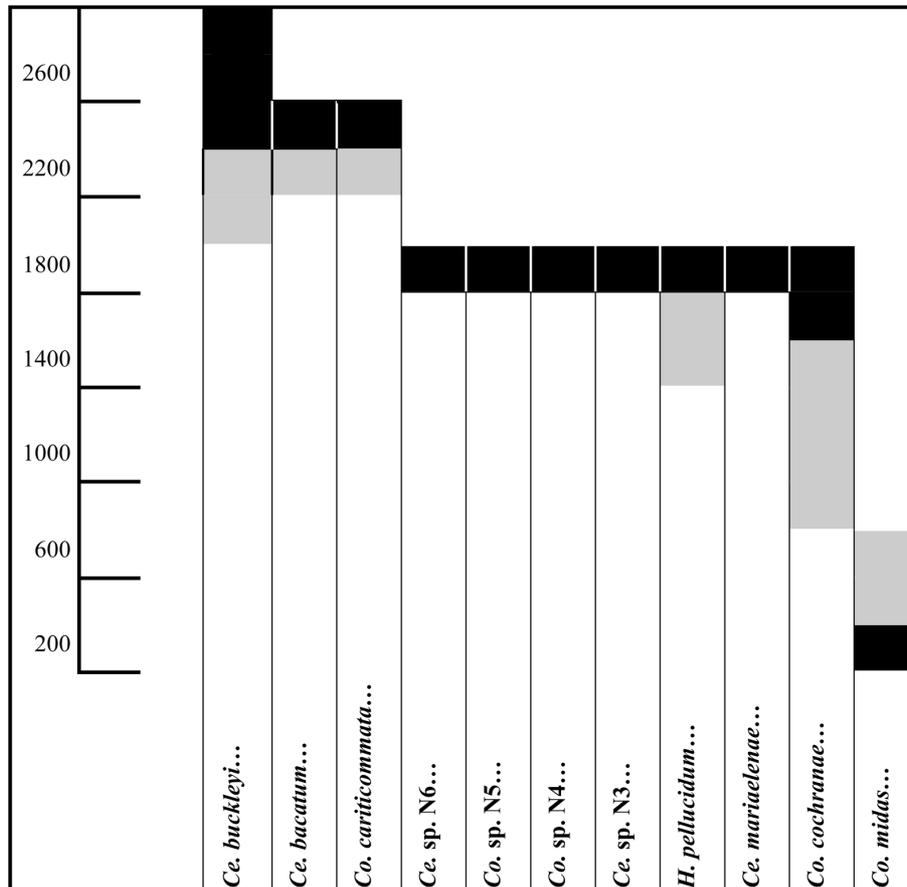


TABLE 4. Altitudinal distribution of the Glassfrogs known from southeastern Ecuador. Ce = *Centrolene*; Co = *Cochranella*; H = *Hyalinobatrachium*; sp. N3–N6 = undescribed species (see text for explanation). Gray areas indicate altitudinal limits reach in northern Ecuador (see Table 3).



Three described species are known to inhabit the Amazonian-versant Foothill forests (600–1300 m above sea level) of Ecuador: *Centrolene puyoensis* (Flores & McDiarmid), *Cochranella flavopunctata* (Lynch & Duellman), and *Cochranella cochranae*. There is at least one undescribed species of *Cochranella* (sp. N2) (Table 3, 4), that is sympatric with *C. cochranae* (Table 5).

Eight described species are currently known from the Amazonian-versant Low Montane and Cloud forests (1300–1900 m a.s.l.) of the northern section: *Centrolene audax* (Lynch & Duellman), *Centrolene pipilatium* (Lynch & Duellman), *Cochranella anomala* (Lynch & Duellman), *Cochranella cochranae*, *Cochranella flavopunctata*, *Cochranella megacheira* (Lynch & Duellman), *Cochranella siren* (Lynch & Duellman), and *Hyalinobatrachium pellucidum* (Lynch & Duellman). On the southern section, only three species (*Centrolene mariaelenae*, *Cochranella cochranae* and *Hyalinobatrachium pellucidum*) have been described from the Low Montane and Cloud forests, but there are at least five undescribed species (*Centrolene* sp. N3, *Cochranella* sp. N4 and N5 from

southern Cordillera Oriental, and N6 from Cordillera del Cóndor). The new record of *Hyalinobatrachium pellucidum* (QCAZ 25950) from the southern section corresponds to a specimen collected at 6.6 Km N of Limón (Limón-Macas road, 1013 m), Province of Morona-Santiago, ca. 280 Km S from previously known localities in northeastern Ecuador (Lynch & Duellman 1973).

The Amazonian-versant Low Montane and Cloud forests have the largest diversity of Glassfrogs in Ecuador; however, the knowledge on most species is still fragmentary with various taxa known just from their type series (eg. *Cochranella anomala*). Further, most species from the northern section would appear to be endemic from the Upper Quijos River basin, but it is an artifact of collections because most areas in eastern Ecuador are poorly known or completely unexplored.

The highest beta diversity in eastern Ecuador for Glassfrogs (14 spp.) occurs in the belt between 1300 and 1800 m a.s.l. (above sea level), with at least six species found sympatrically at the same stream (Table 3, 4, 5). This pattern, with the cloud forest and low montane being more diverse than lowland forests or high montane areas, was also identified in the eastern versant of the Cordillera Oriental of Colombia (Ruíz-Carranza & Lynch 1997), and the Pacific versant of the Andes of Ecuador (Lynch & Duellman 1973, Duellman & Burrowes 1989, Cisneros-Heredia and McDiarmid in prep.).

Above 1900 m, the diversity of Glassfrogs includes three described species: *Centrolene buckleyi* (Boulenger) (distributed up 3200 m a.s.l. on paramos and subparamos), *Centrolene bacatum* Wild, and *Cochranella cariticomata* Wild. Recent studies have revealed the presence of *Cochranella posadae* Ruíz-Carranza and Lynch in northeastern Ecuador (J. M. Guayasamín pers. comm.) and at least three undescribed species: *Centrolene* sp. N7, N8 (Cisneros-Heredia and McDiarmid in prep.), and N9 (Guayasamín *et al.* in prep.). *Centrolene buckleyi*, *Centrolene bacatum*, and *Cochranella cariticomata* are sympatric in northeastern (together with *C. posadae*, J. M. Guayasamín pers. com., Coloma *et al.* 2004) and in southeastern Ecuador (Table 5) (Wild 1994). *Centrolene* sp. N7 and N8 are sympatric over 2000 m a.s.l. at La Bonita, in northeastern Ecuador (Table 5).

The distribution ranges of *Centrolene bacatum*, *Cochranella cariticomata*, and *Centrolene buckleyi* are among the widest for centrolenid frogs from the Andean versants, situation explainable by the rather continuous extension of the high montane forests along the eastern versant of the Cordillera Oriental, in comparison with the low montane and cloud forests which are more dependent of local conditions of isolated valleys and mountain ranges.

Cochranella cariticomata, an Ecuadorian endemic species, has been reported just from two localities (Wild 1994, Coloma *et al.* 2004). Two specimens of *C. cariticomata* collected on leaves in wet grass and shrubs on edge of forest at night at El Cruzado, Province of Morona-Santiago, on 21 August 1962 by M. Olalla. (USNM 288435-6), provide the third locality for the species, extending its range 23 km. NNW from the type locality.

Biogeographic patterns

The *Centrolene gorzulai* group is apparently a monophyletic clade, based on the unique combination of a humeral spine, a transparent peritoneum, and a hepatic peritoneum covered by guanophores (Noonan & Harvey 2000; Duellman & Señaris 2003). The *Centrolene gorzulai* species group was formerly considered as restricted to the Guayana Shield until the description herein of *Centrolene mariaelenae*, the first Andean species. A connection linking the Andes and the Guayana Shield has been identified previously for various groups among plants and animals (Berry & Riina 2005.). This biogeographical connection varies from a situation where the clade is Guayanan-centered with one or a few outliers in the Andes, to the opposite where the clade is basically an Andean lineage with one or few outliers in the Guayana Shield (Berry & Riina 2005). The *Centrolene gorzulai* species group is apparently an example of the first case, a situations shared with several bird groups, among others, for example: The *Streptoprocne rutilus* superspecies includes two species of swifts, the Chestnut-collared Swift *S. rutila* (Vieillot) with an Andean distribution and the Tepui Swift *S. phelpsi* (Collins) endemic to the Guayana Shield; the White-tipped Swift *Aeronautes montivagus* (d'Orbigny & Lafresnaye) comprises two subspecies, the nominate subspecies distributed in the Andes from Venezuela to Bolivia and the subspecies *tatei* (Chapman) from the Tepuis; the nominate subspecies of the Blue-fronted Lancebill, a hummingbird, *Doryfera j. johannae* (Bourcier) occurs in the Andean region and *D. j. guianensis* (Boucard) is restricted to the Guayana Shield; the Buff-fronted Owl, *Aegolius harrisii* (Cassin), comprises two subspecies, the nominate subspecies from the Andes from Venezuela to Peru, and an undescribed subspecies that occurs in the Cerro Neblina, Guayanan Shield; the Foothill Screech-Owl, *Megascops roraimae* (Salvin), includes two subspecies, the nominate subspecies from the Cerros Roraima, Duida and Neblina in the Guayanan region and the *napensis* (Chapman) subspecies from eastern Ecuador to Bolivia; the Masked Trogon, *Trogon personatus* Gould, with several species along the Andes from Venezuela to Bolivia and one subspecies from the Tepuis; the genus *Nannopsittaca* is composed of two species, the Tepui Parrotlet *N. panychlora* (Salvin & Godman) from the Guayana Shield and the Amazonian Parrotlet *N. dachilleae* O'Neill, Munn & Franke from southeastern Peru and northeastern Bolivia (Fjeldså & Krabbe 1990, O'Neill *et al.* 1991, Del Hoyo *et al.* 1992–2004).

Most cases mentioned above are taxa widely distributed along the Andes from Venezuela to Ecuador, Peru and Bolivia, and separated from their Guayanan relatives by a few kilometers, yet, the distance separating *Centrolene mariaelenae* from its apparently closest relatives in the *gorzulai* group is ca. 1500 km. This pattern is also shown by several clades, revealing a particular connection between the Guayana Shield and the sandstone outcrops ranges (cordilleras or contrafuertes) from southeastern Ecuador and northeastern Peru. Berry & Riina (2005) provided information on several taxa of Guayanan-centered plants with some outliers in southeastern Ecuador and northeastern Peru (Pruski 1998,

Berry & Riina 2005).

While the *Centrolene gorzulai* species group is a Guyanan-centered clade; the entire family Centrolenidae is an Andean-centered clade. Most Centrolenid frogs are distributed between Venezuela and Bolivia along the Cordillera de Los Andes, with just few species in Central America, the Guayana Shield, and southeastern Brasil and northern Argentina. This pattern with the larger — most inclusive — clade having an Andean-centered distribution, and other smaller lineages with Guyanan-centered and southern Brazilian-centered distributions, are again observed in other taxa: the *Otus guatemalae* superspecies; the *Trogon personatus* superspecies; the Oilbird *Steatornis caripensis* Humboldt; the genus *Streptoprocne* of Collared Swifts, the genus *Doryfera* of Lancebill Humingbirds (Fjeldså & Krabbe 1990, Del Hoyo *et al.* 1992–2004). Further studies on the systematics and biogeographical history of more clades will probably reveal that all these patterns are more widespread than previously thought in Neotropical lineages, and they reflect a common evolutionary history.

Comments on the infrageneric and generic taxonomy of Glassfrogs

Darst & Cannatella (2004), Wiens *et al.* (2005), and Frost *et al.* (2006) confirm the monophyly of the family Centrolenidae but found that the genera proposed by Ruíz-Carranza & Lynch (1991a) are not monophyletic units. Four genera are currently recognized inside the family Centrolenidae, divided among two subfamilies: *Allophryne* (subfamily Allophryinae), *Centrolene*, *Cochranella*, and *Hyalinobatrachium* (subfamily Centroleninae) (Frost *et al.* 2006). The genus *Centrolene* is solely defined by the presence of humeral spines in males, but it is paraphyletic with respect to *Cochranella* (Darst & Cannatella 2004, Wiens *et al.* 2005, Frost *et al.* 2006). The genus *Hyalinobatrachium* was originally defined over the synapomorphy of a non-trilobate bulbous liver covered by guanophores by Ruíz-Carranza & Lynch (1991a) (character first described by Starrett & Savage 1973). Noonan & Harvey (2000) and Duellman & Señaris (2003) reported that three Guianan species of the genus *Centrolene* have a white hepatic peritoneum and the genus *Hyalinobatrachium* was left defined only by having a bulbous liver. Myers & Donnelly (2001: 20) described *Hyalinobatrachium eccentricum* with a liver with “2 lobes visible”, questioning the real status of this character.

The external appearance of the liver of *C. mariaelenae* (Fig. 4) appears bulbous and closer to the state previously defined for the genus *Hyalinobatrachium* than to the lobate liver of other centrolenid frogs. Yet, the condition could be like *C. gorzulai* where the liver of *Centrolenella auyantepuiana* Señaris & Ayarzagüena (synonym of *Centrolene gorzulai*) was described as having a bulbous liver apparently bilobated under the white hepatic peritoneum (Ayarzagüena & Señaris 1997). Later, after dissection, *C. auyantepuiana*'s liver was described as trilobate (two big lobes and a small lobe), but with a variable external appearance, as it can appear as a unified unlobed structure or as clearly lobate structure (Duellman & Señaris 2003: 251, fig. 4, Señaris & Ayarzagüena 2005). The

precise condition in *C. mariaelenae* must await the collection of additional material, as we prefer not to dissect the holotype.

The observation of Myers & Donnelly (2001) on the form of the liver of *Hyalinobatrachium eccentricum* and our discovery of an apparent bulbous liver in *C. mariaelenae* made us examining several specimens of different species of Centrolenid frogs to analyze the interspecific variation in the form of the liver. All studied species of *Centrolene* (except *C. mariaelenae*) and *Cochranella* have lobate livers (with 3 – 4 clearly separated lobes). *Hyalinobatrachium fleischmanni* (Boettger) (USNM 342162-342213) showed a liver composed of one lobule, but *H. uranoscopum* (Müller) (USNM 243722), *H. eurygnathum* (Lutz) (USNM 208390-1), and *H. ruedai* (DFCH-USFQ 0735) showed bilobate livers, and *H. cardiacalyptum* (McCranie & Wilson) (USNM 530617) a trilobate liver. The lobes in the bilobate and trilobate conditions of *Hyalinobatrachium* are not widely separated as in other Centrolenid frogs, and are better described as livers with lobes entirely fused proximally and discernible only distally. These dissections revealed that, as mentioned by Duellman & Señaris (2003), the guanophores over the hepatic peritoneum and the gallbladder obscures at a first glance the structure of the liver; and the third lobe is not discernible without dissection because its dorsal projection. The form of the liver is apparently a character more variable than previously understood; and the similarity between the liver of the *Hyalinobatrachium* and some members of the *C. gorzulai* (including *C. mariaelenae* and *C. gorzulai*) set up questions about the validity of this character to solely define the generic separation of *Hyalinobatrachium* as presented by Duellman & Señaris (2003).

Further, the genus *Hyalinobatrachium* includes three species groups: *fleischmanni*, *pulveratum*, and *parvulum* (Ruíz-Carranza & Lynch 1991a). The *Hyalinobatrachium pulveratum* group is formed by two poorly-known species: *H. pulveratum* and *H. antisthenesi*, and no apomorphic characters have been diagnosed for this group. We examined a specimen of *Hyalinobatrachium antisthenesi* and obtained information from the detailed descriptions presented by Señaris & Ayarzagüena (2005), Savage (2002) and Ibañez *et al.* (1999) for both species. *Hyalinobatrachium pulveratum* and *H. antisthenesi* greatly differ from taxa assigned to the *H. fleischmanni* group in several chromatic, osteological, and behavioral characteristics, as already stated by Señaris & Ayarzagüena (2005) for *H. antisthenesi*. These strong differences suggest that both taxa are more closely related to the clade formed by the *Centrolene/Cochranella* genera than to the clade determined by the *H. fleischmanni* as type species (= *H. fleischmanni* group) and we propose the new combinations: *Cochranella antisthenesi* n. comb. and *Cochranella pulverata* n. comb.

The *Hyalinobatrachium parvulum* group, from southeastern Brasil and northern Argentina, includes three species. The monophyly of this group is currently supported by the presence of guanophores covering the urinary bladder; further it differs from the *H. fleischmanni* species group by the greencolor of the bones and the presence of vomerine

teeth. The taxonomic position of the three species of glassfrogs from southern Brasil and northern Argentina is uncertain. It is apparently a monophyletic clade, different enough to be considered apart from *Hyalinobatrachium* (*sensu stricto* = *Hyalinobatrachium fleischmanni* group). However available information is not sufficient to determine its relationships, and they are here considered as part of *Hyalinobatrachium* (*sensu lato*).

The *H. fleischmanni* group, which contains most species of the genus (including its type-species), is apparently monophyletic. Its monophyly was suggested by Ruíz-Carranza & Lynch (1991a, 1998) based on the “deposition of one layer of eggs on the underside of leaves”. Yet, this condition is not limited to the *H. fleischmanni* group as it has been reported also in *H. uranoscopum* (which uses both sides of leaves), *Cochranella spinosa* (Taylor) (also with eggs in a single layer), and *Cochranella albomaculata* (Taylor) (Lutz 1947, McCranie & Wilson 1997, Ibañez *et al.* 1999, Savage 2002). Starrett & Savage (1973), Barrera-Rodríguez (2000) and Manzano (2000) described several morphological, miological, and chromatic characters that support a monophyletic *H. fleischmanni* group; six of those characters are also seen in Venezuelan members pictured by Señaris & Ayarzagüena (2005) and in Ecuadorian species studied by us, thus seem to be valid synapomorphies that better defined *H. fleischmanni* group rather than the egg deposition site: reduced nasal bones widely separated; reduced prevomers without dentigerous process or prevomerine teeth; reduced quadratojugals not in contact with the maxillae; little development of the *crista humeralis*, not forming a humeral spine in males; white bones in life; and coloration in preservative mainly white or cream without extensive lavender.

The genus *Centrolene* was divided into three groups by Ruíz-Carranza & Lynch (1991a). This division has been questioned, as the characters used to separate them are variable (Noonan & Harvey 2000). The latter authors discussed the characters defining the *prosolepon* and *peristictum* species groups. They found that both groups, as currently defined, are practically identical and that the differences are subjected to interspecific variation. Although the general appearance of the members of the *prosolepon* species group is slightly more slender than members of the *peristictum* species group, we agree that the recognition of these two groups as currently defined is unsupported by any clear character.

The *C. geckoideum* species group was assigned to taxa with humeral spine in males, small eyes, green bones, trilobate liver, vomerine teeth present, clear visceral peritonea, and guanophores just over the parietal peritoneum and pericardium (Ruíz-Carranza & Lynch 1991a). Ruíz-Carranza & Lynch (1991a) pointed out that *C. acanthidiocephalum* Ruíz-Carranza & Lynch and *C. medemi* (Cochran & Goin) shared derived characters with *C. geckoideum* and *C. paezorum* Ruíz-Carranza, Hernández-Camacho & Ardila-Robayo, as to be considered part of the same group. *Centrolene acanthidiocephalum* and *C. petrophilum* Ruíz-Carranza & Lynch were considered related by sharing the synapomorphy of large labial tubercles in males. Savage (2002) resurrected the genus

Centrolenella from the synonymy of *Centrolene*; and proposed the restriction of the genus *Centrolene* to the three larger species (*geckoideum*, *paezorum*, and *acanthidiocephalum*) of the *geckoideum* species group of Ruíz-Carranza & Lynch (1991a), leaving the other two species (*medemi* and *petrophilum*) under the *prosoblepon* group of his *Centrolenella* genus. The hypotheses by Ruíz-Carranza & Lynch (1991a) and Savage (2002) present different classifications of the same group. We think that the information available is insufficient to determine the real relationships of the species currently under the *geckoideum* group among them and with the other species groups (see Frost *et al.* 2006).

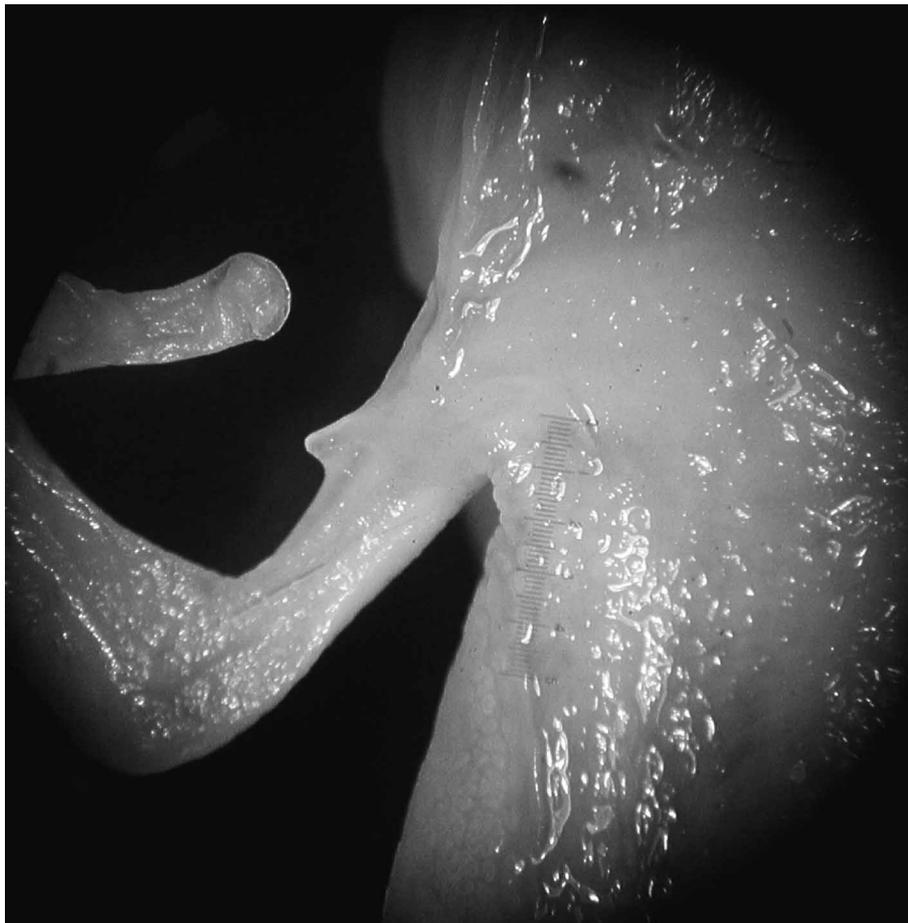


FIGURE 6. Humeral spine of the paratype of *Centrolene balionotum* n. comb. (ICN 23479).

We suggest the following infrageneric division of the genus *Centrolene*: (1) *Centrolene geckoideum* group, (2) *C. prosoblepon* group, and (3) *C. gorzulai* group (Table 2). Otherwise we keep using Ruíz-Carranza & Lynch's (1991a) hypothesis for convenience until a detailed study reveal the relationships of the species currently under *Centrolene*, *Cochranella*, and their species groups.

We take the opportunity herein to propose the transferal of the taxon *Centrolenella*

balionota Duellman from the genus *Cochranella* (where Ruíz-Carranza & Lynch 1991a placed it) to the genus *Centrolene*, as *Centrolene balionotum* n. comb. Duellman (1981) described the presence of a humeral spine in the males of *C. balionota*; but Ruíz-Carranza & Lynch (1991a) consider that it was just a truncate *crista ventralis*, similar to that of *Cochranella griffithsi* and *Cochranella armata* Lynch & Ruíz-Carranza (Ruíz-Carranza & Lynch 1991a, Lynch & Ruíz-Carranza 1996). We studied several paratypes of *balionota* (KU 164701, 164703–11, ICN 23479 [formerly KU 164712]) and found that it does have a well differentiated humeral spine (Fig. 6). The specimens analyzed by Ruíz-Carranza & Lynch (1991a) and Lynch & Ruíz-Carranza (1996) (ICN 13105–13) correspond to an undescribed species. Although *Centrolene* is paraphyletic towards *Cochranella*, we propose this new combination to reflect the state of a humeral spine in *Centrolene balionotum*.

Comments on some characters of the family Centrolenidae

Frogs of the family Centrolenidae (subfamily Centroleninae) have been commonly differentiated from other anurans by a combination of the following characters: fusion of the astragalus and calcaneum, T-shaped terminal phalanges, process on the third metacarpal, and eggs deposited outside of water (Ruíz Carranza & Lynch 1991a). None of these characters are unique synapomorphies of the family Centrolenidae as all are known to have convergent states in other anurans (Ford & Cannatella 1993, Ruíz-Carranza & Lynch 1991a). While the T-shaped terminal phalanges and the eggs deposited outside of water are conditions widely spread among other anuran families; the fusion of the astragalus and calcaneum was thought to be a well-supported character to define the family Centrolenidae, convergent just with a state present in the genus *Pelodytes* (Ford & Cannatella 1993, Ruíz-Carranza & Lynch 1991a). Sanchiz & De la Riva (1993), Barrera-Rodríguez (2000), and specimens studied by us, revealed the existence of variation of this character within the Centrolenidae. There is a complete fusion of the bones (without evidence of suture and forming one element) in some species of *Hyalinobatrachium* (*H. bergeri* Cannatella, *H. fleischmanni*, *H. colymbiphyllum* (Taylor), *H. esmeralda* Ruíz-Carranza & Lynch, and *H. aureoguttatum* Barrera-Rodríguez & Ruíz-Carranza); complete fusion but with evidence of suture between the two bones in *Centrolene prosoblepon*, *Hyalinobatrachium mondolfii* Señaris, and an undescribed species of *Cochranella* related to *C. anomala*; distal partial fusion with the two bones free proximally in *Centrolene geckoideum* and *C. acantidiocephalum*; and proximal and distal fusion with complete separation of middle section in *Cochranella bejaranoi* Cannatella and *Cochranella daidalea* Ruíz-Carranza & Lynch (Eaton 1958, Sanchiz & de la Riva 1993, Rueda 1994, Barrera-Rodríguez 2000, Señaris & Ayarzagüena 2001, Cisneros-Heredia & McDiarmid unpubl. data 2002–2005) (Fig. 7). The degree of interspecific variation of this character obscures its clear definition, with species of *Hyalinobatrachium* presenting the complete fusion state and some *Cochranella* just a peripheral fusion. This wide variation prevents

the use of this character as a synapomorphy to define the family. Further, although it has been suggested that the degree of fusion could be useful to separation at the generic level (Sanchiz & De la Riva 1993, Barrera-Rodríguez 2000), current generic divisions do not match any discernible and consistent pattern. But, as the present taxonomy of the family Centrolenidae does not reflect accurately the evolutionary history of the entities involved, it is possible that closely related groups will show similar patterns of fusion of the tarsal elements.

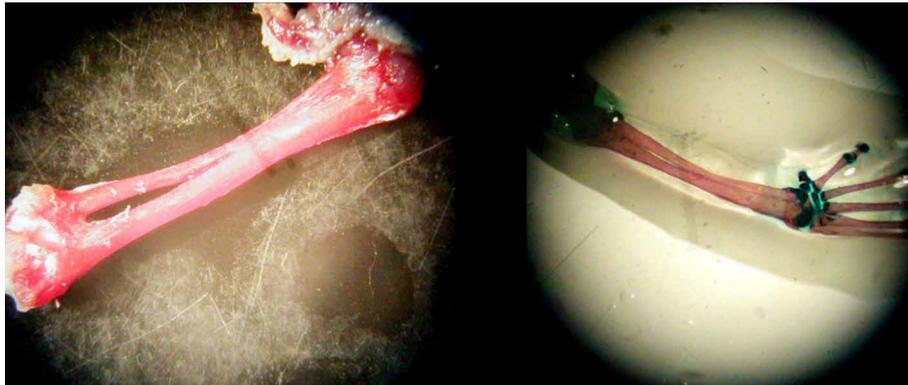


FIGURE 7. State of astragalus and calcaneum in two glassfrogs: *Centrolene acanthidiocephalum* (left), and *Cochranella daidalea* (right).

The process on the medial side of the third metacarpal seems to be present in all species currently assigned to the family Centrolenidae, under any genus. A similar character is found in the distantly related *Litoria* (Tyler & Davies 1978) and in some rhacophorids and hyperoliids (Liem 1970). However, the process in the Centrolenidae is always medial to the third metacarpal while the process in *Litoria meiriana* (Tyler) (Tyler & Davies 1978: Fig. 21) is distal; and in the rhacophorids and hyperoliids is an extended expansion of the dorsolateral tip of the metacarpal (as discussed by Hayes & Starrett 1980). The presence of processes in these different unrelated groups is understood as a congruence of characters between clades independently acquired and apparently related to their arboreal life (Ruíz-Carranza & Lynch 1991a). No intra/inter generic/specific variation on the presence of a process on the medial side of the metacarpal has been observed in the Centrolenid frogs; it was reported by Hayes & Starrett (1980) in 27 species, by Ford & Cannatella (1993) in more than 40 species, Barrera-Rodríguez (2000) in four species, and we found it in at least 78 species (Cisneros-Heredia & McDiarmid unpubl. data 2002–2005) (Fig. 8). This character seems to be a well-supported synapomorphy for the Centrolenidae (Hayes & Starrett 1980, Ford & Cannatella 1993, pers. obs.).

La Marca (1995, 1997) placed without justification the names *Centrolenella estevesi* Rivero and *C. pulidoi* Rivero under the genus *Hyalinobatrachium*; however the absence of the medial process on the metacarpal in *Centrolenella pulidoi* and *Centrolenella estevesi*

regards them as members of the family Hylidae and not Centrolenidae, as suggested by Starret in Frost 2004, and confirmed by Señaris & Ayarzagüena 2005, Faivovich *et al.* 2005, and our direct examination of a paratype of *C. pulidoi* USNM 166854.



FIGURE 8. Process on the medial side of the third metacarpal of *Centrolene acanthidiocephalum* (left), and *Cochranella daidalea* (right).

The hepatic peritoneum, pericardium and the urinary bladder covered by guanophores were considered conditions restricted to the Centrolenidae by Ruíz-Carranza & Lynch (1991a). Noonan & Harvey (2000) commented that the hepatic peritoneum covered by guanophores is not unique to the just to the genus *Hyalinobatrachium* neither restricted to the family Centrolenidae as this character is present in some *Centrolene*, *Cochranella*, and Hylidae. These asseverations are true also for the pericardium and urinary bladder covered by guanophores; as *Hypsiboas pellucens* Werner, *H. cinerascens* Spix, and *Hyloscirtus phyllognatha* have the hepatic peritoneum and the pericardium covered by guanophores, and the last two also the urinary bladder (Cisneros-Heredia & McDiarmid unpubl. data 2002–2005).

The tadpoles of the Centrolenidae are exotroph, lotic and burrower/fossorial larvae with a vermiform body (Altig & McDiarmid 1999) that exhibit dorsal C-shaped eyes (Altig & Brandon 1971) and live buried within leaf packs in still or flowing (mostly slow) water systems (Wassersug & Hoff 1979, Hoff *et al.* 1999). These morphological and ecological characteristics defined a unique type of tadpole which seems to be common to all the species of the family, and also useful as a diagnostic feature of the Centrolenidae.

Several other characters have been suggested as unique to the Centrolenidae: (1) Barrera-Rodríguez (2000) proposed the condition of the *musculus depressor mandibulae* constituted by one slit in the Centrolenidae as a possible apomorphy of the family, however Manzano (2000) found much variation within the centrolenids as to be useful as an apomorphy for the family. (2) Burton (1998) studied eight species of Centrolenidae and found a ventral origin of the *musculus flexor teres digiti III* relative to the *musculus transversi metacarpi I*; proposing this condition as an apomorphy of Centrolenidae. (3)

Cadle & McDiarmid (1990) proposed the mineralized intercalary elements as another apomorphy. (4) Schwalm & McNulty (1980) found that the chromatophore organization and the ultrastructure of melanophore pigment granules differ markedly between *Hyalinobatrachium fleischmanni* and Hylids. Hass (2003) suggested several characters present in the tadpole of *Cochranella granulosa* that could represent synapomorphies of the Centrolenidae. However extensive sampling and a phylogenetic analysis of the family are still necessary to prove the validity of all these suggested characters.

Examined comparative material

Centrolene acanthidiocephalum: Colombia: ICN 5285 (holotype): Santander. *Centrolene audax*: Ecuador: USNM 286622-24: Río Salado, Napo. USNM 286620-22: Cascada de San Rafael, Napo. *Centrolene balionotum*: ICN 23479 (paratype): Mindo, Pichincha. *Centrolene geckoideum*: Ecuador: USNM 167018: Pichincha. Colombia: ICN 5562-63: Boyacá. *Centrolene gemmatum*: Ecuador: QCAZ 467-72: Tandapi, Pichincha. *Centrolene grandisonae*: DFCH-USFQ (field series) 111, 117, 150, 152, 160–1, 175: Río Guajalito Protected Forest, Pichincha. *Centrolene guanacarum*: Colombia: ICN 11686 (holotype), 11685: Cauca. *Centrolene heloderma*: USNM 211216–8: Pichincha. *Centrolene huilense*: Colombia: ICN 7462 (holotype), 7461, 7463 (paratypes): Huila. *Centrolene hybrida*: Colombia: ICN 17897 (holotype), ICN 17898, 10197, 9614: Boyacá. *Centrolene ilex*: Ecuador: MECN 2620–26: Canandé, Esmeraldas; MECN 3199–03: Río Tululbí, Esmeraldas; MECN 3204: Río Verde, Esmeraldas; .DFCH-USFQ D260–1: San Vicente de Andoas, Pichincha. *Centrolene litorale*: Colombia: ICN 13821 (holotype): La Guayacana, Nariño; Ecuador: MECN 3198: Río Cachabí, Esmeraldas. *Centrolene medemi*: Colombia: USNM 15227: Putumayo. *Centrolene notostictum*: Colombia: ICN 12632 (holotype): Santander. *Centrolene paezorum*: Colombia: ICN 11866 (holotype): Inzá, Cauca. *Centrolene peristicta*: Ecuador: USNM 286714: Río Faisanes, Pichincha; QCAZ 6446: Río Guajalito Protected Forest. *Centrolene petrophilum*: Colombia: ICN 9567 (holotype): Boyacá. *Centrolene pipilatum*: Ecuador: ICN 23756: Río Azuela; USNM 286717: Río Salado, Napo. *Centrolene prosoblepon*: Ecuador: USNM 541904-541915: Bilsa Biological Reserve, Esmeraldas; USNM 288438: “Guayaquil”, Guayas; USNM 286738-39: El Oro; USNM 288441: below Sigchos, Cotopaxi; DFCH-USFQ 293-295: Mashpi Reserve, Pichincha. *Centrolene quindianum*: Colombia: ICN 24886 (holotype), ICN 24910-20 (paratypes): Quindío. *Centrolene robledo*: Colombia: ICN 17936–7, 17939–41 (paratypes): Antioquia. *Centrolene* sp. N3: DFCH-USFQ: Ecuador: Zamora-Chinchipe. *Centrolene* sp. N6: Ecuador: MAM032: Cordillera del Cóndor, Morona-Santiago. *Centrolene* sp. N7: Ecuador: USNM 288464: La Bonita, Sucumbíos.

Cochranella adiazeta: Colombia: ICN 17919 (holotype): Santander. *Cochranella ametarsia*: Ecuador: DFCH-USFQ D162: Tiptuni Biodiversity Station, Orellana. QCAZ 28138: Cuyabeno, Sucumbíos. Colombia: ICN unnumbered: Leticia. *Cochranella antisthenesi*: Venezuela: ICN 36589: Aragua, Estación Biológica Rancho Grande.

Cochranella armata: Colombia: ICN 28037–49: El Cairo, Valle del Cauca. *Cochranella cariticommata*: Ecuador: USNM 288435–6: El Cruzado, Province of Morona-Santiago. *Cochranella cochranae*: Ecuador: USNM 284304–6, 286632–36: Cascada de San Rafael, Napo; USNM 288452: “Loreto”, Orellana; DFCH D100-1: Contrafuerte de Tzunantza, Zamora-Chinchipe; FHGO 2804: Romerillos, Zamora-Chinchipe. *Cochranella daidalea*: Colombia: ICN 18008 (holotype): Cundinamarca; ICN 14916. *Cochranella griffithsi*: Ecuador: USNM 286671–77: Tandayapa, Pichincha. *Cochranella ignota*: Colombia: ICN 14748 (holotype), ICN 14749–77 (paratypes): Farallones de Cali, Valle de Cauca. *Cochranella luteopunctata*: Colombia: ICN 20747 (holotype): El Tambo, Cauca. *Cochranella megacheira*: Ecuador: USNM 286701: Río Salado, Napo; EPN s/n: Cordillera de Guayacamayos. *Cochranella midas*: Ecuador: ICN 23755 (paratype): Santa Cecilia, Sucumbíos. DFCH-D102: Tiputini Biodiversity Station, Orellana; QCAZ 22876: Yasuni, Orellana; QCAZ 20001-2: Puerto Misahualli, Napo; USNM 288437: Río Oglán, Curaray, Pastaza. *Cochranella nephelophila*: Colombia: ICN 24297 (holotype): Caquetá. *Cochranella oreonympha*: Colombia: ICN 20765 (holotype), ICN 20766–75 (paratypes): Caquetá. *Cochranella pulverata*: USNM 219379–87: Costa Rica. *Cochranella resplendens*: Ecuador: FHGO 1305, 1324: Pozo Garza, Oryx, Pastaza; DFCH D103-4: Tiputini Biodiversity Station, Orellana. *Cochranella ruizi*: Colombia: ICN 7469, 7470–71 (paratypes): Quebrada Sopladero, Cauca. *Cochranella savagei*: ICN 9769 (holotype): Quindío. *Cochranella siren*: Ecuador: USNM 286740: Río Azuela, Napo. *Cochranella solitaria*: Colombia: ICN 24298 (holotype): Caquetá. *Cochranella* sp. N1: Ecuador: QCAZ: Cuyabeno, Sucumbíos. *Cochranella* sp. N2: Ecuador: USNM 28845: Loreto, Orellana. *Cochranella spinosa*: Ecuador: USNM 288443: Río Blanco, Pichincha. USNM 286741–2: Río Palenque, Los Ríos.

Hyalinobatrachium aureoguttatum: Colombia: ICN 17507, 17509–10, 7252–4, 17515–6, 171250, 17255–7 (paratypes): Chocó. *Hyalinobatrachium cardiacalyptum*: Honduras: USNM 530617: Quebrada Las Marías, Olancho; USNM 5358282: Quebrada El Guasimo, Olancho, Honduras. *Hyalinobatrachium crurifasciatum*: Venezuela: AMNH 131329 (holotipo), AMNH 131331 (paratipo): Pico Tamacuari, Sierra Tapirapecó, Amazonas. *Hyalinobatrachium eccentricum*: Venezuela: AMNH 159164 (paratipo): Cerro Yutajé, Amazonas. *Hyalinobatrachium esmeralda*: Colombia: ICN 9593–4, 9596, 9603 (paratypes): El Descanso, Boyacá. *Hyalinobatrachium eurygnathum*: Brasil: USNM 208390–1: Teresopolis, Rio de Janeiro. *Hyalinobatrachium fleischmanni*: Ecuador: USNM 286639: Río Palenque, Los Ríos; USNM 286645: Patricia Pilar, Los Ríos; USNM 286640: Río Palenque, Los Ríos; USNM 286646: Hacienda Cerro Chico, Los Ríos. Costa Rica: USNM 219303: Tilarán, Guanacaste; USNM 219267: Curridabat, San José. Nicaragua: USNM 220013-18: Matagalpa. Honduras: USNM 342162-342213: Olancho. México: 115499: Salto de Agua, Cerro Obando, Chiapas. *Hyalinobatrachium ibama*: Colombia: ICN 6033-35 (paratypes): Río Cañaverales, Santander. *Hyalinobatrachium munozorum*: Colombia: ICN 5031-34, 39503: Meta. *Hyalinobatrachium* cf. *munozorum*:

Colombia: ICN (serie de campo JMR 4119): Leticia, Amazonas. *Hyalinobatrachium* cf. *nouraguensis*: Brasil: OMNH/MPEG 13042: Río Ituxi. *Hyalinobatrachium pellucidum*: Ecuador: USNM 286708-10: Río Azuela, Napo; USNM 286711-12: Río Reventador, Napo; QCAZ 25950: 6 Km N of Limón, Morona-Santiago. *Hyalinobatrachium ruedai*: ICN 40409 (holotipo), ICN 40410-11, IND-AN 5448-52 (paratipos): Colombia: Parque Nacional Natural de Chiribiquete, Caquetá, Colombia. Ecuador: DFCH-USFQ 0735: Tena, Napo; EPN 6427: Río Manderoyacu, Arajuno, Pastaza. *Hyalinobatrachium* sp. A: Ecuador: USNM 286762-63: Río Faisánes, Pichincha. *Hyalinobatrachium* sp. B: Ecuador: USNM 286746-49: Río Palenque, Los Ríos; MECN: Manta Real, Cañar. *Hyalinobatrachium uranoscopum*: Brasil: USNM 243722: Parque Nacional da Tijuca, Rio de Janeiro. *Hyalinobatrachium valerioi*: Costa Rica: USNM 219429, 219431, 219433, 219438: Río Sarapaquí, Alajuela.

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