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**Revision of the characters of Centrolenidae
(Amphibia: Anura: Athesphatanura),
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DIEGO F. CISNEROS-HEREDIA & ROY W. MCDIARMID

# Revision of the characters of Centrolenidae (Amphibia: Anura: Athesphatanura), with comments on its taxonomy and the description of new taxa of glassfrogs

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## Abstract

Anurans of the family Centrolenidae are a diverse clade of arboreal frogs distributed across tropical America. Knowledge of their taxonomy, systematics, ecology, behavior, morphology, and other evolutionary aspects of their biology is deficient. Relationships among centrolenid species remain largely unresolved, with no satisfactory phylogenetic hypothesis, and none of the current genera has compelling evidence of monophyly. Further, understanding the phylogeny of glassfrogs is constrained by species-level taxonomic problems, including incorrect description of characters, incomplete analyses of intraspecific variation, and lack of appreciation of species diversity. Herein, we define and analyze the 23 characters that are useful, in combination, in diagnosing centrolenid species, and thereby provide a reference for the use of future workers. We propose revised classifications for the parietal and visceral peritoneal pigmentation, liver form and coloration of its associated hepatic peritoneum, nuptial excrescences, and hand ornamentation. We comment on the generic and species-level taxonomy of Centrolenidae, proposing the recognition of a new genus and describing a new species from Ecuador. We treat *Hyla ocellifera* Boulenger as a synonym of *Centrolene prosoblepon* (Boettger), *Hyalinobatrachium cardiacalyptum* McCranie & Wilson as a synonym of *Hyalinobatrachium chirripoi* (Taylor), and *Hyalinobatrachium crybetes* McCranie and Wilson as a synonym of *Hyalinobatrachium colymbiphyllum* (Taylor). We also present an annotated list of the species of glassfrogs from the Republic of Ecuador with some distributional remarks.

**Key words:** Centrolenidae, diagnostic characters, variation, peritoneal coloration, nuptial excrescences, taxonomy, synonyms; *Centrolene*, *Cochranella*, *Hyalinobatrachium, Nymphargus*, new genus; *Nymphargus laurae*, new species

**Resumen**

Los anuros de la familia Centrolenidae forman un clado diverso de ranas arbóreas distribuidas a lo largo de América tropical. El conocimiento sobre su taxonomía, sistemática, ecología, comportamiento, morfología y otros aspectos biológicos y evolutivos es deficiente. Las relaciones entre las especies de centrolénidos permanecen ampliamente sin resolver, sin hipótesis filogenéticas satisfactorias y todos los géneros actuales tienen evidencia clara de su no-monofília. Más aún, el entendimiento de la filogenia de las ranas de cristal está limitado por problemas taxonómicos al nivel de especies, incluyendo la descripción incorrecta de caracteres, análisis incompletos de la variación intraespecífica y la falta de apreciación de la diversidad de especies. En este trabajo, nosotro definimos y analizamos los 23 caracteres que son útiles, en combinación, para diagnosticar todas las especies de centrolénidos, proveyendo una referencia para el uso de futuros investigadores. Proponemos clasificaciones revisadas para la pigmentación de los peritoneos parietal y visceral, la forma del hígado y la coloración del peritoneo hepático asociado, las excrescencias nupciales y las ornamentaciones manuales. Comentamos sobre la taxonomía a nivel genérico y específico de Centrolenidae, proponiendo el reconocimiento de un nuevo género y la descripción de una nueva especie de Ecuador. Colocamos a *Hyla ocellifera* Boulenger como un sinónimo de *Centrolene prosoblepon* (Boettger); a *Hyalinobatrachium cardiacalyptum* McCranie & Wilson como sinónimo de *Hyalinobatrachium chirripoi* (Taylor); y a *Hyalinobatrachium crybetes* McCranie and Wilson como sinónimo de *Hyalinobatrachium colymbiphyllum* (Taylor). Presentamos una lista anotada de las especies de ranas de cristal de la República del Ecuador con algunos comentarios sobre su distribución.

**Palabras clave:** Centrolenidae, caracteres diagnóstico, variación, coloración peritoneal,  excrescencias nupciales, taxonomía, sinonimias; *Centrolene*, *Cochranella*, *Hyalinobatrachium, Nymphargus*, género nuevo; *Nymphargus laurae*, nueva especie

**Introduction**

Centrolenidae is a diverse clade of arboreal frogs endemic to America. They occupy riverine, understory, and canopy layers of evergreen and semi-deciduous forest, rainforests, cloud forests, and páramo habitats from southern Mexico to Panama and through the Andes from Venezuela to Bolivia, with species in the Amazon and Orinoco River basins, the Guiana Shield region, and the Atlantic forests of southeastern Brazil and northern Argentina. As far as is known, all species are nocturnal and lay their egg clutches either on leaves overhanging water or on stones next to streams or waterfalls. Approximately one-fourth of the known species of centrolenids have a transparent ventral skin through which the internal organs are visible—including the beating heart, thereby earning the group its common name: glassfrogs. Many species of centrolenids are conspicuous members of riverine communities in montane forests, but knowledge of their ecology, population dynamics, behavior, breeding biology, and other evolutionary and biological aspects of their natural history is available for only a few species (Noble 1925; Dunn 1931; Duellman & Tulecke 1960; Duellman & Cole 1965; Duellman 1967; McDiarmid & Adler 1974; McDiarmid 1975; Duellman & Savitzky 1976; Schwalm et al. 1977; McDiarmid 1978; Greer & Wells 1980; Villa 1980; Wells & Schwartz 1982; Ardila-Robayo 1983; Hayes 1983; Lynch et al. 1983; Villa 1984; Zimmerman & Bogart 1984; Heyer 1985; Jacobson 1985; Cannatella & Lamar 1986; Jungfer 1988; Ibáñez 1993; Marquez et al. 1996; Grant et al. 1998; Bolívar et al. 1999; Lötters & Köhler 2000; Hero et al. 2001; Bernal et al. 2004; Puschendorf et al. 2004; Guayasamin & Barrio-Amorós 2005; Señaris & Ayarzagüena 2005, Hawley 2006). Further, while the morphology of centrolenid adults, eggs, and larvae provides some interesting glimpses of their life history (e.g., miniaturization, osseous spines, novel dermal chromatophores, tadpole adaptations to fossorial life in stream bottoms), investigations on comparative and developmental morphology and descriptions of tadpoles are also limited (Eaton 1958; Duellman & Tulecke 1960; Starrett 1960; Lynch & Duellman 1973; Duellman 1978; Schwalm & McNulty 1980; Villa & Valerio 1982; Heyer 1985; Hero 1990; Hayes & Starrett 1980; Lynch et al. 1983; Cadle & McDiarmid 1990; Mijares-Urrutia 1990; Ruiz-Carranza & Lynch 1991a–b; 1997; Sanchiz & De la Riva 1993; Rueda-Almonacid 1994; Wild 1994; Jaramillo et al. 1997; Myers & Donnelly 1997; Ibañez et al. 1999; Fab-

rezi & Langone 2000; Barrera-Rodríguez 2000; Myers & Donnelly 2001; Savage 2002; Noonan & Bonett 2003; Hoffmann 2004; Señaris & Ayarzagüena 2005; Cisneros-Heredia & McDiarmid 2006a).

The phylogeny of centrolenids remains poorly understood. The monophyly of the family Centrolenidae has been supported consistently by morphological, behavioral, and molecular synapomorphies (Ruiz-Carranza & Lynch 1991a; Burton 1998; Cisneros-Heredia & McDiarmid 2006a; Frost et al. 2006; Guayasamin et al. 2006c). However, relationships among centrolenid species remain largely unresolved. Morphological studies have produced a number of phenetic groups, which have been proposed and retained mainly as units of convenience facilitating taxonomic work. Such arrangements have not withstood the tests of time because the phylogenetic hypotheses and accompanying taxonomies have been shown to be problematic as more data (characters and taxa) are accumulated (Starrett & Savage 1973; Lynch & Duellman 1973; Cadle & McDiarmid 1990; Ruiz-Carranza & Lynch 1991a; Señaris & Ayarzagüena 2005; Cisneros-Heredia & McDiarmid 2006a; Guayasamin et al. 2006c, Cisneros-Heredia & Meza-Ramos 2007). Recent molecular studies have provided some insights into the phylogeny of the centrolenids. Darst and Cannatella (2004), Faivovich et al. (2005), Wiens et al. (2005), Frost et al. (2006), and Grant et al. (2006) found that centrolenid genera currently in use are non-monophyletic, but these studies were not focused on centrolenids specifically and included only a small portion of the diversity of centrolenids. As a result, no satisfactory phylogenetic hypothesis is available. Further, the understanding of the phylogeny of glassfrogs is limited by species-level taxonomic problems, including incorrect description of characters, incomplete analyses of intraspecific variation, and lack of appreciation of species diversity.

The most generally accepted view of centrolenid systematics is based on the system proposed by Ruiz-Carranza and Lynch (1991a–d, 1995a–d, 1996, 1997, 1998). Their monumental works, based on an explicitly phylogenetic framework, brought some order to the previous chaos where nearly everything was dumped into a single genus (*Centrolenella*). Ruiz-Carranza & Lynch (1991a) divided the species of centrolenids among three genera, *Centrolene* Jiménez de la Espada, 1872, *Cochranella* Taylor, 1951, and *Hyalinobatrachium* Ruiz-Carranza & Lynch, 1991a. *Centrolene* and *Hyalinobatrachium* were defined by having humeral spines in male *Centrolene* or bulbous liver in *Hyalinobatrachium*, characters originally conceived as unique and unreversed synapomorphies. At present, these two genera include about one-half of the named species of glassfrogs. The other half is placed in *Cochranella*, a heterogeneous group of species united by plesiomorphic characters (i.e., absence of humeral spines in males and lobed liver). However, recent investigations of several new species of centrolenids have led to the discovery of morphological characters that conflict with these hypotheses of centrolenid systematics (Noonan & Harvey 2000; Duellman & Señaris 2003; Cisneros-Heredia & McDiarmid 2006a; Guayasamin et al. 2006c, Cisneros-Heredia & Meza-Ramos 2007). Ruiz-Carranza & Lynch´s system is not perfect as this and other recent papers have made clear, but it was a major step forward and greatly facilitated the work accomplished over the last 16 years.

Recent molecular studies have challenged the monophyly of *Centrolene* and *Cochranella* (Darst & Cannatella 2004; Faivovich et al. 2005; Wiens et al. 2005; Frost et al. 2006; Grant et al. 2006), and while compelling evidence supports the monophyly of the *Hyalinobatrachium fleischmanni* group (Ruiz-Carranza & Lynch 1998; Barrera-Rodríguez 2000; Señaris & Ayarzagüena 2005; Cisneros-Heredia & McDiarmid 2006a; Guayasamin et al. 2006c), the phylogenetic relationships of the other two species-groups placed in *Hyalinobatrachium* are unclear—i.e., *pulveratum* group and *parvulum* group (Starrett & Savage 1973; Ruiz-Carranza & Lynch 1991a; Señaris & Ayarzagüena 2005; Cisneros-Heredia & McDiarmid 2006a). While the recent assignment of species of the *Hyalinobatrachium pulveratum* group to *Cochranella* (Cisneros-Heredia & McDiarmid 2006a) has helped to "clean-up" *Hyalinobatrachium*, relationships among the species of *Cochranella*, the most diverse genus of glassfrogs, are still unresolved (Ruiz-Carranza & Lynch 1991a; Señaris & Ayarzagüena 2005; Cisneros-Heredia & McDiarmid 2006a–b; Frost 2006; Guayasamin *et al.* 2006b–c; Aguayo & Harvey 2006). *Cochranella* has been often regarded as a convenient group to hold glassfrogs that do not fit in the putatively monophyletic *Centrolene* or *Hyalinobatrachium*.

Inside each genus, several phenetic species-groups have been proposed. Characters related to the eye size, peritoneal pigmentation (parietal and visceral peritonea), amount of hand webbing, bone coloration, and vomerine teeth have been used to define these species-groups. Ruiz-Carranza and Lynch (1991a, 1995a) proposed three species groups inside each centrolenid genus. Duellman and Señaris (2003) proposed a fourth species-group for *Centrolene*, and Señaris and Ayarzagüena (2005) a fourth species-group for *Cochranella*. Savage (2002) proposed restricting the genus *Centrolene* to the largest species with humeral spines—the *geckoideum* group in part, while resurrecting the genus *Centrolenella* Noble, 1920 for the small species with humeral spines. This proposal has not received wide acceptance. Most species-groups are problematic because many species do not match current definitions, show intermediate conditions, or contradictory combinations of characters. An important factor exacerbating the inadequate knowledge of centrolenid relationships is the problematic descriptions of several species. Several species were differentiated based on erroneous diagnoses due to confusion of the characters involved and insufficient understanding on their intra and interspecific variation. Further, our incomplete knowledge of the diversity of this group of amphibians is highlighted by the large number of species described in recent years. New species will certainly be discovered in the future by surveys of poorly explored areas (e.g., Bolivia: Harvey & Noonan 2005; Aguayo & Harvey 2006; Ecuador: Cisneros-Heredia & McDiarmid 2006a; Guayasamin et al. 2006c; Cisneros-Heredia & Meza-Ramos 2007) and the study of museum collections (Cannatella & Duellman 1982; Cisneros-Heredia & McDiarmid 2002, 2003, 2004a–b, 2006a; Cisneros-Heredia et al. 2006).

Since the 1970s, one of us (RWM) has been studying different biological and evolutionary aspects of centrolenid biology (McDiarmid & Adler 1974; McDiarmid 1975; Schwalm, Starrett & McDiarmid 1977; McDiarmid 1978; McDiarmid & Savage 1984; Flores & McDiarmid 1989; Cadle & McDiarmid 1990). In 2002, the authors of this paper joined as part of the Research Training Program of the National Museum of Natural History, Smithsonian Institution, and started to work on descriptions of new species of glassfrogs (Cisneros-Heredia & McDiarmid 2002). Since 2002, we have been working together on the diversity, taxonomy, biogeography, and conservation biology of centrolenids (Cisneros-Heredia & McDiarmid 2002, 2003, 2004a–b, 2005a–b, 2006a–b, in press; Cisneros-Heredia et al. 2006), and the IUCN Red List–GAA accounts (Bolívar et al. 2004c, 2004e–f, 2004h–i; Coloma et al. 2004c–l, 2004n; Kubicki et al. 2004; Rodríguez et al. 2004b; Solís et al. 2004d; Cisneros & Lynch 2006). Based on our work, we present this paper with the following goals: (1) to define the diagnostic characters used in the taxonomy of Centrolenidae, providing a reference for future workers use; (2) to comment on and analyze the variation in these diagnostic traits; (3) to review the generic and species-level taxonomy of Centrolenidae, propose the recognition of a new genus and the description of a new species from Ecuador; and (4) to present an annotated list of the species of glassfrogs from the Republic of Ecuador.

**Materials and Methods**

To avoid confusion due to differences between past, current, and future taxonomical proposals, we use binominals only when proposing taxonomic changes or when referring to the specific use of the name of a particular taxon. Elsewhere we refer to taxa using only their species name (e.g., *prosoblepon*). We also include several species that are undescribed or of unclear identity by referring to their localities as informal names within quotes (e.g., "Palenque" in reference to an undescribed species from the Rio Palenque Research Center in Ecuador) or as they have been reported in the literature (e.g., "*Cochranella* sp. N2" of Cisneros-Heredia & McDiarmid 2006a). The following abbreviations are used in the text: *Ce.* = *Centrolene*, *Co.* = *Cochranella*, *H.* = *Hyalinobatrachium*, *s.s.* = *sensu stricto*, *s.l.* = *sensu lato*.

This revision is based largely on data assembled from the direct study of nearly 1100 specimens of Centrolenidae from ca. 75% of the species in the family (see Material Examined). Information on the remaining

25% of the described species was obtained from the literature (e.g., Heyer 1978, 1985; Duellman & Schulte 1993; Savage 2002; Señaris & Ayarzagüena 2005; Harvey & Noonan 2005; Guayasamin *et al*. 2006b–c), from the study of photographs (types of *Centrolenella altitudinale*, *Centrolenella buckleyi venezuelensis*, and *Centrolenella gemmata*, available from MCZ collection database at http://collections.oeb.harvard.edu/Herp/AmphSearch.htm), and from direct communication with experienced herpetologists (see Acknowledgments). The collections that provided access to specimens are listed below along with the abbreviations used for them in the text:

| | |
|---|---|
| American Museum of Natural History, New York; | AMNH |
| The Natural History Museum, Department of Zoology, London; | BMNH |
| División de Herpetología, Museo Ecuatoriano de Ciencias Naturales, Quito; | DHMECN |
| EcoCiencia, Fundación Ecuatoriana de Estudios Ecológicos, Quito; | EcoC |
| Departamento de Biología, Escuela Politécnica Nacional, Quito; | EPN |
| Fundación Herpetológica G. Orcés, Quito; | FHGO |
| Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá; | ICN |
| Instituto Nacional de Recursos Naturales Renovables, INDERENA, colección de anfibios, Colombia (now Instituto Alexander von Humboldt, IAvH; specimens examined at ICN); | IND-AN |
| The University of Kansas, Natural History Museum, Lawrence; | KU |
| Museum of Comparative Zoology, Harvard University, Cambridge; | MCZ |
| Museo de Historia Natural, Universidad Nacional Mayor San Marcos, Lima; | MHNSM |
| Museum National d'Histoire Naturelle, Paris; | MNHN |
| Oklahoma Museum of Natural History, Norman; | OMNH |
| Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito; | QCAZ |
| National Museum of Natural History, Washington, D.C.; | USNM |
| Universidad San Francisco de Quito, Quito; | DFCH-USFQ |

The geographic placement and elevation at collection localities were determined using collector's field notes and museum records and revised in accord with the 2000 physical map of the Republic of Ecuador (1:1'000 000) (IGM 2000), and NGA (2006). Classification of vegetation formations in Ecuador follows Sierra (1999), and that of zoogeographic regions follows Albuja et al. (1980) as modified by Cisneros-Heredia (2006).

General characters and terminology used herein follow definitions by Ruiz-Carranza and Lynch (1991a) and Cisneros-Heredia and McDiarmid (2006a). Webbing formulae follow the method of Savage & Heyer (1967), as modified by Guayasamin *et al.* (2006b–c) (Fig. 1). Eye direction angle was calculated as proposed by Wild (1994), and eye diameter was measured following Campbell (1994) (Fig. 2). Sex and sexual maturity was determined by direct examination of the gonads and evaluation of the development of secondary sexual characters. Adult male centrolenids have the following conditions: enlarged testes, developed dorsal spicules [interspecific variation], vocal slits, developed nuptial pads [interspecific variation], humeral spines [interspecific variation]; and adult females have convoluted oviducts or oviductal eggs, and lack nuptial pads and vocal slits. Relative digits lengths were determined by adpressing adjacent digits one to another (Fig. 2). The following measurements, preceded by their abbreviations as cited in the text, were taken with electronic digital calipers (0.05 mm accuracy) at least three times each (Fig. 1–2):
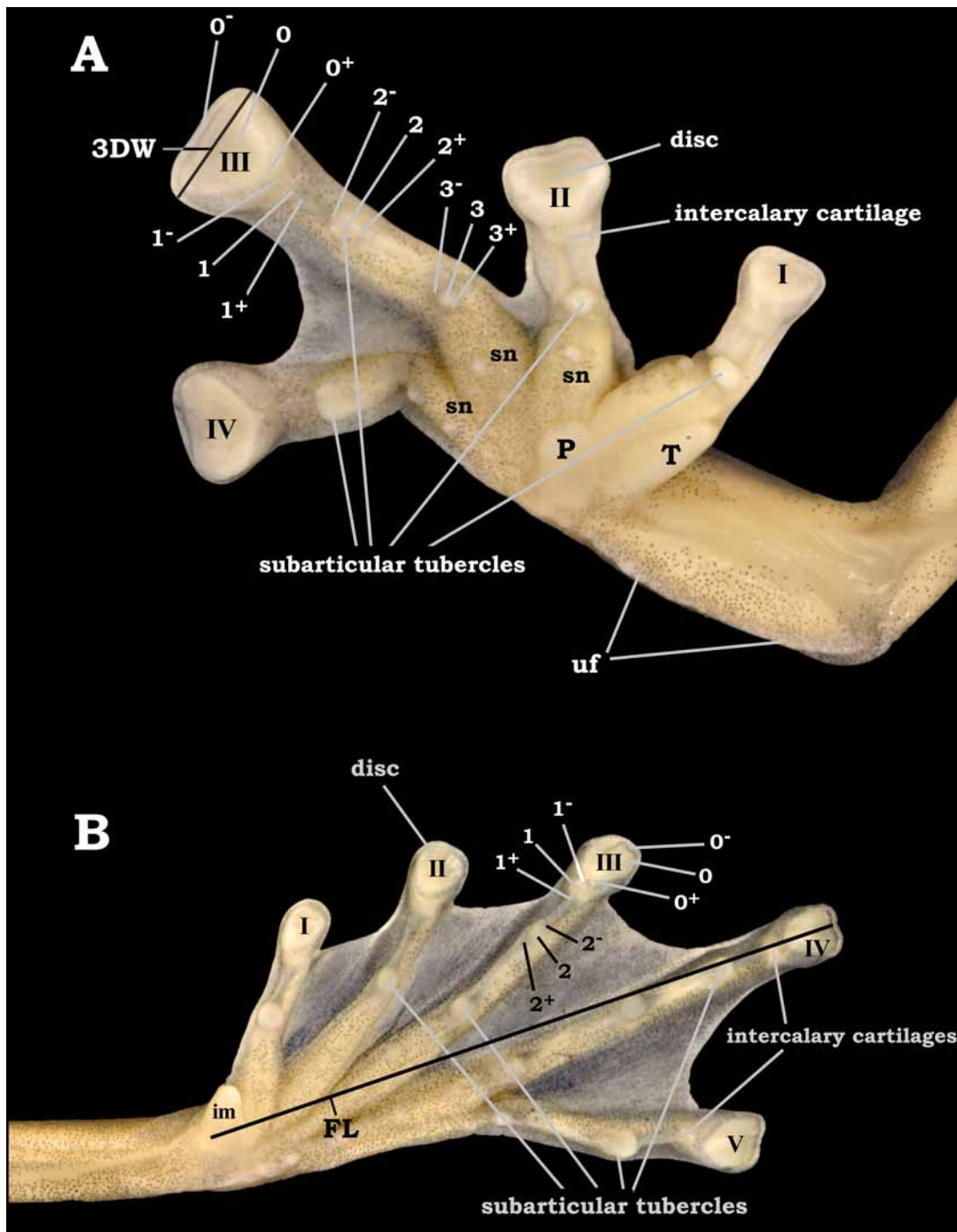
**FIGURE 1.** Measurements and structures of hand and foot of centrolenid frogs. (A) Right hand and distal section of forearm in palmar (ventral) view [SC]. (B) Left foot and distal section of tarsus in palmar view [SC]. Fingers and toes are numbered in order from innermost to outermost (indicated by Roman numerals). Abbreviations: T = thenar tubercle, P = palmar tubercle, sn = supernumerary tubercles, im = inner metatarsal tubercle, 3DW = width of disc on the third finger, FL = foot length. Each finger and toe has one intercalary cartilage (always distal, below disc), and at least one subarticular tubercle; only toe IV has three subarticular tubercles. Webbing formular notations of hand and foot follow the proposal by Savage and Heyer (1967) as modified by Guayasamin et al. (2006b); the following Arabic numerals are used: 0 is assigned to the disc, 1 to the intercalary tubercle, and 2–4 to the subarticular tubercles; these numbers represent the number of phalanges free of webbing (totally or partially). When the web reaches the distal margin of the structure (disc, intercalary tubercle or subarticular tubercle), a minus sign (–) is attached to the Arabic number; when it reaches the proximal margin, a plus sign (+) is attached; and when the web reaches the middle of the structure no sign is attached. When the web reaches a point between structures (between subarticular tubercles or between the intercalary tubercle and the distal subarticular tubercle), not getting to the margins, a notation with fractions is appropriate (e.g., $^1/_2$ when the web reaches a midpoint, or $^2/_3$ when the distal two-thirds of the phalanx are free).
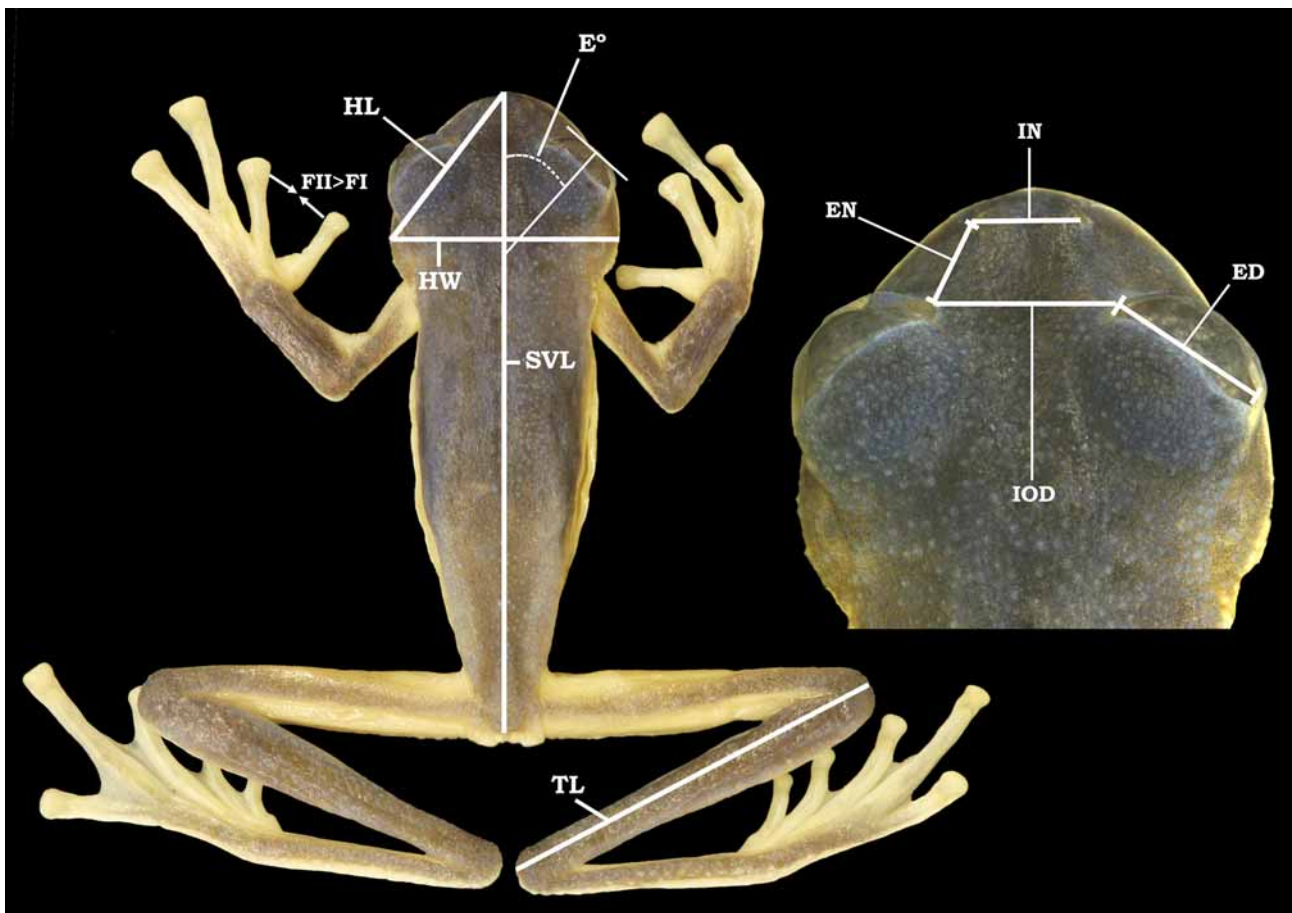
**FIGURE 2.** Standard measurements for centrolenid frogs and size ratio between finger I and finger II when adpressed. Abbreviations: SVL = snout-vent length, HW = head width, HL = head length, ED = horizontal eye diameter, IOD = inter-orbital distance, EN = eye-nostril distance, IN = internarial distance, TL = tibia length, E° = eye direction angle, FI = finger I, FII = finger II (for 3DW and FL see Fig. 1). [SC].

SVL   Snout-vent length,

HW    Head width measured at the corners of the mouth,

HL    Head length, measured 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, measured 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,

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.

    Credits for photographs are placed between brackets and are as follows: SC = Sebastián Cruz, JD = Jesse Delia, WED = William E. Duellman, AR = Arthur Georges, BK = Brian Kubicki, MR = Marco Rada, GR = Gilson Rivas, ETJB = Evan Twomey and Jason Brown, VVA = Viviana Vidal Astudillo, MYM = Mario Yánez-Muñoz, RWM = Roy W. McDiarmid, DFCH = Diego F. Cisneros-Heredia.

**Analysis of the diagnostic characters of Centrolenidae**

We identify 23 characters that are useful, in combination, in diagnosing centrolenid species. Lynch and Duellman (1973) were the first to suggest most of the diagnostic characters, but several authors have revised and added to them (Flores 1985; Heyer 1985; Cadle & McDiarmid 1990; Ruiz-Carranza & Lynch 1991a, 1991b; Wild 1994; Harvey 1996; McCranie & Wilson 1997; Noonan & Bonett 2003; Señaris & Ayarzagüena 2005; Cisneros-Heredia & McDiarmid 2006a; Guayasamin *et al.* 2006a–c; Cisneros-Heredia & Meza-Ramos 2007; Cisneros-Heredia & Yánez-Muñoz 2007b). For all characters, we present an analysis of the available information to provide an overview of their variation, and in certain cases, we propose expanded or revised definitions.

Previous authors (see Lynch & Duellman 1973) have used a numbered sequence of these characters, organized in order of importance. We consider that all characters are equally useful for different centrolenid taxa, and herein employ a more concise arrangement of the diagnostic characters, organized into anatomical and behavioral sequences as follows: teeth and head characters (1–3), skin (4–5), internal anatomy (6–7), limbs (8–14), coloration (15–18), behavior and reproductive biology (19–22), and SVL (23). We trust that future researchers will find this arrangement to be useful in their work.

*(1) Vomerine teeth.* Most species of centrolenids show no intraspecific variation in the presence or absence of vomerine teeth, and the condition is useful in combination with additional character to diagnose species. However, the condition of vomerine teeth is variable in at least the following taxa: *andinum*, *prosoblepon*, *cristinae*, and *cochranae* (Lynch & Duellman 1973; Ruiz-Carranza & Lynch 1991a; Señaris & Ayarzagüena 2005; Guayasamin et al. 2006c; Cisneros-Heredia & McDiarmid pers. obs.). Accordingly, all specimens of a new species should be examined for this condition.

*(2) Snout* (Fig. 3). In dorsal view, the form of the snout may be truncate (e.g., *cochranae*), subovoid (*pulverata*), or rounded (*cariticommata*). In profile or lateral view, the snout may be sloping or gradually inclined (*resplendens*), truncate (*mariaelenae*), or rounded (*adiazeta*). The shape of the nostril region affects the snout form and protruding nostrils usually produce bluntly truncate conditions both in dorsal and lateral views. Intraspecific variation in the form of the snout has been detected in certain species, and intermediate conditions particularly in profile are common (e.g., *puyoensis* has a truncate or round snout in profile, and *posadae* has a subovoid or truncate snout in dorsal view and slightly anteroventrally sloping or truncate one in profile). Some changes in the form of the snout and overall head shape likely are preservation artifacts, especially from desiccation. For example, desiccated specimens often show a post-cephalic constriction, otherwise absent in well-preserved specimens (but see comments about the presence in life of post-cephalic constriction in some specimens of *duranti*, Señaris & Ayarzagüena 2005).

*(3) Tympanum.* A tympanum is present in all species in Centrolenidae, but the visibility, shape, and orientation may vary interspecifically. In most species, a supratympanic fold is present above the tympanum, usually concealing its upper portion. The most evident feature of the tympanum in most centrolenids is the tympanic annulus, while the tympanic membrane itself may vary by being similar in coloration to the surrounding skin or clearly differentiated. Some species have the entire structure (annulus and membrane) clearly visible (e.g., *petrophilum*), while in other species just the annulus is usually evident (e.g., *cariticommata*), in some species the tympanum is entirely concealed and neither the membrane nor the annulus is evident (e.g., *buckleyi*). The tympanum is very sensitive to preservation, and poorly preserved specimens often present distorted tympana, including over or under expressions of the supratympanic fold.

*(4) Dorsal skin texture.* The general dorsal skin texture of centrolenids may be smooth (e.g., *medemi*), microspiculate (very small and closely packed spicules only visible under magnification usually distributed across the dorsum, e.g., *puyoensis*, *luteopunctata*), finely shagreened (e.g., *fleischmanni*), shagreened (e.g., *cochranae*), coarsely granular (*megacheira*), pustular (*heloderma*), or rugose (a condition we

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recently observed in an undescribed species, characterized by having irregular, low wrinkles on an otherwise smooth surface). Many species have different types of dermal elevations on the dorsum of the body, arms, and legs: warts (low, wider that high, and flat), tubercles (elevated, higher than wide, and rounded), and spicules (elevated, higher than wide, conic and pointy, and usually present profusely in reproductive males). Some species, like *acanthidiocephalum*, show spicules over the warts, but in most species, the spicules are not directly linked to tubercles or warts. Dorsal light spots usually yellow, orange or green (produced by iridophores or xanthophores) are associated with warts or tubercles in many species (e.g., *grandisonae, anomala*, *resplendens*), while spicules are typically rather transparent or cream (without associated chromatophores). Lynch and Duellman (1973) established the term enameled to describe "the shiny white elevations found in the skin of some centrolenids" like *resplendens*. The term is used to characterize all kinds of elevations and folds with white pigment (iridophores, sometimes in combination with glandular tissues), not only tubercles but also warts, dermal folds, and flaps.
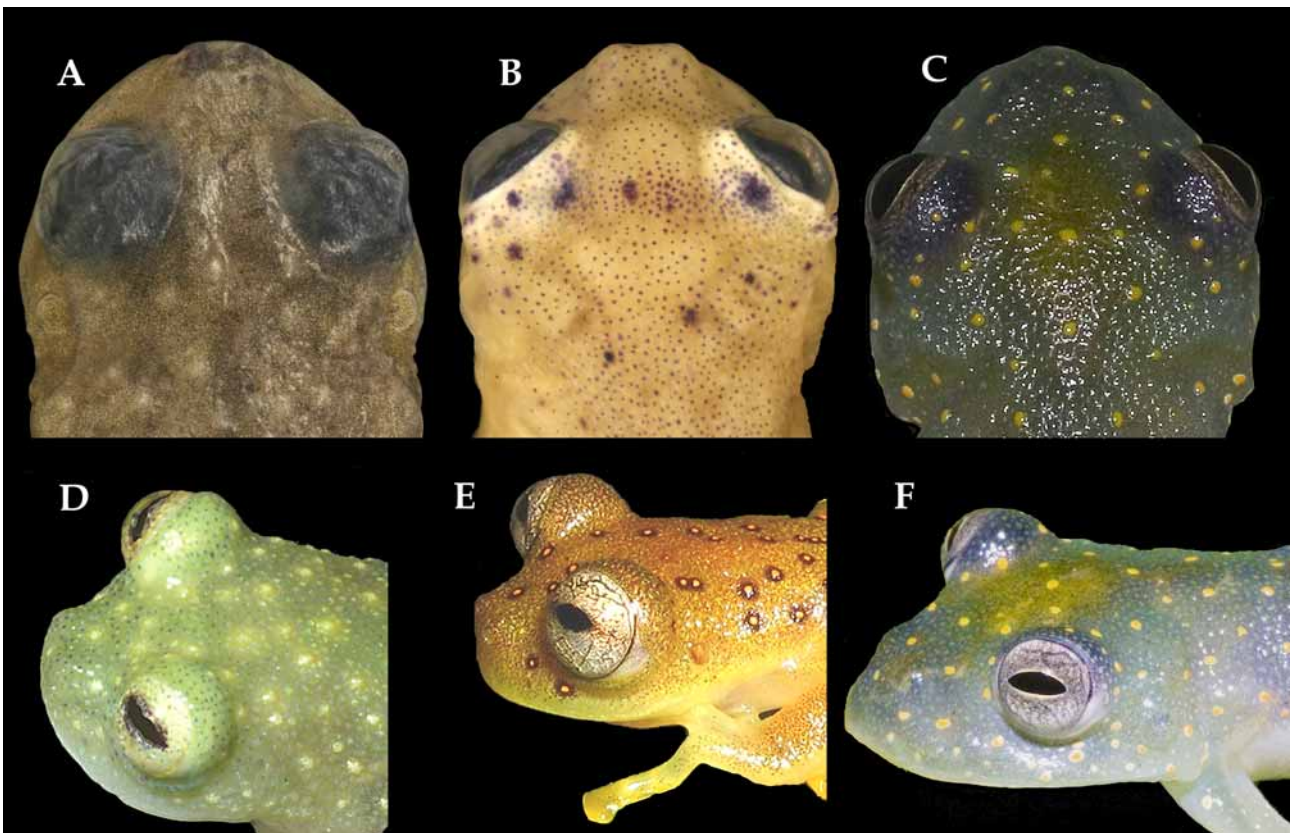


**FIGURE 3.** Most common snout forms in centrolenid frogs. Dorsal view: (A) rounded—*Cochranella* sp. 4 [SC], (B) truncate—*mariaelenae* [SC], (C) subovoid—*mache* [JD]. Lateral view: (D) rounded—*pellucidum* [RWM], (E) truncate—*ignotus* [VVA], (F) sloping—*mache* [JD].

The presence of spicules in most species of centrolenids varies with age and reproductive condition of the specimen (Ruiz-Carranza & Lynch 1991a). Sexually active adult males usually develop abundant, conspicuous spicules, especially on the upper lip and the dorsum of the head and body, while spicules are absent or scarce and low in non-reproductive males, females, and juveniles. The size and concentration of spicules varies among sexually active males; sexually active males with poorly developed spicules are frequently found in the same population at the same time as males with enlarged and conical spicules. Harvey and Noonan (2005) mentioned the presence of melanophores arranged in circular clusters with the same distribution as spicules in *spiculata*, and suggested that they constitute germinal structures associ-

ated with the seasonal appearance of spicules. We have observed similar clusters of melanophores on the dorsum of males of *posadae*. Most sexually active males of this species have the dorsum entirely covered by spicules; but some other sexually active males (with vocal slits and well-developed nuptial excrescences) have clusters of melanophores, especially on the sides of the body and on the limbs, in places where there are no spicules. Under magnification, small dermal elevations (apparently spicules in development) occur over some of the clusters of melanophores. Our observations support Harvey and Noonan's (2005) hypothesis on the germinal nature of the clusters.

*(5) Cloacal ornamentations* (**Fig. 4**). In general, the ventral skin below the vent of most centrolenids is highly granular and enameled (=white). On the ventral surface of the thighs, just below the cloaca, most species have two subcloacal warts that are distinct from the surrounding granular skin by being larger and elevated. The presence of these warts shows interspecific but not intraspecific variation, and they are always paired. In addition, some species of centrolenids have a variety of cloacal ornamentations, varying from simple folds (e.g., *pellucidum*) to intricate ornamentation involving enameled tubercles, folds, and crenulated flaps (e.g., *resplendens*, *mache*, *uranoscopum*). The most complex ornamentation usually occurs to the sides of the cloaca, and may include warts and tubercles of different sizes, dermal folds (low), and dermal flaps (fleshy). When present, these structures are often enameled and formed by glandular tissue. The degree of expression and coloration of these ornamentations shows extensive intraspecific variation, apparently related to the age, sex, and reproductive condition when preserved, and is sensitive to preservation with poorly preserved specimens (due to wrong position of the legs or desiccation) showing distorted cloacal ornamentations, including over or under expressions of the folds and tubercles (Heyer 1978, 1985; Cisneros-Heredia and McDiarmid pers. obs.).

*(6) Color of peritonea* (**Fig. 5a–b**). A white semi-solid substance covers various parts of the peritonea of different species of centrolenids. The pigment cells involved in this coloration are called iridophores or guanophores. We use the term "iridophore" in this document since it has a wider academic use (Google Scholar search returned ca. 200 results for "guanophores" and ca. 800 for "iridophores"), but both terms refer to the same cellular structure. Iridophores reflect light using plates of crystalline schemochromes made from guanine and other purines (Taylor 1969). Iridophores are present on both the parietal and visceral peritonea of centrolenids, including the pericardial (covering the heart), gastrointestinal (covering the digestive tract, including esophagus, stomach, and intestines), hepatic (covering the liver), and urogenital peritonea (covering the urinary bladder, renal capsules [kidneys], and testes). Ventral dissection is usually the best method to determine the state of the peritonea. Simple external examination is not adequate and is strongly discouraged because of the difficulties of differentiating the presence and extent of the iridophores between the parietal and visceral peritonea, and because the ventral skin often impedes the accurate observation of organs like heart, liver, kidney, and testis. Descriptions of the peritoneal pigmentation in many species of centrolenids are highly heterogeneous, and several species have been described based on external examination, resulting in erroneous descriptions (e.g., *peristictum*, *croceopodes*, *griffithsi*, and *orejuela*). Most specimens retain the silvery white pigment on the peritonea after many years in preservative, but preservation sometimes affects the presence and extent of the iridophores. Specimens exposed to extended periods of light or fixed for long periods in formalin are apparently more affected (Starrett & Savage 1973; Ruiz-Carranza & Lynch 1991a; Harvey & Noonan 2005; Cisneros-Heredia & McDiarmid 2006a; pers. obs.).

Patterns of distribution and extent of iridophores (= silvery white pigment) on the ventral parietal peritoneum are represented by the following discrete states (P = parietal peritoneum):

(P0)   Iridophores absent on the ventral parietal peritoneum—clear parietal peritoneum (e.g., *fleischmanni*, *munozorum*, *mariaelenae*, *pulverata*, *antisthenesi*) (Fig. 5A);

(P1)   Iridophores barely covering the anterior part (¼) of the parietal peritoneum (e.g., *oyampiensis*, *ametarsia*), sometimes as a bib-like patch (heart not visible) (e.g., *gorzulai*, *lema*) (Fig. 5A);

(P2)   Iridophores covering at least ⅓ of the parietal peritoneum (e.g., *mache*) (Fig. 5A);

(P3)   Iridophores covering between ½ to ⅔ of the parietal peritoneum (e.g., *buckleyi*, *petrophilum*, *puyoensis*) (Fig. 5A);

(P4)   Iridophores covering almost the entire parietal peritoneum, sometimes to the region of the groin (e.g., *geckoideum, acanthidiocephalum*) (Fig. 5A).
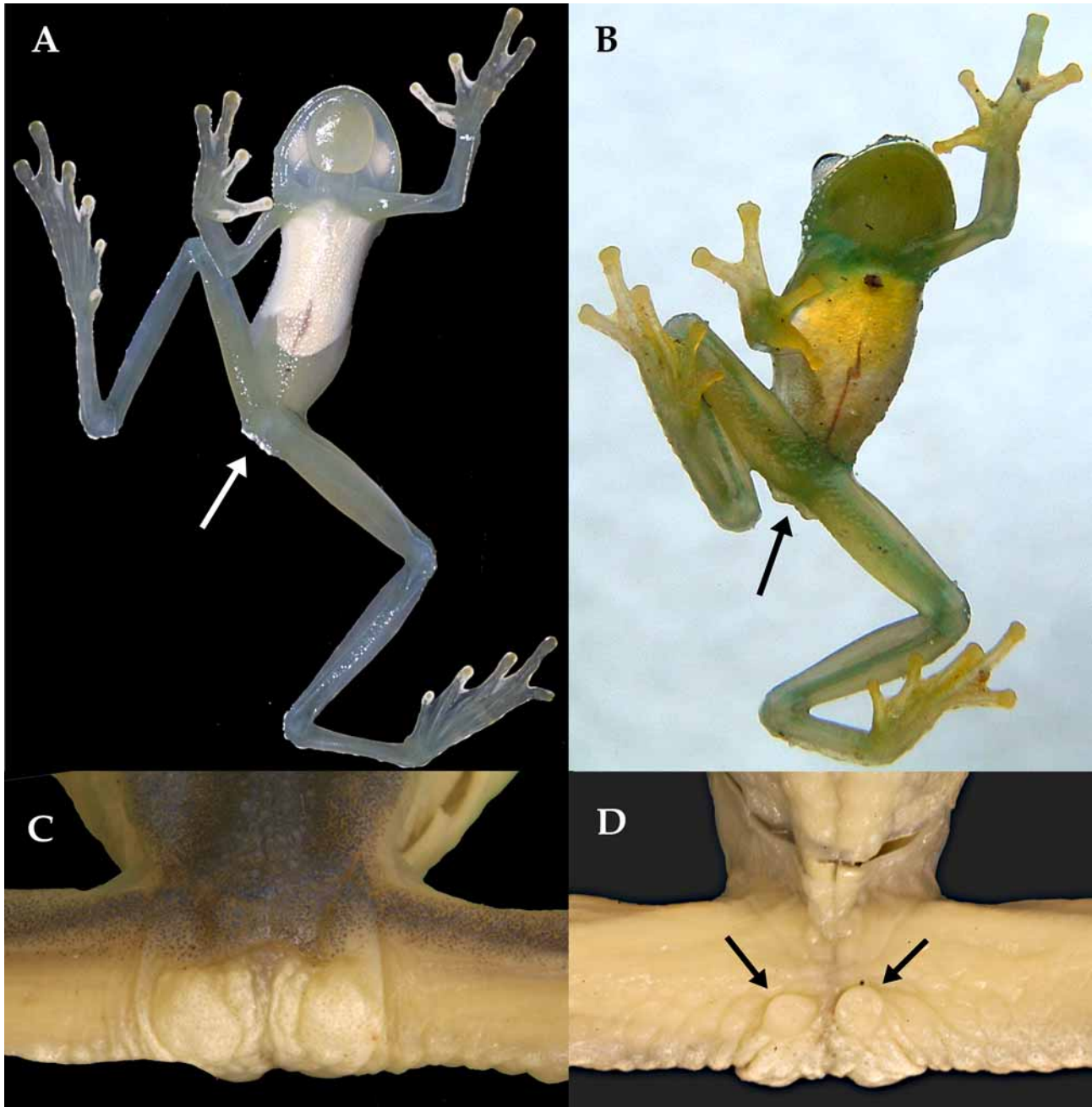


**FIGURE 4.** Cloacal ornamentation in centrolenid frogs. (A) ventral view of *mache*, arrow points to the enameled (white pigmented) cloacal flaps [JD]; (B) ventral view of *resplendens*, arrow points to the cloacal flaps [ETJB]; (C) posterodorsal view of *posadae* showing the enameled swollen area and enameled cloacal folds below the cloacal opening, and the enameled granular area on the posterior surface of the legs [SC]; (D) ventral view of the area between the legs (subcloacal area) of *posadae* showing the two enlarged subcloacal tubercles (arrows) and the enameled swellings, folds, and granular area shown in previously [SC].

In most species, the iridophores of the parietal peritoneum line the dorsal side of the body cavity to

the same extent they line the ventral side, but they are not visible externally because of the dorsal muscles and colored skin. Two distinctive species (i.e., *iaspidiense* and *nouraguensis*) have iridophores absent on the ventral portion of the parietal peritoneum (P0), but show large blotches of white pigment on the dorsal side. We have not established if the iridophores are in or below the skin, but these blotches are visible in dorsal view due to the transparency of the skin. In life, they are colored like the dorsal skin (greenish or yellowish) but in preservative they appear silvery white (Fig. 5AII). Another species, *balionota*, also has a rather transparent dorsal skin, and two large oval patches of iridophores (on the dorsal side of the parietal peritonea) are evident toward the flanks and sides of the dorsum.
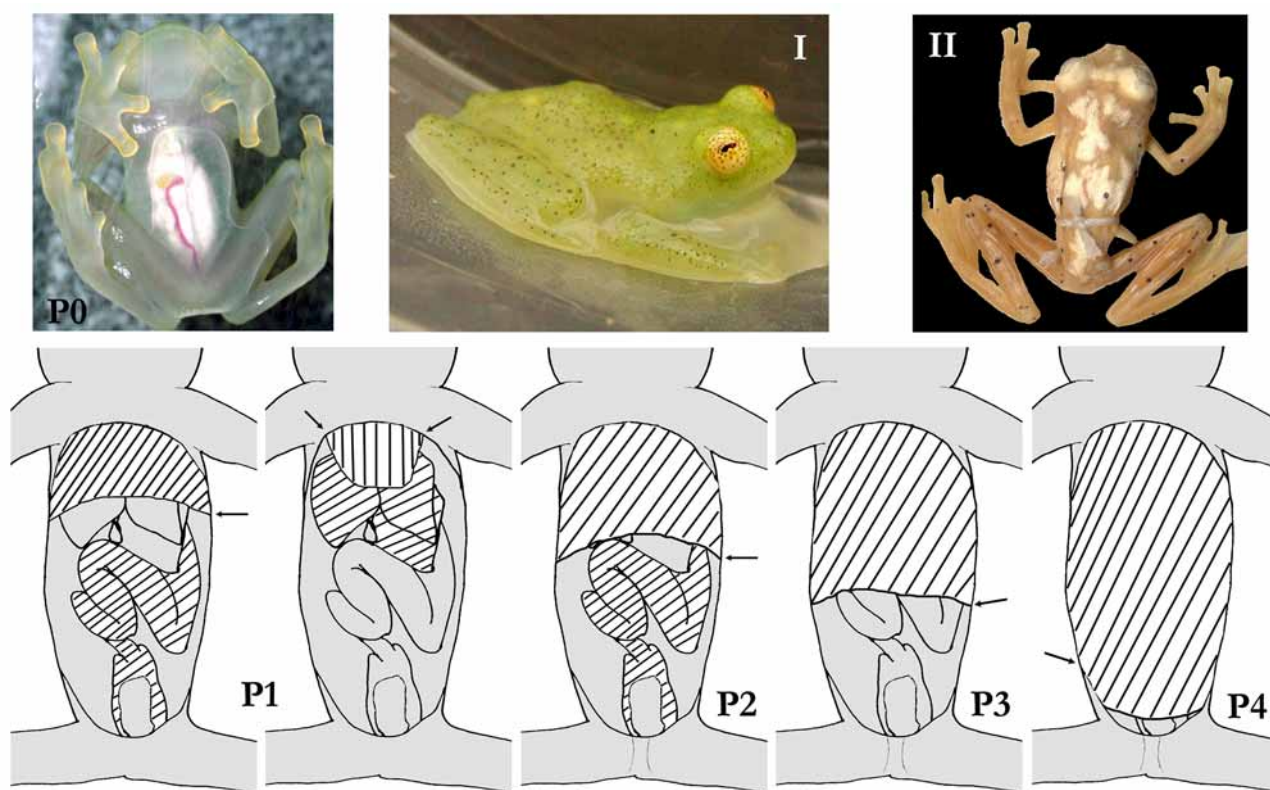


**FIGURE 5A.** Schematic drawings and photographs of the conditions and arrangements of the parietal peritoneum (P0 to P4) and dorsal coloration in *Hyalinobatrachium* (I and II). Color code: grey = without white pigment (iridophores); barred white = covered by white pigment (iridophores). Conditions are shown without dissection, and some of the internal organs are visible beneath; arrows point to the limits of the parietal peritoneum. I = Photo of *ruedai* showing the absence of iridophore-delimited dorsal blotches [DFCH]; II = Photo of *iaspidiense* showing the white dorsal blotches of iridophores [GR].

Señaris and Ayarzagüena (2005) reported a unique design on the parietal peritoneum of *revocata* Rivero, 1985, with the white pigment covering ½ to ⅔ of the parietal peritoneum and with white lateral extensions covering the flanks of the venter. The white lateral extensions are lost in preservative and do not correspond to iridophores, but instead are muscles of the flanks (Señaris and Ayarzagüena 2005) and as such are not considered part of the variation of the parietal peritoneum pigmentation by iridophores. Some intraspecific variation occurs in the extent of the iridophores over the parietal peritoneum (*nola*, Harvey 1996; *buckleyi*, pers. obs.). A few species exhibit intraspecific variation and some individuals in the same population may be intermediate between conditions P3 and P4 (Cisneros-Heredia & McDiarmid pers. obs.).

Variation in the distribution of iridophores (= silvery white pigmentation) on the visceral peritonea falls into the following states (V = visceral peritonea):

(V0)   Iridophores absent on all visceral peritonea, including the pericardium. In some cases, this condition could be an artifact of preservation, but the absence of iridophores has been observed also in freshly euthanized specimens (e.g., *posadae*) (Fig. 5B).

(V1)   Iridophores covering only the pericardium; all other visceral peritonea clear (e.g., *geckoideum*, *acanthidiocephalum*, *cochranae*) (Fig. 5B). All specimens of the Andean *grandisonae* have this condition, but in addition, they show the peritoneum on the urinary bladder covered by iridophores (J. M. Guayasamin pers. comm.). The presence of iridophores on the urinary bladder was previously conceived as unique to the species from the Atlantic forest in southeastern South America (see condition V4).

(V2)   Iridophores covering the pericardium and parts or all of the gastrointestinal peritoneum, but not the hepatic peritoneum nor the urinary bladder (e.g., *ametarsia*, *cariticommata*, *granulosa*, *litorale*, *midas*, *resplendens*, *antioquiense*, *hybrida*, *litorale*, *peristictum*, *quindianum*) (Fig. 5B). The species *cariticommata* is the only reported as having iridophores restricted just to the esophageal peritoneum (Wild 1994); this condition may be overlooked in other species because the liver usually covers this section of the digestive tract.

(V3)   Iridophores covering the pericardial and hepatic peritonea; all other parts of the visceral peritoneum clear (e.g., *lema*) (Fig. 5B);
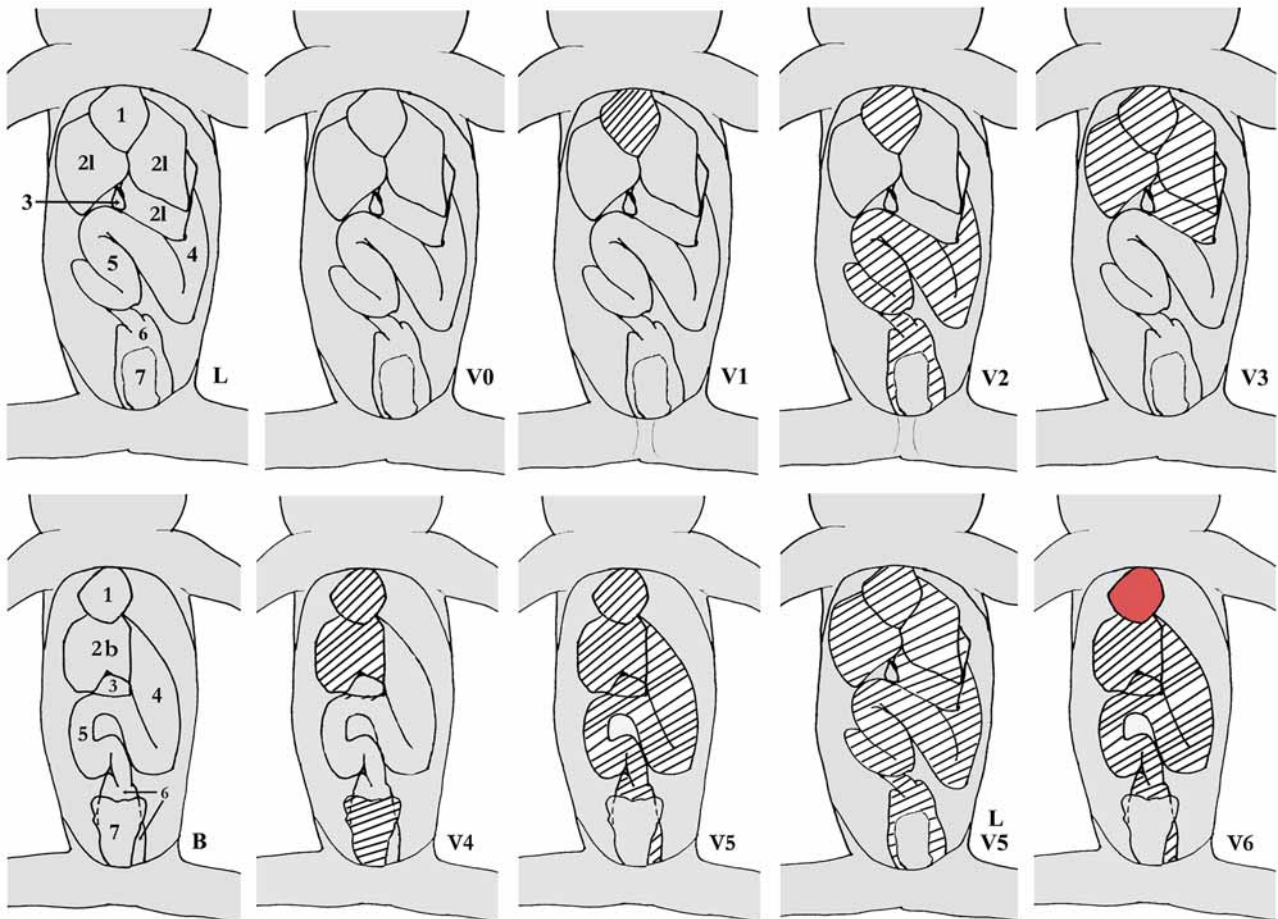


**FIGURE 5B.** Schematic drawings of the internal organs, and conditions and arrangements of the visceral peritonea (V0 to V6) after removal of ventral body wall and ventral parietal peritoneum. Color code: grey = without white pigment (no iridophores); barred white = covered by white pigment (iridophores); in V6, red = bare heart. Internal organs (B, L): 1 = heart, 2 = bulbous liver; 2l = lobed liver, 3 = gallbladder; 4 = stomach; 5 = small intestine; 6 = large intestine; 7 = urinary bladder. B = species with bulbous livers; L = species with lobed livers. Note that condition V5 is present in species with bulbous livers and those with lobed livers.

(V4)  Iridophores covering the pericardial, hepatic, and urinary bladder peritonea, all other parts of the visceral peritoneum clear (e.g., *eurygnathum*, *uranoscopum*) (Fig. 5B);

(V5)  Iridophores covering all parts of the visceral peritoneum—pericardium, digestive tract, and hepatic peritonea, except for the urinary bladder (e.g., *gorzulai*, *mariaelenae*, *oyampiensis*, *ruedai*) (Fig. 5B).

(V6)  Iridophores covering all visceral peritonea except for the urinary bladder and pericardium—bare heart condition (e.g., *munozorum*) (Fig. 5B).

Some centrolenid species show intraspecific variation in the concentration and extent of iridophores on the pericardium. The pericardium of most specimens of *geckoideum*, *buckleyi* or *cochranae* is usually covered by a dense layer of iridophores, but some individuals have only a thin layer, as a yellowish-white or golden pigmentation, and *pallidum* has been reported to have a pericardium usually covered by light golden pigmentation that turns transparent in preservative (intermediate state between conditions V0 and V1; Señaris & Ayarzagüena 2005; Cisneros-Heredia & McDiarmid 2006a). This golden coloration could be related to preservation in certain specimens, but in some cases, data were taken from freshly euthanized frogs. Variation on the iridophore layer of the pericardium in species with white parietal peritoneum (conditions P1–P4) has been overlooked because it usually remains hidden. However, in taxa with transparent parietal peritoneum (condition P0), conditions V5 and V6 have been considered important taxonomic character states, resulting in recognition of two different subgroups within the *fleischmanni* species-group of *Hyalinobatrachium* (white pericardium - condition V5, in the *fleischmanni* subgroup; and bare heart pericardium - condition V6, in the *chirripoi* subgroup; Ruiz-Carranza and Lynch 1998). In several species of *Hyalinobatrachium*, the pericardial peritoneum varies from being completely white, to partial, to transparent (no iridophores) in the same population (Cisneros-Heredia & McDiarmid 2006a; Guayasamin et al. 2006c). Some species, like *crurifasciatum* and *fleischmanni*, have conditions V5, V6, and intermediates in the same population (pericardium covered in some areas by white pigment but clear especially in the central or lower portions; Myers and Donnelly 2001; Señaris and Ayarzagüena 2005; Guayasamin *et al*. 2006c; Cisneros-Heredia and McDiarmid in press). We reject the recognition of two subgroups (*fleischmanni* and *chirripoi*) based solely on the pericardial coloration (Cisneros-Heredia & McDiarmid in press), and recognize that some species that show opposite pericardial coloration could be closely related (*munozorum*, *ruedai*, and *crurifasciatum*). Given our understanding of variation in this trait, we recommend that species diagnosis and separation based solely on the condition of the silver pigmentation on the pericardium be avoided. We suspect that certain species that currently differ from their closest relatives only in pericardial coloration are in fact synonyms (e.g., *nouraguensis* and *iaspidiense*; D. F. Cisneros-Heredia, R. W. McDiarmid, J. P. Caldwell, and G. Rivas unpubl. data).

Different combinations of parietal (P) and visceral peritonea (V) states are known in centrolenids. For example, in *geckoideum* iridophores cover almost the entire parietal peritoneum (P4) but they are present only on the pericardial portion of the visceral peritoneum (V1); in contrast, *chirripoi* has a clear parietal peritoneum (P0) and bare heart condition (V6). In fact, we have noticed an inverse relationship between the presence of iridophores on the visceral peritonea and their presence on the parietal peritoneum. In most species where iridophores cover all or most of the parietal peritoneum (P3, P4), the visceral peritonea usually lack iridophores (V0). In those species with the parietal peritoneum partially covered (P1, P2, and some P3), iridophores are present on various parts of the visceral peritonea, especially on those where transparency of the ventral skin left them exposed (V2). In all species that completely lack iridophores over the parietal peritoneum (P0), the visceral peritonea are mostly covered by iridophores (V4, V5, V6). The only apparent exception is *lema*, which shows just a bib-like patch of iridophores on the parietal peritoneum; yet *lema* has just the pericardial and hepatic peritonea covered by iridophores.

Except for *C. saxiscandens* that has abundant melanophores on the ventral surfaces (Duellman & Schulte 1993), the ventral skin of most centrolenids is essentially transparent and lacking chromatophores (Schwalm & McNulty 1980). It looks creamish colored or whitish when viewed externally due to the

underlying muscles (especially in medium or large species) and the reflection of the iridophores on the parietal/visceral peritonea. As species' SVLs diminish, the skin gets thinner, as do the muscles of the abdominal wall. In small taxa, like *Hyalinobatrachium*, even the dorsal skin is translucent to some degree. We hypothesize that the iridophore layer on centrolenids' peritonea provides a shield protecting the enzymatic activity occurring inside the gastrointestinal tract (and related viscera) against detrimental effects from external factors such as light and heat. In other frogs, protection would be supplied by their thick, non-transparent (with abundant chromatophores) ventral skins. The inverse relationship between the presence of iridophores over the parietal and visceral peritonea supports this hypothesis.

Furthermore, it is interesting to note that most if not all species with visceral iridophores exhibit some form of parental care behaviors (see "(21) Egg clutches and parental care" below; McDiarmid 1978; M. Rada, D.F. Cisneros-Heredia & P. Gutiérrez pers. obs.). Several centrolenid species exhibit exhibit parental care behavior wherein one of the parents, usually the male, remains nearby, next to, or even straddling the egg clutches on the upper or underside of leaves or on rocks (usually at night but in some species during day and night), sometimes for considerable periods. The clutches are usually placed on exposed surfaces allowing hatching tadpoles direct access to water. If a male is successful in attracting females to the site, he may continue to attend the clutches until all have hatched. In some instances, this may continue for a few weeks depending on the periodicity of female arrival. Under these conditions, guarding parents are subjected to extended stresful conditions (i.e., high levels of solar radiation, dry air currents, high temperatures) that may provoke high evaporative water loss (even in parents that retreat during the day, as they typically go to nearby leaves also located in exposed areas of the vegetation). In addition, during periods of clutch attendance, the guarding male apparently does little foraging but continues to call. We suggest that these males must reduce to some degree their metabolic activity during these periods of high activity and low food resources. When the calling period ends, guarding males are usually alert but quiet, just moving when disturbed. The maintenance of low metabolism, yet non-torpid state, means that they must have mechanisms to prevent poisoning by nitrogenous wastes that rapidly accumulate during these periods, and whose accumulation exacerbates osmotic problems caused by dehydration (Schmuck & Linsenmair 1988, Schmuck et al. 1988). In addition, the attending male is often in direct contact with the eggs, and nitrogenous wastes produced by the tadpoles during drier periods may be absorbed by the male during contact bouts to hydrate the eggs. Iridophores are know to have radiation reflective qualities and in some anurans reduce cutaneous water loss and function as an osmoregulatory mechanism to manage nitrogenous waste in some anurans (Kobelt & Linsenmair 1986, 1992, 1995; Schmuck & Linsenmair 1988; Schmuck et al. 1988; Drewes et al. 1997; Lillywhite 2006). We hypothesize that in species of centrolenids that exhibit parental care, the dermal and peritoneal iridophores play important roles as reflectors of radiated energy, reducing the solar radiation load, and thereby helping frogs to reduce over-heating and cutaneous water loss (see Drewes et al. 1977; Kobelt & Linsenmair 1986, 1992, 1995; Schmuck et al. 1988; Lampert 2001, Lillywhite 2006). In addition, iridophores may play a role in osmoregulation by storing nitrogenous wastes in the form of osmotically inactive and nontoxic purines (major compounds of iridophores) instead of toxic urea (see Schmuck & Linsenmair 1988, Schmuck et al. 1988).

*(7) Liver.* The general external structure of the liver of most centrolenids is either bulbous or lobed. However, external examination is usually inadequate to determine the form of the liver, and we recommend dissecting the liver in order to determine its real structure (especially when more than one specimen is available). The presence of white pigment on the hepatic peritoneum, the position of the gallbladder, or the unequal size of lobes (usually the smaller has a dorsal projection) obscure the form of liver, and lobed organs are sometimes reported as bulbous (e.g., *gorzulai*; Duellman & Señaris 2003; Cisneros-Heredia & McDiarmid 2006a). Moreover, bulbous livers are in fact bulbous only proximally but with lobes slightly discernible distally (see a larger discussion in Cisneros-Heredia & McDiarmid 2006a).

Available data on the relation between the form of the liver and the presence of iridophores on the

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liver indicate the following character-states (H = hepatic condition):

(H0) Liver divided into lobes and the hepatic peritoneum lacking an iridophore layer. This is the most wide-spread condition. We are aware of three specimens (the holotype of *phryxa* and two specimens of *mache*) that show patches of iridophores on the ventral and lateral surfaces of the hepatic peritoneum (Aguayo & Harvey 2006; Cisneros-Heredia et al. obs. pers.). All other know specimens of *mache* and all species apparently related to both *mache* and *phryxa* (former "*granulosa* group") lack iridophores on the hepatic peritoneum;

(H1) Liver divided into lobes and the hepatic peritoneum covered by an iridophore layer. This condition is present only in species from the Guiana Shield (e.g., *gorzulai*, *papillahallicum*, *lema*, *oyampiensis*, *helenae*, *castroviejoi*). The species *gorzulai* and *helenae* have livers divided into lobes but externally they appear bulbous;

(H2) Liver bulbous (or with its lobes entirely fused proximally and medially—as a bulb—but slightly discernible distally) with its hepatic peritoneum covered by an iridophore layer. This condition is present in all species currently placed in the genus *Hyalinobatrachium*, and in *mariaelenae*, *amelie*, *antisthenesi*, *pulveratum*, and an undescribed species apparently related to *amelie* (Cisneros-Heredia & McDiarmid 2006a, Cisneros-Heredia & Meza-Ramos 2007; S. Castroviejo-Fisher & I. de la Riva pers. comm.).

The presence of iridophores on the hepatic peritoneum of some centrolenids shows an inverse relationship with the color of the parietal peritoneum described in the previous section. All species with the parietal peritoneum mostly covered by iridophores (parietal conditions P2, P3, and P4) have livers without iridophores (H0). All species with the parietal peritoneum mostly or totally lacking iridophores (at least less than ¼, parietal conditions P0, and P1) have livers with iridophores covering them (H1 and H2).

The relationship between coloration of the hepatic and other visceral peritonea is less clear. Most species with hepatic condition H2 (except for *uranoscopum*, *eurygnathum*, and *parvulum*) have the entire gastrointestinal tract covered by iridophores (visceral conditions V5 and V6). The Brazilian-restricted group formed by *uranoscopum*, *eurygnathum*, and *parvulum* has hepatic condition H2 but visceral condition V4 (iridophores absent from the entire gastrointestinal tract but present on the urinary bladder). Most species with hepatic condition H1 (except for *lema*) have the entire gastrointestinal tract covered by iridophores (visceral condition V5). One species, *lema*, has hepatic condition H1 but its gastrointestinal tract does not have the iridophore cover (V3). Some species with hepatic condition H1 (e.g., *midas*, *cariticommata*, *resplendens*) have visceral condition V2 (iridophores covering only some parts or the gastrointestinal tract). Most species with hepatic condition H1 have visceral condition V1 (and some V0) with the entire gastrointestinal tract lacking an iridophore cover.

*(8)* **Humeral spine** **(Fig. 6)**. Humeral spines are ventrolateral extensions of the humeral *crista ventralis* (Noble 1924; Ruiz-Carranza & Lynch 1991a). Most species of anurans, including the majority of glass-frogs (*Cochranella* and *Hyalinobatrachium*), lack a humeral spine or hook and instead possess a *crista ventralis* that is just slightly elevated (Ruiz-Carranza & Lynch 1991a; Duellman *et al.* 1997; Napoli 2000; De la Riva 2005; Señaris & Ayarzagüena 2005). Among anurans with humeral spines, most species are Centrolenidae (*Centrolene* spp.; Ruiz-Carranza & Lynch 1991a), but humeral spines have also been reported in other species of Athesphatanura (*sensu* Frost et al. 2006): Ceratophryidae (e.g., *Telmatobius bolivianus* Parker, 1940, *Telmatobius yuracare* De la Riva, 1994; Lavilla & Ergueta 1999, De la Riva 2005), and Hylidae (*Bokermannohyla langei* [Bokermann, 1965], *Bokermannohyla martinsi* [Bokermann, 1964], *Litoria humeralis* [Boulenger, 1912]; Zweifel 1958; Napoli 2000; Caramaschi *et al.* 2001; Faivovich *et al.* 2005). In all cases, humeral spines are present in males but not in females.
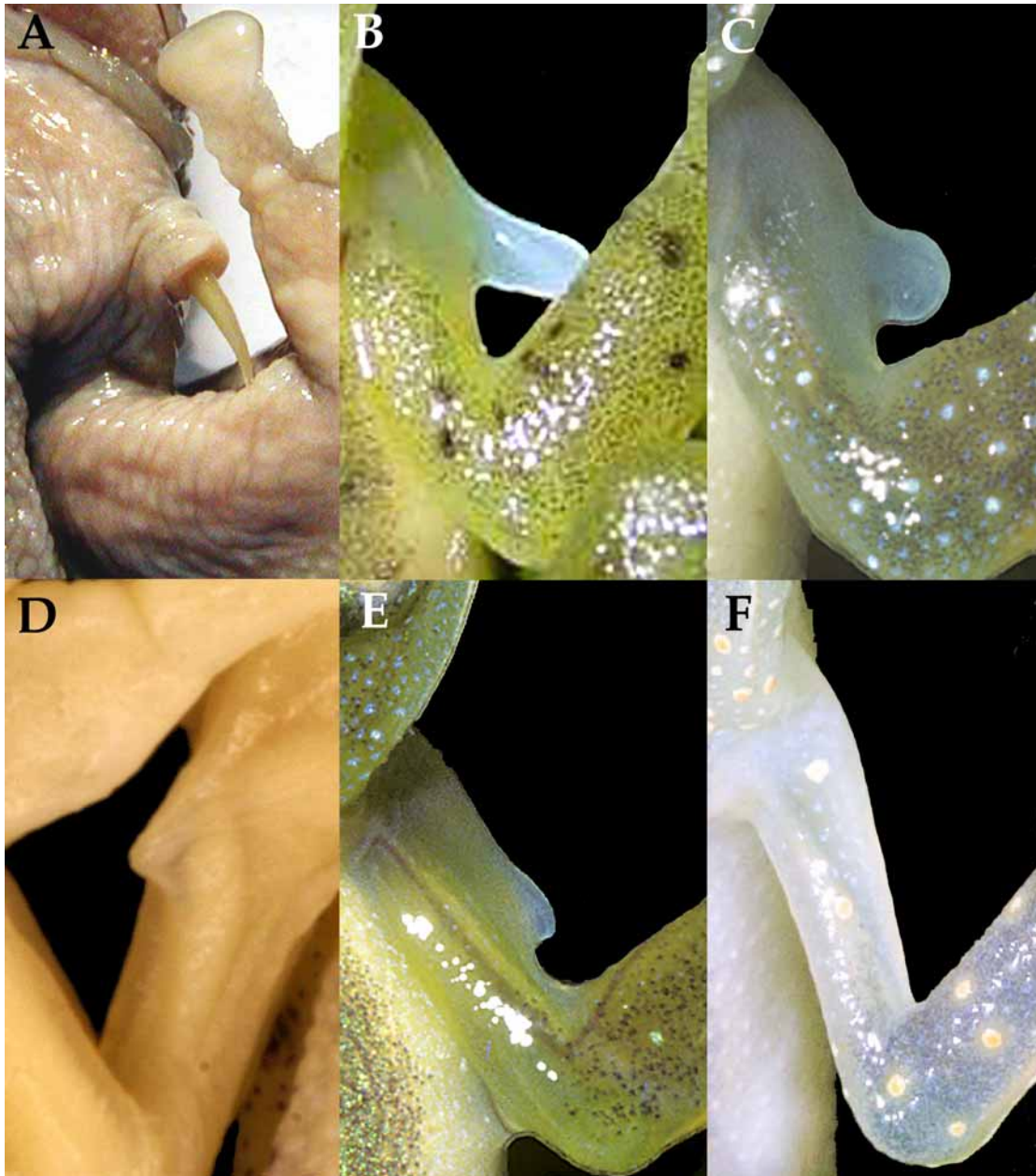
**FIGURE 6.** Humeral spines of centrolenid frogs. (A) *geckoideum* (ventral view) [DFCH], (B) *prosoblepon* (dorsolateral view) [MYM], (C) *pipilatum* (dorsolateral view) [RWM], (D) *mariaelenae* (ventral view) [JD], (E) *audax* (dorsolateral view) [RWM], (F) *mache* (dorsolateral view, humeral spine absent, as in all centrolenid females and in males of all species of the genera *Cochranella*, *Nymphargus*, and *Hyalinobatrachium*) [JD].

Ruiz-Carranza and Lynch (1991a) used the condition of the humeral spine to diagnose *Centrolene* (humeral spine present) from *Cochranella* and *Hyalinobatrachium* (humeral spine absent). However, Darst and Cannatella (2004), Wiens *et al.* (2005), Faivovich et al. (2005), Frost *et al.* (2006), and Grant et al. (2006) found that *Centrolene* and *Cochranella* are non-monophyletic. Frost *et al.* (2006) suggested that coding the humeral spine character just as presence or absence is simplistic, and we agree as considerable variation is known: *geckoideum* Jiménez de la Espada, 1872 has a sharp, smooth, pointed, protruding humeral spine in males, and a poorly developed, non-protruding humeral spine in females; *heloderma* Duellman, 1981 has a blunt, bladelike, projecting humeral spine in males; *ilex* Savage, 1967 has a non-

protruding humeral spine that runs almost parallel to the humerus; *litorale* Ruiz-Carranza & Lynch, 1996 has a very small and poorly-developed spine; *castroviejoi* Ayarzagüena & Señaris, 1997 has a bladelike humeral crest that almost forms a projecting small spine; and *griffithsi* Goin, 1961 and *armata* Lynch and Ruiz-Carranza, 1996 have bladelike, irregular humeral crests which sometimes in *griffithsi* develop non-projecting spines (Ruiz-Carranza & Lynch 1991a,b; Señaris & Ayarzagüena 2005; Frost *et al.* 2006; Cisneros-Heredia & McDiarmid pers. obs.).

The size of the humeral spine increases through ontogeny, and juvenile males usually have a reduced or poorly developed *crista ventralis* similar to the condition in females (Ruiz-Carranza & Lynch 1991a: 12, observations on *buckleyi*; Cisneros-Heredia & McDiarmid pers. obs., observations on *prosoblepon* and *grandisonae*). Some intraspecific variation in the form of the humeral spines is known, but in general, the morphology of the humeral spine seems to be conservative within each species. In comparison, considerable interspecific variation has been observed, and this character is apparently useful for taxonomic purposes (Ruiz-Carranza & Lynch 1991a–b; Wild 1994). Ruiz-Carranza and Lynch (1991b) and Wild (1994) explored the morphology of humeral spines in *Centrolene*, and characterized the variation in terms of: (a) the spine is embedded in the arm musculature and not visible (e.g., *ilex*), visible and projecting (e.g., *prosoblepon*), or even protruding through the skin (e.g., *geckoideum*), (b) length of the base of the *crista ventralis*, (c) angle between the axes of the spine and the humerus, (d) curvature of the axis of the spine, and (e) form of the tip of the spine.

*(9) Hand webbing* **(Fig. 1).** The variation of the webbing between the fingers is extensive in centrolenids; some species have basal webbing (e.g., *cochranae*), and others have extensive webbing, especially between the outer fingers (e.g., *resplendens*). Ruiz-Carranza and Lynch (1991d, 1995a) recognized that variation in hand webbing of the species of *Centrolene* is continuous. However, species currently placed in *Cochranella* have discrete variation, and two conditions are easily recognized: (i) species with basal webbing (not extending beyond the base of distal subarticular tubercle); and, (ii) species with extensive webbing (extending beyond the distal subarticular tubercle, usually to the intercalary cartilage) (Ruiz-Carranza & Lynch 1991d, 1995a). In *Hyalinobatrachium*, the webbing between fingers III and IV is always extensive, but some variation exists in the webbing between fingers II, III, and IV. Ruiz-Carranza and Lynch (1998) described this variation in *Hyalinobatrachium* and recognized three conditions: (i) basal webbing between fingers II and III, at most reaching distal subarticular tubercle, and extensive between fingers III and IV—beyond distal subarticular tubercle or reaching the intercalary cartilage (e.g., *munozorum*); (ii) basal webbing between fingers II and III and less extensive between fingers III and IV—barely reaching distal subarticular tubercle (e.g., *esmeralda*); and, (iii) extensive webbing between fingers II and III—beyond distal subarticular tubercle—, and extensive between fingers III and IV (e.g., *chirripoi*).

Various species with extensive hand webbing (across the different genera) show a bubble-like structure called "bulla" embedded in the webbing between the outer fingers (Myers & Donnelly 2001; Cisneros-Heredia & McDiarmid in press). The bulla has been overlooked in several species (e.g., *fleischmanni*, *prosoblepon*, *spinosa*), so its nature remains undetermined; and its presence and form show intraspecific and interspecific variation (Cisneros-Heredia & McDiarmid in press, pers. obs.).

*(10) Foot webbing* **(Fig. 1).** Toe webbing is less variable than finger webbing; in general, species with reduced hand webbing also have less toe webbing than species with extensive hand webbing.

*(11) Tubercles, fringes, and folds.* Dermal ornamentation in the form of tubercles, folds, or fringes is present on the hands, arms, feet, and legs of several species in the Centrolenidae. In most species with ornamentation on the forearm or tarsus, it usually extends along the outer edges of the outer fingers or toes respectively. These ornaments are enameled in some species and are distinctive in life. In preservative, the white pigment that provides the enameled appearance to these ornaments is usually lost, and low folds are easily overlooked without proper light and magnification. The enameled folds in males are usually formed by glandular tissue and probably are related to the reproductive condition of the frog; in females, the enam-

eled folds are evident but not always formed by glandular tissue (Myers & Donnelly 2001; Cisneros-Heredia & McDiarmid pers. obs.). Dermal elevations on the edges of the forearms and tarsi vary in form from flat (= warts, e.g., *posadae*) to pronounced (= tubercles, e.g., *peristictum*). The fringes or folds are sometimes low, smooth, and without tubercles (*ruedai*, *pellucidum*; a common condition in *Hyalinobatrachium*); well-developed, smooth, and without tubercles (e.g., *adenocheira*); well-developed, scalloped, without tubercles (e.g., *euknemos*, *uranoscopum*); and well developed, scalloped, and with tubercles (e.g., *mache*).

*(12) Nuptial excrescences and hand ornamentation* (**Fig. 7**). Since Taylor's (1949) first mention of prepollical spines and nuptial pads in some centrolenids, most researchers overlooked these structures until the mid-80s. Flores (1985) proposed a classification for the nuptial excrescences of centrolenids based on the form of the nuptial pads on the thumb. Two types of nuptial pads were defined: Type-I as "a large pad, extending from the ventrolateral base of the thumb over the prepollex distally around to the dorsomedial surface, and… about as long as one-half the thumb length and ovoid in shape" (Flores 1985), and Type-II as a "nuptial pad present only on the dorsomedial surface of the thumb, located on the distal half to third of the antepenultimate phalanx, and is round in shape" (Flores 1985). That author also referred to the protruding prepollical spine present in *spinosa* and the hard, sharp prepollical spine concealed beneath the skin of *lynchi*. Flores (1985) mentioned, but never described, a third type of nuptial pad present in Brazilian species and some peculiar glands underlying Type-I and Type-II nuptial pads and on the flanks of many species (Flores 1985: 318). Ayarzagüena (1992) described and pictured the nuptial excrescences of eight species of Venezuelan centrolenids and pointed out additional species with protruding prepollical spine like in *spinosa* (*gorzulai* and *duidaeana*). Ayarzagüena (1992) also noted the existence of additional types from those described by Flores (1985) including: nuptial pads constituted exclusively by individual glands clustered together but not densely packed (*orientalis*, *iaspidiense*, and *duidaeana*), and individual glands concentrated on the thumb but also extending distally along the outer thumb fringe and in the webbing (*taylori*).

Lynch and Ruiz-Carranza (1996) described *armata*, a species with a unique nuptial pad formed of cornified spines, and provided an extensive revision of the nuptial excrescences of the centrolenids. Lynch and Ruiz-Carranza (1996) recognized that prepollical spines are present in most if not all species of centrolenids. They pointed out that most species have concealed prepollical spines (beneath the skin) and mentioned protruding prepollical spines only in *spinosa* (overlooking the descriptions by Ayarzagüena 1992). Further, Lynch and Ruiz-Carranza (1996) described the presence of Type-I nuptial pads in most species of the genera *Centrolene* and *Cochranella*, and in a few *Hyalinobatrachium*, while Type-II pads were reported just from four species of *Centrolene*. The nuptial excrescences described by Ayarzagüena (1992) were fitted into Type-I and Type-II conditions, and the glandular clusters were referred to as diffuse variations of those conditions. Lynch and Ruiz-Carranza (1996) considered Type-II nuptial pads as rudimentary versions of the Type-I nuptial pads in which the central portion is active, and they hypothesized that the spinous pad of *armata* is an autapomorphic modification of Type-I pads. These authors also described "reduced or rudimentary versions of Type-I nuptial excrescences (less extensive, individual glands visible within a patch)" in some species of *Hyalinobatrachium*, suspecting that those structures were what Flores (1985) mentioned as the third type of nuptial pad. Lynch and Ruiz-Carranza (1996) commented that several species lack nuptial pads: *ametarsia*, *resplendens*, *spinosa*, *daidalea*, *savagei*, *solitaria*, *pulverata*, *fleischmanni*, and *lemur* (but see McCranie & Wilson 2002; Savage 2002). Ayarzagüena and Señaris (1997) described protruding prepollical spines in *castroviejoi*. Subsequently, Señaris and Ayarzagüena (2005) used the classification of the nuptial excrescences suggested by Flores (1985) and revised by Lynch and Ruiz-Carranza (1996) but pointed out that the nuptial excrescences of Venezuelan species are made up of a diverse set of structures, and their descriptions were based not only on the position and shape of the nuptial excrescences but also oncharacters such as glandular clusters and protruding

prepollical spines.

We have found that nuptial excrescences and hand ornamentation of centrolenids have a larger morphological diversity than previously recognized, that the current classification is limited and does not describe and diagnose accurately this diversity, and that these structures are important for taxonomic purposes. Some species have structures that are useful in distinguishing them from sympatric or closely related species, and nuptial excrescences are useful for determining the sex of museum specimens. For practical reasons, we propose a revised classification for the nuptial excrescences and hand ornamentation of centrolenid frogs.
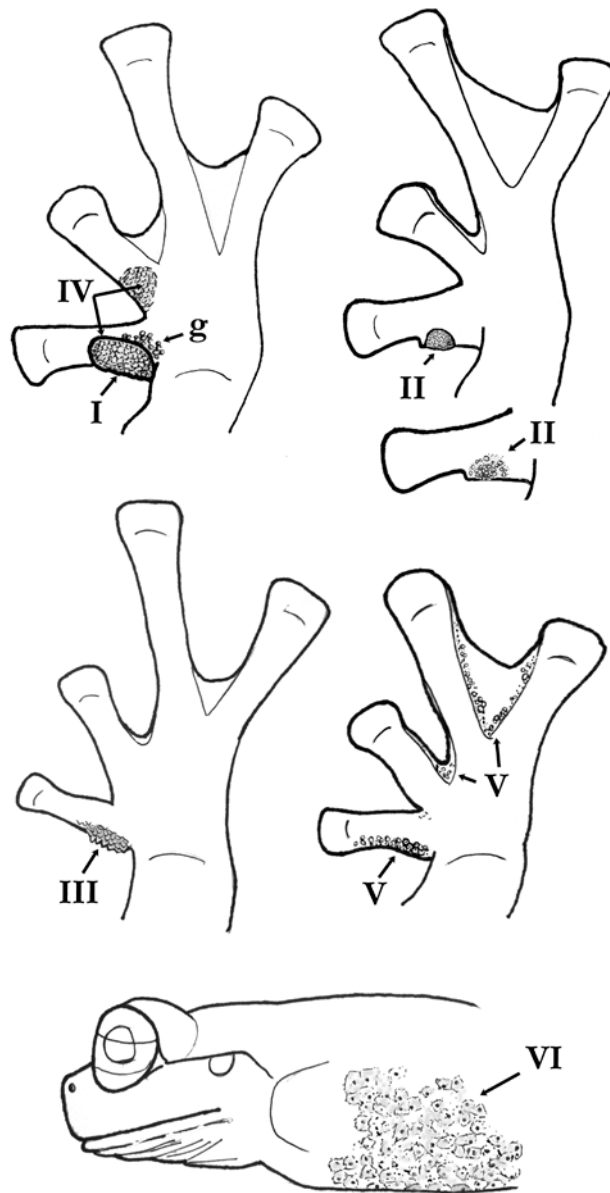


**FIGURE 7.** Schematic drawings of the different types of nuptial excrescences (not to scale). Type–I: Granular pad, sometimes with glandular clusters or individual glands (g); Type–II: Circular or squarish granular pad without glandular clusters or individual glands (note prepollical bulge; above); or circular glandular cluster surrounded by individual glands (note prepollical bulge, below). Type–III: Spinous nuptial excrescence. Type–IV: Granular pad on the thumb and on the dorsal surface of finger II; Type V: Glandular cluster with individual glands on the thumb, and sometimes with glandular clusters and individual glands evenly distributed in the webbing of fingers. Type–VI: Glandular clusters and individual glands distributed (with some variation) along the body.

*Nuptial excrescences classification*

The terms nuptial pad and nuptial excrescence have been used as synonyms by many authors (e.g., Peters 1964; Lynch & Ruiz-Carranza 1996). However, we prefer to use the term *nuptial excrescence* to refer to the entire area (spinous/cornified, roughened, or granular) formed by glands in different morphological arrangements (pads, clusters, or individual glands), which is associated with the breeding cycle. Nuptial excrescences have been mostly described in the thumb area, but they are present also on other fingers, on hand and foot webbing, and as patches along the flanks of the body and on the limbs (concept modified from Peters 1964; Flores 1985; Lynch & Ruiz-Carranza 1996). The term *pad* is herein restricted to the white or cream-colored, rough or granular, cushioned, thick patch formed by densely packed glands (not discernible as separated, individual glands). The term *cluster* is herein used to describe the smooth, thin, non-cushioned patches formed by dense aggregation of individual glands.

We propose six character-states of nuptial excrescences based on distribution and morphology:

*Type-I* (**Fig. 7**)*:* Large to medium-size nuptial excrescence present on the dorsal, lateral, and/or ventral sides of the thumb. This is the most common nuptial excrescence type in centrolenids, equivalent to Flores' (1985) Type-I. The granular pad is pale colored. Glandular clusters or individual glands are usually absent, but some species like *riveroi*, have underlying glandular clusters or loosely distributed individual glands at the base or on the perimeter of the pad. The glands forming the pad are usually similar in form and size, but some heterogeneity is observed in some species.

*Type-II* (**Fig. 7**)*:* Small circular or squarish nuptial excrescence present only on the dorsal or dorsolateral face of the thumb. A glandular pad is absent in most species (e.g., *lynchi*) and the excrescence is usually formed just by one circular glandular cluster with many individual glands along its perimeter. A granular pad without glandular clusters or individual glands is present in some specimens of *pipilatum*. This type is equivalent to Flores' (1985) Type-II.

*Type-III* (**Fig. 7**)*:* Medium-size spinous nuptial excrescence extending from the lateral side of the thumb to its dorsomedial surface (Lynch & Ruiz-Carranza 1996, designated as Type-III by Señaris & Ayarzagüena 2005). Spines are weakly keratinized and pale brown. This condition is known only in *armata*.

*Type-IV* (**Fig. 7**)*:* Large nuptial excrescence formed by a granular pad that extends from the side of the thumb to its dorsomedial surface, and on the proximal dorsolateral surface of finger II.

*Type-V* (**Fig. 7**)*:* Medium-size diffuse nuptial excrescence formed by glandular clusters and individual glands. A pad as such is absent. Glandular clusters are not circular but usually distributed along the edge of the thenar tubercle to the dorsomedial surface of the thumb, often with individual glands surrounding the area. Inter and intraspecific variation is observed in the distribution of individual glands in the webbing and fringes of the hand and foot, and they could be absent (e.g., most *fleischmanni*) or evenly distributed (e.g., *taylori*).

*Type-VI* (**Fig. 7**)*:* Nuptial excrescences formed by a combination of clustered and individual glands. These excrescences are common to sparse along the body flanks from the axilla to the groin; extend to the ventrolateral sides of the body but abruptly terminate at the dorsal margin of the flanks. They are also present on the ventral and dorsal surfaces of the forearms, arms, and legs, and sometimes extend to the throat. The presence of this extensive glandular tissue has previously been overlooked; we have seen this character in many species in different genera in Centrolenidae (e.g., *balionotum*, *posadae, buckleyi*) in active reproductive males (Cisneros-Heredia and McDiarmid unpubl. data).

*Hand ornamentation classification*

We define hand ornamentation as the morphologies associated with the prepollex. Lynch & Ruiz-Carranza (1996) reported the presence of enlarged but concealed prepollices in most if not all species of Centrolenidae, but noted that it was distinct only in *spinosa*. Since their review, a distinct prepollex has been

reported from other species. We propose two character-states describing hand ornamentation in centrolenids:

*Distinct prepollex* (**Fig. 7**)*:* The enlarged prepollex is well separated from finger I and noticeable by external examination. In most species with this condition, the prepollex forms a rounded "prepollical bulge" at the base of the thumb but does not pierce the skin (a condition known in *lynchi* some specimens of of *ametarsia*, *castroviejoi*, *oyampiensis*, *pipilatum*, *riveroi*). In some species, the tip of the prepollex pierces the skin to form a protruding "prepollical spine" that is visible externally at the base of thumb (condition known in *gorzulai*, some specimens of *castroviejoi*, *duidaeana*, and *spinosa*). Further studies are needed to understand the nature of the variation of this character in species such as *castroviejoi* and *pipilatum*, and whether it is polymorphic or influenced by ontogeny, age, sex, or preservation.

*Concealed prepollex:* The enlarged prepollex is not separated from finger I, not apparent externally. This condition is widespread among centrolenids.

*(13) Length of finger I vs. II* (**Fig. 2**)*.* This relationship is determined by equally adpressing both fingers one to another. The conditions are usually I>II or II>I, but some species have both fingers of equal length. The differences in finger length in centrolenids are due to variation in the length of both fingers (in contrast, in dendrobatids it appears that it is entirely due to variation in the length of finger I, T. Grant pers. comm.). Desiccation and bad preservation can result in smaller discs or curly fingers, somtimes making it difficult to evaluate relative finger length. When the fingers are well preserved, measuring the length of both fingers from the base of the thenar tubercle is a good option for comparison.

*(14) Eye-diameter vs. width of disc on finger III.* Ruiz-Carranza & Lynch (1991a) provided a detailed discussion of this relationship. The most common condition is ED>3DW, except for *geckoideum* and *paezorum*. Preservation sometimes affects eye-diameter and disc width, and measurements should be taken only on well-preserved specimens, and not on desiccated discs or crushed eyes.

*(15) Coloration in life (including bones).* Schwalm & McNulty (1980) and Ramírez et al. (1989) described four cellular structures (chromatophores) involved in the coloration of the skin of *fleischmanni* and *acanthidiocephalum*: xanthophores, iridophores, melanophores, and chromatophores "C". In most anurans, the coloration depends on the arrangement of these four cells in the skin, and a green skin may be produced in centrolenids by two different physiological factors. Some species have the four cells arranged in layers as dermal chromatophore units (see Bagnara et al. 1968), where most wavelengths are absorbed by melanophores and xanthophores (yellows, oranges, blues, and lavender) and only the greens are transmitted (Goin & Goin 1968). Species that are green due to the predominance of dermal chromatophore units in their skin turn lavender or blue in preservative (because the xanthophores are destroyed by the preserving fluid). However, in other species, like *fleischmanni*, dermal chromatophore units are not predominant in the skin, and the green coloration is in fact produced by the accumulation of the pigment biliverdin in the cell called chromatophore "C" by Schwalm & McNulty (1980). Species where biliverdin is responsible for the green coloration turn cream or white in preservative because the preserving fluid either dilutes or destroys this pigment. In life, the background color of centrolenids varies from various shades of green (most species), to pale or dark brown / tan (e.g., *anomala*, *rosada*), dark greenish black or gray (e.g., *saxiscandens*), or blue (*mache*, a coloration previously unreported for a centrolenid, Cisneros-Heredia *et al.* pers. obs.). Unfortunately, there are no studies on the morphology and organization of the chromatophore structures that are responsible for the intra and interspecific color variation. The different dorsal shades of centrolenids are certainly cryptic. Species that occur in vegetation are usually green (providing protection from predators with visual sensitivity in the visible light spectrum from 400 to 700 nm). Species that occur on rocks next to waterfalls are usually dark green or grey (e.g., *orejuela*, *saxiscandens*, Duellman & Burrowes 1989; Duellman & Schulte 1993). In addition, centrolenids reflect light in the near infrared region (700 to 900 nm) similar to green plants, thus they have an infrared cryptic coloration (Schwalm et al. 1977).

While some species of centrolenids have a uniform dorsal coloration (e.g., *prasina*, *adiazeta*, *papilla-hallicum*), most centrolenids have distinctive marks (listed from small to large size): punctuations (the smallest mark, formed by just one star-like melanophore; it is a common condition in *Hyalinobatrachium*); flecks (formed by small aggregations of chromatophores with irregular borders; e.g., *mariaelenae* has dark flecks formed by small aggregations of melanophores, and abundant, small punctuations; *lynchi* has pale irregular flecks formed by small groups [less than 0.5 mm] of iridophores or xanthophores, and large, dark, irregular spots); circular dots (e.g., formed by round aggregations of chromatophores, usually elevated; e.g., *midas* and *siren* have pale [yellow in life] circular dots; *megacheira* has dark black or blue circular dots; some specimens of *prosoblepon* have dark circular dots and pale circular dots); spots (formed by large aggregations of chromatophores or by individual spaces lacking melanophores [but not forming a net like in reticulations] with irregular borders, usually not greatly elevated; e.g., *luteopunctata* has pale spots; *litorale* has dark spots); true ocelli (dark circles formed by melanophores with orange or yellow centers formed by xanthophores; e.g. *cochranae*, *anomalus*); false ocelli (irregular light spots formed by iridophores surrounded by ill-defined dark borders forming a reticulated pattern, sometimes resembling ocelli or reticulations; e.g. *ocellata*, some specimens of *prosoblepon*); and reticulations (formed by melanophores distributed across the dorsal surfaces, usually as a green net surrounding yellow or cream spots which completely lack melanophores; e.g., *valerioi*, *puyoensis*). Searis and Ayarzagena (2005) used the term ocelli to describe the color pattern of some *Hyalinobatrachium*. The definition of ocellus (plural ocelli) is an eyelike colored spot (as on a peacock feather or the wings of some butterflies) (Merriam-Webster Online Dictionary 2004). Therefore, we consider that the term is best applied to the dark circles with light centers found on the dorsum of species such as *cochranae* and *anomalus*, while the coloration of some *Hyalinobatrachium*, or of *puyoensis* and *mariae*, with green background color and yellow round spots is best termed as reticulate.

Most authors have considered the coloration of bones in life as having three conditions: white, light green and dark green (Lynch & Duellman 1973, Ruiz-Carranza & Lynch 1991a). However, we have noted some intraspecific variation in the green coloration of bones in life—e.g., the bones are pale green in some specimens of *grandisonae*, *prosoblepon*, *resplendens*, and *mache*, but dark green in others. Thus, we prefer to code this character as either green or white. Green color in bones seems to be produced by biliverdin.

*(16) Coloration in preservative.* Most green centrolenid species turn lavender or purple in preservative (e.g., *prosoblepon*, *mache*, *cochranae*), but *pulverata* and *revocata* lose their lavender coloration after some time in preservative and turn cream. The species *vozmedianoi* is unique because its dorsal color remains greenish in preservative (Señaris & Ayarzagüena 2005). Most species of the genus *Hyalinobatrachium* turn white or cream, whereas *uranoscopum*, *eurygnathum*, and *taylori* retain some lavender in preservative. Most brown, tan, black, or gray species turn dark grey or dark brown with a lavender tint in preservative. The pale colors (yellow or orange in life) of the dorsal markings usually turn cream. The green reticulum of most species of *Hyalinobatrachium* is lost after some time in preservative, and just a fine dusting of lavender melanophores is usually visible under great magnification. In preservative, green bones usually turn white due to loss of the green pigment, but some specimens can retain the green coloration for several decades, especially in the articular (joint) regions, (e.g., some specimens of *puyoensis* show green bone epiphysis in the knees).

*(17) Iris coloration (in life and preservative)* **(Fig. 8)**. Little attention has been paid to the eyes of centrolenids, such that very few species descriptions provide accurate data on the coloration of the iris, either in life (ideal) or in preservative. Iris coloration is related to two features, the background coloration and the pattern. Background coloration has wide interspecific variation and usually low intraspecific variation (mainly related to different shades rather than dramatic color differences): silver white (e.g., *ilex*), different shades of grey (e.g., *grandisonae*, *cochranae*), different shades of yellow (e.g., *ruedai*, *fleischmanni*),

salmon (e.g., *litorale*), or lavender (e.g., *mache*). The iris shows wide interspecific variation and low intraspecific variation in the concentration and extent of the pattern rather than in its presence or absence: dark flecks (e.g., *ruedai*), red flecks (e.g., *ignioculus*), reddish marks (e.g., "Palenque"), fine dark reticulations (e.g., *grandisonae*, *prosoblepon*), fine russet or gray reticulations (e.g., *uranoscopum*), fine lavender to light blue reticulations (e.g., *mache*), and thick dark reticulations (e.g., *ilex*) are representative of the diversity. The shape of the pupil also is variable but we have no information on how or if pupils change shape and size in different light conditions. Myers and Donnelly (2001) reported the presence of a bicolored iris in *Hyalinobatrachium eccentricum* Myers and Donnelly, 2001 that was characterized by the presence of a dark, dome-shaped circumpupillary zone that conceals the pupil, separating the pupil from the colored peripheral zone. This character is present also in *ruedai* (although with a grey circumpupillary zone less marked than eccentricum) and probably is present in other species of *Hyalinobatrachium*, but detailed information for most species is lacking. Photographs of some specimens of *mariaelenae* suggest that it too may have a bicolored iris.
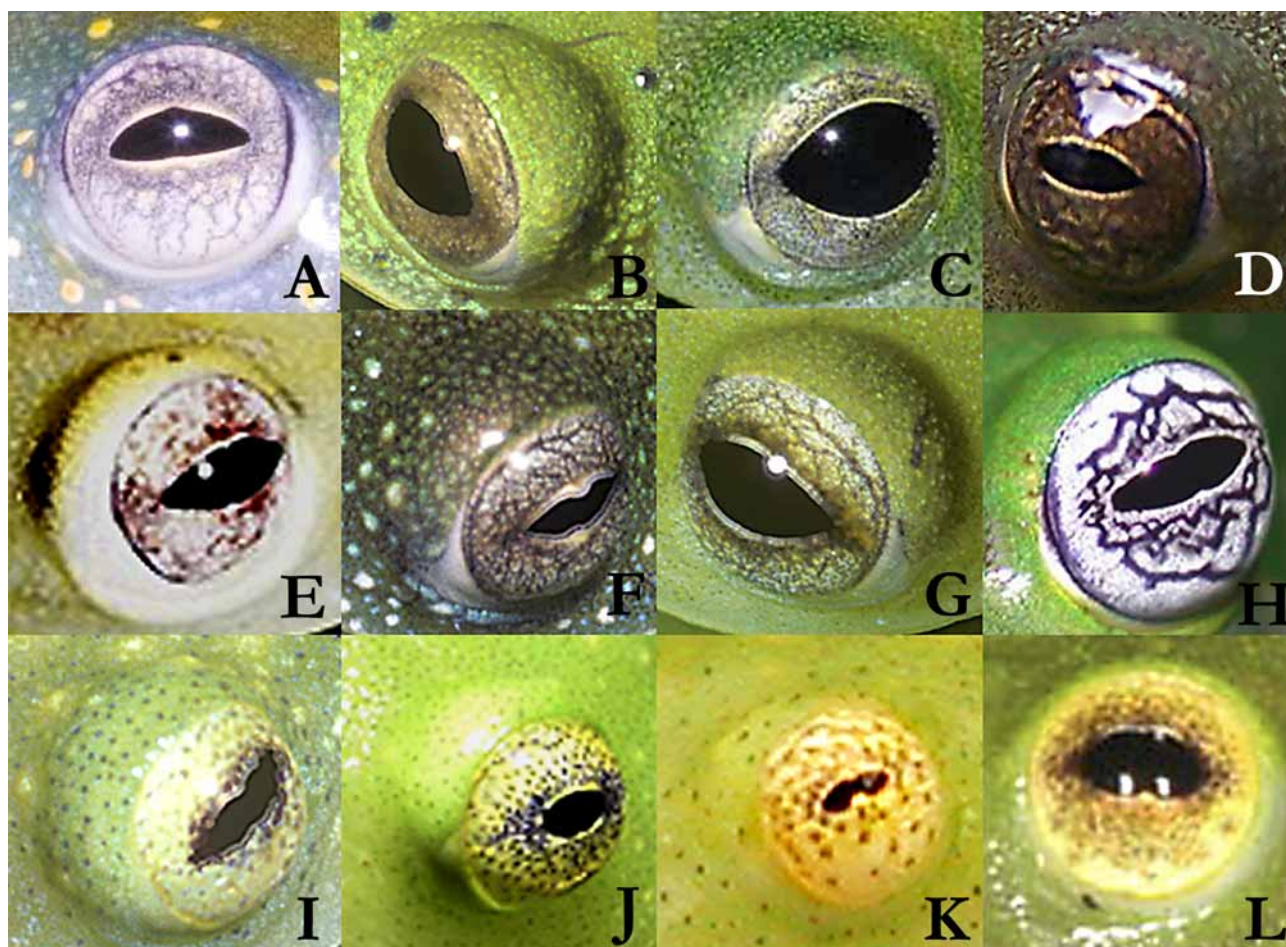


**FIGURE 8.** Assortment of irises of centrolenid frogs (all in life). (A) *mache*, note fine lavender reticulation [JD], (B) *megacheira*, note apparent absence of circumpupillary ring [RWM], (C) *midas*, note general grayish coloration and presence of circumpupillary ring [AR], (D) *adiazeta*, note general brown coloration and presence of circumpupillary ring [MR], (E) *Centrolene* sp. "Palenque", note unique red marks and reticulations and presence of circumpupillary ring [RWM], (F) *pipilatum*, note fine reticulations and rounded points on the upper and lower side of the iris [RWM], (G) *prosoblepon*, note fine reticulation, dark colored area toward the midline and presence of circumpupillary ring [RWM], (H) *ilex*, note thick reticulations, inconspicuous points on the upper and lower side of the iris, and presence of circumpupillary ring [MYM], (I) *pellucidum*, note dark flecks, dark circumpupillary zone of pupil, absence of circumpupillary ring, and irregular edges of the iris [RWM], (J) *colymbiphyllum*, note presence of circumpupillary rings and dark flecks concentrated toward the midline [BK], (K) *ruedai*, note dark flecks, absence of circumpupillary ring, and more conspicuous point on the lower side of the iris than on upper side [DFCH], (L) *fleischmanni*, note dark flecks surrounding the iris, presence of circumpupillary ring, and rounded point on the lower side of the iris [BK].

*(18) **Coloration of fingers and toes.*** The color of fingers and toes and the presence of melanophores on them are usually not reported in species descriptions. In most species, the fingers and toes are colored like the dorsum, or slightly paler (e.g., *prosoblepon*), but in some species the hands and feet are distinctively pale colored, usually yellow or cream (e.g., *cariticommata*). In preservative, species with pale colored hands and feet have melanophores reaching the base of finger IV and toe V or lack them completely; while in most species without distinctive hand and foot coloration, the melanophores cover most of the fingers and toes. Some species show intraspecific variation in the coloration of fingers and toes, but the coloration of the digits is still useful in combination with additional character to diagnose species. Two species have coloration not reported in other centrolenid taxa: *mache* has silvery white pigment on the inner fingers and toes, and *adenocheira* has white glands along the fingers and onto the webbing.

*(19) **Advertisement calls and calling sites.*** Available information indicates that adult male centrolenids call from three different sites: (i) from the upper side of leaves, usually with the snout directed towards the tip of the leaf; (ii) from the underside of leaves, usually with the snout toward the base of the leaf; (iii) from rocks on the walls of waterfalls or within or near spray zones of fast-flowing streams. Unfortunately, calling sites for many species are unknown. Available information suggests that males of all species currently assigned to *Hyalinobatrachium* s.s. (= *fleischmanni* group) call from the underside of leaves; while most other taxa (those currently assigned to *Centrolene* and *Cochranella*; e.g., *acanthidiocephalum*, *albomaculata*, *antisthenesi*, *grandisonae*, *griffithsi*, *ilex*, *prosoblepon*, *pulverata*) call from the upper side of leaves. The Brazilian *uranoscopum* apparently uses both sides of leaves (Lutz 1947). Just a few species are known to call from rocks near waterfalls or from the sprayzones of streams (e.g., *geckoideum*, *euhystrix*; see Grant et al. 1998).

Field observations of *fleischmanni* in northwestern Ecuador revealed that males started calling from the upper sides of leaves at sunset, but shortly after dark, all individuals were found calling from the undersides of leaves (D.F. Cisneros-Heredia pers. obs.). Kubicki (2004) reported that most individual of *chirripoi* call from the undersides of leaves, but some were seen calling from the upper sides of vegetation, but much less frequently. Information on the advertisement calls of a few species of centrolenids is available (McDiarmid & Adler 1974; Wells & Schwartz 1982; Zimmerman & Bogart 1984; Marquez et al. 1996; Grant et al. 1998; Bolivar et al. 1999; Ltters & Khler 2000; Bernal et al. 2004; Searis, 2001; Searis & Ayarzagena 2005, Guayasamin et al. 2006c), but much remains to be learned.. Some taxa have been differentiated from similar species by their calls (e.g., *guairarepanensis* Señaris, 2001). The variation of advertisement calls is characterized in terms of: (a) duration of the call, (b) call repetition rate, (c) number of notes, (d) duration of notes, (e) number of pulses, (f) duration of pulse, (g) dominant frequency, (h) initial frequency, and (i) maximum frequency.

*(20) **Fighting behavior.*** Behavioral information about centrolenids is scarce and mostly anecdotal. Information about the fighting behaviors in centrolenids is known for less than 10% of the described species. Two character-states have been reported for the fighting behavior: (i) males grasp each other venter-to-venter and dangle upside down while holding onto vegetation with their hind legs; and, (ii) an amplexus-like embrace between males. The first state has been reported in eight species currently assigned to *Centrolene* and *Cochranella*, and the latter in three species currently assigned to *Hyalinobatrachium* (McDiarmid & Adler 1974, Duellman & Savitzky 1976; Greer & Wells 1980; Jacobson 1985; Jungfer 1988; Bolívar et al. 1999; Savage 2002; Guayasamin & Barrio-Amorós 2005; Kubicki 2007). Bolivar et al. (1999) hypothesized that the venter-to-venter fighting behaviour is a derived character while the amplexus-like fighting behaviour is primitive; unfortunately, data are too few to allow further comment.

*(21) **Egg clutches and parental care.*** The egg clutches of centrolenids have interesting features but are poorly known. Egg masses vary widely among species and show differences related to location, form, egg coloration, and clutch size. All species of centrolenids deposit their egg clutches outside of water. Most species place their eggs next to or over lotic water systems (rivulets, streams, waterfalls), but a few species occa-

sionally place them over lentic waters (e.g., sometimes *grandisonae* deposits egg clutches over small permanent pools or ditches; D. F. Cisneros-Heredia & A. León-Reyes pers. obs.). A population of *buckleyi* recorded at a highland locality in Ecuador (Cuicocha) had access to just two water reservoirs, a lake and terrestrial bromeliads, and Lynch & Duellman (1973) suggested that the frogs might use the latter for egg deposition. 1973). However, centrolenid tadpoles have not been found in bromeliads. Available information indicates that egg clutches are usually deposited at the calling site of the male; thus, clutches are located on the upper side of leaves, on the underside of leaves, or attached to twigs or rocks. Some species reportedly place their eggs indiscriminately on either the upper or undersides of leaves (e.g., *uranoscopum*, Lutz 1947).

In most species, the eggs are deposited as a monolayer and each is attached individually to the leaf surface. This configuration, called a laminar array by Altig and McDiarmid (in press), may change dramatically depending on the species, placement of the clutch, and subsequent hydration of the eggs. In some species, eggs deposited on top of a leaf frequently absorb water from rain and swell considerably, so that the jelly layer and eggs meld together and appear as a 3-dimensional clump or mass and the array actually hangs of the leaf tip (e.g., *pulverata*, *granulosa*). In other species that deposit on the tops of leaves, the eggs do not absorb as much water and develop to hatching in a single slightly globular tier (e.g., *prosoblepon*). Some of the surface clutches are "doughnut-shaped" with an empty space in the middle of the array (e.g., *albomaculata*, *geckoideum*, Lynch et al. 1983; Puschendorf et al. 2004; Kubicki 2007). The eggs of species that deposit on the upper surface of leaves are usually dark brown. Eggs deposited on the undersides of leaves generally maintain their single layer morphology throughout development and are typically white or greenish and lack the protective melanophores characteristic of most surface clutches.

Some species of centrolenids (most *Hyalinobatrachium*) show parental care behavior (McDiarmid 1978). In those species one of the parents (usually the male, but the female has been reported in one species, *tayrona*, M. Rada pers. comm.) remains nearby (= on the same leaf but not in contact with the eggs, e.g., *buenaventura*), next to (on the same leaf and touching the eggs but not over them, *daidalea*), or on top of the eggs (*valerioi*; M. Rada, D.F. Cisneros-Heredia, and P. Gutirrez pers. obs.). In most species, the guarding parent remains with the eggs during the night but retreats to nearby leaves during the day. In some taxa, the attending parent remains with the egg clutches day and night. If a male is successful in attracting several females to the site, he may continue to attend the clutches until all have hatched. In some instances, this may continue for a few weeks depending on the periodicity of female arrival. An especially fit male of one species of Hyalinobatrachium (*valerioi*, R.W. McDiarmid pers. obs.) successfully attracted seven females and attended all clutches through to hatching over a minimum period of 28 days. When the calling period ends, guarding males are usually alert but quiet, just moving when disturbed (especially when insects like wasps or flies approach the eggs). Little information is available about parental care for most species of centrolenids, and we recommend that egg clutches of centrolenids should be monitored over several days in order to determine if a guarding parent is present, its sex, the position(s) that it adopts while attending the eggs, the diel behaviour of the parent, and the stage of development of the eggs when first discovered.

*(22) Tadpoles.* The tadpoles of centrolenids are exotrophs with a vermiform body (Altig & McDiarmid 1999) and dorsal C-shaped eyes (Altig & Brandon 1971); they live buried within leaf packs along the edges of still or slow-flowing water systems (Wassersug & Hoff 1979, Hoff et al. 1999; Kubicki 2007). These morphological and ecological characteristics define a unique type of tadpole with a morphology that seems to be common to all the species in the family. Unfortunately, little information is available about the tadpoles of most glassfrog species. Extensive information about useful characters and standards for tadpole descriptions are presented in McDiarmid and Altig (1999).

**(23) Snout-vent length (SVL) of adult males and females.** Body size in centrolenids varies continuously, including small species (< 22 mm; e.g., *ruedai*), medium-sized ones (22–35 mm; e.g., *acanthidioceph-alum*, *grandisonae*, *posadae*), large-sized ones (35–55 mm; e.g., *paezorum*), and giants (> 55 mm; e.g., *geckoideum*). Sexual dimorphism is apparent in most centrolenids, with females attaining a larger SVL than males. The only known exception is *geckoideum*, where males are larger than females. Interestingly, male *geckoideum* have a formidable humeral spine (Fig. 6A) and commonly have many scars on the head and body, which suggest that they are frequently involved in male-male combat (Bolivar et al. 1999; pers. obs.).

## Comments on the generic and infrageneric-level taxonomy of Centrolenidae

Ruiz-Carranza and Lynch (1991a) recognized three species-groups in the genus *Centrolene* using the eye size, bone coloration, visceral peritonea coloration, and vomerine teeth to characterize the groups: the *geckoideum* group (small eyes, green bones, clear visceral peritonea, and vomerine teeth present), the *prosoblepon* group (large eyes, green or white bones, clear or white visceral peritonea, and vomerine teeth present or absent), and the *peristictum* group (large eyes, green bones, white visceral peritonea, and vomerine teeth absent). These authors also proposed two species-groups for the genus *Cochranella* primarily based on the condition of the visceral peritonea: the *granulosa* group (with white visceral peritonea) and the *ocellata* group (with clear visceral peritonea). The three species-groups within *Hyalinobatrachium* were based on the condition of the visceral peritonea, bone coloration, and vomerine teeth: the *fleischmanni* group (white visceral peritonea except for the clear urinary bladder, white bones, vomerine teeth absent), the *pulveratum* group (white visceral peritonea except for the clear urinary bladder, green bones, vomerine teeth present), and the *parvulum* group (white urinary bladder and hepatic peritoneum, green or white bones, vomerine teeth present or absent) (Ruiz-Carranza and Lynch 1991a). Ruiz-Carranza and Lynch (1991d) also analyzed webbing on the outer fingers and vomerine teeth among the centrolenids, and found that the species assigned to the genus *Cochranella* can be divided among four discrete groups. Based on their previous analysis, Ruiz-Carranza and Lynch (1995a) separated the species originally classified under their *ocellata* group into two groups: the *spinosa* group (extensive hand webbing and presence of vomerine teeth) and the *ocellata* group (reduced hand webbing and most species without vomerine teeth). Duellman and Señaris (2003) recognized a *gorzulai* group for the Guianan species of *Centrolene* that have a white hepatic peritoneum. Señaris and Ayarzagüena (2005) proposed the *oyampiensis* group to include the species of *Cochranella* with white hepatic peritoneum. Noonan & Harvey (2000) commented that the separation of the species of the *peristictum* group from the *prosoblepon* group was questionable, but they did not examine all members of those groups and did not take further action. Señaris and Ayarzagüena (2005) presented information on *antisthenesi* that suggested its closer relationship to members of the clade *Centrolene/Cochranella* rather than with *Hyalinobatrachium*. We (Cisneros-Heredia & McDiarmid 2006a) regarded the separation of the *peristictum* group from the *prosoblepon* group as unwarranted due to the ambiguity of the characters used to separate them. We also separated the species of the former *pulveratum* group (*sensu* Ruiz-Carranza & Lynch 1991) from *Hyalinobatrachium* and placed them in *Cochranella* (as *Co. pulverata* and *Co. antisthenesi*), but did not comment on their relationships with other species (Cisneros-Heredia & McDiarmid 2006a).

Ruiz-Carranza & Lynch remarked that their groups were only phenetically based and groups of convenience to aid in the identification of species, and not formal statements of phylogenetic relationships (Ruiz-Carranza & Lynch 1991a–d, 1995a–d). Currently, most species-groups in Centrolenidae are simply used for convenience, and their monophyly remains untested (Ruiz-Carranza & Lynch 1991a, Cisneros-Heredia & McDiarmid 2006a, Frost *et al.* 2006, Guayasamin et al. 2006c). In the present paper, we refrain from recognizing species-groups because their effectiveness for identification purposes (their main function) has dimin-

ished with the discovery of many new species in the last decades and morphological characters that conflict with group diagnoses. We agree that it is inappropriate to continue to recognize or expand species-groups in the Centrolenidae when their utility is very limited and their recognition uninformative. The former groups were not defined as evolutionary entities, and new species could only be assigned to a species group using a reduced set of non-objective characters.

**Comments about taxa under *Hyalinobatrachium*.**—With the removal of *pulverata* and *antisthenesi* from *Hyalinobatrachium s.l.* by Cisneros-Heredia and McDiarmid (2006a), two species-groups were left in *Hyalinobatrachium s.l.*: the "*fleischmanni* group" and the "*parvulum* group". The three species (i.e., *eurygnathum*, *parvulum*, and *uranoscopum*) assigned to the "*parvulum* group" are characterized by having white pigment on the peritoneum of the urinary bladder. Until recently, this condition was thought to be restricted to the taxa from southeastern Brazil, but recently it was found also in an Andean species (*grandisonae*, J. M. Guayasamin pers. comm.). Contrary to species in the former "*fleischmanni* group", *eurygnathum*, *parvulum*, and *uranoscopum* have green bones in life, are lavender in preservative, and have vomerine teeth. Their morphology has not been described in detail. We have examined a cleared-and-stained *uranoscopum* and found it to have some osteological conditions that are intermediate between *Cochranella* and *Hyalinobatrachium*. The combination of lavender dorsum, white bulbous liver, and incomplete fusion of the astragalus and calcaneum present in *eurygnathum*, *parvulum*, and *uranoscopum* is otherwise known in the Guianan *antisthenesi*, *gorzulai*, *papillahallicum*, and *lema*, in the Andean *mariaelenae* and *amelie*, and in the Pacific *pulveratum*. Biogeographic affinities would suggest that the relationships of the species from southeastern Brazil are likely with the Guianan taxa. For these and other reasons, we prefer to restrict the genus *Hyalinobatrachium s.s.* to those taxa related to its type-species *fleischmanni* and leaving the relationships of *eurygnathum*, *parvulum*, and *uranoscopum* as uncertain, pending further phylogenetic study. Ruiz-Carranza and Lynch (1991a) placed *taylori* in the former "*fleischmanni* group", but Señaris and Ayarzagüena (2005) left *taylori* outside of any speciesgroup because it has green bones, pale lavender coloration in preservative, a distinctive tympanum, fused astragalus and calcaneum but with an evident suture, and males calling from the upper side of leaves (Goin 1968; Señaris & Ayarzagüena 2005, Noonan & Bonett 2003). These characters would seem to ally *taylori* more closely to *Cochranella*, but the osteology of *taylori* is in general similar to that of species of *Hyalinobatrachium s.s.* (see Señaris & Ayarzagüena 2005). Phylogenetic studies are needed to determine the phylogenetic placement of *taylori*.

Two species of *Hyalinobatrachium*, i.e. *iaspidiense* and *nouraguensis*, show a unique color arrangement of the parietal peritoneum, with large dorsal blotches of iridophores (Ayarzagüena 1992; Lescure & Marty 2000; Señaris & Ayarzagüena 2005; D. F. Cisneros-Heredia, R. W. McDiarmid, J. P. Caldwell, and G. Rivas pers. obs.). At least two apparently undescribed taxa also show the same color pattern, one from Venezuela (C. Barrio-Amoros pers. comm.), and another from Amazonian Peru (*Hyalinobatrachium* sp. "Tambopata"; Cocroft *et al.* 2001, Cisneros-Heredia & McDiarmid unpubl. data). We hypothesize that they form a monophyletic group delimited by the synapomorphic occurrence of large blotches of iridophores on the dorsum (versus blotches of iridophores completely absent from the dorsum in other Centrolenidae and in fact apparently from all other anurans). We are uncertain about the relationships of this group with the taxa herein recognized as *Hyalinobatrachium s.s.*, and additional phylogenetic studies are needed to determine if it is embedded within *Hyalinobatrachium* or corresponds to a different clade deserving generic recognition.

**Comments about taxa under *Centrolene/Cochranella*.**—The species *acanthidiocephalum*, *geckoideum*, *medemi*, *paezorum*, and *petrophilum* were joined under the *Centrolene geckoideum* group (Ruiz-Carranza & Lynch 1991a). These species were united by sharing the following characters: humeral spine in males, small eyes (ED<3DW), green bones, trilobed liver, white pigment on the parietal and pericardial peritonea while absent on the visceral peritonea, and vomerine teeth present (Ruiz-Carranza and Lynch 1991a). However, the only unique and distinctive feature for the group was the ratio between the eye-diameter and the width of disc on finger III (ED/3DW). Most analyses of the phylogenetic relationships of the glassfrogs based on morpho-

logical characters used the ED/3DW ratio as a well-supported character for the "*geckoideum* group" (e.g., Ruiz-Carranza & Lynch 1991, Guayasamin et al. 2006b). Savage (2002) proposed the restriction of the genus *Centrolene* to *geckoideum, acanthidiocephalum*, and *paezorum* based on the ED relative size, ED<3DW, and resurrected *Centrolenella* from the synonymy of *Centrolene* to include the species with ED>3DW. This proposal was not follow by subsequent researchers (Cisneros-Heredia and McDiarmid 2006a, Guayasamin et al. 2006b) because it did not address Ruiz-Carranza and Lynch's (1991a) evaluation and discussion of the eye-size character, and was based on insufficient information to determine the true relationships of the taxa involved. We examined specimens of *acanthidiocephalum, geckoideum, medemi, paezorum*, and *petrophilum*, and found that only *geckoideum* and *paezorum* have ED=3DW (small eyes, *geckoideum* ED/3DW = 0.70–0.94; *paezorum* ED/3DW = 1), while the other three species have ED>3DW (medium to large eyes, *acanthidiocephalum* ED/3DW = 1.12–1.63; *medemi* ED/3DW = 1.11–1.57; *petrophilum* ED/3DW = 1.19–1.65) (Ruiz-Carranza et al. 1986, Ruiz-Carranza & Lynch 1989, Ruiz-Carranza & Lynch 1991a, Rueda-Almonacid 1994, Cisneros-Heredia & McDiarmid pers. obs.). This pattern is also apparent from the figures presented by Ruiz-Carranza and Lynch (1991a: 16–17), where only *geckoideum* and *paezorum* were distinctive in terms of 3DW vs. SVL and ED vs. SVL, while *acanthidiocephalum, medemi*, and *petrophilum* clustered together with the smaller species. Guayasamin et al. (2006b) redefined the diagnostic character of the "*geckoideum* group" to "disc of Finger III large (> 80% of eye diameter)". Yet, again inconsistencies exist as only *geckoideum* and *paezorum* have this condition, while the other species in the group (*acanthidiocephalum, medemi*, and *petrophilum*) have ranges between 60–88%, and other centrolenids also have similar intermediate values (e.g., *tayrona* with 53–80%). The ED/3DW ratio is inversely proportional to the SVL of the species; small-sized taxa have higher ED/3DW values (= 1.70), medium-sized taxa have intermediate ED/3DW values (1.10–1.70), a large-sized taxon like *paezorum* has a low ED/3DW value (1.00), and a giant-sized glassfrog like *geckoideum* has the lowest ED/3DW values (0.70–0.94). Further, larger discs may be a reflection of the saxicolous habits (on rocks along streams or waterfalls borders) of *geckoideum, paezorum, medemi, euhystrix, orejuela*, and *Cochranella* sp. 4 (Cisneros-Heredia & McDiarmid 2006a, M. Rada pers. comm.; pers. obs.). The ED-3DW ratio and the disc size are uninformative characters that provide little evidence about the relationships of taxa because they show continuous variation and reflect adaptations to a particular microhabitat. Thus, there is no basis to recognize a phenetically defined "*geckoideum* group".

The species *geckoideum*, type-species of the genus *Centrolene*, is different in many morphological and behavioural characters from most centrolenid species. The humeral spine of *geckoideum* (Fig. 6) is a sharply pointed, almost needle-like (neither laminar nor blade-like), smooth, curved spine that protrudes through the skin in some males. The spine is separated from the *crista ventralis* by a deep notch, and projects from the proximal portion of the *crista ventralis* and not from its distal portion (Ruiz-Carranza & Lynch 1991b, Rueda-Almonacid 1994, Cisneros-Heredia & McDiarmid unpubl. data). The size of the spine of *geckoideum* is directly related to the species SVL (i.e., the larger the species the larger its spine), but most centrolenid species, including the large *acanthidiocephalum* and *tayrona*, have laminar spines. Although some species such as *andinum* and *ilex* have sharp pointed spines, they are not needle-like nor separated from the *crista ventralis*; and while *tayrona* has the spine projecting from the center of the *crista ventralis* rather than from its distal end, it is laminar and otherwise very similar to spines of other centrolenids. Further, *geckoideum* is the only centrolenid species reported to produce skin secretions, a condition probably related to the developed and abundant dorsal glands. The species *paezorum* is known only from the female type; thus, it is currently impossible to determine the morphology of its humeral spines, and no information about secretions has been reported, although the species has abundant dorsal glands. The general morphology of *paezorum* is similar to *geckoideum* as previously recognized by Ruiz-Carranza et al. (1986), and we hypothesize that they are sister-species.

As presently defined, the genus *Centrolene* includes all species with humeral spines and was found to be paraphyletic with regards to *Cochranella* by Frost et al. (2006). Further phylogenetic analysis may call for a

resurrection of the name *Centrolenella*, currently under the synonymy of *Centrolene*. The type-species of *Centrolenella* is *antioquiensis*; it is a taxon characterized by having white pigment on the visceral peritonea, and as such it was placed in the "*peristictum* group" (Ruiz-Carranza & Lynch 1991a). The "*peristictum* group" was formed by *antioquiense*, *gemmatum*, *litorale*, *lynchi*, *peristictum*, and *sanchezi*. The presence of silver white pigment over the visceral peritonea (excluding the hepatic peritoneum that is clear) was defined as the distinctive character for most of its members (Ruiz-Carranza & Lynch 1991a, Guayasamin et al. 2006b). However, white pigment on the visceral peritoneum, condition V2, is found in *antioquiense*, *litorale*, *peristictum*, and "Palenque"; but also in species of the "*prosoblepon* group": *hybrida* and *quindianum*, and outside of *Centrolene* in several species of *Cochranella*. In contrast, *sanchezi* has clear visceral peritonea (Ruiz-Carranza & Lynch 1991b), and we have examined several fresh specimens of *lynchi* and have found no trace of white pigment on the visceral peritonea (*contra* Ruiz-Carranza & Lynch 1991a, 1991d). The taxa *peristictum*, *lynchi*, *antioquiensis*, and *pipilatum* share two conditions that we considered derived: dorsum with light flecks and diffuse dark spots (versus the primitive state of uniform green), and Type-II nuptial excrescence (versus the primitive state of Type-I nuptial excrescence). In addition, *lynchi* and *pipilatum* have distinct prepollices (versus the primitive state of concealed prepollex; this condition was previously unreported in *pipilatum*, but revealed by our examination of one paratype [ICN 23756] and additional specimens [MCZ 97803, USNM 286717]). Further, *peristictum*, *lynchi*, *antioquiensis*, and *pipilatum* have similar humeral spines (small, curved, with a relatively short *crista ventralis*), and *antioquiensis* and *lynchi* show similar reproductive behaviors, placing their egg clutches on the undersides of leaves and having parental care (M. Rada & P. Gutiérrez pers. comm.; pers. obs.). In contrast, *litorale* and the undescribed "Palenque" share four characters that we consider derived and that clearly separate them from the previous species: Type-IV nuptial excrescence (versus the primitive state of Type-I nuptial excrescence), dorsolateral yellow lines (a unique condition, otherwise known only in *duranti*), distinct prepollex (versus the primitive state of concealed prepollex), and reddish tinted irises (a unique condition in the family; Fig. 8). The humeral spines of *litorale* and "Palenque" are very different from those of other species (including *peristictum*, *lynchi*, *antioquiensis*, and *pipilatum*), being very small and poorly developed, Nothing is known about the reproductive behaviors of *litorale* or "Palenque". These data suggest that (i) the "*peristictum* group" is non-monophyletic, supporting conclusions by Noonan & Harvey (2000) and Cisneros-Heredia & McDiarmid (2006a); (ii) *peristictum*, *lynchi*, *antioquiensis*, and *pipilatum* apparently form a monophyletic group; (iii) the relationships of these species with other phenetically similar species must be tested, i.e., *quindianum*, *huilense*, *sanchezi*; and (iv) *litorale* and "Palenque" apparently form a monophyletic group, that may not be related to *peristictum*, *lynchi*, *antioquiensis*, and *pipilatum*.

The relationships of the various other species with white visceral peritonea are problematic. The following five Guianan taxa share the presence of distinct prepollices (either as prepollical bulges or as spines) and white visceral peritonea (including the hepatic peritoneum): *lema*, *gorzulai*, *papillahallicum*, *oyampiensis*, and *castroviejoi*. The first three species were placed as the "*gorzulai* group" of the genus *Centrolene* by Duellman & Señaris (2003), while the last two were clustered with *helenae* under the "*oyampiensis* group" of the genus *Cochranella* by Señaris & Ayarzagüena (2005). Together with *antisthenesi*, and the Brazilian *eurygnathum*, *parvulum*, and *uranoscopum*, these species are the only centrolenid taxa that are lavender in preservative and have iridophores over the hepatic peritoneum. Species currently placed under *Hyalinobatrachium*, and *pulveratum*, *revocata*, and *mariaelenae* have iridophores on the hepatic peritoneum (and *mariaelenae* humeral spines); but, their chromatic structure is different, turning white or cream in preservative. The species *antisthenesi*, *eurygnathum*, *parvulum*, and *uranoscopum* have bulbous liver, and *helenae* and *gorzulai* have livers that may appear completely or partially bulbous. Based on these characters and the biogeographical affinities of the taxa involved, we suggest that *antisthenesi*, *castroviejoi*, *gorzulai*, *helenae*, *lema*, *papillahallicum*, *oyampiensis* and probably *eurygnathum*, *parvulum*, and *uranoscopum* may form a monophyletic clade, but a phylogenetic study must determine its real affinities. Earlier we regarded the Andean *mariaelenae* as a

member of the *gorzulai* group (Cisneros-Heredia & McDiarmid 2006); yet the chromatophore structure (turns cream or pale lavender in preservative) and its geographical distribution suggest that it may not be related to the Guianan species. The species *mariaelenae* shows derived conditions otherwise attributed as unique to different groups: it has humeral spines, and a bulbous liver covered by iridophores; its phylogenetic relationships are uncertain.

In addition to the species mentioned in the two paragraphs above, iridophores over the visceral peritonea are present in *ametarsia*, *cariticommata*, *midas*, and *pulverata*, and species of the former "*granulosa* group". The following eight species were considered part of the former "*granulosa* group", i.e., *daidalea*, *euknemos*, *granulosa*, *mache*, *phryxa*, *resplendens*, *savagei*, and *solitaria*. Duellman and Schulte (1993) described *croceopodes* and placed it in the former "*granulosa* group". Ruiz-Carranza and Lynch (1995a) removed the species from the "*granulosa* group" and included it in the "*spinosa* group"; but Guayasamin and Bonnacorso (2004) moved it back, arguing that "according to the original description… *croceopodes* has a white visceral peritoneum"; however they did not dissect specimens since only the types were available (J.M. Guayasamin pers. com). Recent surveys in northeastern Peru found additional specimens of *croceopodes* and confirmed that the species has clear visceral peritonea (uncovered by iridophores) (M. Rada pers. comm.). Since *croceopodes* also lacks dermal folds on the arms and legs, we follow Ruiz-Carranza & Lynch (1995a) in considering it to be unrelated to species in the former "*granulosa* group". The visceral peritonea of *orejuela* were originally described as white by Duellman and Burrowes (1989); however, review of additional material showed that the species has clear visceral peritonea (M. Rada pers. comm.). In contrast, the recently described *adenocheira* was placed in the former "*ocellata* group" by Harvey and Noonan (2005) but it has white visceral peritonea, dermal folds on arms and legs, green bones, vomerine teeth, and extensive hand webbing, and we regard it as related to species of the former "*granulosa* group. The species *adenocheira*, *daidalea*, *euknemos*, *granulosa*, *mache*, *phryxa*, *resplendens*, *savagei*, and *solitaria* have white visceral peritonea, clear hepatic peritoneum, dermal folds on arms and legs, green bones, vomerine teeth, and extensive hand webbing (Guayasamin & Bonnacorso 2004; Aguayo & Harvey 2006). Morphologically, they seem to form a fairly uniform group of species; however, differences in their reproductive behaviors suggest that these species may not be as closely related as previously conceived. Little information about the natural history of these species is available, but *granulosa* and *euknemos* lack parental care of the eggs (Savage 2002), while *daidalea* and *savagei* show parental care of the eggs (M. Rada and P. Gutiérrez pers. comm.). Further phylogenetic analysis including molecular data may clarify the relationships of these species. Since *granulosa* is the type-species of the genus *Cochranella*, this generic name is best reserved for species related to *granulosa*. The species *midas* has iridophores over some visceral peritonea (covering the esophagus, stomach, intestines, and renal capsules), but, *midas* is morphologically different from species assigned to the former "*granulosa* group", particularly by lacking any dermal folds, having a rounded snout, and small SVL. The relationships of *midas* are uncertain, but it is morphologically similar to *spinosa*, and other species previously included in the former "*spinosa* group". We are uncertain about the relationships of the species of the former "*spinosa* group", but if the generic name *Cochranella* were to be restricted to species related to *granulosa*, the name *Teratohyla* would be available for *spinosa* (its type-species) and the species related to it.

The species *pulverata*, *ametarsia*, and *cariticommata* have iridophores partially or completely covering the visceral peritonea. The species *pulverata* has all visceral peritonea covered by iridophores, and externally is similar to *mache* and *euknemos*. However, *mache* and *euknemos* are apparently related to *granulosa*, and differ from *pulverata* by having iridophores on the parietal peritonea and by having lobed livers without iridophores on the peritoneum. The relationships of *pulverata* are uncertain, and further phylogenetic analyses including molecular data are needed. The species *ametarsia* has iridophores on the peritonea of the esophagus, stomach, and renal capsule (lacks them on the intestinal and hepatic peritonea) but was originally placed in the former "*spinosa* group" (Ruiz-Carranza & Lynch 1995a, Savage 2002, Guayasamin et al. 2006b). It, *ametarsia*, is very similar to *oyampiensis* in terms of morphology and coloration (see below for details). If

future research confirms they are closely related, the different coloration of their hepatic peritoneum would suggest the non-monophyly of the former "*oyampiensis* group", and the existence of variation in the hepatic peritoneum coloration in closely related species, thus challenging the previous concept about the value of this character for separating supraspecific clades. The species *cariticommata* is the only species with basal hand webbing that has been reported to have iridophores covering its esophageal peritoneum; otherwise, it is similar to other species with basal hand webbing that lack vomerine teeth, especially *buenaventura*, *griffithsi*, and *wileyi* (see Cisneros-Heredia & Yánez-Muñoz 2007). However, the presence of iridophores on the esophageal peritoneum may be easily overlooked because that area is covered by the lobes of the liver, thus white pigment on the esophagus could occur in other species but has been overlooked.

Three centrolenid species, *ocellata*, *puyoensis*, and *mariae* share a unique dorsal color pattern, and basal webbing between fingers II, III and IV. Cisneros-Heredia and McDiarmid (2006b) moved *puyoensis* from *Centrolene* to *Cochranella* because males lack humeral spines; they also suggested that *ocellata* was probably related to *puyoensis* (Cisneros-Heredia & McDiarmid 2006b). The three species show a reticulate pattern formed by the presence of abundant pale spots (medium to large) over a darker background; to the best of our knowledge, this is a unique color pattern among glassfrogs (see pictures of *puyoensis* in Flores & McDiarmid 1989, and of *ocellata* and *mariae* in Guayasamin et al. 2006b). In fact, *mariae* seems to be almost indistinguishable from *puyoensis* according to the original description of the later (but has some differences in hand webbing and cloacal ornaments), and we suggest that they may be related if not conspecific. Any further speculation or discussion about their relationships requires more data from these three rare species (*ocellata*, *puyoensis*, and *mariae*). Meanwhile, we leave them in the non-monophyletic *Cochranella*.

The following species formerly placed in the "*ocellata* group" by Ruiz-Carranza & Lynch (1995a) are homogeneous in their morphologies, known osteology, and basic coloration and peritoneal patterns: *anomala*, *armata*, *bejaranoi*, *buenaventura*, *cariticommata*, *chami*, *chancas*, *cristinae*, *cochranae*, *ignota*, *garciae*, *griffithsi*, *luminosa*, *luteopunctata*, *megacheira*, *mixomaculata*, *nephelophila*, *oreonympha*, *phenax*, *posadae*, *pluvialis*, *prasina*, *ruizi*, *rosada*, *siren*, *spilota*, *truebae*, *wileyi*, and a new species described below. The reduced or absent webbing between all fingers is a character-state shared by all species, and we consider it a derived character (versus the ancestral state of extensive hand webbing), and a synapomorphy for this group that supports its monophyly. In addition, all species lack humeral spines, have clear intestinal and hepatic peritonea (lacking iridophore layers), are lavender or brownish in preservative (but not cream like *fleischmanni* or green like *vozmedianoi*), and most species lack vomerine teeth. All genera currently available in the family Centrolenidae, as defined by their type species, have extensive webbing between the fingers (*Centrolene*, type-species *geckoideum*; *Centrolenella*, type-species *antioquiensis*; *Cochranella*, type-species *granulosa*; *Teratohyla*, type-species *spinosa*; and *Hyalinobatrachium*, type-species *fleischmanni*). We consider that the group of species mentioned above forms a clade, and that no available name is applicable to it; thus,, we propose a new generic name for it.

## GENUS *NYMPHARGUS* new genus

*Type species.*—*Nymphargus cochranae* new combination

*Content.*—29 species: *Nymphargus anomalus* (Lynch & Duellman, 1973) new comb.; *N. armatus* (Lynch & Ruiz-Carranza, 1996) new comb; *N. bejaranoi* (Cannatella, 1980) new comb.; *N. buenaventura* (Cisneros-Heredia & Yánez-Muñoz, 2007) new comb.; *N. cariticommatus* (Wild, 1994) new comb.; *N. chami* (Ruiz-Carranza & Lynch, 1995) new comb.; *N. chancas* (Duellman & Schulte, 1993;) new comb.; *N. cochranae* (Goin, 1961) new comb.; *N. cristinae* (Ruiz-Carranza & Lynch, 1995) new comb.; *N. garciae* (Ruiz-Carranza & Lynch, 1995) new comb.; *N. griffithsi* (Goin, 1961) new comb.; *N. ignotus* (Lynch, 1990) new comb.; *N. laurae* Cisneros-Heredia & McDiarmid, new species; *N. luminosa* (Ruiz-Carranza & Lynch, 1995) new comb.; *N. luteopunctatus* (Ruiz-Carranza & Lynch, 1996) new comb.; *N. megacheirus* (Lynch & Duellman,

1973) new comb.; *N. mixomaculatus* (Guayasamin et al. 2006b) new comb.; *N. nephelophila* (Ruiz-Carranza & Lynch, 1991) new comb.; *N. oreonympha* (Ruiz-Carranza & Lynch, 1991) new comb.; *N. phenax* (Cannatella & Duellman, 1982) new comb.; *N. pluvialis* (Cannatella & Duellman, 1982) new comb.; *N. posadae* (Ruiz-Carranza & Lynch, 1995) new comb.; *N. prasinus* (Duellman, 1981) new comb.; *N. rosada* (Ruiz-Carranza & Lynch, 1997) new comb.; *N. ruizi* (Lynch, 1993) new comb.; *N. siren* (Lynch & Duellman, 1973) new comb.; *N. spilotus* (Ruiz-Carranza & Lynch, 1997) new comb.; *N. siren* (Lynch & Duellman, 1973) new comb.; *N. spilota* (Ruiz-Carranza & Lynch, 1997) new comb.; *N. truebae* (Duellman, 1976) new comb.; and *N. wileyi* (Guayasamin et al., 2006c) new comb.

*Characterization and diagnosis.*—Absence of webbing between fingers I, II, and III, and reduced (basal) webbing between fingers III and IV. Humeral spines absent. Iridophores on the parietal peritoneum covering at least its anterior half. Lobed livers with hepatic peritonea lacking iridophores (clear). Iridophores absent from the peritonea covering the intestines in all species. Vomerine teeth absent in most species. Most species green in life and lavender in preservative, but some with a brownish tint both in life and in preservative.

*Distribution.*—Western Andean slopes and adjacent lowlands of Colombia and Ecuador; and eastern Andean slopes of Colombia, Ecuador, Peru, and Bolivia.

*Etymology.*—*Nymphargus* is formed from the Greek *nýmphaē* in allusion to the nymphs, beautiful goddesses in Greek mythology that personify the creative and fostering activities of nature, living in mountains, valley, springs and rivers; and, *argus* in allusion to the mythological Greek Argus, nephew of the nymph *Io*, a giant with a hundred eyes, whose eyes became the ocelli in the peacock's tail. The name is masculine and alludes to the true ocelli found on the dorsum of four of the most peculiar species of the genus: *anomalus*, *cochranae*, *ignotus*, and *laurae* sp. nov.

*Remarks.*—As found by recent studies (Darst & Cannatella 2005, Frost et al. 2006) and from the information presented above, *Centrolene* and *Cochranella* are non-monophyletic. Although present evidence is insufficient to allow an exhaustive phylogenetic hypothesis to solve this problem, the recognition of *Nymphargus* as a monophyletic group is the first step, and concerns about future improvements in our knowledge should not prevent present progress.

The genus *Nymphargus* differs from all other genera available for centrolenid taxa (*Centrolene*, *Centrolenella*, *Cochranella*, *Teratohyla*, and *Hyalinobatrachium*) by having clear visceral peritonea (white visceral peritonea in the type-species of *Centrolenella*, *Cochranella*, and *Hyalinobatrachium*), lacking a protruding cresta ventralis forming a humeral spine (present in *Centrolene* and *Centrolenella*), having the hand webbing very reduced or absent on all fingers (extensive hand webbing in *Centrolene*, *Centrolenella*, *Cochranella*, *Teratohyla*, and *Hyalinobatrachium*), having a concealed prepollex (distinct prepollex in the type-species of *Centrolenella* and its related species and in the type species of *Teratohyla*), being lavender or brownish lavender in preservative (*Hyalinobatrachium* are cream in preservative, *vozmedianoi* is green and cream in preservative, the type-species of *Centrolene* is grey in preservative), and placing the egg clutches on the upper sides of leaves and with males showing parental care, at least for the species where information is available (*Hyalinobatrachium* place them on the underside of leaves and show parental care, the type-species of *Teratohyla* uses both sides but no parental care has been recorded; the type-species of *Centrolenella* and its related-species place them on the undersides of leaves and at least *peristictum* exhibits parental care; and the type-species of *Centrolene* attaches egg clutches to waterfall walls but no parental care has been recorded).

Available information does not allow a complete evaluation of the relationships among the species included in *Nymphargus*. However, two groups of species inside *Nymphargus* are apparently monophyletic. The species *buenaventura*, *cariticommatus*, *griffithsi* and *wileyi* share several characteristics, including snout form, general appearance, and presence of low ulnar folds. Cisneros-Heredia & Yánez-Muñoz (2007b) suggested that *buenaventura*, *cariticommatus*, *griffithsi*, and *wileyi* formed a monophyletic group, which they called the "*griffithsi* clade". Until recently, the presence of iridophores on the renal capsules was considered as unique to these four species, but it seems to be more widespread across different centrolenid genera (pers.

obs.). However, we agree that these four species are extremely similar and appear to be closely related. The second group is formed by the ocellated species, *anomalus*, *cochranae*, *ignotus*, and a new species described below. Lynch (1990) suggested that *anomalus*, *cochranae*, and *ignotus* seemed to constitute a monophyletic group characterized by having ocelli on the dorsum and by *anomalus* and *ignotus* having a tan dorsal coloration instead of green. Their ocelli are always elevated over tubercles or warts and characterized by being completely circular with clear-cut edges and clear-colored centers. We consider that the presence of these true ocelli is a unique synapomorphy for this clade within *Nymphargus*. Three other centrolenid frogs have been mentioned in the literature as having dorsal markings similar to ocelli: *ocellata*, *luteopunctata*, and *ocellifera*. Lynch (1990) suggested that the ocellate pattern of *ocellata* was more similar to the open reticulations found in some *Hyalinobatrachium* rather than being truly ocellated. We agree with Lynch (1990) about the presence of a reticulated rather than ocellated pattern in *ocellata*, but consider *ocellata* to be more similar to *puyoensis* or to *luteopunctata* (see above). Ruiz-Carranza and Lynch (1996) described the dorsal pattern of *luteopunctata* as "green with irregular, large yellow spots delimited by black" (free translation from Spanish). These dorsal markings could be interpreted as ocelli, but they are not circular, the dark borders (black in life, lavender in preservative) are irregular and not uniformly delimited, and although the yellow spots are slightly elevated, they do not correspond to tubercles. The species *ocellifera* is a synonym of *prosoblepon* (see below), and its dorsal spotted pattern corresponds to the random association of dark spots around clear spots and may best be considered as false ocelli (Fig. 9). Ruiz-Carranza and Lynch (1997) considered *rosada* closely related to the ocellated species (particularly *anomalus* and *ignotus*) by having a brownish dorsum. These authors suggested that the pallid dorsal dots over a small tubercle could be "primitive ocelli". However, light dots over tubercles or warts are present in other species of *Nymphargus* (e.g., *siren*), as is brown dorsal coloration (e.g., *ruizi* Lynch 1993). Additional studies are required to evaluate the current position of *rosada* within *Nymphargus*.
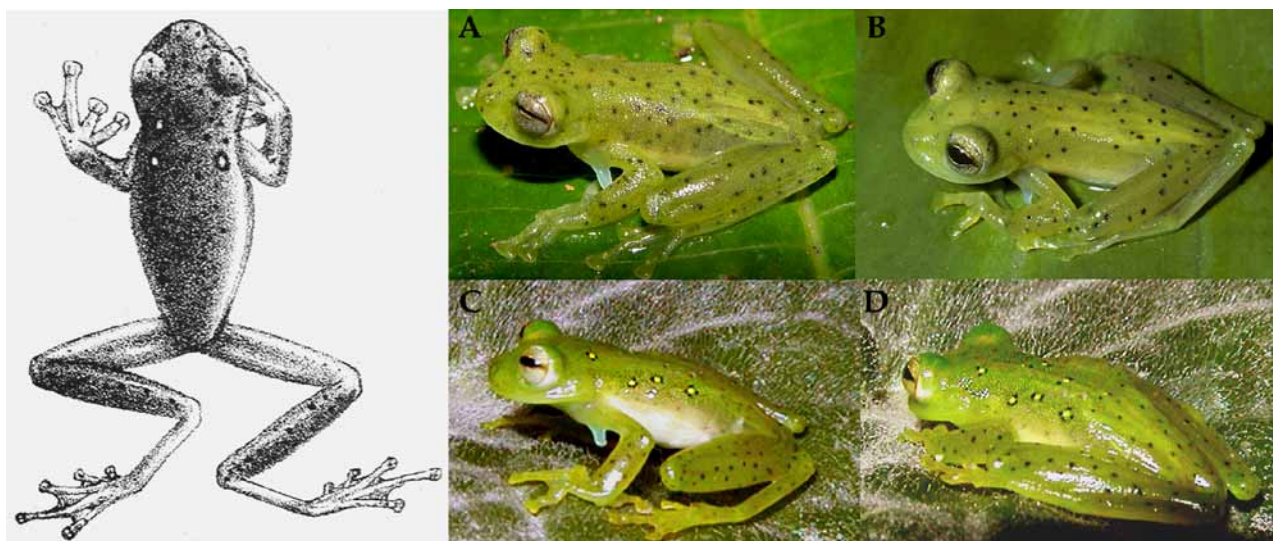


**FIGURE 9.** Left: Drawing of the female holotype of *Hyla ocellifera* Boulenger, 1899 = "*Cochranella ocellifera*" (reprinted from Boulenger 1899). Right (A–D): Photographs of *Centrolene prosoblepon* showing the variation in dorsal pattern. (A) Dark spots only, no yellow spots [MYM]; (B) Dark spots and few yellow spots (e.g., over the shoulder) [RWM]; (C–D) Dark and yellow spots forming false ocelli (same pattern as the holotype of "*Cochranella ocellifera*") [DFCH].

**Description of a new species of *Nymphargus* gen. nov.**—The northern Andean region in Colombia, and Ecuador holds a remarkably high diversity of species in the family Centrolenidae. The northeastern Andean slopes of Ecuador have the highest diversity of centrolenids in the country. However, only a small fraction of this region in Ecuador has been thoroughly surveyed (the Upper Quijos River basin; Cisneros-Heredia &

McDiarmid 2006a); and several museum specimens remain unidentified (Cisneros-Heredia & McDiarmid 2003, 2006a). A specimen (USNM 288453) collected in the Loreto region of eastern Ecuador has such distinctive characters that we conclude that it is well separated from all described centrolenid frogs and we are pleased to describe it as a new taxon:

### Nymphargus laurae Cisneros-Heredia & McDiarmid, new species
(Fig. 10)

*Holotype*

USNM 288453 (original number, Gustavo Orcés-Villagómez collection OV 3298), an adult male (Fig. 10) from "Loreto, Upper Rio Napo" [= Loreto region, near the town of Loreto](ca. 77°20'S, 00°40'W, ca. 500 m elevation), lower slopes of the Sumaco Volcano, on the Cordillera Oriental, eastern slopes of the Andes, Provincia de Orellana, República del Ecuador, collected on October 1955 by Jorge Olalla (Fig. 11).
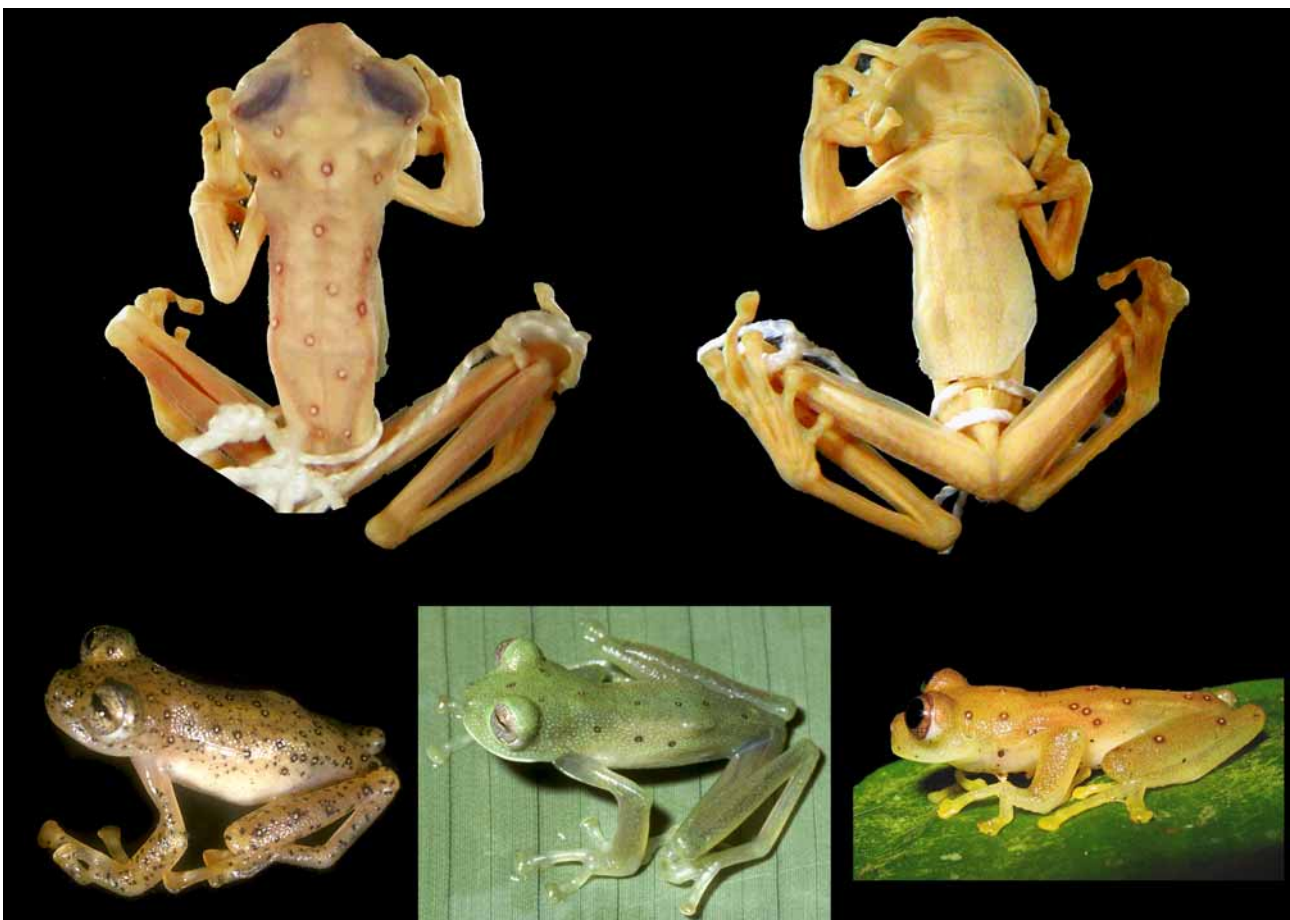


**FIGURE 10. Above:** Dorsal (left) and ventral (right) view of the holotype of *Nymphargus laurae* (USNM 288453), SVL = 19.9 mm, adult male. Below for comparison, from left to right, *Nymphargus anomalus* (KU 14443299, holotype) [WED], *Nymphargus cochranae* (USNM RW 12260) [RWM], *Nymphargus* C) *Nymphargus ignotus* [VVA].

*Diagnosis*

*Nymphargus laurae* (Fig. 10) is diagnosed from all other glassfrogs by the combination of the following characters: (1) vomerine teeth absent; (2) snout truncate in dorsal view and in profile; nostrils slightly elevated producing an slight depression in the internarial area; loreal region concave; (3) tympanic annulus evident,

oriented dorsolaterally with dorsal inclination; weak supratympanic fold from behind the eye to the insertion of the arm; (4) dorsal skin slightly shagreened with elevated warts corresponding to ocelli, and scattered spicules; (5) ventral skin granular; pair of large, round, flat tubercles on ventral surfaces of thighs below vent; other cloacal ornamentation absent; (6) parietal peritoneum white, covering ca. $^2/_3$ of the abdomen (condition P3), all other peritonea clear; (7) liver lobed, hepatic peritoneum clear (no iridophores); (8) humeral spine absent in male holotype, forearm moderately robust; (9) webbing basal between fingers I, II and III, outer fingers III$2^2/_3$-$2^1/_2$IV; (10) webbing on feet I$2^-$–$2^+$II$1^1/_2$–$2^+$III$1^+$–$2^1/_2$IV$2^1/_2$–$1^1/_2$V; (11) no dermal folds or tubercles on hands, forearms, feet, or tarsi; (12) unpigmented nuptial pad Type I; concealed prepollex; (13) second finger longer than first, (14) eye diameter larger than width of disc on finger III; (15) color in line, green with yellow spots surrounded by black; (16) color in preservative, dorsal surfaces tan cream with dark reddish lavender ocelli; (17) iris coloration unknown; (18) melanophores absent on fingers and toes; (19, 20, 21, 22, 23) calling site, advertisement call, fighting behavior, egg clutches, parental care, and tadpoles unknown; (24) snout-vent length in male holotype 19.9 mm; females unknown.
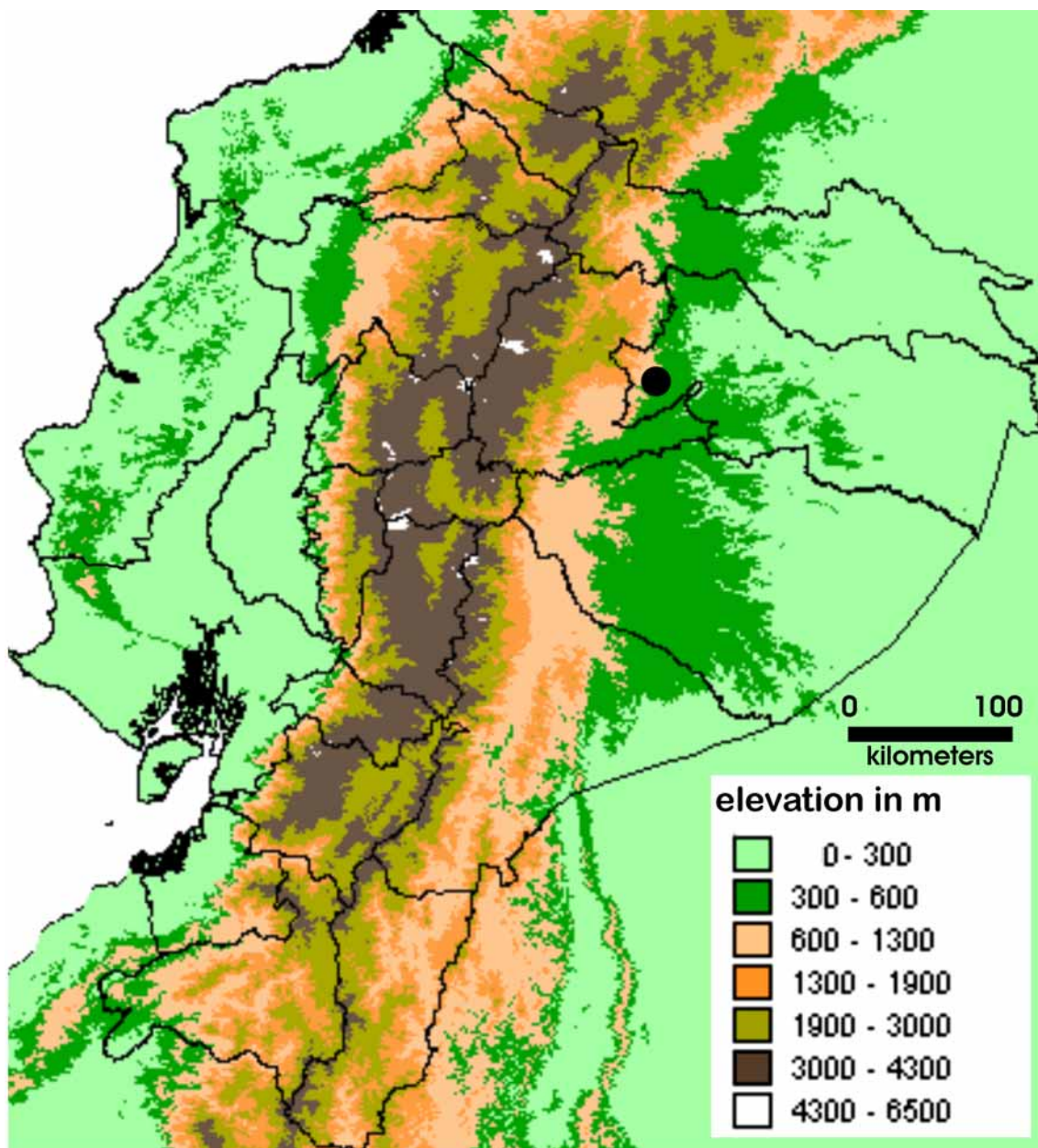


**FIGURE 11.** Distribution map of *Nymphargus laurae* in Ecuador.

CISNEROS-HEREDIA & MCDIARMID

*Comparisons*

The presence of ocelli on the dorsum separates *Nymphargus laurae* from most glassfrogs, except for the three ocellated species of the genus *Nymphargus*: *N. anomalus* (Lynch & Duellman, 1973), *N. cochranae* (Goin, 1961), and *N. ignotus* (Lynch, 1990). All four species are very similar in their general appearance, but *N. laurae* differs from *N. anomalus* by having larger (at least twice) and fewer ocelli; by completely lacking ocelli on forearms and shanks; and by its smaller size (19.9 mm SVL male holotype of *N. laurae* versus 24.1 mm SVL male holotype *N. anomalus*). In addition, *N. laurae* has the second finger longer than first finger; distal subarticular tubercle on forth finger bifurcate; supernumerary tubercles present; and indistinct outer metatarsal tubercle. *Nymphargus laurae*, *N. ignotus* and *N. cochranae* differ from *N. anomalus* by lacking dark brown flecks interspersed among the ocelli; examination of a large series of *ignotus* and several specimens of *cochranae* shows that there is no interspecific variation in this character. Besides, *N. anomalus* is known from higher elevations (1740 m above sea level). *Nymphargus laurae* differs from *N. ignotus* by having larger (at least two times) and fewer ocelli (19 ocelli in *laurae*, vs. 28–95 ocelli [mean 48, n = 30] in *ignotus*); lacking ocelli on forearms and shanks (vs. 7–20 ocelli [mean 10, n = 30] in *ignotus*); having a bifurcate distal subarticular tubercle of fourth finger; having supernumerary tubercles; and by being smaller (22.3 – 25.4 mm SVL in males of *N. ignota*). Further, *Nymphargus ignotus* is known only from western Colombia around 1900 m above sea level. *Nymphargus laurae* differs from *N. cochranae* by having much larger ocelli (the light-colored centers of the ocelli in *cochranae* are so small in some specimens that without close inspection, they appear to be just dark spots); second finger longer than first; distal subarticular tubercle of fourth finger bifurcate; indistinct outer metatarsal tubercle; supernumerary tubercles present; no ocelli on forearms and shanks; no vomerine teeth (present in some *N. cochranae*); and, smaller size (23.8–26.7 mm SVL in males of *N. cochranae*). *Cochranella ocellata* has a reticulate pattern similar to ocelli but without warts or tubercles; larger and ill-defined pale spots; slightly more webbing on hand; and a rounded snout in dorsal and lateral views; lacks subcloacal tubercles; and is slightly larger (adult males 21.0 – 25.1 mm SVL).

*Description of the holotype*

Adult male, SVL = 19.9 mm (Fig. 10). Body slender. Head distinct, slightly wider than long, and wider than body; HW/HL = 1.07, HW/SVL = 0.37, HL/SVL = 0.35. Snout short, truncate in dorsal view and in profile, EN/HL = 0.25; nostrils slightly elevated producing slight depression in internarial area; loreal region concave; canthus rostralis indistinct separated by a shallow platform; concave loreal region; lips slightly flared. Eyes large, ED/HL = 0.42, directed anterolaterally at about 45° from midline, eyes visible when viewed from below, interorbital area wider than eye diameter, IOD/ED = 1.31, EN/ED = 0.59, EN/IOD = 0.45. Tympanic annulus evident, oriented dorsolaterally with dorsal inclination; weak supratympanic fold from behind eye to insertion of arm, separated from orbit by distance less than diameter of tympanum. Dentigerous processes of vomers absent; choanae of moderate size, round, near margin of mouth; tongue round, slightly notched behind, not indented posteriorly; vocal slits paired, extending from anterior base of tongue to angles of jaws.

Skin of dorsal surfaces of head, body, and limbs slightly shagreened with scattered spicules and elevated warts corresponding to ocelli; ventral surfaces granular. Some spicules below the tympanum appear to be enameled. Cloacal opening directed posteriorly at upper level of thighs; no distinct cloacal sheath; a pair of large, round, flat subcloacal warts on ventral surfaces of thighs below vent, other cloacal ornamentation absent, ventral skin granular but not enameled (at least in preservative).

Upper arm thin, forearm moderately robust, width of upper arm about half that of forearm. Humeral spine absent (Fig. 10); ulnar fold and tubercles absent. Relative lengths of fingers III > IV > II > I; webbing basal between fingers I, II and III, outer fingers III2⅔-2½IV; bulla absent; finger discs wide, nearly truncate; disc on third finger slightly larger than those on toes, and smaller than eye diameter, 3DW/ED = 0.41; subarticular tubercles rounded and elevated except distal subarticular tubercle of fourth finger, which is bifurcate supernumerary tubercles present; palmar tubercle large, rounded, elevated; thenar tubercle elliptic. Concealed pre-

pollex, unpigmented nuptial excrescences Type I present.

Hind limbs slender; TL/SVL = 0.59, FL/SVL = 0.44. Tarsal fold apparent but probably an artifact of preservation; inner metatarsal tubercle large and elliptical; outer metatarsal tubercle indistinct. Subarticular tubercles rounded and low; supernumerary tubercles small, rather indistinct. Webbing on feet I $2^-$–$2^+$ II $1^1/_2$–$2^+$ III $1^+$–$2^1/_2$ IV $2^1/_2$–$1^1/_2$V; disc on toe I round not expanded, all other discs bluntly truncate, two pointed projections on all toe discs except for toe V.

*Coloration of holotype*

In preservative (Fig. 10), all dorsal surfaces cream-colored with minute reddish lavender melanophores as punctuations (visible under magnification); these punctuations more concentrated toward flanks, forming a reddish lavender shadow on sides of body. Dark reddish lavender ocelli over head and body. In center of each ocelli is a cream-colored warts. Upper eyelid dark lavender. Venter cream. Bones white in preservative. Parietal peritoneum with a light layer of iridophores, condition P3 (fading of iridophores probably due to preservation and time); all other peritonea clear, condition V0. The coloration of the holotype in life is briefly described as green with yellow spots surrounded by black in correspondence between Gustavo Orcés-Villagómez and James A. Peters (Archives of Field Notes, Division of Amphibians and Reptiles, National Museum of Natural History [DAR-NMNH]).

Measurements

Snout-vent length, 19.9 mm; head width, 7.4 mm; head length, 6.9 mm; horizontal eye diameter, 2.9 mm; inter-orbital distance, 3.8 mm; eye-nostril distance, 1.7 mm; internarial distance, 1.6 mm; tibia length, 11.7 mm; foot length, 8.7 mm; width of disc on the third finger, 1.2 mm.

*Etymology*

This new species is named in honor of Laura Heredia, D. F. Cisneros-Heredia's grandmother and friend, who has always fostered Diego's interest for animals and science with infinite love, patience, and wisdom.

*Distribution and natural history*

The type locality of *Nymphargus laurae* indicated in the USNM catalog is "Loreto, Upper Rio Napo". Gustavo Orcés-Villagomez, in a letter to James A. Peters (Archives DAR-NMNH) described in detail the Loreto region where Jorge Olalla collected a great deal of material. This area of Amazonian foothills corresponds to the trapezoidal plateau limited to the northeast and west by the Cordillera Oriental (the eastern range of the Andes in Ecuador), to the southeast by the Cordillera de Galeras, to the south by the Napo River, and to the north and east by the Payamino River. This plateau covers almost 1,200 km$^2$, and the small town of Loreto is located within it (Hudelson 1987, IGM 2000). The elevational range of the plateau extends from ca. 300 m at the Napo River up to ca. 700 m on the slopes of the Sumaco Volcano (Hudelson 1987, IGM 2000). According to the letters between G. Orcés-Villagomez and J. A. Peters, the collections by J. Olalla were concentrated near the town, this information has been confirmed by surviving members of the Olalla family (A. Almendáriz pers. comm.). The type locality of *N. laurae* is better defined as near Loreto (ca. 77º20'S, 00º40'W, ca. 500 m elevation), Province of Orellana, Ecuador (Fig. 11). The adult male holotype of *N. laurae* likely was found along a stream that runs through the Foothill Evergreen forests of the Loreto plateau. *Nymphargus cochranae* (USNM 288452), *Cochranella flavopunctata* (USNM 288456), an undescribed centrolenid (USNM 288455), and an unidentified glassfrog (USNM 288457) were also collected in the Loreto region and may occur in sympatry with *N. laurae*. In addition, *Hypsiboas boans* and *Dendropsophus triangulum* were collected by J. Olalla at the locality in the same month that *N. laurae* was collected, which suggests possible sympatry. *Nymphargus laurae* (together with *N. cochranae*, *Cochranella flavopunctata*, *Co. puyoensis*, and the undescribed species) is part of an ecological group of glassfrogs that inhabits intermediate elevations (600–1300 m) between the ranges of lowland species (up to 600 m) and cloud forest taxa (1300–1900 m)

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(Lynch & Duellman 1973, Cisneros-Heredia & McDiarmid 2006a).

*Remarks*

*Nymphargus laurae* corresponds to the species cited as "*Cochranella* sp. N2" by Cisneros-Heredia and McDiarmid (2006a). The holotype of *Nymphargus laurae* was incorrectly reported as "*Centrolenella ocellifera*" by Lynch and Duellman (1973, p. 43), who erroneously noted its locality as Pilaló a site at 2,468 m elevation on the Pacific versant in the Province of Cotopaxi.. The correct locality of the holotype of *N. laurae* is in the Amazonian lowlands. The holotype of *Nymphargus laurae* has two pointed projections (papillae) on each toe discs, except for toe V. The pointed projections of *N. laurae* are distinctive on all digits and are not artifacts of preservation. Some paratypes of *Nymphargus ignotus* also have pointed projections on their toes (D. F. Cisneros-Heredia & R. W. McDiarmid pers. obs.). Noonan and Harvey (2000) reported the presence of a projection at the end of toe I in their specimens of *Centrolene papillahallicum* from Guyana, and Harvey and Noonan (2005) reported pointed toes in *Cochranella adenocheira* from Bolivia (but lacking papillae). As Noonan and Harvey (2000) and Harvey and Noonan (2005) commented, the presence of pointed projections has not been reported in other species of the Centrolenidae, but these structures could have been overlooked previously. We agree that this morphological character may have been gone unnoticed by previous researchers, who looked only at typical features, such as webbing and subarticular tubercles. Non-typical centrolenid structures, such as pointed projections or the bulla—a "bubble" structure on hand webbing, first described by Myers and Donnelly (2001)—have been overlooked in most descriptions. The bulla has been reported in just two species of *Hyalinobatrachium*, but its presence is widespread (with intra and interspecific variation) among species with extensive webbing between the outer fingers in the genera *Centrolene*, *Cochranella*, and *Hyalinobatrachium* (Cisneros-Heredia & McDiarmid in press).

**Comments on the species-level taxonomy of some Centrolenidae.**—The species *lema*, *gorzulai*, and *papillahallicum* were diagnosed from each other with strong emphasis on the distribution of white pigment on the peritonea; *lema* differs from *gorzulai* and *papillahallicum* by having (among others) condition V3 on the visceral peritonea instead of condition V5. However, the distinction between *gorzulai* and *papillahallicum* seems tenuous. When Noonan and Harvey (2000) described *papillahallicum*, the status of *gorzulai* and *lema* (= "*Centrolene* Escalera region" of Noonan & Harvey 2000) was unclear. Ayarzagüena (1992) described *gorzulai* based on one specimen, and several characters were imprecise or of unknown variation. Noonan and Harvey (2000) differentiated *gorzulai* from *papillahallicum* by the following (characters of *papillahallicum* in parentheses): notch in the lower lip absent (present); dorsal skin smooth (shagreened); pericardium clear (white); visceral peritoneum clear (white); hepatic peritoneum clear (white); prepollical spine protruding externally (not protruding externally); inner metatarsal tubercle absent (present); postaxial edge of fifth toe without fringe (fringe present); ED/HL = 0.44 (0.36). Subsequent reviews of the holotype and additional material of *gorzulai* (including the type of *auyantepuiana*, a synonym of *gorzulai*) showed that it has shagreened dorsal skin; white pigment on the pericardial, hepatic, and visceral peritonea; prepollex showing both conditions: protruding and not protruding (prepollical spine and prepollical bulge; see *Hand ornament classification* under character *(12) Nuptial excrescences and hand ornamentation* above); and inner metatarsal tubercle present (Señaris & Ayarzagüena 1994, Duellman & Señaris 2003, Señaris & Ayarzagüena 2005). Therefore, only three characters remain as diagnostic between *papillahallicum* and *gorzulai*: the notch in the lower lip, the fringe on the postaxial edge of fifth toe, and the ED/HL ratio. A notch in the lower lip is a character present in juveniles and not a diagnostic feature, and the ED/HL ratiocould have been affected by the sample size of *gorzulai*. The descriptions of *Centrolene papillahallicum* Noonan & Harvey, 2000 and *Centrolenella gorzulai* Ayarzagüena, 1992 do not justify recognition of these as different species. Independently, Santiago Castroviejo-Fisher and associates have reached the same conclusion about *papillahallicum* and gorzulai; since they have reviewed the type specimens of both species and additional material, we refer to them

for a definitive conclusion.

Boulenger (1899) described *ocellifera* from an adult female (BMHN 98.5.19.3) collected at Paramba, an hacienda at ca. 780 m elevation on the Pacific versant in the Province of Imbabura, Ecuador. Only one additional specimen of *ocellifera* has been reported, a subadult male (KU 118046) collected at Tandapi, Province of Pichincha, Ecuador (Lynch & Duellman 1973; they erroneously reported another specimen from Pilalo, but see remarks on the description of the new ocellated species above). Lynch (1990) suggested that the ocellated pattern of *ocellifera* was similar to the open reticulations found in some *Hyalinobatrachium* rather than to that of the ocellate centrolenids. We studied the holotype of *ocellifera* (Boulenger 1899, Fig. 9), an additional specimen collected at the type locality and by the same collector deposited at the BMNH, and the KU specimen. We regard the dorsal pattern of *ocellifera* as identical to the dorsal pattern of some specimens of *prosoblepon* that show false ocelli formed from the random association of dark spots surrounding clear spots (yellow in life, white in preservative) without a tubercle or wart, often incomplete or with irregular borders (Fig. 9). In species with "true ocelli", the well-defined circular ocelli surround pale colored warts (yellow or orange), and the coloration appears to be related to the presence of xanthophores in the most external dermal layers (pers. obs.). In specimens of *prosoblepon* and "*ocellifera*" with "false ocelli", the ocelli are not placed on tubercles or warts, and their coloration seems to be produced by the presence of iridophores in the most external dermal layers (pers. obs.). Boulenger (1899) described the adult female holotype *ocellifera* as having "vomerine teeth in two round groups close together between the choanae", and Lynch and Duellman (1973) mentioned that "*ocellifera*" lacks vomerine teeth, but these conditions are known to be intraspecifically variable in *prosoblepon*. The reference to the absence of humeral spines in males of *ocellifera* is based on the subadult male (SVL 20.0 mm) studied by Lynch and Duellman (1973). The expression of the humeral spine is related to ontogenic development, and subadult and juvenile males of *Centrolene* show a *crista ventralis* that does not project into a humeral spine, and does not protrude through the skin, similar to female condition. The shape of the snout in profile and dorsal view of *ocellifera* and *prosoblepon* is identical, as well as webbing on the hands and feet. Our studies of *ocellifera* and *prosoblepon* show that there are no characters to differentiate between them. Accordingly, we regard *Hyla ocellifera* Boulenger, 1899 as a synonym of *Centrolene prosoblepon* (Boettger, 1892).

The Ecuadorian populations assigned to *albomaculata* are characterized by having a dark indigo granular dorsum with many large orange-yellow spots almost forming a reticulum. McCranie & Wilson (2002) and Savage (2002) described *albomaculata* as having a green dorsum with numerous pale yellow small to medium-size spots, a coloration different from Ecuadorian specimens. Currently, *albomaculata* is considered as a highly polymorphic species, and at least three different geographical color variants occur in Costa Rica (Caribbean versant, central-southern Pacific, and northern Pacific foothills) (Savage 2002, Kubicki 2007). Pictures presented by Savage (2002) correspond to the forms from the Pacific region. Since the type locality of *albomaculata* is "Los Diamantes" in the Caribbean zone (Taylor 1949) and the holotype of *albomaculata* has color pattern similar to the Ecuadorian populations, the latter were assigned to *albomaculata* (Guayasamin et al. 2006a). A detailed study of the populations currently assigned to *Co. albomaculata* throughout its range is needed, as probably more than one species is included.

Lynch (2005) considered *resplendens* as a synonym of *ritae* (Lutz in Lutz and Kloss 1952), but did not provide additional information or details for his conclusion. The holotype of *ritae* was formerly deposited at the Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janerio (MNRJ). At our request in 2006, Dr. Jose P. Pombal Jr., curator of the collections of amphibians of the MNRJ, searched for the holotype of *ritae*. He kindly indicated to us that the specimen was not found in the collections of the MNRJ. Thus, the holotype of *ritae* is lost or destroyed, as noted by Duellman (1977). Given that certain characters described for *ritae*, such as the presence of dark dorsal spots and an exposed prepollex (Lutz & Kloss 1952), do not match juveniles or adults of *resplendens*, we do not adopt Lynch's (2005) proposal. We consider *ritae* more similar to *ametarsia* than to *resplendens*, and in fact, *ametarsia* may be a synonym of *ritae*. The species *ametarsia* is the

only Amazonian centrolenid with dark dorsal spots and an exposed prepollex. The only significant difference between *ritae* and *ametarsia* is the reference to large discs on the fingers pointed out by Lutz in Lutz and Kloss (1952) for *ritae*. All known specimens of *ametarsia* have the discs of the hand smaller than the diameter of eye and the tympanum; nevertheless, this character may be influenced by preservation or condition of the specimen. The type locality of *ametarsia* is at the headwaters of Río Caiwima, ca. 70 km NNE of Puerto Nariño, Colombia, and it is located at ca. 140 km from the type locality of *ritae*, in Benjamin Constant, Brazil. The species *ametarsia* is widely distributed in the Amazon basin across southeastern Colombia, Ecuador, and northeastern Peru, south to Bolivia (Flores 1985, Lynch 2005, Guayasamin et al. 2006, D.F. Cisneros-Heredia pers. obs, J. Lynch pers. comm., W. Lamar pers. comm., A. Muñoz pers. comm.).

In the description of *ametarsia*, Flores (1987) diagnosed it from *oyampiensis* by having (*oyampiensis* characters in parenthesis): less extensive webbing on outer fingers (fully webbed outer fingers), parietal peritoneum clear (parietal peritoneum white), visceral peritonea white (visceral peritonea clear), exposed tympanum (concealed tympanum), and prepollical spine present (absent). Some of Flores's (1987) assertions about *oyampiensis* are incorrect. Based on the original description of *oyampiensis* by Lescure (1975) and additional data presented by Lescure and Marty (2000), *oyampiensis* has a clear parietal peritoneum, white visceral peritonea, small but visible tympanum, and a prepollical spine at the base of the thumb. Señaris and Ayarzagüena (2005) agreed with these descriptions except that they reported the parietal peritoneum covered by white, but reduced to the anterior $^1/_4$ or $^1/_3$ portion, and previous workers apparently misinterpreted the characters because of its small size. Flores (1987) described the parietal peritoneum of *ametarsia* as clear; however, it is also covered by iridophores for at least ¼ of its extent (our state P1) as in *oyampiensis* (pers. obs.). We have examined specimens of *ametarsia* and it is so similar to the descriptions of *oyampiensis* that we are tempted to place them in synonymy, but unfortunately, we have not reviewed specimens of *oyampiensis*. Future researchers should check for the following three characters: hand webbing in *ametarsia* seems to be slightly reduced in comparison to that reported for *oyampiensis* (a character that could be related to intraspecific variation); iris and background coloration and pattern appear to be different (compare photographs presented by Guayasamin *et al*. 2006a and Lescure & Marty 2000); and most importantly, *ametaria* has a clear hepatic peritoneum while the hepatic peritoneum in *oyampiensis* has been reported as white (Señaris and Ayarzagüena 2005).

The study of several specimens of *mache* has revealed intraspecific variation in this species (particularly the distinctiveness of the tympanum, relative size of fingers, and form of the cloacal folds). The same variable characters were used to separate *resplendens* and the recently described *phryxa* (Aguayo and Harvey 2006), suggesting that in fact, they could be synonyms. Definitive conclusions require the comparison of material assigned to the rare *resplendens* with the only known specimen of *phryxa*. The species *mache* and *phryxa* are the only known taxa related to *granulosa* that have patches of iridophores over the hepatic peritoneum; in *mache* this character shows intraspecific variation.

The recently described *wileyi* is morphologically very similar to *cariticommata*. Guayasamin *et al*. (2006c) used the presence of iridophores covering the renal capsule (= layer surrounding the kidneys) of *wileyi* to differentiate it from *cariticommata*. Examination of recently collected specimens of *cariticommata* (DHMECN) showed that it has iridophores on the renal capsule. The absence of iridophores covering the renal capsule in the types of *cariticommata* is likely an artifact of preservation since they were collected almost 20 years ago. The great similarity of *wileyi* and *cariticommata* suggests their synonymy, but one discrete character separates them: in life, *cariticommata* has yellow spots on a green dorsum, and *wileyi* has a uniform green dorsum. In addition, the snout of *cariticommata* in dorsal view is round, while in *wileyi* it is truncate, and *cariticommata* has light yellow hands, and *wileyi* has light green hands (pers. obs.).

We examined the type specimens of two recently described species from the Guianan Shield: *eccentricum* and *crurifasciatum*. We found that they are nearly identical. Myers & Donnelly (2001) separated the species based on the "bicolored iris" of *eccentricum* formed by the presence of a dark dome-shaped circumpupillary zone that conceals the pupil, separating the pupil from the colored peripheral zone. The form and expression

of the circumpupillary zone was found to vary in relation to its exposure to light (Myers & Donnelly 2001). A circumpupillary zone also is known in *ruedai* (although grey and less marked than in *eccentricum*; Cisneros-Heredia & McDiarmid 2007), and *mariaelenae*. In *ruedai* and *mariaelenae*, the circumpupillary zone may remain undetected even after several observations of the same specimen under different light conditions, and becomes apparent after the light changes or is noticeable when a photographic series is available, such as in *eccentricum* or *ruedai*. In preservative, the circumpupillary zone is barely noticeable in specimens that have it expanded when euthanized, but completely hidden in specimens that have it contracted when preserved (pers. obs.). The separation between *eccentricum* and *crurifasciatum* based solely on the degree of expression of the circumpupillary zone seems unwarranted. If the same criterion were applied, several specimens of *ruedai* and *mariaelenae* would be considered different taxa. A third Guianan taxon, *ignioculus*, was recently described and diagnosed from the morphologically similar *eccentricum* and *crurifasciatum* by having a yellow iris with a reddish ring, green limb bands in life, SVL range, and skin texture (Noonan & Bonett 2003). The last three characters are commonly affected by intraspecific variation in centrolenids, i.e., skin texture is affected by sex, age variation, and also preservation; the SVL ranges of *ignioculus* and *crurifasciatum* overlap; and the green limb band coloration has been found to vary among specimens of the apparently related *ruedai* (Cisneros-Heredia & McDiarmid in press). Thus, the only prominent difference between *ignioculus*, *eccentricum*, and *crurifasciatum* is the iris coloration. Independently, Santiago Castroviejo-Fisher and associates have reached a similar conclusion while studying *crurifasciatum*, *eccentricum*, and *ignioculus*; since they have reviewed abundant additional material to address adequately the nature of differences among the species, we defer to them for a definitive conclusion on their status.

We have examined the types of *nouraguensis* and photographs of the types of *iaspidiense* and found them also to be almost identical. The condition of the iridophores over the pericardium (V5 vs. V6) is the only character that differs between *nouraguensis* and *iaspidiense*, this character has been found to vary intraspecifically in other *Hyalinobatrachium* (Guayasamin et al. 2006c, Cisneros-Heredia & McDiarmid in press, pers. obs.). Independently, Santiago Castroviejo-Fisher and associates have reached the same conclusion about *iaspidiense* and *nouraguensis*, and since they have reviewed considerable additional material to address adequately the intraspecific variation of the species involved, we defer to them for a definitive conclusion.

McCranie and Wilson (1997) described *cardiacalyptum* as a new species from Central America with extensive webbing between finger II and III. They pointed out that *cardiacalyptum* is most similar to *chirripoi*, and distinguished between them based on preserved specimens of *chirripoi* lacking or having only a few brown flecks on dorsal surfaces; having a strongly granular dorsal skin; "a tympanum covered by thin skin, annulus distinct or evident but indistinct"; skin below the vent with large granules; eyes protuberant and extending the lip margin when viewed from above; long loreal region; and nostrils more swollen and indented medially than *cardiacalyptum*. We have examined the type series of *cardiacalyptum* and ffound that all noted differences from chirripoi are related to intraspecific variation and effects of preservation, and none is valid. The brown flecks on the dorsal surfaces usually are indistinct or disappear in many specimens in preservative; the tympanum of both species is indistinct; and the smooth ventral skin, loreal region size, nostril form, and eye distinctiveness are affected by preservation and interspecific variation. We herein place *Hyalinobatrachium cardiacalyptum* McCranie & Wilson, 1997 in the synonymy of *Hyalinobatrachium chirripoi* (Taylor, 1958). McCranie and Wilson (1997) also described crybetes and diagnosed it from *colymbiphyllum* by the latter having brown flecks on dorsal surfaces in preserved specimens, a visible tympanic annulus, and a markedly swollen nasal region. McCranie and Wilson (1997) distinguished *crybetes* from *fleischmanni* by the latter having a white pericardium, numerous brown flecks in preserved specimens, and a longer head. All differences of *crybetes* from *colymbiphyllum* and *fleischmanni* are related to intraspecific variation, effects of preservation, or the small sample size of *crybetes*, and none diagnoses *crybetes* as a valid taxon. Due to the bare heart condition described for "*crybetes*" by Starrett and Savage (1973) and McCranie and Wilson (1997), herein we place *Hyalinobatrachium crybetes* McCranie and Wilson, 1997 as a synonym of *Hyalinobatrach-*

*ium colymbiphyllum* (Taylor, 1949). However, the identity of this Honduran population must be confirmed by examining fresh material to determine if it corresponds to *colymbiphyllum* or *fleischmanni*, since variation in the pericardial coloration has been observed in these species (D.F. Cisneros-Heredia & R.W. McDiarmid pers. obs.).

**Annotated list of the species of Centrolenidae from the Republic of Ecuador**

Species are listed alphabetically by their specific names, followed by the currently accepted generic placement. Abbreviations include GD = Global distribution and ED = Ecuadorian distribution.

*Centrolenidae* Taylor, 1951
    *GD*.—Tropical America (= Neotropics) from southern Mexico to Panama, through the Andes from Venezuela to Bolivia, with species in the Amazon and Orinoco river basins, the Guiana Shield region, and the Atlantic forests of southeastern Brazil and northeastern Argentina.
    *ED*.—Across Ecuador, with records in most vegetation formations (except Mangrove, Open Savanna, and Dry Forest) and all mainland provinces (absent from the insular province of Galápagos), in the Pacific lowlands, Cordillera de la Costa, Andean highlands and slopes, and Amazonian lowlands, between 0 and 3300 m elevation.

*albomaculata* Taylor, 1949
—*Cochranella albomaculata* (Taylor, 1949)
    *GD*.—Honduras, Costa Rica, Panama, Colombia, and Ecuador.
    *ED*.—Recently reported from three localities in Lowland Non-Seasonal Evergreen and Foothill Non-Seasonal Evergreen Forests on the northern Pacific Andean slopes, between 200 and 700 m elevation, in the provinces of Esmeraldas and Imbabura.
    *Relevant literature*.—Taylor (1949), Solís et al. (2004b), Guayasamin et al. (2006a).

*amelie* Cisneros-Heredia & Meza-Ramos, 2007
—*Cochranella amelie* Cisneros-Heredia & Meza-Ramos, 2007
    *GD*.—Ecuador.
    *ED*.—Recently described from a single locality on the Río Oglan, Province of Pastaza, in Foothill Evergreen Forests on the central Amazonian slopes at 600 m elevation.
    *Relevant literature*.—Cisneros-Heredia & Meza-Ramos (2007).

*ametarsia* Flores, 1987
—*Cochranella ametarsia* (Flores, 1987)
    *GD*.—Colombia, Ecuador, Peru and Bolivia.
    *ED*.—Recently reported from two localities: Estación de Biodiversidad Tiputini and Puerto Bolívar. Additional localities are: Estación Científica Yasuní, Pontificia Universidad Católica del Ecuador, Province of Orellana (ca. 250 m elevation) (QCAZ 16652, 22709) and Hosteria La Selva, Province of Sucumbíos (250 m elevation). All localities are in Lowland Evergreen Forests in the northern Amazonian lowlands below 300 m elevation in the provinces of Sucumbíos and Orellana (Fig. 12).
    *Relevant literature*.—Flores (1987), Bolívar et al. (2004b), Cisneros-Heredia and McDiarmid (2006a), Guayasamin et al. (2006a), Kubicki (2007).

*anomalus* Lynch & Duellman, 1973

—*Nymphargus anomalus* (Lynch & Duellman, 1973)

   *GD*.—Endemic to Ecuador

   *ED*.—Only known from the type locality (Azuela River) in Low Montane Evergreen Forests on the northern Amazonian Andean slopes at ca. 1740 m elevation in the Province of Napo.
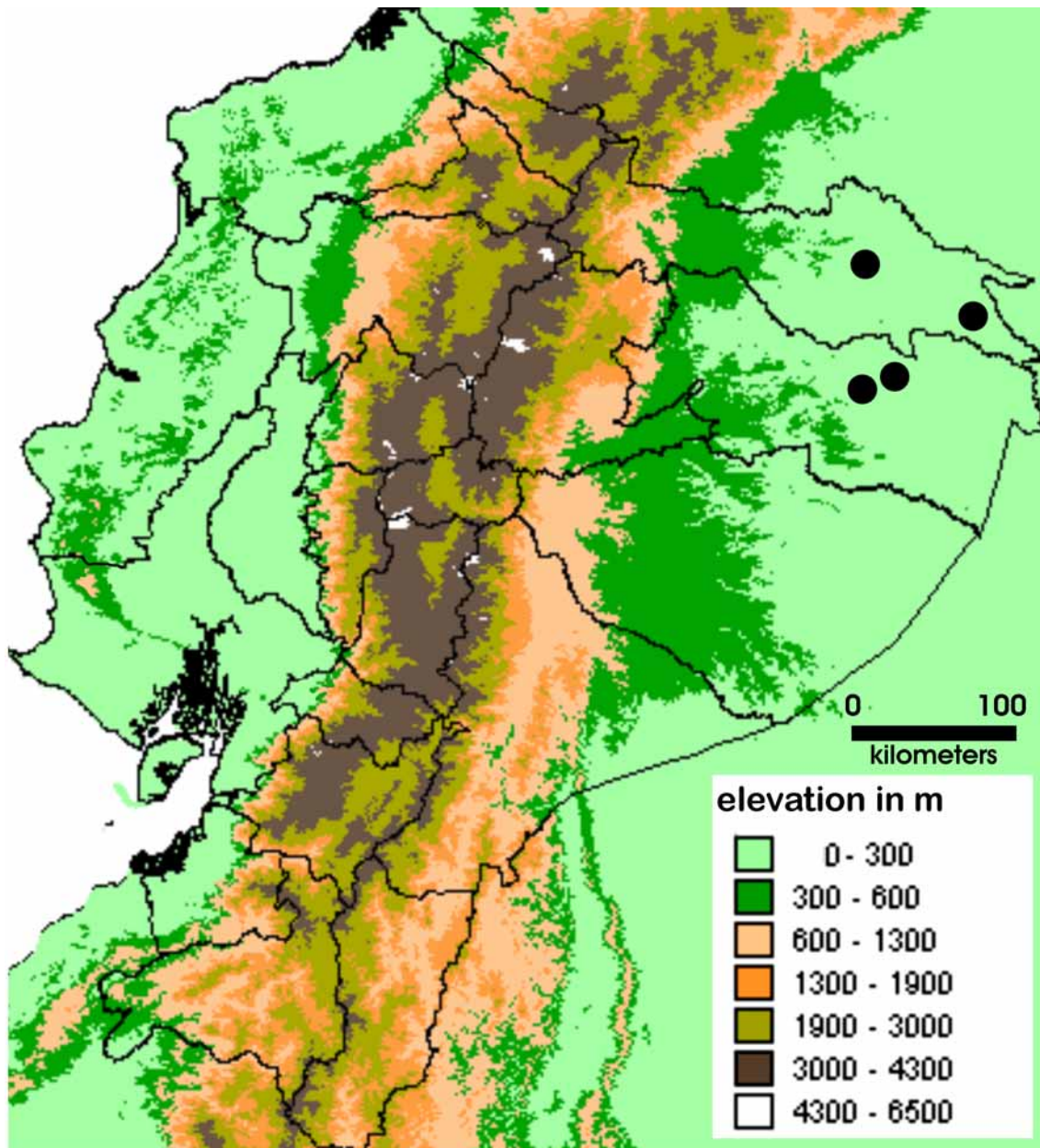


**FIGURE 12.** Distribution of *Cochranella ametarsia* in Ecuador.

   *Remarks*.—The original description indicated that the holotype lacks subcloacal warts; however a pair is present in the holotype on the ventral surface of limbs, below the cloaca.

   *Relevant literature*.—Lynch and Duellman (1973), Lynch (1990), Coloma and Ron (2004b), Cisneros-Heredia & McDiarmid (2006a).

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*audax* Lynch & Duellman, 1973

—*Centrolene audax* (Lynch & Duellman, 1973)

　　*GD*.—Colombia and Ecuador.

　　*ED*.—It has been reported from two localities: the type locality at Salto de Agua, 2.5 km NNE of Río Reventador on Quito-Lago Agrio road, 1660 m, and 16.5 km NNE of Santa Rosa on Quito-Lago Agrio road, 1700 m elevation. Two additional localities are presented herein: 14.7 km by road NE of Río Salado, 1310 m, Province of Napo (USNM 286623-24, collected on 24 February 1979), and near the Cascada de San Rafael, on Rio Quijos, at km 102, INECEL Station, 1350 m, Province of Napo (USNM 286620-22, collected on 23 February 1979). All four localities are located in Low Montane Evergreen Forest of the northern Amazonian Andean slopes between 1350 and 1700 m, elevation in the Province of Napo (Fig. 13).

　　*Relevant literature*.—Lynch and Duellman (1973), Wild (1994), Coloma et al. (2004c), Mueses-Cisneros 2005, Cisneros-Heredia and McDiarmid (2006a).
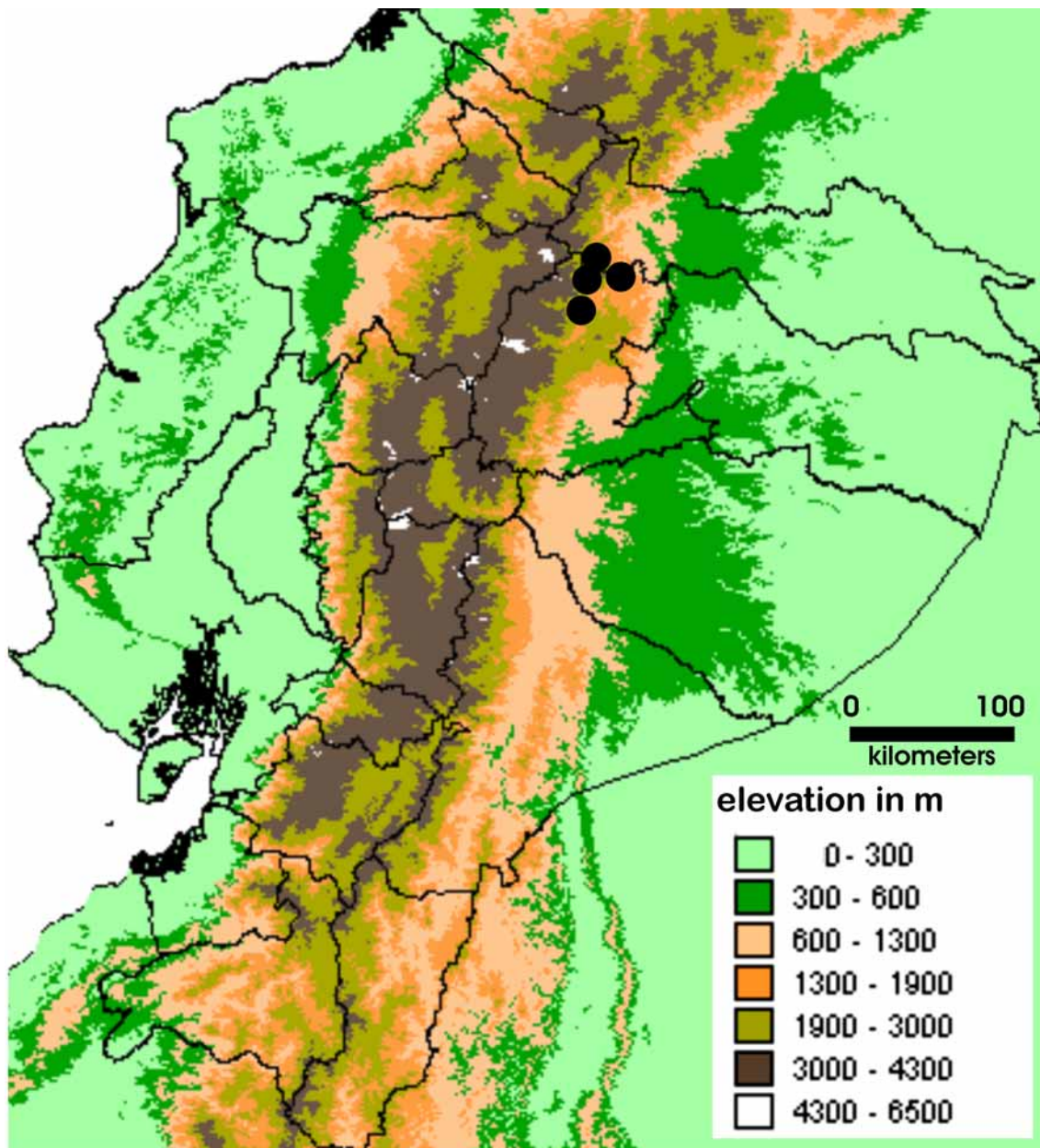


**FIGURE 13.** Distribution of *Centrolene audax* in Ecuador.

*aureoguttatum* Barrera-Rodríguez & Ruiz-Carranza, 1989

—*Hyalinobatrachium aureoguttatum* (Barrera-Rodríguez & Ruiz-Carranza, 1989)

*GD*.—Panama, Colombia, and Ecuador

*ED*.—Recently found at two localities in the Lowland Non-Seasonal Evergreen Forest in the northern Pacific lowlands below 300 m elevation, in the Province of Esmeraldas (Fig. 14).

*Remarks*.—The identification of this Ecuadorian population is preliminary, further details will be publish elsewhere (Bustamante et al. in press). The Ecuadorian specimens are similar to Colombian *H. aureoguttatum* in most morphological and chromatic characters, except that most Ecuadorian specimens show a bare heart condition (intraspecific variation similar to the reports for *H. crurifasciatum* and *H. fleischmanni*, Guayasamin et al. 2006; Cisneros-Heredia & McDiarmid in press), and all lack dark dorsal marks (Bustamante et al. in press).

*Relevant literature*.—Barrera-Rodríguez and Ruiz-Carranza (1989), Bustamante et al. (in press).
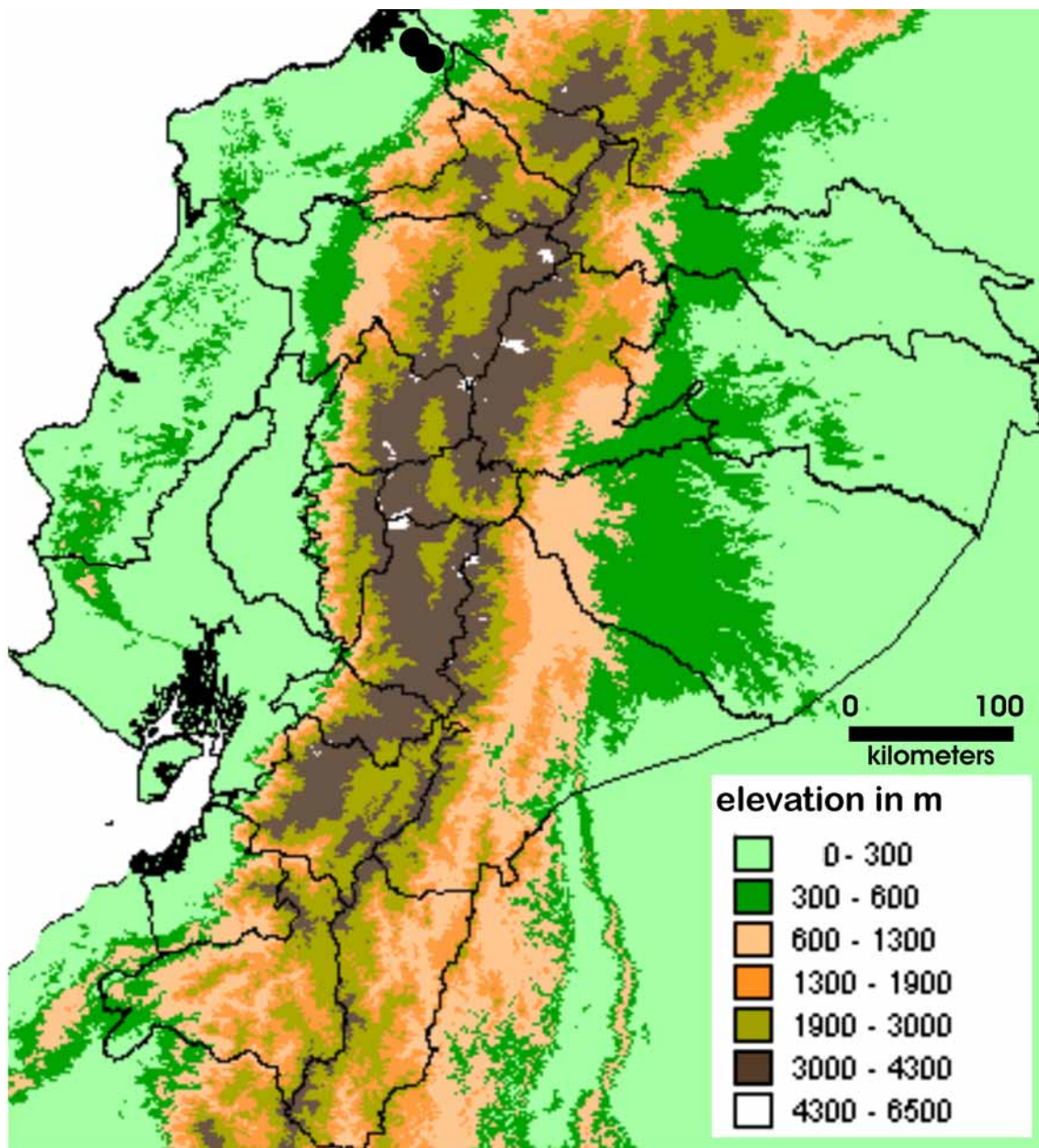


**FIGURE 14.** Distribution of *Hyalinobatrachium aureoguttatum* in Ecuador

*bacatum* Wild, 1994

—*Centrolene bacatum* Wild, 1994

GD.—Colombia and Ecuador.

ED.—Known from two localities in Montane Cloud Forest of the Amazonian Andean slopes between 1950 and 2350 m elevation, in the provinces of Napo and Morona-Santiago.

*Relevant literature*.—Wild (1994), Coloma et al. (2004h), Mueses-Cisneros 2005, Cisneros-Heredia and McDiarmid (2006a), Guayasamin et al. (2006b).

*balionotum* Duellman, 1981

—*Centrolene balionotum* (Duellman, 1981)

GD.—Colombia and Ecuador.

ED.—Known from two localities in Low Montane Evergreen Forest of the northern Pacific Andean slopes between 1400 and 1540 m elevation, in the provinces of Carchi and Pichincha.

*Relevant literature*.—Duellman (1981), Bolívar et al. (2004h), Cisneros-Heredia and McDiarmid (2006a), Cisneros-Heredia and Yánez-Muñoz (2007a).

*ballux* Duellman & Burrowes, 1989

—*Centrolene ballux* (Duellman & Burrowes, 1989)

GD.—Colombia and Ecuador.

ED.—Reported from two nearby localities in Montane Cloud Forest of the Saloya River Basin, northern Pacific Andean slopes between 1900 and 1960 m elevation, in the Province of Pichincha. The locality reported by Marquez et al. (1996) (= Río Guajalito Protected Forest) is as close as 2 km from the type locality (14 km [by road] west of Chiriboga [00°18'S, 78°49'W], 1960 m, Provincia de Pichincha), and we consider them as one locality. The Río Guajalito Protected Forest is a private reserve of almost 1000 ha located at ca.12 km by road west of the town of Chiriboga, and the type locality is either within its borders or very near.

*Relevant literature*.—Duellman and Burrowes (1989), Wild (1994), Marquez et al. (1996), Bolívar et al. (2004e).

*buckleyi* Boulenger, 1882

—*Centrolene buckleyi* (Boulenger, 1882)

GD.—Colombia, Ecuador, and Peru.

ED.—It has been reported from several localities in different vegetation formations including Montane Cloud Forest, Montane Humid Scrub, High Montane Evergreen Forest, and Herbaceous Pramo, along the Andean highlands and high slopes on the Pacific and Amazonian versants between ca. 1900 and 3300 m elevation (Fig. 15). *Centrolene buckleyi* formerly occurred in the provinces of Carchi, Sucumbos, Imbabura, Pichincha, Cotopaxi, Chimborazo, Bolvar, Tungurahua, Caar, Azuay, Loja; however, most populations have apparently disappeared. Only four populations have been recorded in the last ten years; at Moran, Province of Carchi (M. Yánez-Muñoz pers. comm.); Cashca Totoras, Province of Bolvar (Bustamante et al. 2005); Yanayacu, Province of Napo (Guayasamin et al. 2006b); and Zamorahuaico (near Loja), Province of Loja (F. Nogales & D. Almeida pers. comm.; not found in recent expeditions, D.F. Cisneros-Heredia et al. pers. obs.). *Remarks*.—We follow Señaris and Ayarzagüena (2005) in separating the Venezuelan populations as *Centrolene venezuelense*; however, further research is needed to clarify the relationships of *venezuelense* and *buckleyi* as their current separation is unclear (Rivero 1968, Señaris & Ayarzagüena 2005, Guayasamin et al. 2006c). Rada de Martinez (1990) identified a series of tadpoles with 6-7 upper and 7-8 lower tooth rows as *venezuelense* (cited as *buckleyi*). We are convinced that the identification was erroneous, as no centrolenid tadpole is known to have such a high LRTF; her specimens almost surely represent a hylid tadpole.

*Relevant literature*.—Boulenger (1882), Lynch and Duellman (1973), Bolívar-G. et al. (1999), Coloma et al. (2006m), Cisneros-Heredia and McDiarmid (2006a), Guayasaminet al. (2006b)

*buenaventura* Cisneros-Heredia & Yánez-Muñoz, 2007

—*Nymphargus buenaventura* (Cisneros-Heredia & Yánez-Muñoz, 2007)

    *GD*.—Ecuador.

    *ED*.—Recently described; known only from the type locality, Reserva Buenaventura, Province of El Oro, in Foothill Evergreen Forest on the southernwestern Andean slopes at 1200 m elevation.

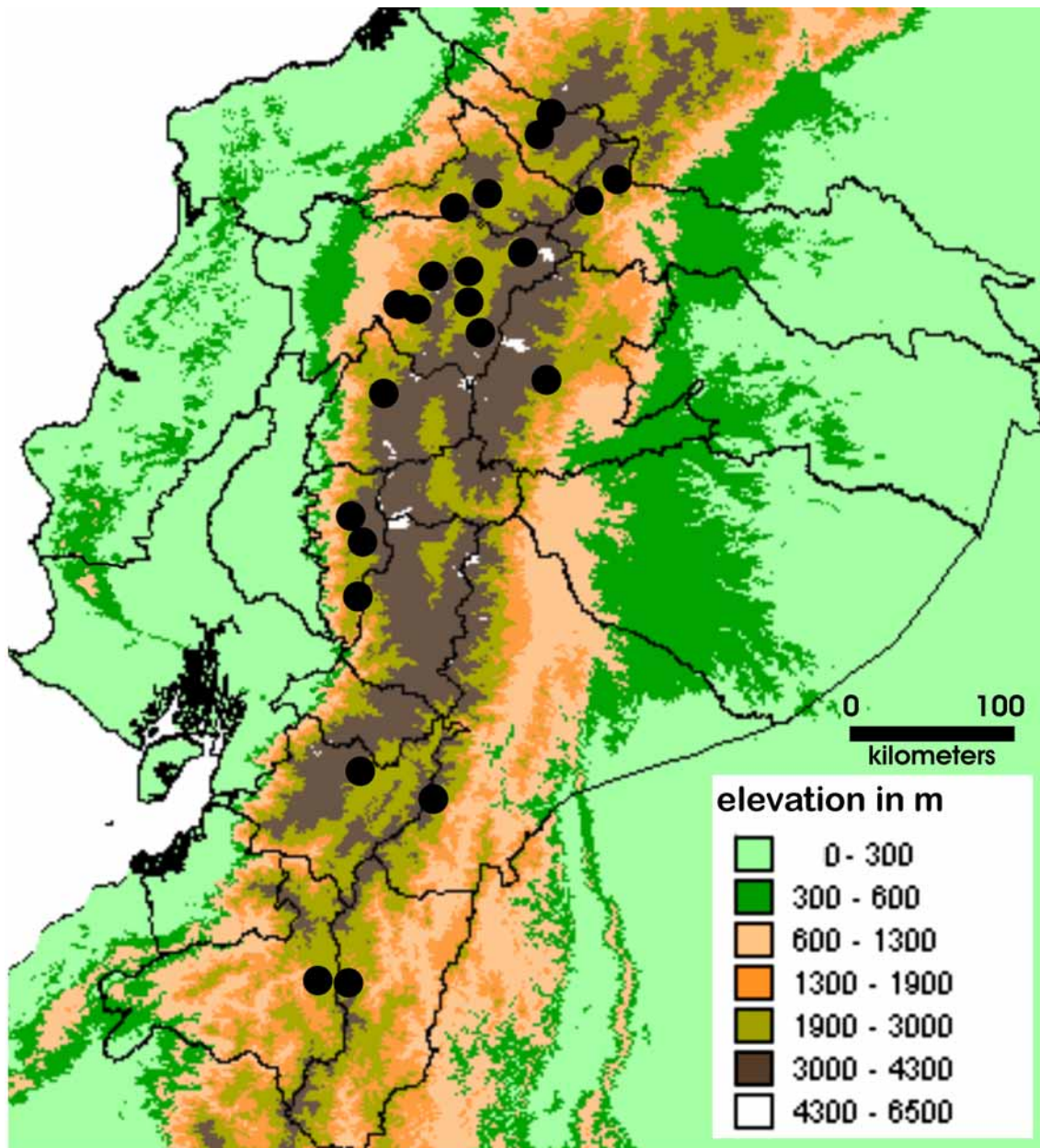    *Relevant literature*.—Cisneros-Heredia & Yánez-Muñoz (2007b).



**FIGURE 15.** Distribution of *Centrolene buckleyi* in Ecuador

*cariticommatus* Wild, 1994

—*Nymphargus cariticommatus* (Wild, 1994)

    *GD*.—Endemic to Ecuador.

    *ED*.—It is known from three localities in Montane Cloud Forest on the southern Amazonian Andean slopes between 2350 – 2500 m elevation, in the provinces of Morona Santiago and Zamora-Chinchipe. The report of *Co. cariticommata* by Coloma et al. (2004a) from Yanayacu corresponds to *Co. wileyi* (see Guayasamin et al. 2006c).

*Relevant literature.*—Wild (1994), Coloma et al. (2004a), Yáñez-Muñoz et al. (2004), Cisneros-Heredia and McDiarmid (2006a), Guayasamin et al. (2006c), Cisneros-Heredia and Yánez-Muñoz (2007a).

*cochranae* Goin, 1961
—*Nymphargus cochranae* (Goin, 1961)

GD.—Ecuador (Colombia?).

*ED.*—Known from several localities in the Low Montane Evergreen and Foothill Evergreen forests across the Amazonian Andean slopes between 700 and 1800 m elevation, in the provinces of Sucumbíos, Napo, Orellana, Pastaza, and Zamora-Chinchipe.

*Remarks.*—This species was reported from the Serranía de los Churumbelos, southeastern Andean slopes of Colombia by Salaman and Donegan (1998), but this report remains to be confirmed.

*Relevant literature.*—Goin (1961), Lynch and Duellman (1973), Lynch (1990), Coloma et al. (2004b), Cisneros-Heredia & McDiarmid (2005), Cisneros-Heredia and McDiarmid (2006a).


*durrellorum* Cisneros-Heredia, 2007
—*Centrolene durrellorum* Cisneros-Heredia, 2007

*GD.*— Ecuador.

*ED.*— Recently described; known from two localities in Foothill Evergreen Forest on the Amazonian Andean slopes between 800 and 1150 m elevation, in the provinces of Zamora-Chinchipe and Napo.

*Relevant literature.*—Cisneros-Heredia (2007).


*flavopunctata* Lynch & Duellman, 1973
—*Cochranella flavopunctata* (Lynch & Duellman, 1973)

*GD.*—Colombia and Ecuador.

*ED.*—Known from several localities in Foothill Evergreen and Low Montane Evergreen forests across the northern and central Amazonian Andean slopes between 700 and 1800 m elevation, in the provinces of Sucumbíos, Napo, Orellana, and Pastaza.

*Relevant literature.*—Lynch & Duellman (1973), Castro et al. (2004a), Cisneros-Heredia and McDiarmid (2006a), Lynch (2006).


*fleischmanni* Boettger, 1893
—*Hyalinobatrachium fleischmanni* (Boettger, 1893)

*GD.*—Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.

*ED.*—Known from several localities in Lowland Seasonal and Non-Seasonal Evergreen forests in the northern and central Pacific lowlands below 800 m elevation, in the provinces of Esmeraldas, Manabí, Pichincha, and Los Ríos.

*Remarks.*—The populations from Venezuela, Guyana, and Suriname are not conspecific with *fleischmanni*. Venezuelan populations previously reported as *fleischmanni* are currently assigned to *guairarepanensis* and *revocata* (Señaris & Ayarzagüena 2005). The name *Hyalinobatrachium cappellei* is available for the Guyana and Suriname populations. The species *petersi* Goin, 1961 was revalidated by Ruiz-Carranza & Lynch (1998) as different from *fleischmanni* because it has a bare heart. Ruiz-Carranza & Lynch (1998) use the name *petersi* for a population of *Hyalinobatrachium* from the southwestern Andean slopes of Colombia. The species from the southwestern Colombian Andes was found to be different from *petersi* (Cisneros-Heredia & McDiarmir in press), and herein we are assigning it to *valerioi* (see below). One of us (DFCH) recently reviewed the holotype of petersi and found it to be conspecific with fleischmanni (unpublished data).

*Relevant literature.*—Goin (1961), Lynch and Duellman (1973), Starrett and Savage (1973), Ruiz-Carranza and Lynch (1998), Barrera-Rodríguez (2000), Coloma et al. (2004l), Cisneros-Heredia and Lynch

(2006), Cisneros-Heredia and McDiarmid (2007), Kubicki (2007).

*geckoideum* Jiménez de la Espada, 1872

—*Centrolene geckoideum* Jiménez de la Espada, 1872

    *GD*.—Colombia and Ecuador.

    *ED*.—On the western side of the Andes, it has been reported from three localities in the provinces of Carchi and Pichincha in Montane Cloud Forest between 1800 and 2000 m elevation: (1) km 45 on the Chillogallo to Santo Domingo de los Colorados road (Goodman & Goin 1970; = Quebrada Zapadores, 1910 m, sensu Lynch et al. 1983, Ruiz-Carranza et al. 1986); (2) 1 km by road SW of San Ignacio, 1920 m (Lynch et al. 1983), and (3) on the Tufiño - Maldonado road, Carchi (Cisneros-Heredia & Yánez-Muñoz 2007a). A small population of *Ce. geckoideum* found in the Río Guajalito Protected Forest, km 59 on the Chillogallo - Chiriboga - Santo Domingo de los Colorados road (78°49'W, 0°14'S, 1800-2200 m), Province of Pichincha, is the fourth known locality for the species in Ecuador. Males at Guajalito were observed during the rainy season from January to May between 1998 and 1999, usually on rocks on the spray area of the waterfalls and behind the waterfalls.

    The type locality of *geckoideum* ("Rio Napo") is the only record from the eastern Andean slopes of Ecuador (see Ruiz-Carranza et al. 1986). It has been suggested that it is in error, but pending new information, we consider the type locality correct. The species is distributed in all three cordilleras in Colombia, and we suspect that the absence of additional localities for this species in eastern Ecuador is the result of inadequate sampling. Many areas in eastern Ecuador remain unexplored, and *geckoideum* is restricted to very specific and hard-to-sample habitats (waterfalls and rocky streams in cloud forest) (Fig. 16).

    *Relevant literature*.—Jiménez de la Espada (1872), Goodman and Goin (1970), Lynch et al. (1983), Ruiz-Carranza et al. (1986), Rueda-Almonacid (1994), Bolívar et al. (2004i), Cisneros-Heredia and Yánez-Muñoz (2007a).

*grandisonae* Cochran & Goin, 1970

—*Centrolene grandisonae* (Cochran & Goin, 1970)

    *GD*.—Colombia and Ecuador.

    *ED*.—It is widely distributed in Low Montane Evergreen and Montane Cloud forests on the northern Pacific Andean slopes between 1100 and 2700 m elevation, in the provinces of Carchi, Imbabura, Pichincha, and Cotopaxi.

    *Remarks*.—Lynch and Duellman (1973), by error, applied this name to specimens of *lynchi*.

    *Relevant literature*.—Cochran and Goin (1970), Duellman 1980, Bolívar et al. (2004f).

*griffithsi* Goin, 1961

—*Nymphargus griffithsi* (Goin, 1961)

    *GD*.—Colombia and Ecuador.

    *ED*.—Known from various localities in Montane Cloud Forest in the Saloya River Basin, northern Pacific Andean slopes between 1460 and 2600 m elevation, in the Province of Pichincha.

    *Remarks*.—*Cochranella griffithsi* is probably a species complex (Cisneros-Heredia & Yánez-Muñoz 2007b; R. W. McDiarmid pers. obs.).

    *Relevant literature*.—Goin (1961), Lynch and Duellman (1973), Bolívar et al. (2004g), Guayasamin et al. (2006c).

*heloderma* Duellman, 1981

—*Centrolene heloderma* (Duellman, 1981)

    *GD*.—Colombia and Ecuador.

    *ED*.—Known from four localities in Montane Cloud Forests on the northern Pacific Andean slopes, between 1900 and 2400 m elevation, in the Province of Pichincha. Most, if not all, populations have apparently gone extinct.
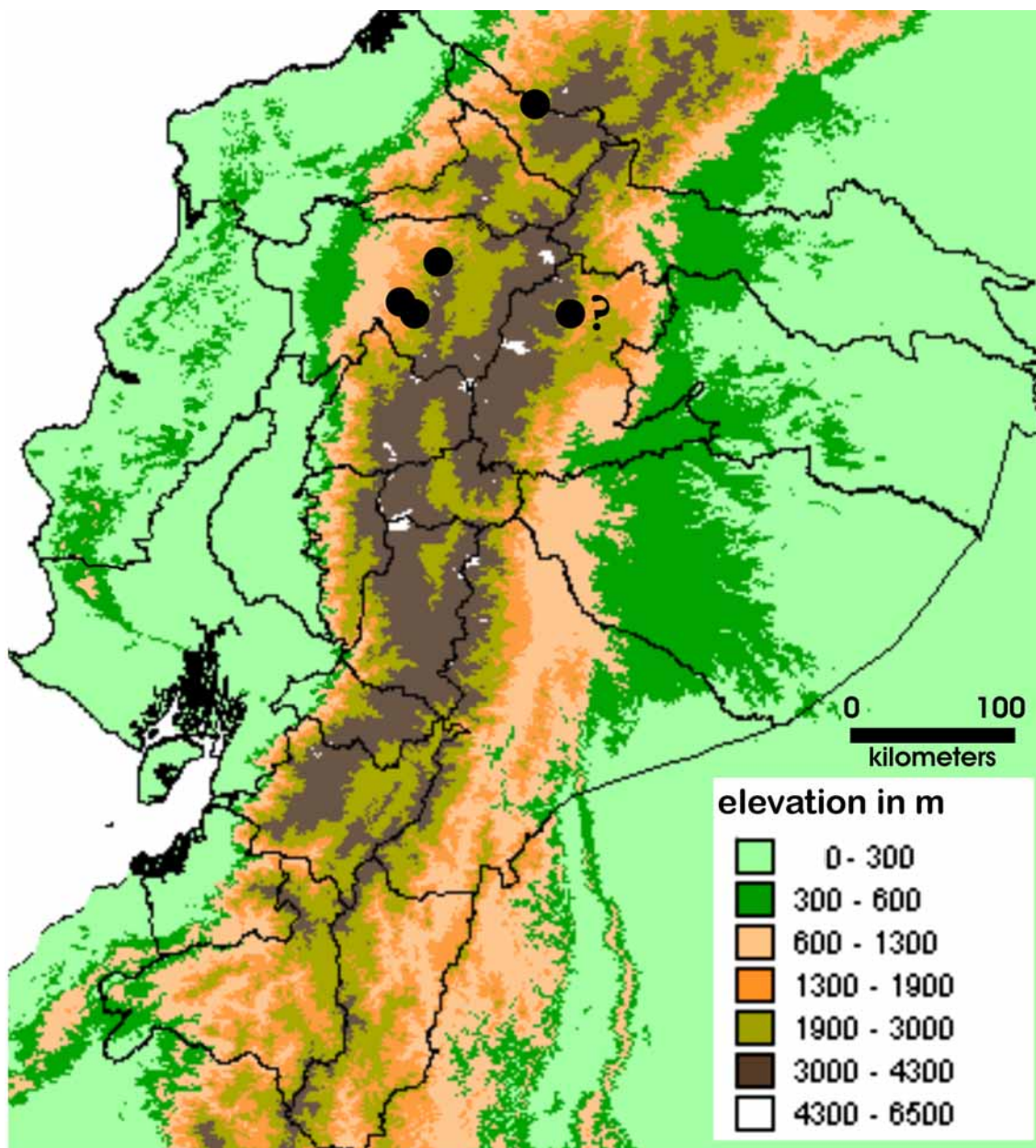
*Relevant literature.*—Duellman (1981), Coloma et al. (2004j)



**FIGURE 16.** Distribution of *Centrolene geckoideum* in Ecuador; question mark next to the type locality indicates the uncertainty of its exact location

*ilex* Savage, 1967
—*Centrolene ilex* (Savage, 1967)

   *GD.*—Nicaragua, Costa Rica, Panamá, Colombia, and Ecuador.

   *ED.*—Recently reported from several localities in Lowland Non-Seasonal Evergreen and Foothill Seasonal Evergreen forests of the northern Pacific lowlands between 180 and 800 m elevation, in the provinces of Esmeraldas and Pichincha.

   *Remarks.*—The Colombian *luteopunctata* Ruiz-Carranza & Lynch 1996 was erroneously reported as *ilex* from Colombia by Lynch and Duellman (1973). Its occurrence in Ecuador is possible, but it remains unrecorded.

*Relevant literature.*—Savage (1967), Hayes and Starrett (1980), Savage (2002), Solís et al. (2004a), Guayasamin et al. (2006a), Kubicki (2007).

*laurae* Cisneros-Heredia & McDiarmid, new species
—*Nymphargus laurae* Cisneros-Heredia & McDiarmid, new species
   *GD.*—Endemic to Ecuador.
   *ED.*—Known only from the type locality in the Foothill Evergreen Forest on the northern Amazonian slopes at ca. 500 m elevation, in the Province of Orellana (Fig. 11).
   *Relevant literature.*—This paper.

*litorale* Ruíz-Carranza & Lynch, 1996
—*Centrolene litorale* Ruíz-Carranza & Lynch, 1996
   *GD.*—Colombia and Ecuador.
   *ED.*—It was recently reported from two localities in Lowland Seasonal Evergreen Forests of the northern Pacific lowlands between 150 and 200 m elevation, in the Province of Esmeraldas.
   *Remarks.*—An apparently undescribed taxon, herein referred to as *Centrolene* sp. "Palenque" (USNM 286751–52), is apparently the sister-taxon of *Ce. litorale*. It appears to be endemic to the Seasonal-Evergreen Forest of the West Ecuadorian Region (Cisneros-Heredia 2006).
   *Relevant literature.*—Ruiz-Carranza and Lynch (1996), Grant and Morales (2004), Guayasamin et al. (2006a).

*lynchi* Duellman, 1980
—*Centrolene lynchi* (Duellman, 1980)
   *GD.*—Colombia and Ecuador.
   *ED.*—Known from various nearby localities in Foothill Seasonal Evergreen and Low Montane Evergreen forests on the northern Pacific Andean slopes between 1100 and 1800 m elevation, in the provinces of Pichincha and Cotopaxi.
   *Remarks.*—This species was called "*Centrolenella grandisonae*" by Lynch and Duellman (1973), an error later corrected by Duellman (1980) who clarified the status of *grandisonae* and described *lynchi*. The original description of *scirtetes* compared it only with *peristictum*, but did not make any comparisons with *lynchi*. The holotype of *Centrolenella scirtetes* Duellman & Burrowes, 1989 (KU 202720) is extremely similar to *lynchi*, if not conspecific. *Centrolenella gemmata* Flores, 1985 is also very similar if not conspecific with *lynchi*. Both species were separated by differences in the snout form, hand webbing, and in overall head shape, characters that seem to be within the intraspecific variation of *lynchi*. The presence of a marked post-cephalic constriction in the type series of *gemmatum* suggests that the specimens were affected by desiccation; and, the differences between *gemmatum* and *lynchi* could be also artifacts of preservation. We do not include *scirtetes* and *gemmatum* in this list, and a detailed analysis and conclusions about the status of both names will be presented elsewhere.
   *Relevant literature.*—Lynch and Duellman (1973, as "*Centrolenella grandisonae*"), Duellman (1980), Duellman & Burrowes (1989), Flores (1985), Coloma et al. (2004i).

*mache* Guayasamin & Bonnacorso, 2004
—*Cochranella mache* Guayasamin & Bonnacorso, 2004
   *GD.*—Endemic to Ecuador.
   *ED.*—Currently known from three localities in Foothill Seasonal Evergreen forests of the northern Pacific lowlands below 550 m elevation, in the Province of Esmeraldas.
   *Relevant literature.*—Guayasamin & Bonnacorso (2004), Guayasamin (2006)

*mariaelenae* Cisneros-Heredia & McDiarmid, 2006

—*Centrolene mariaelenae* Cisneros-Heredia & McDiarmid, 2006

   *GD*.—Endemic to Ecuador.

   *ED*.—Known from four localities in Low Montane Evergreen Forests on the Amazonian Andean slope, between 1400 and 1820 m elevation, in the Provinces of Napo, Tungurahua, and Zamora-Chinchipe (Fig. 17). An additional record is reported herein; a specimen (DFCH-USFQ ZZ2) was collected at the Cascada de San Rafael, province of Napo, providing the northernmost locality for the species. The species has also been collected recently in the province of Morona-Santiago (M. Bustamante pers. comm. QCAZ).

   *Relevant literature*.—Cisneros-Heredia and McDiarmid (2006a), Cisneros-Heredia and Guayasamin (2006).
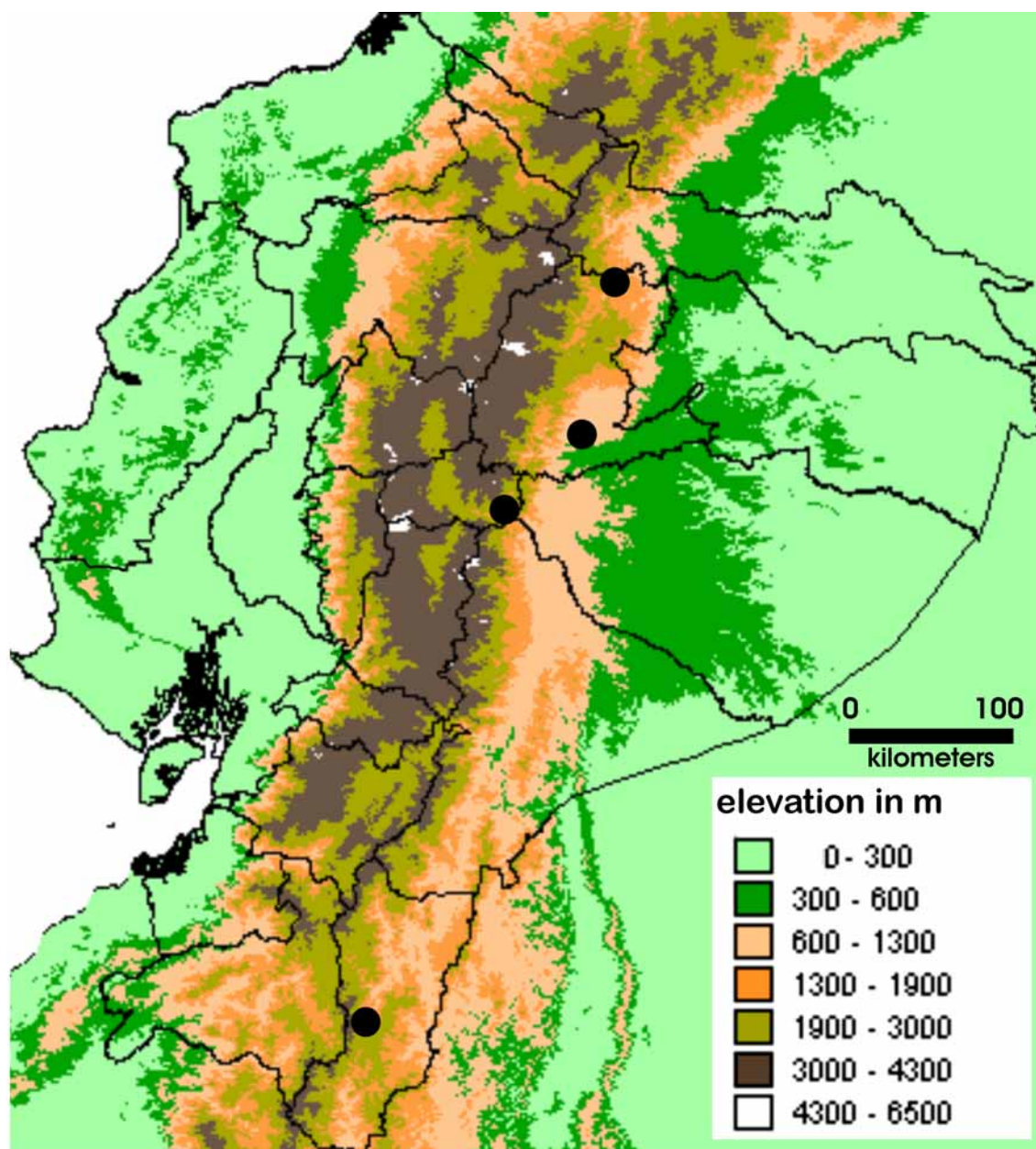


**FIGURE 17.** Distribution of *Centrolene mariaelenae* in Ecuador

*medemi* Cochran & Goin 1970

—*Centrolene medemi* (Cochran & Goin 1970)

  *GD*.—Colombia and Ecuador.

  *ED*.—It is known from one locality in Low Montane Evergreen Forest on the northern Amazonian Andean slopes at 1490 m elevation, in the Province of Napo.

  *Relevant literature*.—Cochran and Goin (1970), Lynch & Duellman (1973), Ruiz-Carranza and Lynch (1991b), Suárez-Mayorga (1999), Bolívar et al. (2004a), Guayasamin et al. (2006a).


*megacheirus* Lynch & Duellman, 1973

—*Nymphargus megacheirus* (Lynch & Duellman, 1973)

  *GD*.—Colombia and Ecuador.

  *ED*.—It has been reported from two localities: the type locality (16.5 km NNE of Santa Rosa on Quito-Lago Agrio road, 1700 m elevation) and the Azuela River. Additionally a specimen from the EPN collection has been reported from the Cordillera de Guacamayos. An additional locality is herein presented; 14.7 km by road NE of Río Salado, 1310 m, Province of Napo (USNM 286700-01, collected in 24 February 1979). All four localities are in Low Montane Evergreen Forests on the northern Amazonian Andean slopes between 1300 and 1750 m elevation in the Province of Napo (Fig. 18).

  *Relevant literature*.—Lynch & Duellman (1973), Bolívar et al. (2004d), Cisneros-Heredia & McDiarmid (2006a).


*midas* Lynch & Duellman, 1973

—*Cochranella midas* Lynch & Duellman, 1973

  *GD*.—Ecuador, Perú, and Brazil, probably also in Colombia.

  *ED*.—Known from several localities in Lowland Evergreen Forests on the Amazonian lowlands below 600 m elevation, in the provinces of Sucumbíos, Orellana, Napo, and Pastaza.

  *Relevant literature*.—Lynch & Duellman (1973), Rodríguez et al. (2004a), Cisneros-Heredia and McDiarmid (2005b), Cisneros-Heredia and McDiarmid (2006a).


*munozorum* Lynch & Duellman, 1973

—*Hyalinobatrachium munozorum* (Lynch & Duellman, 1973)

  *GD*.—Colombia, Ecuador, and Peru.

  *ED*.—Known from few localities in Lowland Evergreen Forests on the northern Amazonian lowlands below 400 m elevation, in the provinces of Sucumbíos and Orellana.

  *Relevant literature*.—Lynch and Duellman (1973), Duellman (1976), Rodríguez et al. (2004b).


*orejuela* Duellman & Burrowes, 1989

—*Cochranella orejuela* (Duellman & Burrowes, 1989)

  *GD*.—Colombia and Ecuador.

  *ED*.—Recently collected in Ecuador in two localities in the Lowland Seasonal Evergreen and Evergreen Foothill Evergreen forests on the northwestern Pacific Andean slopes between 600 and 1200 m elevation, in the Province of Pichincha (Yánez-Muñoz & Cisneros-Heredia in press).
Relevant literature.—Yánez-Muñoz & Cisneros-Heredia (in press).


*pellucidum* Lynch & Duellman, 1973

—*Hyalinobatrachium pellucidum* (Lynch & Duellman, 1973)

  *GD*.—Endemic to Ecuador.

  *ED*.—It has been reported from the type locality (Azuela River) and from near Limón. An additional

locality is reported herein: 14.7 km by road NE of Río Salado, 1310 m, province of Napo (USNM 286712). Thus, the species is distributed in Low Montane Evergreen Forest on the Amazonian Andean slopes between 1000 and 1740 m elevation, in the provinces of Napo and Morona-Santiago (Fig. 19).

*Remarks*.—The species *lemur* is very similar to *pellucidum*, if not conspecific. Both species were separated by differences in hand webbing and other characters that are within the intraspecific variation of *pellucidum*. We do not include *lemur* in our list of the species of Centrolenidae (see below), and a detailed analysis and conclusions about the status of *lemur* will be presented elsewhere.
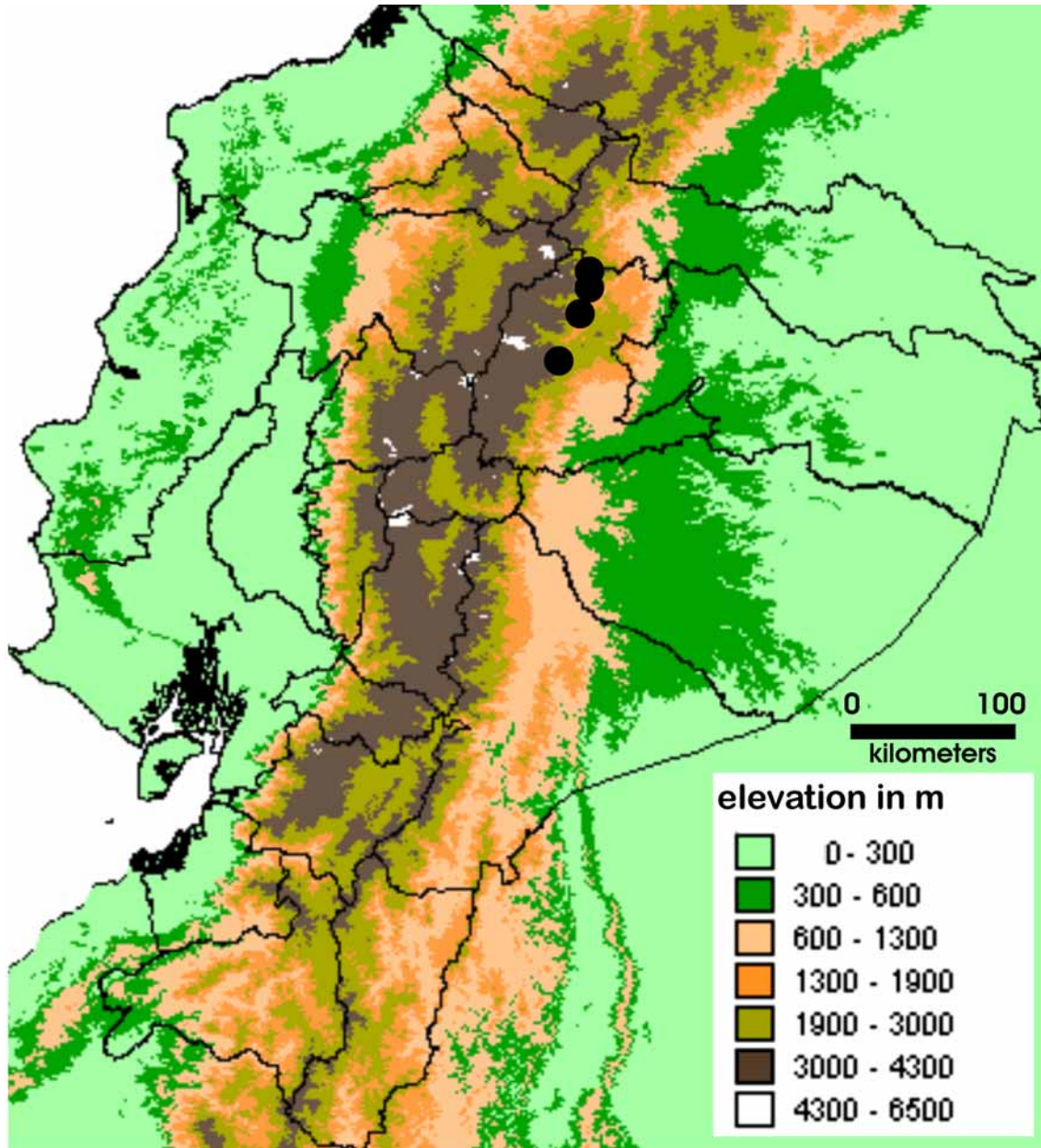


**FIGURE 18.** Distribution of *Nymphargus megacheirus* in Ecuador

*Relevant literature*.—Lynch and Duellman (1973), Coloma et al. (2004f), Cisneros-Heredia and McDiarmid (2005), Cisneros-Heredia and McDiarmid (2006a).

*peristictum* Lynch & Duellman, 1973
—*Centrolene peristictum* (Lynch & Duellman, 1973)

*GD.*—Colombia and Ecuador.

*ED.*—It is known from three localities in Low Montane Evergreen Forests on the northern Pacific Andean slopes between 1380 and 1900 m elevation, in the Province of Pichincha.

*Remarks.*—The species *peristictum* and *lynchi* are strikingly similar, and normally we would regard them as synonyms, but *lynchi* is larger than *peristictum* (*lynchi* 23.0–26.9 mm SVL in males, n = 23; 23.8–24.9 mm SVL in females, n = 8; *peristictum* 18.7–20.6 mm SVL in males, n = 2; 20.5 mm SVL in female, n = 1), all *lynchi* lack iridophores on the visceral peritonea while some populations of *peristictum* show them, and they are apparently sympatric at least at one locality (Río Faisanes, Bustamante et al. 2005, Cisneros-Heredia & McDiarmid 2005).

*Relevant literature.*—Lynch & Duellman (1973), Coloma et al. (2004k), Cisneros-Heredia and McDiarmid (2005b).
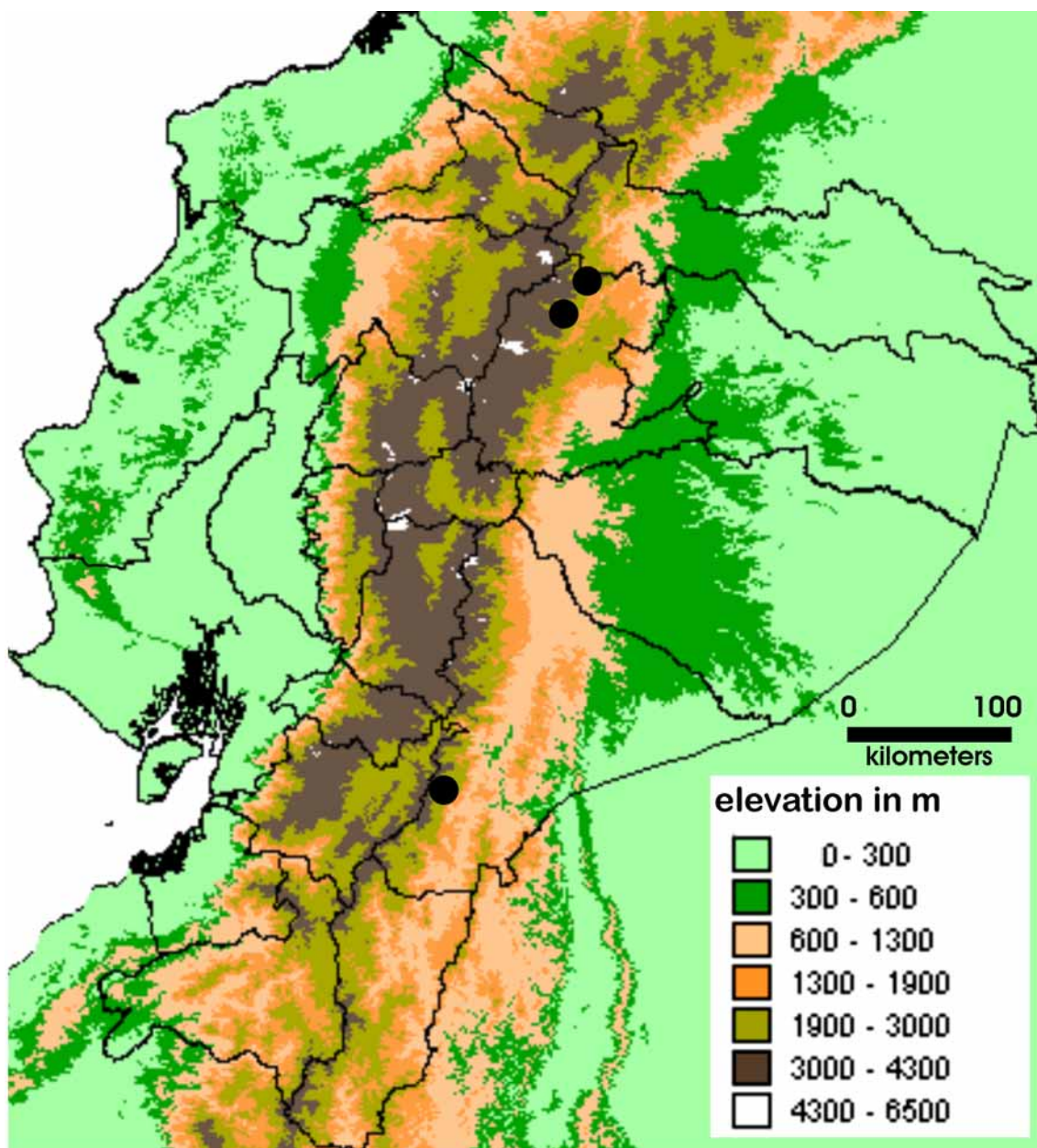


**FIGURE 19.** Distribution of *Hyalinobatrachium pellucidum* in Ecuador.

*pipilatum* Lynch & Duellman, 1973
—*Centrolene pipilatum* (Lynch & Duellman, 1973)

*GD*.—Endemic to Ecuador.

*ED*.—It has been reported from two localities: the type locality (16.5 km NNE of Santa Rosa on Quito-Lago Agrio road, 1700 m elevation), and the Azuela River. An additional locality is herein reported; 14.7 km by road NE of Río Salado, 1310 m, Province of Napo (USNM 286717 and MCZ A-97803, collected on 24 February 1979). All three localities are located in Low Montane Evergreen Forests on the northern Amazonian Andean slopes between 1300 and 1740 m elevation, in the Province of Napo (Fig. 20).

*Relevant literature*.—Lynch & Duellman (1973), Coloma et al. (2004d)
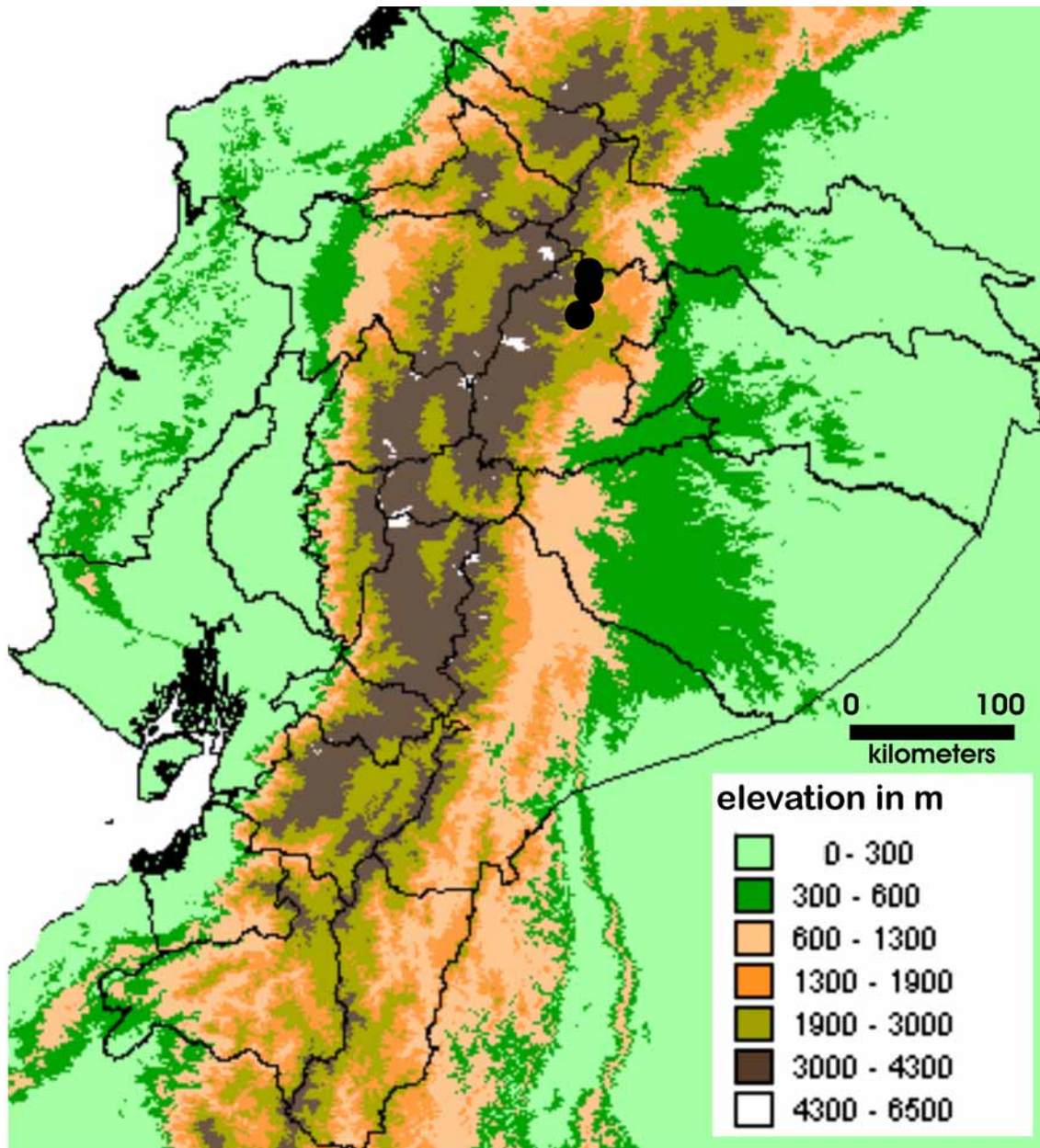


**FIGURE 20.** Distribution of *Centrolene pipilatum* in Ecuador

*posadae* Ruiz-Carranza & Lynch, 1995

—*Nymphargus posadae* (Ruiz-Carranza & Lynch, 1995)

    *GD*.—Colombia and Ecuador.

    *ED*.—The species *posadae* was described from the eastern versant of the Cordillera Central of Colombia, from the departments of Caldas, Huila, and Cauca between 1900 and 2800 m elevation (Ruiz-Carranza &

Lynch 1995a). The species was first reported in Ecuador from specimens collected in the area of Yanayacu (2100 m elevation), Province of Napo (Guayasamin et al. 2006). Herein we report additional localities. A male of *posadae* (DFCH-USFQ) was collected along a small stream, lower tributary of the Jambue River, ca. 15 km S from Zamora, (ca. 04°14'S, 78°57'W, 1750 m), on the western slope of Contrafuerte de Tzunantza, Cordillera Oriental, eastern slopes of the Andes, Province of Zamora-Chinchipe, on 30 April 2002. Two adult males of *Co. posadae* (USNM 288464-5) were collected at "L'Alegria, on Rio Chingual, ca. 3 km N of Sebundoy, ca. 20 km N of La Bonita, 6248 ft" [Province of Sucumbíos, Ecuador], on 25 June 1962 by Manuel Olalla. La Alegría is a small settlement in the Cordillera del Mirador, a small range that is part of the Cordillera Oriental of Ecuador; however, it is located at ca. 2400 m, and is not close to the Chingual River. We consider that the two specimens were collected somewhere near La Alegría but at a lower elevation (6248 ft = ca. 1890 m elevation], where the road from La Alegria crosses the Chingual River (Fig. 21). Specimen USNM 288464 of *Cochranella posadae* was cited as *Centrolene* sp. N7 in Cisneros-Heredia and McDiarmid (2006a) by a lapsus. All three localities are in Montane Cloud Forest on the Amazonian Andean slopes between 1750 and 2100 m elevation, in the provinces of Sucumbíos, Napo, and Zamora-Chinchipe.

*Remarks.*—The three specimens reported herein coincide very well with the description of *Co. posadae* provided by Ruiz-Carranza and Lynch (1995a) and have the following characteristics: vomerine teeth absent; snout in dorsal view from subovoid to truncate (due to nostril elevation), in lateral view from slightly sloping to truncate; tympanum weakly differentiated, with vertical posterior inclination; dorsal skin from shagreen to granular with low warts and tubercles; liver lobed (four lobes); humeral spine absent; hand webbing basal between fingers I–III, and III 3⁻⁻ 3⁻ IV; feet webbing I 2⁻⁻ 2½ II 1⅓ – 2⅓ III 1½ – 2⅔ IV 3⁻ – 2⁻ V;; dermal folds absent but a row of low warts along the ventrolateral external edge of the tarsus; nuptial pad type I, prepollex concealed; finger I shorter than finger II; eye diameter larger than width of disc on finger III; color in preservative, dorsum purple-lavender with some traces of pale spots; fingers and toes without melanophores (mostly cream, except for some melanophores restricted to the base of toe IV). Two characters not mentioned in the original description of *Cochranella posadae* are present in the specimens herein reported: Type-VI nuptial pads (extensive glandular tissue along the body sides, arms, and legs); and cloacal ornamentation consisting of a pair of large, round subcloacal tubercles on the ventral surface of the thighs, and thick vertical glandular folds on the sides of the vent. The entire area below the vent is granular and enameled. The poor development or absence of cloacal ornamentation in the type series of *Co. posadae* could be related to intraspecific variation or to preservation.

*Relevant literature.*—Ruiz-Carranza & Lynch (1995a), Wild and Lynch (2004), Guayasamin et al. (2006c).

*prosoblepon* Boettger, 1892
—*Centrolene prosoblepon* (Boettger, 1892)
—*Hyla ocellifera* Boulenger, 1899 - New synonym, see justification above.

*GD.*—Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador.

*ED.*—It is widely distributed across different vegetation formations, including Lowland Seasonal and Non-Seasonal Evergreen forests, Foothill Seasonal and Non-Seasonal Evergreen forests, and Semideciduous Evergreen forests on the Pacific Andean slopes, between 200 and 1100 m elevation, in the provinces of Esmeraldas, Guayas, Los Ríos, El Oro, Carchi, Imbabura, Pichincha, Bolívar, and Cotopaxi.

*Relevant literature.*—Boettger (1892), Boulenger (1899), Lynch & Duellman (1973), Ruiz-Carranza and Lynch (1995c), Kubicki et al. (2004), Cisneros-Heredia and McDiarmid (2005b), Kubicki (2007).

*pulverata* Peters, 1873
—*Cochranella pulverata* (Peters, 1873)

*GD*.—Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.

*ED*.—Known from two localities in Lowland Non-Seasonal Evergreen Forest in the northern Pacific lowlands below 200 m elevation, in the Province of Esmeraldas (Bustamante et al. in press).

*Relevant literature*.—Peters (1873), Savage (2002), Solís et al. (2004c), Kubicki (2007), Bustamante et al. (in press.).
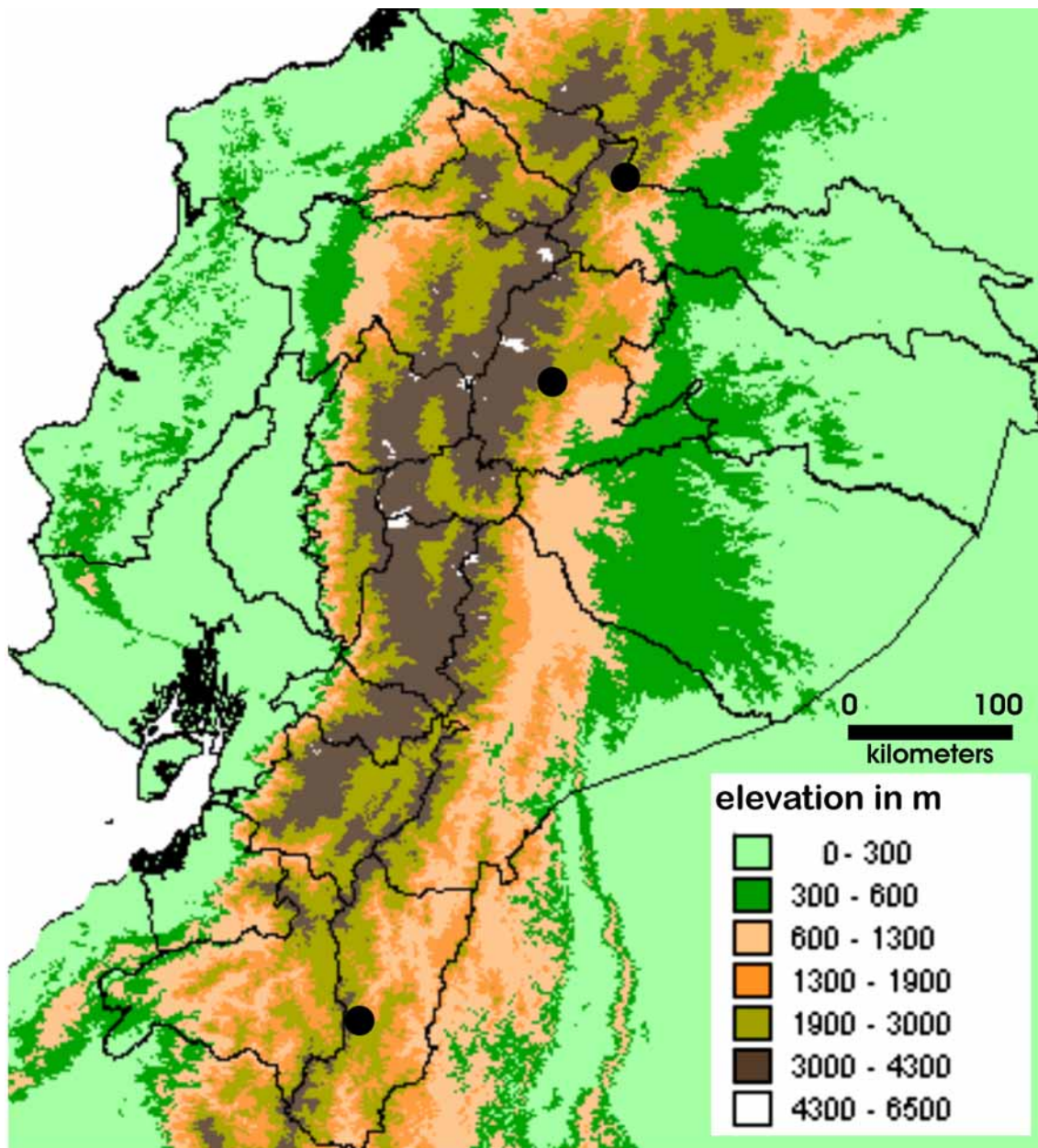


**FIGURE 21.** Distribution of *Nymphargus posadae* in Ecuador

*puyoensis* Flores & McDiarmid, 1989

—*Cochranella puyoensis* (Flores & McDiarmid, 1989)

    *GD*.—Endemic to Ecuador

    *ED*.—Known from four localities in the Huataracu River basin, and near Puyo (type locality) in Foothill Evergreen Forest on the northern and central Amazonian Andean slopes between 350 and 1000 m elevation, in the provinces of Napo, Orellana, and Pastaza.

    *Relevant literature*.—Flores & McDiarmid (1989), Coloma and Ron (2004a), Cisneros-Heredia and McDiarmid (2006b).

*resplendens* Lynch & Duellman, 1973

—*Cochranella resplendens* (Lynch & Duellman, 1973)

*GD*.—Colombia, Ecuador, and Peru (Alto Cainarachi Valley, Department of San Martín, R. Schulte, pers. comm.).

*ED*.—Reported from three localities: the type locality, the Pozo Garza-Oryx, and the Tiputini Biodiversity Station. A fourth Ecuadorian locality is herein reported: A juvenile (USNM 288460) collected by Jorge Olalla at "San José Viejo de Sumaco, upper Rio Napo" on January 1955. San José Viejo de Sumaco is a settlement located ca. 15 km SSW of the town of San José de Payamino, and ca. 18 km NW of the town of Loreto (ca. 900 m elevation), Province of Orellana. Although a juvenile, this specimen shows the characteristic features of the species: snout gradually inclined in lateral view, pronounced dermal folds on ventrolateral edges of arms and feet, cloacal ornaments consisting of cloacal flaps, and extensive webbing on outer fingers. This locality extends the elevational range of the species to the Amazonian foothills at ca. 900 m elevation (previously known just from the Amazonian lowlands up to 300 m). All four localities are in the Lowland Evergreen and Foothill Evergreen forests in the northern and central Amazonian lowlands, between 250 and 900 m elevation, in the provinces of Sucumbíos, Napo, Orellana, and Pastaza (Fig. 22).
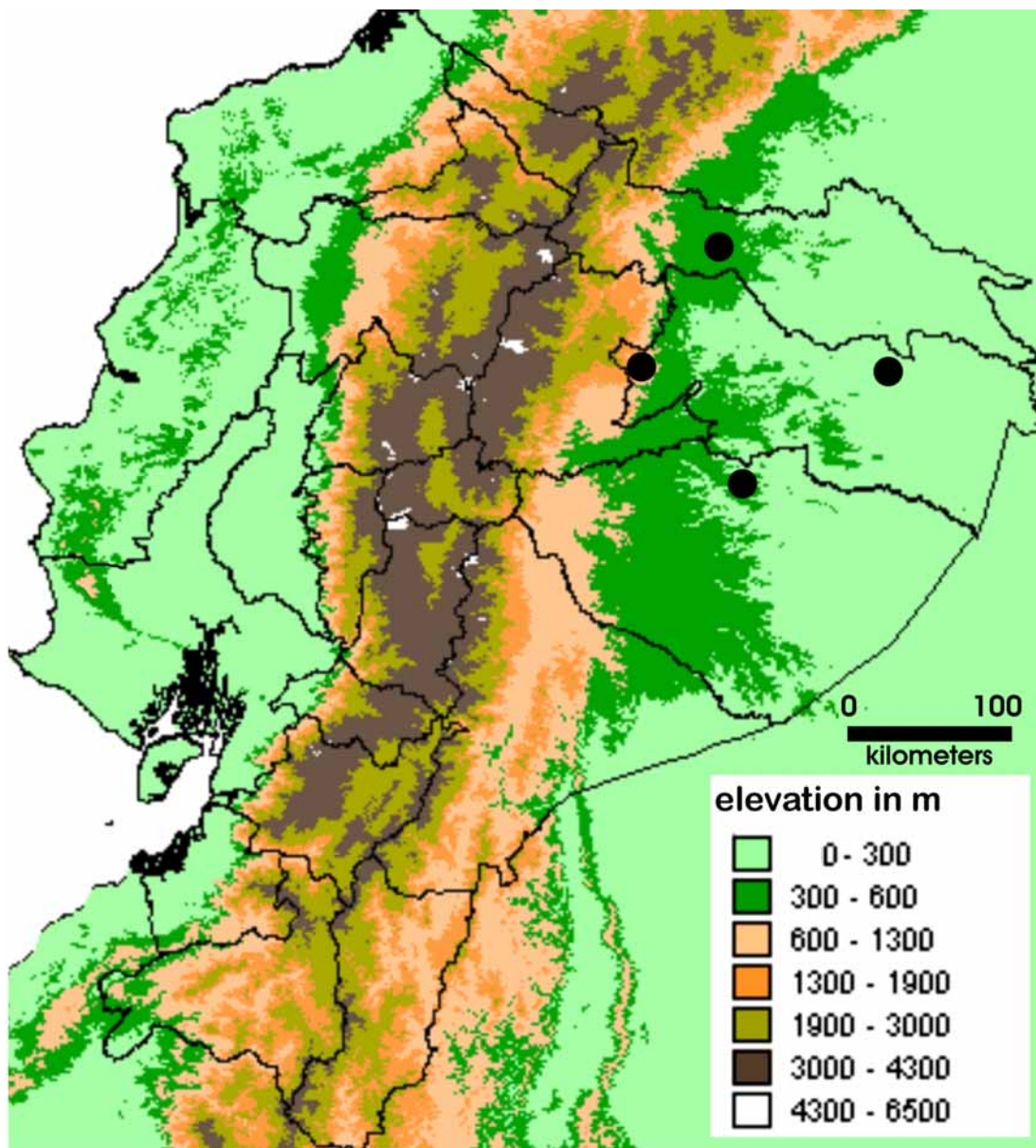


**FIGURE 22.** Distribution of *Cochranella resplendens* in Ecuador

*Relevant literature.*—Lynch and Duellman (1973), Castro et al. (2004b), Guayasamin and Bonnacorso (2004), Cisneros-Heredia and McDiarmid (2005b), Lynch (2005), Cisneros-Heredia and McDiarmid (2006a).

*ruedai* Ruiz-Carranza & Lynch, 1998
—*Hyalinobatrachium ruedai* Ruiz-Carranza & Lynch, 1998
    *GD*.—Colombia and Ecuador
    *ED*.—Known from two localities in the Foothill Evergreen Forests of the Upper Arajuno River Basin, central Amazonian Andean slopes, at ca. 500 m elevation, in the provinces of Napo and Pastaza (Fig. 23).
    *Relevant literature.*—Ruiz-Carranza & Lynch (1998), Bolívar and Rueda (2004), Cisneros-Heredia and McDiarmid (2006a), Cisneros-Heredia and McDiarmid (in press).
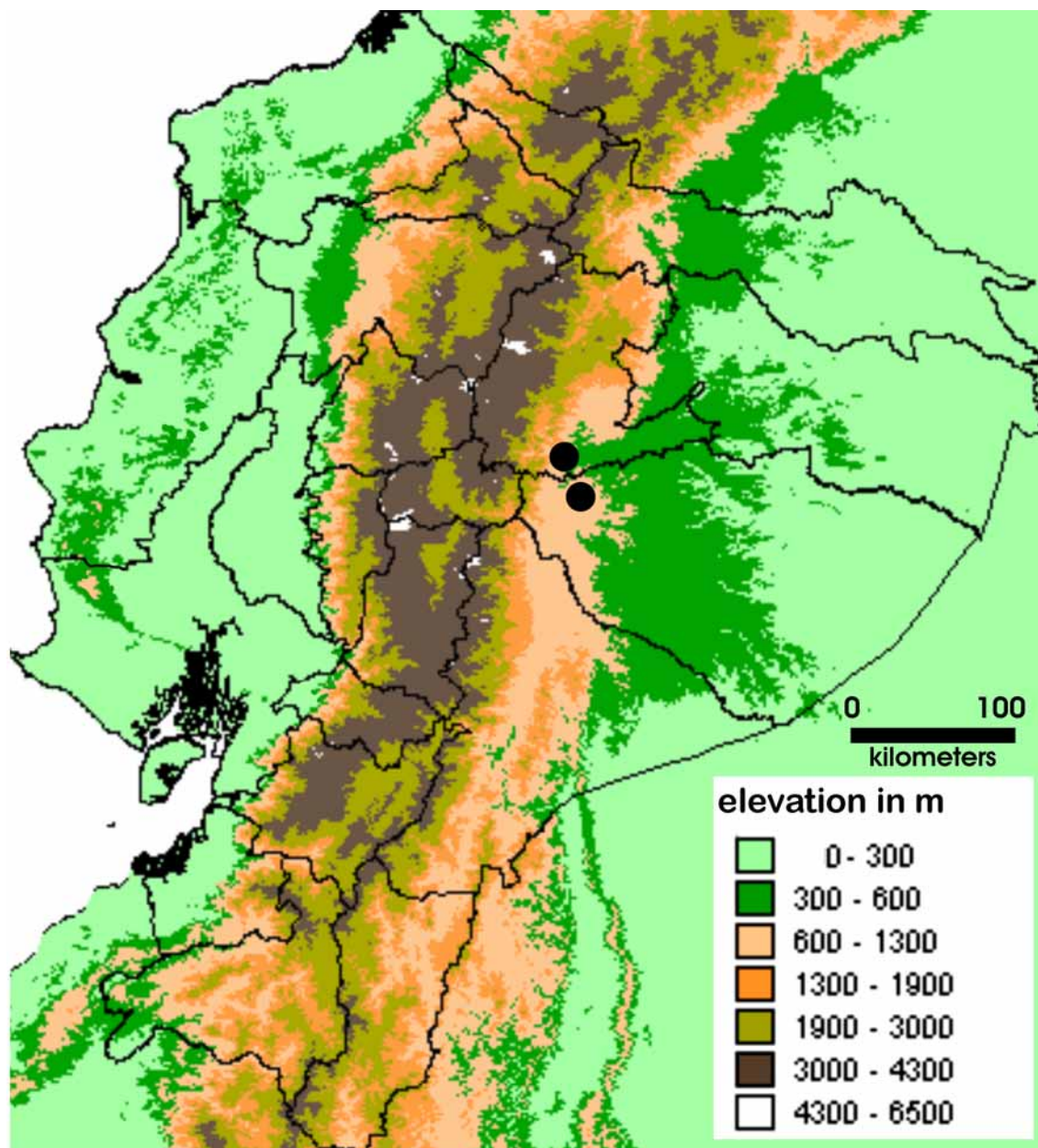


**FIGURE 23.** Distribution of *Hyalinobatrachium ruedai* in Ecuador

*siren* Lynch & Duellman, 1973

—*Nymphargus siren* (Lynch & Duellman, 1973)

 *GD*.—Colombia and Ecuador

 *ED*.—Reported from three localities: the type locality (Salado River), the Azuela River, and 16.5 km NNE of Santa Rosa on Quito-Lago Agrio road. A fourth locality is reported herein: ca. 6 km SW of Huaticocha, Cordillera de Galeras, ca. 1250 m elevation, Province of Orellana (DFCH-USFQ D292-295). All four localities are in Low Montane Evergreen Forest on, province of Orellana (DFCH-USFQ D292-295). All four localities are in Low Montane Evergreen forests on the northern Amazonian Andean slopes, between 1250 and 1700 m elevation, in the provinces of Napo and Orellana (Fig. 24).

 *Relevant literature*.—Lynch & Duellman (1973), Coloma et al. (2004h), Cisneros-Heredia and McDiarmid (2006e).
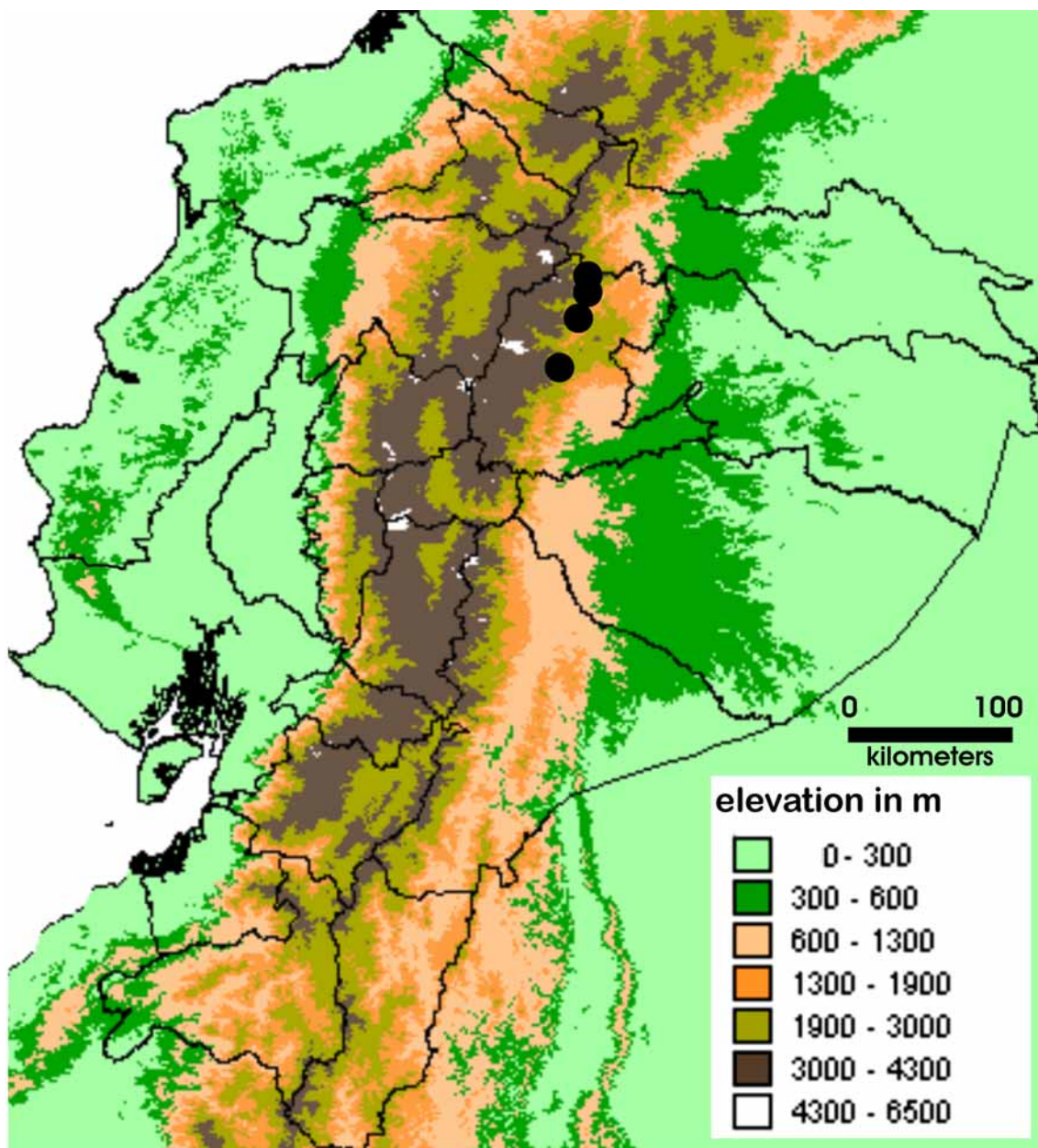


**FIGURE 24.** Distribution of *Nymphargus siren* in Ecuador

*spinosa* Taylor, 1949

—*Cochranella spinosa* (Taylor, 1949)

    *GD*.—Honduras, Costa Rica, Panama, Colombia, and Ecuador.

    *ED*.—Known from localities in Lowland Non-Seasonal and Seasonal Evergreen forests and Foothill Non-Seasonal and Seasonal Evergreen forests in the northern and central Pacific lowlands, below 800 m, in the provinces of Esmeraldas, Pichincha, and Los Ríos.

    *Relevant literature*.—Duellman and Burrowes (1989), Savage (2002), Coloma et al. (2004n), Cisneros-Heredia and McDiarmid (2005b), Kubicki (2007).


*valerioi* Dunn, 1931

—*Hyalinobatrachium valerioi* (Dunn, 1931)

    *GD*.—Costa Rica, Panama, Colombia, and Ecuador

    *ED*.—Known from five localities in Lowland Non-Seasonal Evergreen, Lowland Seasonal Evergreen, and Foothill Seasonal Evergreen forests in the northern and southern Pacific lowlands, foothills and slopes below 1400 m in the provinces of Carchi, Pichincha, Los Ríos, and Azuay.

    *Remarks*.—*Hyalinobatrachium valerioi* was first reported from Ecuador by Duellman and Burrowes (1989). The populations from the slopes seem to have slightly more webbing between finger II and III than those on the lowlands and could correspond to an undescribed species, yet more information is needed to elucidate their identity (Cisneros-Heredia & McDiarmid 2007).

    *Relevant literature*.—Duellman and Burrowes (1989); Ruiz-Carranza and Lynch (1998); Savage (2002), Kubicki (2007), Cisneros-Heredia & McDiarmid (2007).


*wileyi* Guayasamin, Bustamante, Almeida-Reinoso & Funk, 2006c

—*Nymphargus wileyi* (Guayasamin, Bustamante, Almeida-Reinoso & Funk, 2006c)

    *GD*.—Endemic to Ecuador.

    *ED*.—Only known from the type locality (Yanayacu) in Montane Cloud Forests on the northern Amazonian Andean slope at ca. 2100 m elevation, in the Province of Napo.

    *Remarks*.—Guayasamin et al. (2006c) pointed out the strong similarity of *wileyi* with *griffithsi*, a species currently restricted to the Pacific versant of Ecuador and Colombia. Some unicolored specimens of *griffithsi* are practically identical to *wileyi*. The species *wileyi* is also very similar to *cariticommata* (see above).

    *Relevant literature*.—Guayasamin et al. (2006c).

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**APPENDIX I**

**EXAMINED MATERIAL**

To avoid confusion due to disagreements between past, present, and future taxonomic proposals, we refer to species using only their trivial names (e.g., *prosoblepon*). We also include several species that are undescribed or of unclear identity by referring to their localities as informal names within quotes (e.g., "Palenque" in reference to an undescribed species from the Río Palenque Research Center in Ecuador). Locality details are provided only for Ecuadorian specimens. Names of countries are in capital letters; provinces, departments, or states in small capital letters; and localities in lowercase letters. The following abbreviations are used: H = holotype; P = paratype; C&S = cleared and stained.

*acanthidiocephalum*: COLOMBIA: SANTANDER: ICN 5285 (H), ICN 5431 (P, C&S), ICN 60007 (P, C&S), ICN 5429, ICN 5274, ICN 5283–4.

*adiazeta*: COLOMBIA: SANTANDER: ICN 17919 (H).

*albomaculata*: HONDURAS: OLANCHO: USNM 342226–61. COSTA RICA: ALAJUELA: USNM 219182-84; GUANACASTE: USNM 219167-73; PUNTARENAS: USNM 219185-95; SAN JOSE: USNM 219174-81. USNM 219167-95. ECUADOR: IMBABURA: QCAZ 4324–25: 6 km SE of Lita. ESMERALDAS: QCAZ 11369–70: Estero Vicente; DHMECN 2618–19: Reserva Biológica Canandé.

*altitudinale*: VENEZUELA: MERIDA: USNM 166841 (P).

*ametarsia*: COLOMBIA: LETICIA: ICN (JDL 24472). ECUADOR: ORELLANA: DFCH-USFQ D162: Tiputini Biodiversity Station; QCAZ 16652, QCAZ 22709: Estación Científica Yasuní. SUCUMBÍOS: QCAZ 28138: Cuyabeno.

*andinum*: VENEZUELA: MÉRIDA: USNM 166842 (P), USNM 291061 (P). COLOMBIA: SANTANDER: ICN 5432, 6014–6020, 5535–5537.

*anomalus*: ECUADOR: NAPO: KU 143299 (H): Río Azuela.

*antioquiense*: COLOMBIA: ANTIOQUIA: ICN 9773. CALDAS: ICN 35194.

*antisthenesi*: VENEZUELA: ARAGUA: ICN 36589.

*armatus*: COLOMBIA: VALLE DEL CAUCA: ICN 25000 (H), ICN 28037–49 (P).

*audax*: ECUADOR: NAPO: USNM 286620–22: Cascada de San Rafael; USNM 286623–25, MCZ A97807–8: 14.6 km (by road) NE of Río Salado.

*aureoguttatum*: COLOMBIA: CHOCÓ: ICN 17507 (P), ICN 17509–10 (P), ICN 7252–4 (P), ICN 17515–6 (P), ICN 171250 (P), ICN 17255–7 (P). ECUADOR: ESMERALDAS: DHMECN 3221–5: Río Bogotá.

*azulae*: PERU: HUÁNUCO: USNM 195988 (H).

*bacatum*: ECUADOR: NAPO: QCAZ 16212, 17807, 22386–87: Yanayacu Biological Station.

*balionotum*: ECUADOR: CARCHI: DHMECN 0865: Cabeceras del Río Baboso. PICHINCHA: KU 164701 (P), KU 164703–11 (P), ICN 23479 [formerly KU 164712] (P): 3.5 km (by road) northeast of Mindo.

*ballux*: ECUADOR: PICHINCHA: KU 164726–32 (P): 14 km (by road) west of Chiriboga; KU 164733 (P): Quebrada Zapadores.

*bejaranoi*: BOLIVIA: COCHABAMBA: KU 182369 (H), KU 182370-71 (P).

*bergeri*: PERU: CUZCO: KU 162248-49 (P), USNM 298173–75. AYACUCHO: KU 162251 (P), KU 162255 (P), KU 162257 (P).

*buckleyi*: ECUADOR: BOLÍVAR: DHMECN 0866–67: Guanujo. CARCHI: DHMECN 1246: Los Encinos. COTOPAXI: USNM 288428: Pilalo. NAPO: USNM 311113–14: Santa Bárbara. PICHINCHA: USNM 288423: Quito; USNM 286626–27: 8.5 km (by road) NW of Nono; 286628–29: Machachi; 286630–31: 21.2 km (by road) ESE of Chiriboga; USNM 288424: 8 km to Chiriboga. SUCUMBÍOS: DHMECN 0868–93: La Alegría, Santa Barbara.

*buenaventura*: ECUADOR: El Oro: DHMECN 3561-63: Reserva Buenaventura.

*cardiacalyptum*: HONDURAS: OLANCHO: USNM 342161 (H), USNM 530617, USNM 535828–34.

*cariticommata*: ECUADOR: MORONA-SANTIAGO: USNM 288435-6: El Cruzado. ZAMORA-CHINCHIPE: DHMECN 1974, 2429: Reserva Tapichalaca.

*chami*: COLOMBIA: Risaralda: ICN 32079 (H). Antioquia: ICN 8666 (P), ICN 10640 (P).

*cochranae*: ECUADOR: Napo: USNM 284304–6, 286632–36: Cascada de San Rafael; USNM 286638: Río Salado. Orellana: USNM 288452: "Loreto". ZAMORA-CHINCHIPE: DFCH D100-1: Contrafuerte de Tzunantza; FHGO 2804: Romerillos

*colymbiphyllum*: COSTA RICA: Puntarenas: USNM 219196–225. Cartago: USNM 219245–47.

*cristinae*: COLOMBIA: Antioquia: ICN 18645 (H), ICN 18643–4 (P), 18646–9 (P).

*crurifasciatum*: VENEZUELA: Amazonas: AMNH 131329 (H), AMNH 131331 (P).

*daidalea*: COLOMBIA: Cundinamarca: ICN 18008 (H). Santander: ICN 14916 (P, C&S), ICN 8459-60 (P).

*eccentricum*: VENEZUELA: Amazonas: AMNH 159164 (P).

*esmeralda*: COLOMBIA: Boyacá: ICN 9593–4 (P), ICN 9596 (P), ICN 9603 (P).

*euhystrix*: PERU: Cajamarca: USNM 292588 (P), USNM 292587 (P).

*euknemos*: COSTA RICA: San José: USNM 219248.

*eurygnathum*: BRAZIL: São Paulo: USNM 96558, 96560–3, 207734, 217662–69. Minas Gerais: 207762–74. Rio de Janeiro: USNM 208388–95, USNM 232360–64.

*flavopunctata*: ECUADOR: Pastaza: KU 121048 (H), KU 121041 (P), KU 121043–46 (P): Mera.

*fleischmanni*: COSTA RICA: Alajuela: USNM 219249–61. San José: USNM 219263–80. Guanacaste: USNM 219282–303. NICARAGUA: MATAGALPA: USNM 220013-18. NUEVA SEGOVIA: USNM 220019-36. HONDURAS: Olancho: USNM 342162-342213. MÉXICO: Chiapas: USNM 115499. ECUADOR: Los Ríos: USNM 60520: Quevedo; USNM 286639–40: Río Palenque; USNM 286645: Patricia Pilar; USNM 286646: Hacienda Cerro Chico. Esmeraldas: DFCH-USFQ: Río Bogota.

*garciae*: COLOMBIA: Cauca: ICN 11752 (H), ICN 11715–20 (P).

*geckoideum*: COLOMBIA: Boyacá: ICN 5559, 5560–63, 5598 (C&S). Quindío: ICN 8694–97. ECUADOR: Carchi: DHMECN 0900: Río La Plata, Maldonado-Tulcán road. Pichincha: USNM 167018: 45 km SWS of Quito, at km 45 on Chillogallo–Santo Domingo de los Colorados road.

*grandisonae*: ECUADOR: Carchi: USNM 286647–52: 5.9 km E of Maldonado. Pichincha: DFCH-USFQ (field series) 111, 117, 150, 152, 160–1, 175: Guajalito Protection Forest; USNM 211211: Quebrada La Plata; USNM 211212–15: 2.9 km SW of Tandayapa; MCZ A-106952–56: "Santo Domingo de los Colorados" [probably refers to the general area rather than to the Santo Domingo de los Colorados city or surroundings].

*granulosa*: COSTA RICA: Puntarenas: USNM 219304–13.

*griffithsi*: ECUADOR: Pichincha: USNM 286659: Quebrada La Plata; USNM 286662–64, 286667–77: 1.0 km SW of Tandayapa.

*guanacarum*: COLOMBIA: Cauca: ICN 11686 (H), ICN 11685 (P).

*heloderma*: ECUADOR: Pichincha: USNM 211219–21 (P): Quebrada Zapadores; USNM 211216–7: 13.1 km NW of Nono; USNM 211218: 8.6 km SE of Tandayapa.

*hesperium*: PERU: Cajamarca: USNM 292582–84 (P).

*huilense*: COLOMBIA: Huila: ICN 7462 (H), 7461, 7463 (P).

*hybrida*: COLOMBIA: Boyacá: ICN 17897 (H), ICN 17898 (P), ICN 9614 (P), ICN 10197 (P).

*ibama*: COLOMBIA: Santander: ICN 6033-35 (P).

*ignotus*: COLOMBIA: Valle del Cauca: ICN 14748 (H), ICN 14749-77 (P).

*ilex*: ECUADOR: Esmeraldas: DHMECN 2620–26: Reserva Biológica Canandé; DHMECN 3199–03: Río Tululbí; DHMECN 3204: Cantón San Lorenzo, parroquia Santa Rita, recinto Ventanas; DHMECN 3217-3220, 3232, 3283. Pichincha: DFCH-USFQ D260–1: Hacienda La Joya, km 109 Calacalí–Nanegalito–P.V.Maldonado road.

*laurae*: ECUADOR: Orellana: Loreto (H).

"Leticia (cf. *midas*)": COLOMBIA: Amazonas: ICN (JDL) 25379.

"Leticia (cf. *munozorum*)": COLOMBIA: AMAZONAS: ICN (JMR) 4119.

*litorale*: ECUADOR: ESMERALDAS: DHMECN 3198: Río Cachabí; EcoC 141: Tsejpu, Rio Zapallo. COLOMBIA: NARIÑO: ICN 13821 (H).

*luminosa*: COLOMBIA: ANTIOQUIA: ICN 15930 (H), ICN 15931–6 (P), ICN 15918–23 (P).

*luteopunctatus*: COLOMBIA: CAUCA: ICN 20747 (H).

*lynchi*: ECUADOR: PICHINCHA: KU 164691 (H), KU 164692–99, ICN 23753 [formerly KU 164700] (P): 4 km northeast (by road) of Dos Ríos; KU 202720 (H of *Centrolenella scirtetes*): 1.4 km (by road) southwest of Tandayapa; USNM 284345–48: Mindo, Hacienda San Vicente; USNM 286687–89: 14.3 km NE of La Palma; USNM 286690–91: Quebrada La Plata; USNM 286692–95: 1.0 km of Tandayapa; MCZ A105463–64: Tandapi; QCAZ 106–109, 506: Las Pampas; QCAZ 468–72: Tandapi; DHMECN: Chiriboga.

*mache*: ECUADOR: ESMERALDAS: DHMECN 3560: Canandé; DHMECN 2611: Punta Galeras.

*mariae*: PERU: HUÁNUCO: KU 174713 (H).

*mariaelenae*: ECUADOR: ZAMORA-CHINCHIPE: DFCH-USFQ D125 (holotype): Río Jambue, Cordillera de Tzunantza. NAPO: QCAZ 18618–19: Río Hollín.

*medemi*: COLOMBIA: PUTUMAYO: USNM 15227 (H). ECUADOR: NAPO: KU 164493–94: 2 km SSW of Río Reventador.

*megacheirus*: ECUADOR: NAPO: USNM 286700: Rio Azuela; USNM 286701: Río Salado; EPN: Cordillera de Guacamayos.

*midas*: ECUADOR: SUCUMBÍOS: ICN 23755 [formerly KU 150623] (P): Santa Cecilia. ORELLANA: DFCH-D102: Tiputini Biodiversity Station; QCAZ 22876: Yasuní. NAPO: QCAZ 20001-2: Puerto Misahualli; USNM 286702–05, USNM 286707: trail between Tambo Unión and Rosario Yacu. PASTAZA: USNM 288437: Río Oglán, Curaray. PERU: MADRE DE DIOS: USNM 342716.

*munozorum*: COLOMBIA: META: ICN 5031-34, ICN 39503. ECUADOR: ORELLANA: DFCH-USFQ D105: Tiputini Biodiversity Station.

*nephelophila*: COLOMBIA: CAQUETÁ: ICN 24297 (H).

*notostictum*: COLOMBIA: SANTANDER: ICN 12632 (H).

*nouraguensis*: BRAZIL: OMNH/MPEG 13042.

*ocellata*: PERU: AYACUCHO: KU 192030.

*orejuela*: COLOMBIA: CAUCA: KU 145081 (H).

*oreonympha*: COLOMBIA: CAQUETÁ: ICN 20765 (H), ICN 20766–75 (P).

*orientalis*: TRINIDAD & TOBAGO: SAINT PAUL: USNM 194999–5000 (P *tobagoensis*), USNM 195031 – 35 (P *tobagoensis*).

*orocostalis*: VENEZUELA: GUARICO: USNM 166843 (P). ARAGUA: USNM 259138–40.

*paezorum*: COLOMBIA: CAUCA: ICN 11866 (H).

"Palenque": ECUADOR: LOS RÍOS: USNM 286751–2: Rio Palenque Science Center.

*pellucidum*: ECUADOR: NAPO: USNM 286708-10: Río Azuela; USNM 286711-12: Río Reventador. MORONA-SANTIAGO: QCAZ 25950: 6 Km N of Limón.

*peristictum*: ECUADOR: PICHINCHA: USNM 286714: Río Faisanes; QCAZ 6446: Bosque Protector Río Guajalito.

*petrophilum*: COLOMBIA: BOYACÁ: ICN 9567 (H).

*phenax*: PERU: AYACUCHO: KU 162264 (P), 162266–7 (P).

*pipilatum*: ECUADOR: NAPO: ICN 23756 [formerly KU 143283] (P); USNM 286717, MCZ A-97803: 14.7 km NE Rio Salado.

*pluvialis*: PERU: CUZCO: KU 173225–27 (P), USNM 298950–52.

*posadae*: COLOMBIA: CAUCA: ICN 11307 (H), ICN 7447–50 (P). ECUADOR: SUCUMBÍOS: USNM 288464–5: La Bonita.

*prasinus*: COLOMBIA: VALLE DEL CAUCA: KU 169693 (H), KU 169691–92 (P).

*prosoblepon*: ECUADOR: BOLÍVAR: QCAZ 10925: Balsapamba. COTOPAXI: USNM 288441: "below Sigchos". EL ORO: USNM 286738-39: 16.8 km W of Piñas. ESMERALDAS: USNM 541904-541915: Bilsa Biological Reserve. GUAYAS: USNM 288438: "Guayaquil". LOS RÍOS: USNM 286718–27, MCZ A-88573, 89878: Río Palenque Scientific Center; USNM 286734–35: Montañas de Ila. IMBABURA: QCAZ 4318, 4893: 5–6 km W of Lita; QCAZ 20704: Río Verde. PICHINCHA: DFCH-USFQ 293-295: Mashpi Reserve; KU 118041: Tandapi; USNM 285830: Santo Domingo de los Colorados; MCZ A-88434–35, 89877, 91189, 91191, 91460: Tinalandia. COSTA RICA: ALAJUELA: USNM 219329-33. CARTAGO 219334-47. PUNTARENAS: USNM 219314-28, USNM 219348-49. SAN JOSE: USNM 219350-78.

*pulverata*: HONDURAS: OLANCHO: USNM 342214–21. COSTA RICA: PUNTARENAS: USNM 219379–87. ECUADOR: ESMERALDAS: DHMECN 2612, 3195, 3194: Cabo San Francisco.

*punctulata*: COLOMBIA: ANTIOQUIA: ICN 15800 (H). CALDAS: ICN 34745–59 (P).

*puyoensis*: ECUADOR: PASTAZA: MCZ 91187 (H): 1 km W Puyo; USNM 291298: Río Pucayacu. NAPO: DFCH-USFQ D285: ca. 45 km E of Narupa. ORELLANA: QCAZ 7104, 7499: Río Huataracu.

*quindianum*: COLOMBIA: QUINDÍO: ICN 24886 (H), ICN 24910-20 (P).

*ramirezi*: COLOMBIA: ANTIOQUIA: ICN 19684 (H), 19682–3 (P).

*resplendens*: ECUADOR: SUCUMBÍOS: KU 118053 (H): Santa Cecilia. PASTAZA: FHGO 1305, FHGO 1324: Pozo Garza, Oryx. ORELLANA: DFCH D103-4: Tiputini Biodiversity Station; USNM 288460: San José Viejo de Sumaco.

*robledoi*: COLOMBIA: ANTIOQUIA: ICN 17936–7 (P), ICN 17939–41 (P).

*rosada*: COLOMBIA: CALDAS: ICN 34761 (H), ICN 34764–5 (P).

*ruedai*: COLOMBIA: CAQUETÁ: ICN 40409 (H), ICN 40410-11 (P), IND-AN 5448-52 (P). ECUADOR: NAPO: DFCH-USFQ 0735: Tena. PASTAZA: EPN 6427: Río Manderoyacu.

*ruizi*: COLOMBIA: CAUCA: ICN 7469 (H), ICN 7470–71 (P).

*sanchezi*: COLOMBIA: CAQUETÁ: ICN 24293 (H).

*savagei*: COLOMBIA: QUINDÍO: ICN 9769 (H), ICN 9767–8 (P).

*siren*: ECUADOR: NAPO: USNM 286740: R®™o Azuela; KU 146610 (H), KU 146611-23 (P): Rio Salado, ca. 1 km upstream from Rio Coca; MCZ A97809: 6.5 km S Baeza. ORELLANA: DFCH-USFQ D292-295: Cordillera de Galeras.

*solitaria*: COLOMBIA: CAQUETÁ: ICN 24298 (H).

sp. A (of Cisneros-Heredia & McDiarmid in press): ECUADOR: PICHINCHA: USNM 286762-63: Río Faisánes.

*spiculata*: PERU: CUZCO: KU 162283 (P), USNM 298176–77, USNM 342772–77.

*spilotus*: COLOMBIA: CALDAS: ICN 35155 (H).

*spinosa*: ECUADOR: PICHINCHA: USNM 288443: Río Blanco. LOS RÍOS: USNM 286741–44: Río Palenque. COSTA RICA: ALAJUELA: USNM 219388–94.

*susatamai*: COLOMBIA: TOLIMA: ICN 18641 (H). ANTIOQUIA: ICN 15801 (P).

"Tambopata": PERU: MADRE DE DIOS: USNM 300000, 343293, 344821–23.

*tayrona*: COLOMBIA: MAGDALENA: ICN 12997 (H), ICN 12998 (P), ICN 12867 (P), ICN 12869–72 (P).

*truebae*: PERU: CUZCO: KU 162269-81 (P), USNM 298178–80, USNM 346056–59, USNM 346310–13.

*uranoscopum*: BRAZIL: RIO DE JANEIRO: USNM 232353–59, USNM 243722.

*valerioi*: COSTA RICA: PUNTARENAS: USNM 219398–424. ALAJUELA: USNM 219425–38. ECUADOR: LOS RÍOS: USNM 286746-49: Río Palenque (= sp. B, Cisneros-Heredia & McDiarmid 2006a). CAÑAR: DHMECN: Manta Real.

*wileyi*: ECUADOR: Napo: QCAZ 26024, 26028–29, 26057: Yanayacu Biological Station.

*xanthocheridia*: COLOMBIA: RISARALDA: ICN 27758 (H), ICN 27757 (P). ANTIOQUIA: ICN 10643–6 (P).

# APPENDIX II
# CLASSIFICATION OF THE SPECIES OF THE FAMILY CENTROLENIDAE.


## Family CENTROLENIDAE Taylor, 1951

*Type species.*—*Centrolene geckoideum* Jiménez de la Espada, 1872.

*Content.*—Five genera: *Allophryne* Gaige 1926; *Centrolene* Jiménez de la Espada, 1872; *Cochranella* Taylor, 1951; *Hyalinobatrachium* Ruiz-Carranza & Lynch, 1991; *Nymphargus* Cisneros-Heredia & McDiarmid new genus.

*Diagnosis.*—A monophyletic clade defined by the following apomorphies: presence of a dilated process on the medial side of the third metacarpal; T-shaped terminal phalanges; intercalary element between distal and penultimate phalanges; complete or partial fusion of tibiale and fibulare; ventral skin partially or completely transparent due to the absence of chromatophores; egg clutches deposited outside of water on vegetation or rocks above still or flowing water systems; exotroph, lotic, burrowing fossorial larvae with vermiform body and dorsal C-shaped eyes, that live buried within leaf packs amidst mud in bottom of still or flowing water systems (Taylor 1951; Ruiz-Carranza & Lynch 1991a; Sanchiz & de la Riva 1993; Burton 1998; Cisneros-Heredia & McDiarmid 2006a). Frost et al. (2006) presented several molecular synapomorphies of the family. Haas (2003), Burton (1998), and Schwalm and McNulty (1980) suggested several characters that could be synapomorphies of Centrolenidae, but a wider taxon sampling is needed to confirm their validity.


## Genus *ALLOPHRYNE* Gaige, 1926

*Content.*—1 species; *Allophryne ruthveni* Gaige, 1926.

*Remarks.*—Noble (1931) considered that *Allophryne* was closely related to centrolenids. However, Centrolenidae was usually conceived as related to Hylidae (Ford and Cannatella 1993). Recent studies have found evidence that support a sister relationship between Allophrynidae and Centrolenidae (Austin et al. 2002; Faivovich et al. 2005; Frost et al. 2006; Grant et al. 2006). Frost et al. (2006) treated Allophrynidae as a subfamily of Centrolenidae (as Allophryninae). Morphological information about *Allophryne* are described by Lynch and Freeman (1966), Caldwell and Hoogmoed (1998), and Fabrezi and Langone (2000).


## Genus *CENTROLENE* Jiménez de la Espada, 1872

*Content.*—40 species; *Centrolene acanthidiocephalum* (Ruiz-Carranza & Lynch, 1989); *Ce. altitudinale* (Rivero, 1968); *Ce. andinum* (Rivero, 1968); *Ce. antioquiense* (Noble, 1920); *Ce. audax* (Lynch & Duellman, 1973); *Ce. azulae* (Flores & McDiarmid, 1989); *Ce. bacatum* Wild, 1994; *Ce. balionotum* (Duellman, 1981); *Ce. ballux* (Duellman & Burrowes, 1989); *Ce. buckleyi* (Boulenger, 1882); *Ce. callistommum* Guayasamin & Trueb, 2007; Ce. *durrellorum* Cisneros-Heredia, 2007; *Ce. fernandoi* Duellman & Schulte, 1993; *Ce. geckoideum* Jiménez de la Espada, 1872; *Ce. gorzulai* (Ayarzagüena, 1992); *Ce. grandisonae* (Cochran & Goin, 1970); *Ce. guanacarum* Ruiz-Carranza & Lynch, 1995; *Ce. heloderma* (Duellman, 1981); *Ce. hesperium* (Cadle & McDiarmid, 1990); *Ce. huilense* Ruiz-Carranza & Lynch, 1995; *Ce. hybrida* Ruiz-Carranza & Lynch, 1991; *Ce. ilex* (Savage, 1967); *Ce. lema* Duellman & Señaris, 2003; *Ce. lemniscatum* Duellman & Schulte, 1993; *Ce. litorale* Ruiz-Carranza & Lynch, 1996; *Ce. lynchi* (Duellman, 1980); *Ce. mariaelenae* Cisneros-Heredia & McDiarmid 2006a; *Ce. medemi* (Cochran & Goin, 1970); *Ce. muelleri* Duellman & Schulte, 1993; *Ce. notostictum* Ruiz-Carranza & Lynch, 1991; *Ce. paezorum* Ruiz-Carranza, Hernández-Camacho & Ardila-Robayo, 1986; *Ce. peristictum* (Lynch & Duellman, 1973); *Ce. petrophilum* Ruiz-Carranza & Lynch, 1991; *Ce. pipilatum* (Lynch & Duellman, 1973); *Ce. prosoblepon* (Boettger, 1892); *Ce. quindianum* Ruiz-Carranza & Lynch, 1995; *Ce. robledoi* Ruiz-Carranza & Lynch, 1995; *Ce. sanchezi* Ruiz-Carranza & Lynch, 1991; *Ce. tayrona* Ruiz-Carranza & Lynch, 1991; *Ce. venezuelense* (Rivero, 1968).

*Remarks.*—The genus *Centrolene* is currently diagnosed only by the presence of humeral spines on males. However, molecular evidence presented by Frost et al. (2006) indicated that *Centrolene* is paraphyletic with respect to *Cochranella*. Most species have trilobed or tetralobed livers (except for *Ce. mariaelenae*

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which has a liver that is bulbous proximally and bilobed distally—revealed by dissection of specimens QCAZ 18618-9). Venter-to-venter combat behavior has been reported for some species of this genus. All species are lavender in preservative, without ocelli on the dorsal pattern, and most have green bones in life (except for *Ce. tayrona,* which has white bones). Parietal and visceral peritoneal pigmentation is variable; parietal peritoneum shows conditions P0, P2, P3, and P4, while visceral peritonea show conditions V1, V2, V3, and V5. The species currently assigned to *Centrolene* occur from Honduras to Panama, along the Andes from Venezuela to Peru, and on the Cordillera de la Costa of Venezuela and the Guiana region. In Ecuador, they inhabit the Pacific lowlands, Cordillera de la Costa, Pacific Andean slopes, Andean highlands, and Amazonian Andean slopes (no species known from the Amazonian lowlands) between 0 and 3300 m elevation.

### Genus *COCHRANELLA* Taylor, 1951

*Content.*—42 described species; *Cochranella adenocheira* Harvey & Noonan, 2005; *Co. adiazeta* Ruiz-Carranza & Lynch, 1991; *Co. albomaculata* (Taylor, 1949); *Co. amelie* Cisneros-Heredia & Meza-Ramos, 2007; *Co. ametarsia* (Flores, 1987); *Co. antisthenesi* (Goin, 1963); *Co. castroviejoi* Ayarzagüena & Señaris, 1997; *Co. croceopodes* Duellman & Schulte, 1993; *Co. daidalea* Ruiz-Carranza & Lynch, 1991; *Co. duidaeana* (Ayarzagüena, 1992); *Co. euhystrix* (Cadle & McDiarmid, 1990); *Co. euknemos* (Savage & Starrett, 1967); *Co. flavopunctata* (Lynch & Duellman, 1973); *Co. geijskesi* (Goin, 1966); *Co. granulosa* (Taylor, 1949); *Co. helenae* (Ayarzagüena, 1992); *Co. mache* Guayasamin & Bonaccorso, 2004; *Co. mariae* (Duellman and Toft, 1979); *Co. megistra* (Rivero, 1985); *Co. midas* (Lynch & Duellman, 1973); *Co. nola* Harvey, 1996; *Co. ocellata* (Boulenger, 1918); *Co. orejuela* (Duellman & Burrowes, 1989); *Co. oyampiensis* (Lescure, 1975); *Co. phryxa* Aguayo & Harvey, 2006; *Co. pulverata* (Peters, 1873); *Co. punctulata* Ruiz-Carranza & Lynch, 1995; *Co. puyoensis* (Flores & McDiarmid, 1989); *Co. ramirezi* Ruiz-Carranza & Lynch, 1991; *Co. resplendens* (Lynch & Duellman, 1973); *Co. revocata* (Rivero, 1985); *Co. ritae* (Lutz in Lutz & Kloss, 1952); *Co. riveroi* (Ayarzagüena, 1992); *Co. savagei* Ruiz-Carranza & Lynch, 1991; *Co. saxiscandens* Duellman & Schulte, 1993; *Co. solitaria* Ruiz-Carranza & Lynch, 1991; *Co. spiculata* (Duellman, 1976); *Co. spinosa* (Taylor, 1949); *Co. susatamai* Ruiz-Carranza & Lynch, 1995; *Co. tangarana* Duellman & Schulte, 1993; *Co. vozmedianoi* Ayarzagüena & Señaris, 1997; *Co. xanthocheridia* Ruiz-Carranza & Lynch, 1995.

*Remarks.*—The genus *Cochranella* was originally diagnosed by certain plesiomorphic conditions; i.e., absence of humeral spines and lobed liver. The second condition is no longer diagnostic following the inclusion of *Co. antisthenesi* and *Co. pulveratum*. Species currently assigned to *Cochranella* are diagnosed by absence of humeral spines and presence of trilobed or tetralobed livers (except for *Co. antisthenesi* and *Co. pulveratum* with bulbous livers). Venter-to-venter combat behavior has been reported for some species of this genus. All species are lavender in preservative, lack ocelli in the dorsal pattern, and variable bone coloration in life (from green to white). Parietal and visceral peritoneal pigmentation is variable; parietal peritoneum shows conditions P0, P1, P2, P3, and P4, while visceral peritonea show conditions V1, V2, and V5. The species currently assigned to *Cochranella* occur from Honduras to Panama, along the Andes from Venezuela to Bolivia, also in the Cordillera de la Costa of Venezuela and the Guiana region. In Ecuador, they inhabit the Pacific lowlands, Pacific Andean slopes, Andean highlands, Amazonian Andean slopes, and Amazonian lowlands between 0 and 2500 m elevation.

### Genus *HYALINOBATRACHIUM*  Ruiz-Carranza & Lynch, 1991a

*Contents.*—32 described species; *Hyalinobatrachium aureoguttatum* (Barrera-Rodrigues & Ruiz-Carranza, 1989); *H. bergeri* (Cannatella, 1980); *H. cappellei* (Van Lidth de Jeude, 1904); *H. chirripoi* (Taylor, 1958); *H. colymbiphyllum* (Taylor, 1949); *H. crurifasciatum* Myers & Donnelly, 1997; *H. duranti* (Rivero, 1985); *H. esmeralda* Ruiz-Carranza & Lynch, 1998; *H. fleischmanni* (Boettger, 1893); *H. fragile* (Rivero, 1985); *H. guairarepanensis* Señaris, 2001; *H. iaspidiense* (Ayarzagüena, 1992); *H. ibama* Ruiz-Carranza & Lynch, 1998; *H. ignioculus* Noonan & Bonett, 2003; *H. mondolfii* Señaris & Ayarzagüena, 2001; *H. munozorum* (Lynch & Duellman, 1973); *H. nouraguensis* Lescure & Marty, 2000; *H. orientale* (Rivero, 1968); *H. pallidum* (Rivero, 1985); *H. pellucidum* (Lynch & Duellman, 1973); *H. ruedai* Ruiz-Carranza & Lynch, 1998; *H. talamancae* (Taylor, 1952); *H. tatayoi* Castroviejo-Fisher, Ayarzagüena & Vila, 2007; *H. taylori* (Goin,

1968); *H. valerioi* (Dunn, 1931); *H. vireovittatum* (Starrett & Savage, 1973);

*Remarks.*—All species of the genus *Hyalinobatrachium* as herein defined have a bulbous liver with an iridophore layer over the hepatic peritoneum, condition H2; yet, species with this condition are also known in *Centrolene* and *Cochranella*. All species lack humeral spines. Amplexus-like combat behaviour has been reported for some species of this genus. All species are cream-colored in preservative, all have white bones in life, and all lack vomerine teeth. Just one condition of the parietal peritoneum has been reported, P0; and two conditions of the visceral peritonea, V5, and V6. Species of *Hyalinobatrachium* occur from southern Mexico to Panama, along the Andes from Venezuela to Bolivia, in the Cordillera de la Costa of Venezuela, the Guiana region, and the Amazon and Orinoco River basins. In Ecuador, they inhabit the Pacific lowlands, Pacific Andean slopes, Amazonian Andean slopes and Amazonian lowlands between 0 and 1740 m elevation.

### Genus *NYMPHARGUS* Cisneros-Heredia & McDiarmid, new genus

*Content.*—29 species: *Nymphargus anomalus* (Lynch & Duellman, 1973); *N. armatus* (Lynch & Ruiz-Carranza, 1996); *N. bejaranoi* (Cannatella, 1980); *N. buenaventura* (Cisneros-Heredia & Yánez-Muñoz, 2007); *N. cariticommatus* (Wild, 1994); *N. chami* (Ruiz-Carranza & Lynch, 1995); *N. chancas* (Duellman & Schulte, 1993;); *N. cochranae* (Goin, 1961); *N. cristinae* (Ruiz-Carranza & Lynch, 1995); *N. garciae* (Ruiz-Carranza & Lynch, 1995); *N. ignotus* (Lynch, 1990); *N. griffithsi* (Goin, 1961); *N. laurae* Cisneros-Heredia & McDiarmid, new species (Fig. 10); *N. luminosa* (Ruiz-Carranza & Lynch, 1995); *N. luteopunctatus* (Ruiz-Carranza & Lynch, 1996); *N. megacheirus* (Lynch & Duellman, 1973); *N. mixomaculatus* (Guayasamin et al. 2006b); *N. nephelophila* (Ruiz-Carranza & Lynch, 1991); *N. oreonympha* (Ruiz-Carranza & Lynch, 1991); *N. phenax* (Cannatella & Duellman, 1982); *N. pluvialis* (Cannatella & Duellman, 1982); *N. posadae* (Ruiz-Carranza & Lynch, 1995); *N. prasinus* (Duellman, 1981); *N. rosada* (Ruiz-Carranza & Lynch, 1997); *N. ruizi* (Lynch, 1993); *N. siren* (Lynch & Duellman, 1973); *N. spilotus* (Ruiz-Carranza & Lynch, 1997); *N. truebae* (Duellman, 1976); and *N. wileyi* (Guayasamin et al., 2006c).

*Remarks.*—All species lack webbing between fingers I, II, and III, and have reduced (basal) webbing between fingers III and IV. All lack humeral spines. Iridophores on the parietal peritoneum cover at least its anterior half, conditions P3 and P4. All species have liver condition H0. Iridophores are absent from the peritoneum covering the intestines in all species, conditions V0, V1 and V2. Most species lack vomerine teeth. Most species are green in life and lavender in preservative, or have a brownish tint both in life and in preservative. Species of *Nymphargus* occur across the western Andean slopes of Colombia and Ecuador and the eastern Andean slopes of Colombia, Ecuador, Peru, and Bolivia.

**Incerta sedis:** *Hyla (Hylella) eurygnatha* Lutz, 1925; *Hylella parvula* Boulenger, 1895; *Hyla (Hylella) uranoscopa* Müller, 1924. Species previsouly placed in the "*H. parvulum* species-group". All have a light lavender dorsum in preservative, green bones, vomerine teeth, and an iridophore layer over the urinary bladder. The three species inhabit the Atlantic forests of southeastern Brazil and northeastern Argentina.