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**Phylogenetic systematics of Glassfrogs (Amphibia: Centrolenidae)
and their sister taxon *Allophryne ruthveni***

JUAN M. GUAYASAMIN, SANTIAGO CASTROVIEJO-FISHER, LINDA TRUEB,
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Phylogenetic systematics of Glassfrogs (Amphibia: Centrolenidae) and their sister taxon *Allophryne ruthveni*

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Table of contents

Abstract	4
Resumen	4
Introduction	5
Centrolenidae, its monophyly and relationships with other anurans	7
Historical review of the systematics of Glassfrogs and <i>Allophryne ruthveni</i>	9
Material and Methods	17
Nomenclature and Terminology.....	17
Phylogenetic framework for the new classification	17
Criteria for taxon naming	17
Results	19
A monophyletic taxonomy	19
Unranked Taxon: Allocentroleninae	19
Family: Allophrynidae Goin, Goin, & Zug 1978.....	20
Genus: <i>Allophryne</i> Gaige 1926	22
Family: Centrolenidae Taylor 1951	22
Subfamily: Centroleninae Taylor 1951	23
Genus: <i>Centrolene</i> Jiménez de la Espada 1872	25
Genus: <i>Nymphargus</i> Cisneros-Heredia & McDiarmid 2007	26
Tribe: Cochranellini new tribe	29
Genus: <i>Chimerella</i> new genus	31
Genus: <i>Cochranella</i> Taylor 1951	32
Genus: <i>Espadarana</i> new genus	34
Genus: <i>Rulyrana</i> new genus	36
Genus: <i>Sachatamia</i> new genus	37
Genus: <i>Teratohyla</i> Taylor 1951	36
Genus: <i>Vitreorana</i> new genus	38
Subfamily: Hyalinobatrachinae new subfamily	39
Genus: <i>Celsiella</i> new genus	40

Genus: <i>Hyalinobatrachium</i> Ruiz-Carranza & Lynch 1991a	41
Incertae sedis within Centrolenidae: <i>Ikakogi</i> new genus	43
Discussion	43
Centrolenidae, Allophrynidae, and Neobatrachia	43
The new taxonomy	44
Conclusions	46
Acknowledgments	46
References	47
Appendix I.	54
Appendix II.	60
Appendix III.	62
Appendix IV.	63

Abstract

Based on a molecular phylogeny, a new phylogenetic taxonomy that is compatible with both the International Code of Zoological Nomenclature (ICZN) and the PhyloCode is proposed for Glassfrogs and their sister taxon, *Allophryne ruthveni*. The arrangement presented herein emphasizes the recognition of clades having (i) significant statistical support and congruence among phylogenetic estimation methods (i.e., parsimony, maximum likelihood, and Bayesian inference criteria), (ii) congruence among genetic markers, and (iii) morphological and/or behavioral distinctiveness. Also, when previously recognized groups are recovered as monophyletic or nearly monophyletic, we propose taxa that minimize the number of name changes required to make these groups monophyletic, preserving the names and contents of previous classifications (i.e., nomenclatural stability). The evolutionary proximity of Centrolenidae and Allophrynidae is recognized by combining these families into an unraked taxon, Allocentroleniinae—a proposal that maintains the traditional names and species contents of Centrolenidae and Allophrynidae. We arrange centrolenid diversity in two subfamilies: Centroleninae and Hyalinobatrachinae. Within Centroleninae, the diagnosis and species content of the genera *Centrolene*, *Cochranella*, and *Nymphargus* are modified; *Teratohyla* is resurrected and modified, and *Chimerella*, *Espadarana*, *Rulyrana*, *Sachatamia*, and *Vitreorana* are proposed as new genera. The other subfamily, Hyalinobatrachinae, contains the new genus *Celsiella* and a modified *Hyalinobatrachium* that fully corresponds to the former *fleischmanni* Group. Additionally, the genus *Ikakogi* is described. *Ikakogi* could not be assigned with confidence to either subfamily and it is placed as *incertae sedis* in Centrolenidae. The data at hand suggest that *Ikakogi tayrona* is a lineage as old as the subfamilies Hyalinobatrachinae and Centroleninae. The revised taxonomy differs markedly from previous arrangements, which were based on phenetics and few morphological characters. Most of the genera defined herein are confined to distinct biogeographic regions, highlighting the importance of geography in the speciation of Glassfrogs. The principal limitation of this proposal is that it is based on an incomplete sampling of taxa (54% of the recognized Glassfrogs). Although diagnoses are based on phenotypic traits, there are several cases (16% of all species) in which the allocation of species is ambiguous because of morphological homoplasy and the lack of molecular data. Finally, in an attempt to facilitate species identification, comparison, and generic placement, we provide photographs for most (~ 96%) of the recognized centrolenid species.

Key words: Allophrynidae, Amazon, Andes, Anura, Centrolenid frogs, Classification, Cordillera de la Costa, Central America, Diversity, Guiana Shield, Hyloidea, Neobatrachia, Neotropics, Phylogeny, South America, Systematics

Resumen

[Sistemática filogenética de las ranas de cristal (Amphibia: Centrolenidae) y su taxón hermano *Allophryne ruthveni*]

Basándonos en una filogenia molecular, proponemos una nueva taxonomía para las ranas de cristal y su taxón hermano, *Allophryne ruthveni*, que es compatible con el Código Internacional de Nomenclatura Zoológica (ICZN) y el PhyloCode. La clasificación que presentamos aquí enfatiza el reconocimiento formal de clados que (i) tienen soporte estadístico significativo mediante diferentes métodos de inferencia filogenética (parsimonia, máxima verosimilitud y Bayesiano), (ii) son congruentes usando diferentes genes y (iii) son diagnosticables a través de su morfología y/o comportamiento.

Adicionalmente, en situaciones en las que se infieren como casi monofiléticos a grupos reconocidos en clasificaciones previas, proponemos taxa en los que se minimiza el número de cambios requeridos para que estos grupos sean monofiléticos, preservando de esta manera los nombres y contenidos tradicionalmente utilizados (i.e., estabilidad nomenclatural). Proponemos el taxon sin rango Allocentroleniinae, el cual contiene a las ranas de cristal y a su taxon hermano, *Allophryne ruthveni*. De esta manera, reconocemos la proximidad evolutiva entre estos taxa y preservamos el uso tradicional de los nombres Centroleniidae y Allophrynidae, así como las especies que contienen. Organizamos la diversidad de Centroleniidae en dos subfamilias: Centroleninae y Hyalinobatrachinae. En Centroleninae, modificamos la diagnosis y contenido de especies de los géneros *Centrolene*, *Cochranella* y *Nymphargus*, resucitamos y modificamos *Teratohyla* y proponemos los nuevos géneros *Chimerella*, *Espadarana*, *Rulyrana*, *Sachatamia* y *Vitreorana*. La subfamilia Hyalinobatrachinae contiene al nuevo género *Celsiella* y a *Hyalinobatrachium*, el cuál corresponde exactamente al grupo *fleischmanni*. Además, describimos el género monotípico *Ikakogi*, al que tratamos como *incertae sedis* dentro de Centroleniidae. Nuestros datos sugieren que *Ikakogi tayrona* es un linaje tan antiguo como las subfamilias Hyalinobatrachinae y Centroleninae. La taxonomía aquí propuesta difiere drásticamente de todas las propuestas previas, las cuáles se basaron en pocos caracteres fenotípicos y en la similitud general entre las especies. La mayoría de los géneros aquí propuestos están restringidos a regiones biogeográficas concretas, lo cuál resalta la importancia de la geografía en la especiación de los centrolénidos. La principal limitación de nuestra propuesta taxonómica es que está basada en un muestreo incompleto (54% de las especies descritas). Aunque presentamos diagnosis basadas en caracteres fenotípicos, hay varios casos (16% del total de especies) en los cuales la asignación de especies a géneros es ambigua debido a la carencia de datos moleculares y a la homoplasia de los caracteres morfológicos. Finalmente, para facilitar la identificación y comparación de especies y su asignación genérica, proveemos fotografías de la gran mayoría (~ 96%) de centrolénidos reconocidos.

Palabras claves: Allophrynidae, Amazonas, América Central, Andes, Anura, Clasificación, Cordillera de la Costa, Diversidad, Escudo Guayanés, Filogenia, Hyloidea, Neobatrachia, Neotrópico, Ranas de cristal, Sistemática, Sudamérica.

Introduction

Our classifications will come to be, as far as they can be so made, genealogies
Darwin (1859).

Our knowledge of amphibian species diversity has dramatically increased, with the numbers of species growing about 48.2% since 1985 according to Frost *et al.* (2006). For many years, this increment in species richness has not been paralleled by reevaluations of taxonomic arrangements. Thus, we frequently find ourselves in taxonomic quandaries whereby we must deal with broadly distributed, highly species-rich taxa about which we understand little or nothing of their evolutionary relationships and history. Arguably, this could be attributed in part to taxonomists having relied primarily on morphology to develop hypotheses of relationships, with a number of characters that is insufficient to resolve the amphibian tree of life (6485 species; AmphibiaWeb 2009). However, the advent of large molecular datasets has produced a cascade of novel hypotheses of amphibian relationships (e.g., Darst & Cannatella 2004; San Mauro *et al.* 2004; Faivovich *et al.* 2005; Hillis & Wilcox 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Heinicke *et al.* 2007; Hedges *et al.* 2008, Guayasamin *et al.* 2008a), although not all resulted in new taxonomies (see Padial & De la Riva 2007). One of the latest, major contributions is the *The Amphibian Tree of Life* by Frost *et al.* (2006); these authors proposed a revised classification of living amphibians that has generated an intense debate among evolutionary biologists and systematists (AmphibiaWeb 2009; Wiens 2007; Frost *et al.* 2008; Wiens 2008). Although we are far from a consensus, several groups are attempting to provide a taxonomy that combines name stability and information on the evolutionary history of amphibians. In this context, the present study focuses on the Family Centroleniidae, also known as Glassfrogs or centrolenids, and its sister taxon, *Allophryne ruthveni* Gaige 1926.

Glassfrogs constitute one of the most interesting anuran groups in the Neotropics because of their morphological and ecological characteristics (Ruiz-Carranza & Lynch 1991a; Señaris & Ayarzagüena 2005;

Castroviejo-Fisher *et al.* 2007a; Cisneros-Heredia & McDiarmid 2007), as well as their phylogenetic and biogeographic complexity (Guayasamin *et al.* 2008a). Currently, 147 species of centrolenids are recognized (Appendix I). This number is unstable, with new species and/or new synonyms added every year (e.g., Cisneros-Heredia & McDiarmid 2007; Guayasamin *et al.* 2008b; Kok & Castroviejo-Fisher *et al.* 2008; Castroviejo-Fisher *et al.* 2009; Appendix I).

Glassfrogs are distributed throughout the Neotropics, from Mexico to Bolivia, with an isolated group of species occurring in southeastern Brazil and northeastern Argentina. They are nocturnal, epiphyllous, and arboreal. All species have a partially or completely transparent venter (Fig. 1A), and deposit their eggs out of the water on vegetation (leaves, mosses or branches) overhanging streams, or on rocks above streams (Ruiz-Carranza & Lynch 1991a; Fig. 2), although at least two species are reported to breed in ponds occasionally (*Centrolene buckelyi*, *Cochranella granulosa*; Duellman & Burrowes 1989; Kubicki 2007). Cisneros-Heredia and McDiarmid (2007) published a detailed review on centrolenids that compiles the main references and information concerning their biological attributes; to avoid repetition, we refer the reader to them for details.

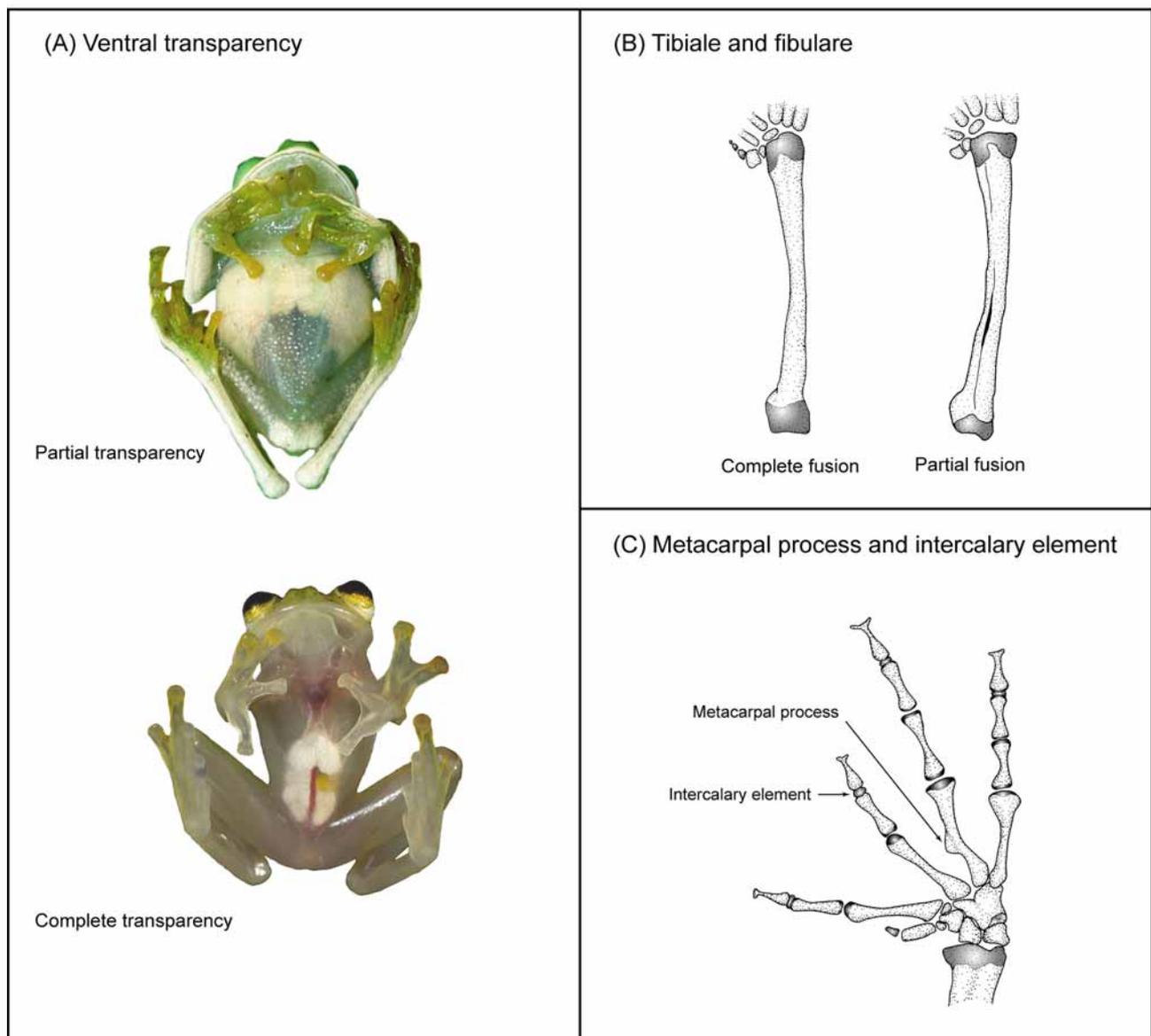


FIGURE 1. Synapomorphies of Centrolenidae. **(A)** Partial (*Nymphargus posadae*, QCAZ 25090) and complete ventral transparency (*Hyalinobatrachium aureoguttatum*, QCAZ 32070). **(B)** Partial (*N. wileyi*, QCAZ 26029) and complete fusion between tibiale and fibulare (*H. munozorum*, KU 155497). **(C)** Medial process on Metacarpal III and intercalary element (*Teratohyla spinosa*, KU 32935). The presence of T or Y-shaped terminal phalanges is a synapomorphy of Allocentroleniinae (Allophryninae + Centrolenidae). Photos in (A) by M. Bustamante.

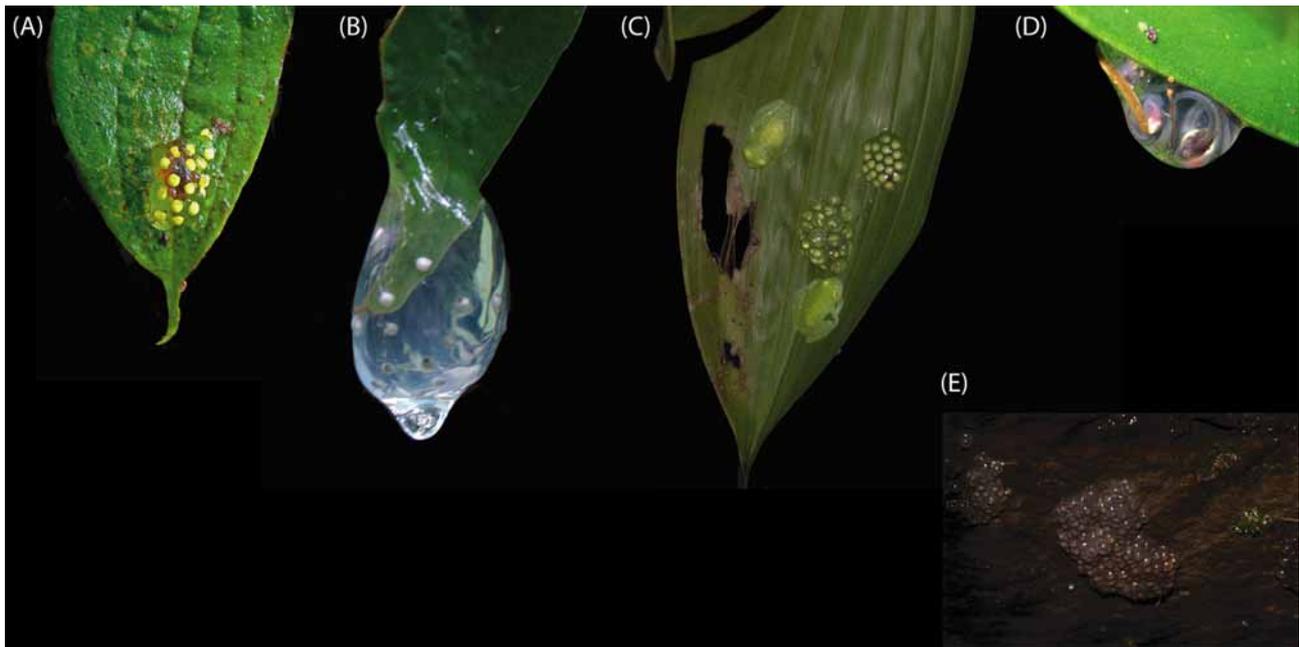


FIGURE 2. Egg deposition sites in Centrolenidae. **Type A:** On the anterior part of upper side of leaves (e.g., *Centrolene bacatum*, photo by JMG). **Type B:** On the tip of upper side of leaves (e.g., *Nymphargus wileyi*, photo by JMG). **Type C:** On the underside of leaves (e.g., *Hyalinobatrachium crurifasciatum*, photo by C. Barrio-Amorós). **Type D:** On the margin of under side of leaves (e.g., *Teratohyla spinosa*, photo by R. Puschendorf). **Type E:** On rocks (e.g., *Sachatamia albomaculata*, photo by R. Puschendorf).

Recently, we presented a novel hypothesis of the evolutionary relationships of Glassfrogs (Guayasamin *et al.* 2008a; Fig. 3) and commented on the differences with previous hypotheses of relationships (Ruiz-Carranza & Lynch 1991a, 1995a, 1998; Savage 2002; Guayasamin *et al.* 2006a; Cisneros-Heredia & McDiarmid 2007). Also, we demonstrated that our inferred phylogeny was significantly better than alternative evolutionary hypotheses. The main goal of this study is to provide a classification that is congruent with the inferred phylogeny. Also, we review briefly the taxonomic history of Glassfrogs and the hypotheses of relationships between them and other anurans.

Centrolenidae, its monophyly and relationships with other anurans

Jiménez de la Espada (1872) described the first genus and species of Glassfrog, *Centrolene geckoideum*, and placed it the family Polypedatidae (now a synonym of Rhacophoridae). It was not until the work of Taylor (1951) that the family Centrolenidae was proposed and defined mainly by the fusion of the tibiale (astragalus) and fibulare (calcaneum). Since then, the monophyly of Centrolenidae (*sensu* Taylor 1951) has not been questioned. Characters shared by all Glassfrogs include a dilated medial process on Metacarpal III (Hayes & Starrett 1980), T-shaped terminal phalanges (Taylor 1951), intercalary element between distal and penultimate phalanges (Taylor 1951), complete or partial fusion of tibiale and fibulare (Taylor 1951; Sanchiz & De la Riva 1993), eggs deposited out of water (Ruiz-Carranza & Lynch 1991a), and ventral parietal peritoneum partially or completely transparent (Fig. 1). Additional derived characters may include myological (Burton 1998, 2004; da Silva 1998; Señaris & Ayarzagüena 2005), osteological (Guayasamin & Trueb 2007), chromatic (Schwalm & McNulty 1980), and larval traits (Haas 2003); however, their relevance remains to be tested at a general scale.

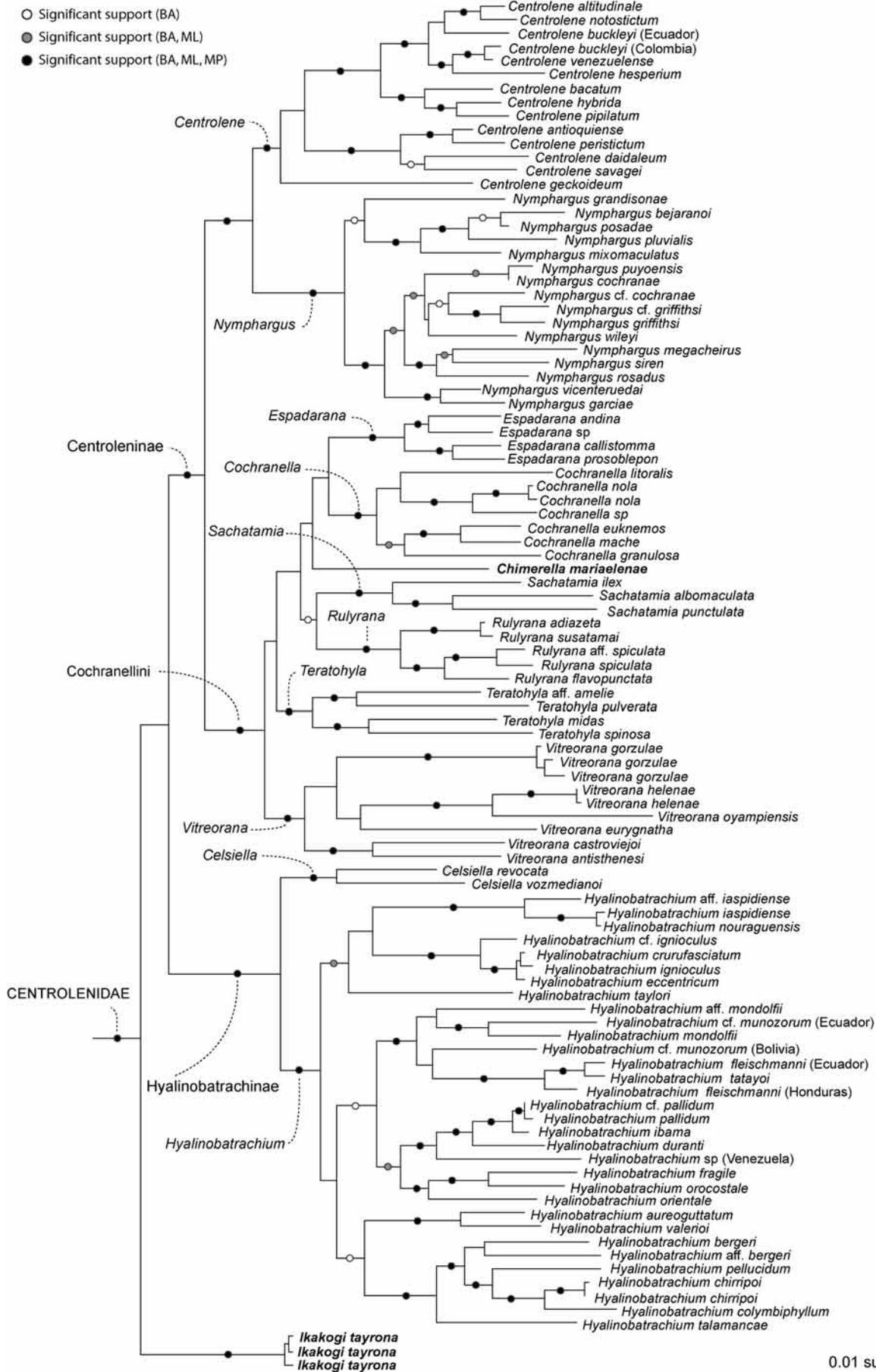


FIGURE 3. Phylogenetic taxonomy of Glassfrogs. Maximum likelihood topology inferred from mitochondrial and nuclear genes (4362 aligned base-pairs) using RAxML (Stamatakis 2006). Circles on branches indicate significant support values for clades recovered by Bayesian (BA, posterior probability ≥ 0.95), maximum likelihood (ML, bootstrap $\geq 70\%$), and maximum parsimony analyses (MP, bootstrap $\geq 70\%$). Species and supraspecific taxa are according to the phylogenetic taxonomy presented herein (see Appendix I). Monotypic genera (*Chimerella* and *Ikakogy*) are shown in bold. Figure modified from Guayasamin *et al.* (2008a).

Molecular phylogenies have supported the view of centrolenids as a natural group. Several independent studies based on different datasets and methods have shown high levels of congruence at retrieving a monophyletic Centrolenidae (e.g., Darst & Cannatella 2004; Faivovich *et al.* 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Guayasamin *et al.* 2008a). The relationship of Glassfrogs with other anurans, however, has remained controversial. After Jiménez de la Espada (1872) considered that *Centrolene geckoideum* was related to *Rhacophorus*, and Taylor (1951) suggested a close affinity with Heleophryinae, most researchers associated centrolenids with Hylidae and Pseudidae based on the presence of intercalary elements (Lynch 1973; Ford & Cannatella 1993; Rueda-Almonacid 1994; Duellman & Trueb 1994). Using larval morphology, Haas (2003) suggested Centrolenidae as sister group of Neobatrachia except *Limnodynastes*. In a molecular study, Darst and Cannatella (2004) explicitly rejected a Centrolenidae + Hylidae + Pseudidae clade, and presented evidence supporting a Centrolenidae + Leptodactylidae clade (see also Roelants *et al.* 2007). Contrary to the latter hypothesis, Biju and Bossuyt (2003) and Heinicke *et al.* (2007) suggested Centrolenidae to be the sister taxon of Bufonidae + Dendrobatidae, although with low support.

Several studies have inferred a close affinity between Centrolenidae and *Allophryne ruthveni*, a hypothesis first suggested by Noble (1931). Morphological (Duellman 2001; Burton 2004; Wiens *et al.* 2005) and molecular (Austin *et al.* 2002; Faivovich *et al.* 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Guayasamin *et al.* 2008a) studies have corroborated Allophrynidae as the sister taxon of Centrolenidae. This probably led Frost *et al.* (2006) to propose that the family Centrolenidae should contain the subfamilies Allophryninae and Centroleninae. This classification was followed in some works (e.g., Cisneros-Heredia & McDiarmid 2006a, 2007; Castroviejo-Fisher *et al.* 2007b), but Guayasamin and Trueb (2007) stated that the proposal led to unnecessary taxonomic instability, an argument that we expand herein (Results and Discussion).

Phylogenetic studies that include in their sampling *Allophryne* and Centrolenidae show total congruence in placing *Allophryne* as the sister taxon of Glassfrogs (Austin *et al.* 2002; Faivovich *et al.* 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Guayasamin *et al.* 2008a), but moderate congruence about the placement of this clade with respect to other anurans (Frost *et al.* 2006; Grant *et al.* 2006; Guayasamin *et al.* 2008a). Given that each study has intrinsic limitations (e.g., criteria for phylogenetic inference, taxon and gene sampling), it is difficult to evaluate the significance of the different results. Nonetheless, we have enough information to conclude that the close evolutionary relationship between *Allophryne ruthveni* and Centrolenidae is real, whereas the relationship of this clade with other frogs remains uncertain (Fig. 4).

Historical review of the systematics of Glassfrogs and *Allophryne ruthveni*

The grouping of Glassfrog species into genera and infrageneric categories has been complex and unstable mainly because hypotheses of relationships have been based on the arbitrary application of a few characters and the lack of cladistic analyses (e.g., proposals by Savage 2002; Cisneros-Heredia & McDiarmid 2007). In this section, we summarize in chronological order the main studies that focus on the systematics of glassfrogs (Fig. 5) and *Allophryne ruthveni*. We exclude from this review papers with species descriptions, which are listed in Appendix 1, but mention extensive reviews of species and/or characters. Taxonomically relevant characters in Glassfrogs are illustrated in Figures 1, 6, and 7.

Jiménez de la Espada (1872).—Description of *Centrolene geckoideum*, type species for the genus *Centrolene*, characterized by having vomerine teeth and humeral spine in males. Jiménez de la Espada placed *C. geckoideum* in the family Polypedatidae (now a synonym of Rhacophoridae) and suggested that *Centrolene* could be regarded as the American representative of the Old World genus *Rhacophorus*.

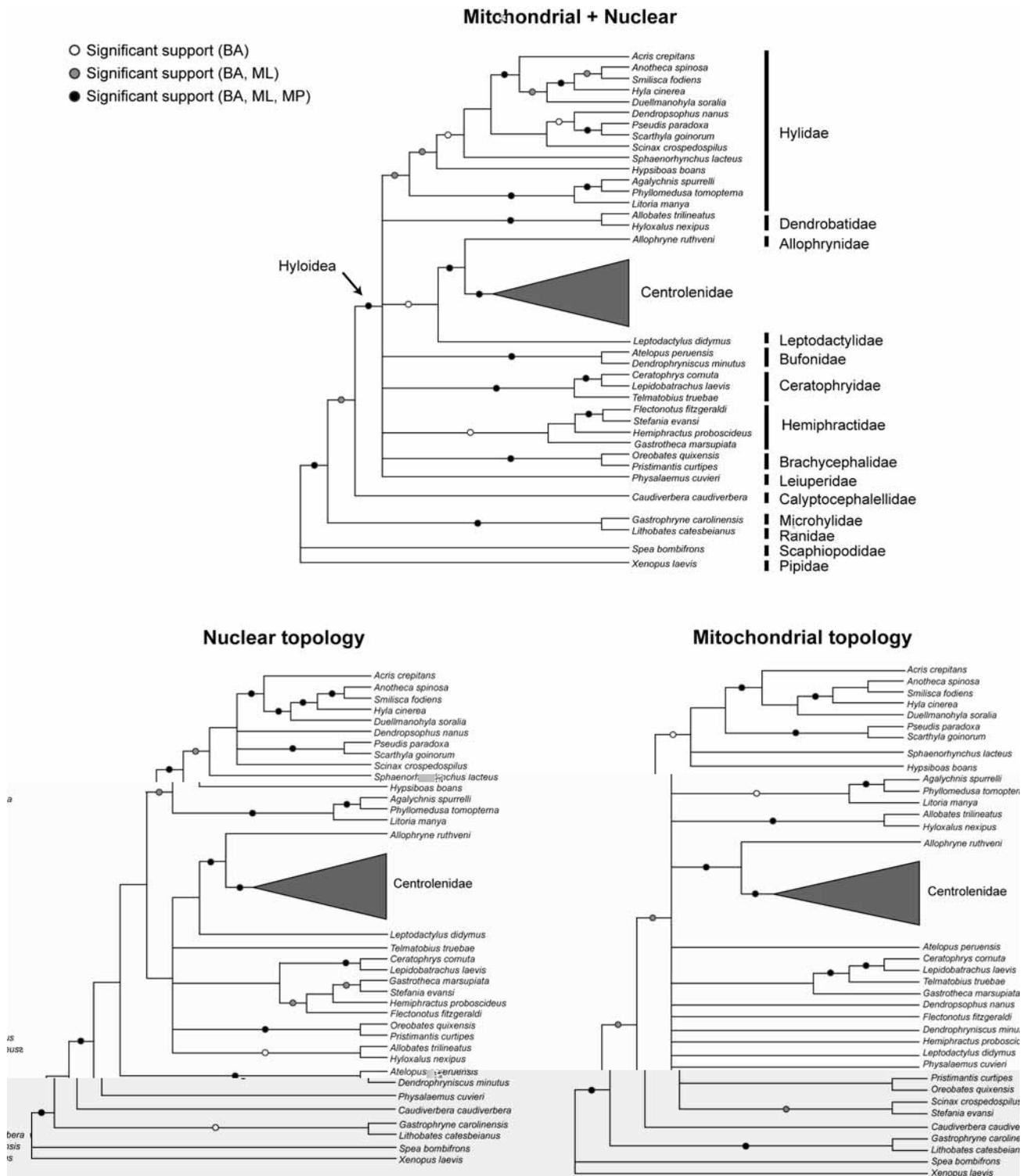


FIGURE 4. Schematic trees summarizing relationships between Centrolenidae and other anurans (Guayasamin *et al.*, 2008a). Note that the *Allophryne* + Centrolenidae clade is recovered consistently. Circles indicate significant support values for clades recovered by Bayesian (BA, posterior probability ≥ 0.95), maximum likelihood (ML, bootstrap $\geq 70\%$), and maximum parsimony (MP, bootstrap $\geq 70\%$) analyses.

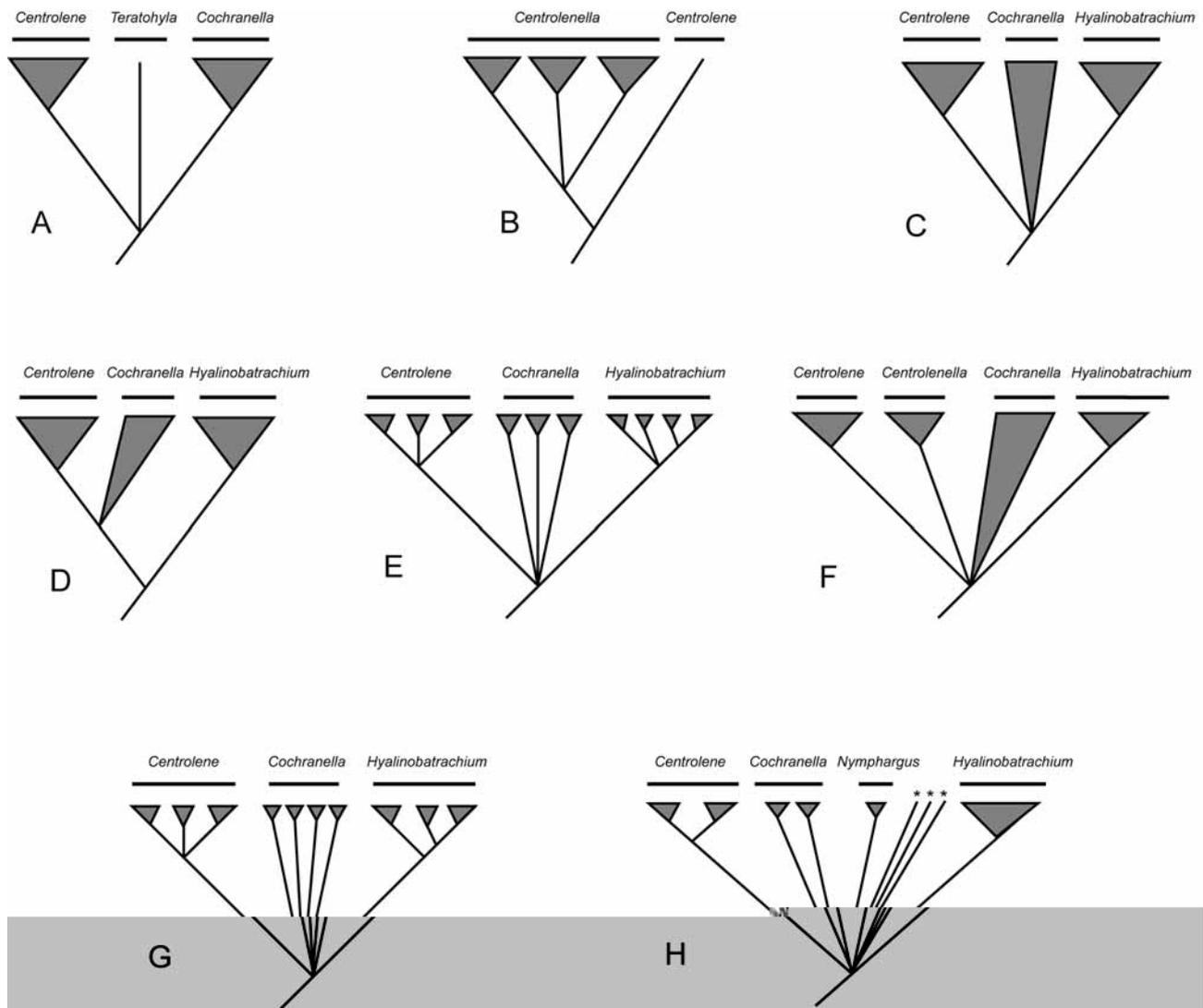


FIGURE 5. Previous taxonomic hypotheses for centrolenid frogs. (A) Taxonomy *sensu* Taylor (1949, 1951). (B) Taxonomy *sensu* Savage (1967). (C) Generic arrangement by Ruiz-Carranza and Lynch (1991a). (D) Hypothesis of relationships *sensu* Ruiz-Carranza and Lynch (1991a), as modified by Bolívar *et al.* (1999). (E) Hypothesis of relationships *sensu* Ruiz-Carranza and Lynch (1991a, 1995a, 1998). (F) Hypothesis of relationships *sensu* Ruiz-Carranza and Lynch (1991a), as modified by Savage (2002). (G) Hypothesis of relationships *sensu* Ruiz-Carranza and Lynch (1991a, 1995a, 1998), as modified by Duellman and Señaris (2003), Señaris and Ayarzagüena (2005), and Cisneros-Heredia and McDiarmid (2006a, b). (H) Hypothesis of relationships *sensu* Ruiz-Carranza and Lynch (1991a, 1995a, 1998), as modified by Cisneros-Heredia and McDiarmid (2007a); asterisks denote uncertain placement of *eurygnathum*, *parvulum*, and *uranoscopum*. Figure from Guayasamin *et al.* (2008a).

- Noble (1920)—Description of the genus *Centrolenella* (type species *C. antioquiensis*) characterized by lacking vomerine teeth and humeral spines. Noble commented on similarities and differences between *Centrolenella* and *Centrolene*; additionally, he suggested the possibility of including *Hyla prosoblepon* Boettger 1892 in *Centrolenella* (formally assigned by Noble [1924]) and the placement of both genera (*Centrolene* and *Centrolenella*) in Leptodactylidae.
- Gaige (1926)—Description of *Allophryne ruthveni*. Gaige mentioned that *Allophryne* apparently belongs to the family Bufonidae, as defined by Noble (1922).
- Noble (1931)—Considered *Allophryne ruthveni* to be a "toothless *Centrolenella*". Other morphological studies showing the evolutionary relatedness between Glassfrogs and *Allophryne* include Duellman (2001), Burton (2004), and Wiens *et al.* (2005).

- Dunn (1931)—Placement of *Centrolenella* under the synonymy of *Centrolene*.
- Taylor (1949)—Recognition of *Centrolene* for species in which males had humeral spines. Species lacking spines were assigned to the genus *Centrolenella*.
- Taylor (1951)—Description of the family Centrolenidae and recognition of three genera: *Centrolene* for species in which males have humeral spines (*Centrolenella* is a synonym); *Teratohyla* (type species: *Centrolenella spinosa* Taylor 1949) for species with prepollical spines and lacking humeral spine; *Cochranella* (type species: *Centrolenella granulosa* Taylor 1949) for species lacking both humeral and prepollical spines. Taylor (1951) diagnosed Centrolenidae based, mainly, on complete fusion of the tibiale and fibulare, T-shaped terminal phalanges, and the presence of an intercalary cartilage between penultimate and ultimate phalanges. He considered centrolenids to be related to African frogs (Heleophrynidae).
- Goin (1964)—Recognition of *Centrolenella* and a monotypic *Centrolene*. Goin characterized *Centrolene* by its large body size, diameter of the disc of Finger III wider than that of the eye, and a developed humeral spine in males.
- Savage (1967)—Followed Goin's arrangement and placed Central American Glassfrogs in *Centrolenella*. Within this genus, Savage proposed three species groups: *fleischmanni* Group for species with white bones, white dorsal coloration in preservative, transparent parietal peritoneum, white hepatic and visceral peritonea, and absence of humeral spine and vomerine teeth; *prosoblepon* Group for species with green bones, lavender dorsal coloration in preservative, white (or partially white) parietal peritoneum, transparent hepatic peritoneum, and presence or not of humeral spines in males and vomerine teeth; *pulverata* Group for species having green bones, white dorsal coloration in preservative, transparent parietal peritoneum, white hepatic and visceral peritonea, absence of humeral spine in males but presence of vomerine teeth. Savage's grouping was fundamental for the development of a new taxonomy (Ruiz-Carranza & Lynch 1991a).

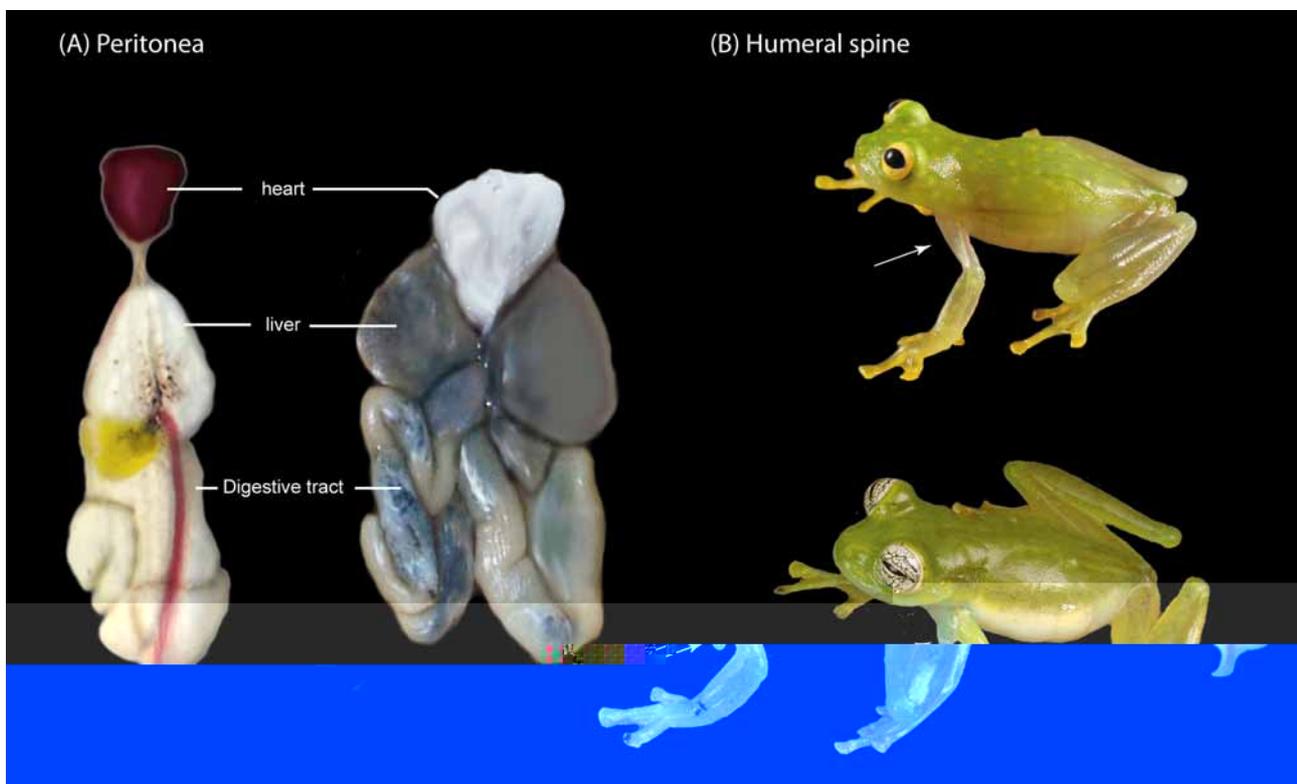


FIGURE 6. Taxonomically relevant characters in Glassfrogs. **(A)** Transparent pericardium, white hepatic and visceral peritonea (left; *Hyalinobatrachium aureoguttatum*); white pericardium, translucent hepatic and visceral peritonea (right; *Centrolene buckleyi*). **(B)** Absence of humeral spine (top; *H. fleischmanni*); presence of humeral spine (bottom; *Espadarana callistomma*).

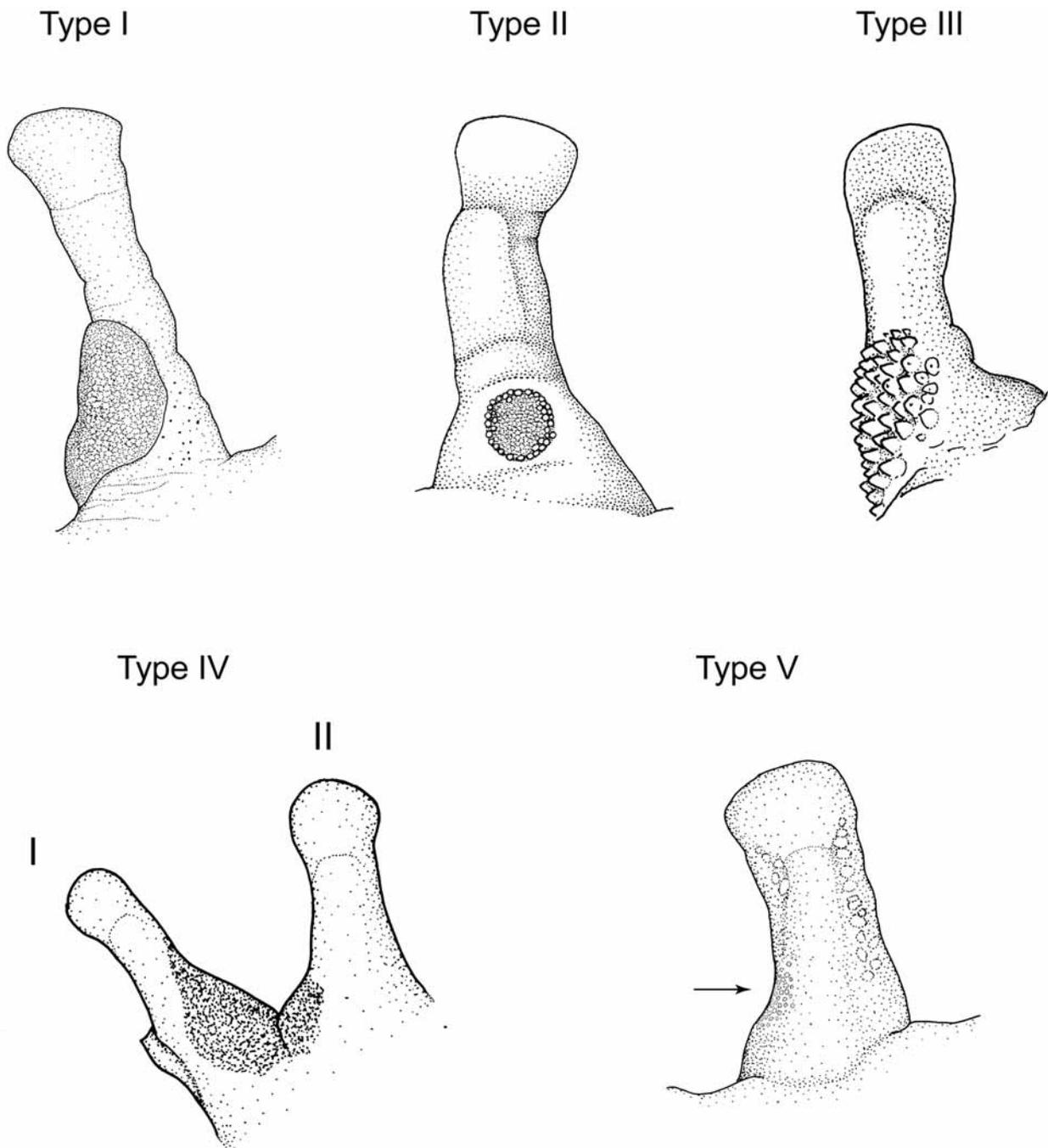


FIGURE 7. Common nuptial pad morphologies in Centrolenidae (*sensu* Cisneros-Heredia & McDiarmid 2007). Arrow indicates glandular cluster typical in species of *Hyalinobatrachium*, as defined herein. Note that Morphology IV has only been reported in *Cochranella litoralis*, and differs from the description provided by Cisneros-Heredia & McDiarmid (2007). Species illustrated: Type I, *Cochranella posadae*, QCAZ 26023; Type II, *Centrolene lynchi*, MCZ 97846 (figure modified from Flores 1985); Type III, *Nymphargus armatus*, UVC 9400 (figure modified from Lynch & Ruiz-Carranza 1996); Type IV, *Cochranella litoralis*, ICN 13821; Type V, *Hyalinobatrachium aureoguttatum*, QCAZ 27429. Morphology VI (glands distributed on the body) is not illustrated.

- Rivero (1968)—Revision of the centrolenid frogs of Venezuela following the generic proposal suggested by Goin (1964).
- Savage (1973).—Considered *Allophryne ruthveni* to form a monotypic family (Allophrynidae), but neither described or diagnosed the family.

- Starrett and Savage (1973)—Addition of liver shape (bulb-shaped/bulbous vs. trilobed) and egg coloration (green vs. dark) as taxonomically important characters for centrolenids. These authors also mention that species in the *fleischmanni* Group usually deposit green eggs on the underside of leaves overhanging streams.
- Lynch and Duellman (1973)—Revision of the centrolenid frogs of Ecuador following the generic proposal suggested by Goin (1964) and the infrageneric groups of Savage (1967). Additionally, these authors presented a review of taxonomic characters.
- Goin *et al.* (1978).—Provided the first diagnosis of Allophryinae.
- Hayes and Starrett (1980).—Description of a dilated medial process on Metacarpal III as diagnostic character for Centrolenidae (Fig. 1C). The validity of this character as synapomorphy (= derived homology) of Centrolenidae is well established; to date, it has been observed in 71 species (Guayasamin & Trueb 2007).
- Lynch (1981)—Association of the name *Hyloopsis platycephalus* Werner 1894 with a centrolenid species from the Sierra Nevada de Santa Marta in Colombia, making *Centrolenella* a synonym of *Hyloopsis*.
- McDiarmid and Savage (1984)—Rejection of the association of *Hyloopsis platycephalus* with a centrolenid species from the Sierra Nevada de Santa Marta in Colombia. These authors argued that Lynch (1981) forced *Centrolenella* into *Hyloopsis* by assuming that the original description of *H. platycephalus* by Werner was incorrect. They also mentioned that the type and only known specimen of *H. platycephalus* was lost, precluding a resolution of this problem, and that to preserve nomenclatural stability the name *Centrolenella* should be conserved.
- Flores (1985).—Description of nuptial pad morphologies as an important taxonomic character in centrolenids.
- Rivero (1985)—Revision of the Venezuelan centrolenid species, with their placement into three groups within the genus *Centrolenella*. The *andina* Group included species with humeral spines in males, Finger I shorter than II, presence of vomerine teeth (not in all species), lavender dorsal coloration in preservative and presence of dark spots in dorsum (not in all species). The *pulidoi* Group was diagnosed by lacking humeral spine in males, having a Finger I shorter than II, presence of vomerine teeth, a well defined *canthus rostralis*, vertical loreal region, reduced webbing between fingers, and dark brown dorsal coloration in preservative. The *fleischmanni* Group included species lacking humeral spines and vomerine teeth, and having a Finger I shorter or longer than II, white dorsal coloration in preservative, transparent parietal peritoneum, and white visceral peritonea.
- Ruiz-Carranza *et al.* (1986).—Provided a new diagnosis of the genus *Centrolene*. They added the black egg coloration as a characteristic of *Centrolene*.
- Ruiz-Carranza & Lynch (1991a)—Proposal of a new generic classification of Glassfrogs explicitly based on the principle of synapomorphy and outgroup comparison. This seminal work provided a testable hypothesis of relationships within Centrolenidae. The classification was based on two putative synapomorphies and divided Glassfrogs in three genera: (1) *Centrolene* was considered monophyletic, with *Centrolenella* as a synonym, being the presence of a humeral spine in adult males the only character supporting the genus. *Centrolene* was subdivided into three phenetic groups. The *geckoideum* Group contains species with small eyes, green bones, trilobated liver covered by transparent peritoneum, white parietal peritoneum, white parietal pericardium, and vomerine teeth. The *prosolepon* Group includes species with large eyes, green bones (white in *Centrolene tayrona* Ruiz-Carranza & Lynch 1991b), trilobated liver covered by transparent peritoneum, white parietal peritoneum, white pericardium, visceral peritoneum white or transparent, vomerine teeth present or absent. The *peristictum* Group includes species with large eyes, pale green bones, trilobated liver covered by transparent peritoneum, white visceral peritoneum, white pericardium, and absence of vomerine teeth. (2) *Hyalinobatrachium* was considered as a monophyletic genus. Ruiz-Carranza & Lynch (1991a) hypothesized that the presence of a bulbous liver covered by white peritoneum was an

unambiguous synapomorphy. The genus was divided in three phenetic groups: *fleischmanni* Group for species with large eyes, white bones in life, white visceral peritonea, white or transparent pericardium, and no vomerine teeth; *parvulum* Group containing species with large eyes, green or white bones, white peritoneum covering the urinary bladder and heart, and vomerine teeth present; *pulveratum* Group, large eyes, pale green bones, white pericardium and visceral peritonea, vomerine teeth present. (3) Species that lacked humeral spines and a white bulbous liver were placed in the genus *Cochranella*, which Ruiz-Carranza & Lynch (1991a) considered a non-monophyletic group. Initially, two phenetic groups were recognized with *Cochranella*: the *granulosa* Group for species with large eyes, pale green bones, three-lobed liver, white pericardium, partially white parietal peritoneum, and white visceral peritonea, and vomerine teeth present; and the *ocellata* Group, for species with large eyes, bones from green to white, trilobated liver, partially white parietal peritoneum (transparent in *C. phenax*, but see Guayasamin *et al.* [2006b]), vomerine teeth present or absent.

- Ruiz-Carranza and Lynch (1995a; 1998)—Redefinition of the infrageneric classification presented by the same authors in 1991a. Most species in the *granulosa* Group were characterized as having sloping snouts in lateral view, protruding upper lip, and fleshy ulnar and tarsal folds. The former *ocellata* Group was split into two groups—a newly defined *ocellata* Group, with reduced webbing between external fingers added to the previous characters, and the new *spinosa* Group, with the same characters than the former *ocellata* Group, but with moderate to extensive webbing between external fingers. The *fleischmanni* Group was proposed as a clade based on a putative synapomorphy: eggs held in a single layer on the undersides of leaves. Furthermore, this group was divided into the *fleischmanni* Subgroup with white pericardium, and the *chirripoi* Subgroup with transparent pericardium.
- Bolívar *et al.* (1999).—Addition of combat behavior between males as a character to resolve the intergeneric relationships *sensu* Ruiz-Carranza and Lynch (1991a). Bolívar *et al.* (1999) proposed that an elaborate combat behavior is a synapomorphy that clusters *Centrolene* and *Cochranella*. In this behavior, first described by Duellman & Savitzky (1976), males fight dangling upside down while holding the vegetation by their hind legs, grasping one another venter-to-venter; this fighting behavior is considered to be derived given that it has been observed only within Centrolenidae. In contrast, all *Hyalinobatrachium* (*sensu* Ruiz-Carranza & Lynch 1991a) males are hypothesized to have an amplexus-like fighting behavior, which was considered to be primitive. Further observations of the derived behavior were summarized by Guayasamin and Barrio-Amorós (2005) and Kubicki (2007).
- Fabrezi and Langone (2000)—Morphological and myological study of *Allophryne ruthveni*, discussing the relationships between *Allophryne* and other anurans.
- Austin *et al.* (2002).—First molecular study supporting the sister-group relationship between *Allophryne ruthveni* and glassfrogs. This finding has been sustained by several subsequent molecular studies (Faivovich *et al.* 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Guayasamin *et al.* 2008a).
- Savage (2002)—Generic-level modifications of the classification by Ruiz-Carranza & Lynch (1991a). Savage limited the genus *Centrolene* to species in the *geckoideum* Group *sensu* Ruiz-Carranza and Lynch (1991a), and resurrected *Centrolenella* for the remaining Glassfrogs that have humeral spine. Also, this study includes species accounts for all Costa Rican Glassfrogs.
- Duellman and Señaris (2003)—Erection of the *gorzulai* Group and modification of the diagnosis of *Hyalinobatrachium*. The *gorzulai* Group was diagnosed, mainly, by having a white hepatic peritoneum and males with a small humeral spine. Other defining characters included large eyes, green bones, parietal peritoneum reduced to the area covering the heart, white or transparent visceral peritoneum, and vomerine teeth absent. This rendered *Hyalinobatrachium* defined by a sole unambiguous synapomorphy, the presence of a bulbous liver.

- Señaris and Ayarzagüena (2005)—Review of Venezuelan Glassfrogs and erection of the *oyampiensis* Group within *Cochranella*. The main characteristics in the *oyampiensis* Group are the absence of humeral spines and the presence of a white hepatic peritoneum; other characters include large eyes, green or pale green in life, white parietal peritoneum (reduced to the anterior quarter), white pericardium, and white visceral peritonea.
- Frost *et al.* (2006).—Placement of Glassfrogs and *Allophryne ruthveni* in a single family, Centrolenidae. Glassfrogs were placed into the subfamily Centroleninae; the monotypic subfamily Allophryninae contained *A. ruthveni*. The arrangement by Frost *et al.* (2006) was disputed by Guayasamin and Trueb (2007) and is discussed in detail below. Additionally, Frost *et al.* (2006) questioned the monophyly of *Centrolene* and *Cochranella* (*sensu* Ruiz-Carranza & Lynch 1991a), although their taxon sampling was limited (4 species).
- Cisneros-Heredia and McDiarmid (2006a)—Modifications at the infrageneric level and comments on genera and characters. These authors introduced several changes: redescription of the *gorzulai* Group as having complete or almost complete transparent peritoneum and a trilobated or bulbous liver; re-allocation of the *pulveratum* Group into the genus *Cochranella*; and fusion of the *peristictum* Group with the *prosoblepon* Group. Also, they reviewed the characters supporting each of the genera and phenetic groups and concluded that the only monophyletic unit was the *fleischmanni* Group, although without analyzing the data in a cladistic framework.
- Guayasamin *et al.* (2006a).—Questioning of the monophyly of generic and infrageneric grouping in Centrolenidae. Based on a cladistic analysis of morphological and behavioral characters, these authors argue that only *Hyalinobatrachium* and the *H. fleischmanni* Group could be seen with confidence as a monophyletic unit. Also, they summarize the classification of Glassfrogs, excluding the changes of Savage (2002) and Cisneros-Heredia and McDiarmid (2006a).
- Cisneros-Heredia and McDiarmid (2007)—Description of the genus *Nymphargus*, comprehensive study of the morphological and behavioral characters of Glassfrogs, and generic and infrageneric redefinitions. These authors elevated the *ocellata* Group (except *Cochranella balionota* [Duellman 1981], *Cochranella ocellata* [Boulenger 1918] and *Cochranella vozmedianoii* [Ayarzagüena & Señaris 1996]) to the rank of genus under the name *Nymphargus*. Also, they eliminated the *geckoideum* Group and the *chirripoi* Subgroup. Species previously assigned to the *parvulum* Group were considered as *incertae sedis* within Centrolenidae. They also provided a summary of the classification of Centrolenidae (including Allophryninae) with the proposed modifications. They expanded the description of types of nuptial excrescences first developed by Flores (1985).
- Kubicki (2007)—Detailed review of the Glassfrogs of Costa Rica, with emphasis on their biology.
- Kok and Castroviejo-Fisher (2008)—Transferred *Cochranella oyampiensis* (Lescure 1975) to the *spinosa* Group, and renamed the former *oyampiensis* Group as the *helenae* Group, stressing that the change does not imply a hypothesis of relationships, but allows diagnosable phenetic groups for species comparisons, identification, and description.
- Guayasamin *et al.* (2008a).—Molecular phylogeny of centrolenid frogs. These authors provided the first extensive molecular phylogeny of centrolenid frogs using mitochondrial and nuclear genes, with a taxon sampling that included more than half of the described diversity of Centrolenidae. According to these authors, the new topology implies a South American origin of Glassfrogs and reveals allopatric speciation as the most important speciation mechanism. The molecular phylogeny differs significantly from previous morphology-based hypotheses of relationships, and shows that morphological homoplasy is not a rare phenomenon in glassfrogs. The work by Guayasamin *et al.* (2008a) is the base for the taxonomic proposal presented below.

Material and Methods

Nomenclature and Terminology

Throughout this work, we use the name Centrolenidae as originally intended by Taylor (1951), exclusive of *Allophryne ruthveni*. An alternate taxonomy can be found in Frost *et al.* (2006). When referring to the current taxonomy, we follow the generic and infrageneric classifications as proposed by Ruiz-Carranza and Lynch (1991a, 1995a, 1998), with the addition of the recently described *Nymphargus* (Cisneros-Heredia & McDiarmid 2007). Fingers are numbered preaxially to postaxially from I–IV to facilitate comparison with previous literature dealing with anurans. However, we stress that in an evolutionary perspective, anuran fingers should be numbered from II–V, consistent with the hypothesis that Digit I was lost in anurans (Shubin & Alberch 1986; Fabrezi & Alberch 1996). Osteological terminology is that of Trueb (1973), Fabrezi (1992, 1993), and Duellman and Trueb (1994). Morphology of nuptial excrescences is as described by Flores (1985) and Cisneros-Heredia and McDiarmid (2007), with a minor modification presented in Figure 7. Institutional acronyms follow those of Frost (2009). Material examined is listed in Appendix II.

Phylogenetic framework for the new classification

The phylogeny inferred by Guayasamin *et al.* (2008a) included 54% of the recognized taxa in Centrolenidae and 35 outgroups. Gene sampling consisted of complete or partial sequences for the following markers: mitochondrial 12S rRNA (~974 bp), fragment of mitochondrial 16S rRNA (895 bp), mitochondrial ND1 (~973 bp), nuclear POMC (~634 bp), nuclear

Mitochondrial tree (ND1 + 12S + 16S)

Nuclear tree (RAG1 + c-myc + POMC)

- Significant support (BA)
- Sig. sup. (BA, ML)
- Sig. sup. (BA, ML, MP)

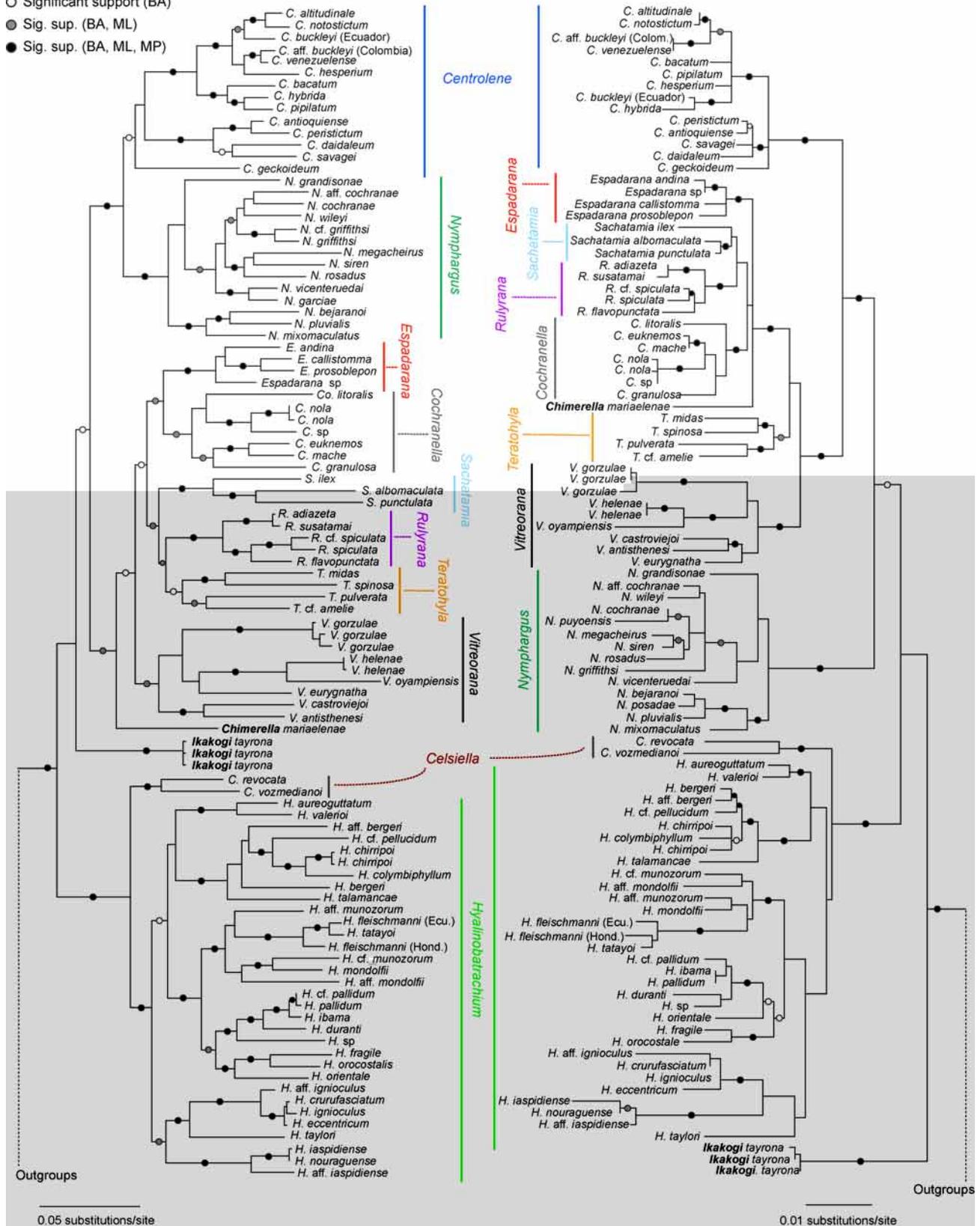


FIGURE 8. Maximum likelihood phylogeny of Glassfrogs inferred from mitochondrial genes (*12S*, *16S*, *ND1*, 2842 aligned base-pairs; $\ln L = -74810.404$) and nuclear genes (*c-myc exon 2*, *RAG1*, *POMC*, 1520 aligned base-pairs; $\ln L = -17244.283$) using RAxML (Stamatakis 2006). Circles indicate significant support values for clades recovered by Bayesian (BA, posterior probability ≥ 0.95), maximum likelihood (ML, bootstrap $\geq 70\%$), and maximum parsimony (MP, bootstrap $\geq 70\%$) analyses. Monotypic genera (*Chimerella* and *Ikakogi*) are shown in bold. Figure modified from Guayasamin *et al.* (2008a).

Briefly, our *modus operandi* was to (i) identify phylogenetically stable clades (Criteria 1 and 2), (ii) recognize which of these clades were diagnosable by phenotypic characters (Criterion 3), and (iii) if more than one clade fit to the previous criteria, provide a name that would produce the fewer number of changes when compared to previous classifications (Criterion 4). We first allocated genera because this rank is linked to the species name in the form of a binomen, one of the most important natural units in evolutionary biology (e.g., Mayr 2004; de Queiroz 2005; Wilson 2005). As a consequence, our taxonomy emphasizes the recognition of phylogenetically stable and phenotypically diagnosable genera.

Criteria 3 and 4 are commonly used in taxonomy and it is clear how they promote stability. However Criteria 1 and 2 need further explanation. The aim of these two criteria is to reduce the probability of naming clades that would change in content and position within the phylogeny as a consequence of the method used for tree inference or a particular combination of datasets. In other words, we try to present a phylogenetic taxonomy that is stable under different phylogenetic methods and datasets. Admittedly, our evaluation of methods and data partitions is far from being exhaustive, given the numerous available options. Instead, we have named clades that are inferred and supported by the most accepted cladistic methods (i.e., parsimony, Bayesian, and Maximum Likelihood), and are congruent using independent datasets (nuclear and mitochondrial genes; Figs. 3, 8; Guayasamin *et al.* 2008a).

Results

A monophyletic taxonomy

Based on the topology presented in Figures 3 and 8, and on the criteria described in the previous section, we propose a revised taxonomy that is congruent with the evolutionary history of Glassfrogs and their closest relative, *Allophryne ruthveni*. A list of all currently recognized centrolenid species with their previous generic placements and names proposed herein is provided in Appendix I. Several species are considered as *incertae sedis* because molecular data are not available, and phenotypic characters are not sufficient to place them into monophyletic genera with confidence (Appendix I).

Within Centrolenidae we recognize two subfamilies and a total of 12 genera, seven of which are new. At the end of this work, we provide an indented classification to facilitate visualizing the new arrangement (Appendix III), and photographs for most recognized centrolenid species (Appendix IV).

UNRANKED TAXON: **Allocentroleniae** new taxon

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Centrolene geckoideum* Jiménez de la Espada 1872 and *Allophryne ruthveni* Gaige 1926.

SISTER TAXON: The affinities of other anurans to the clade Centrolenidae + Allophrynidae are poorly resolved (Guayasamin *et al.* 2008).

DIAGNOSIS: Some of the most conspicuous characters shared by *Allophryne ruthveni* and centrolenid frogs include presence of T-shaped terminal phalanges (Duellman 2001), ventral process on terminal phalanges of fingers (da Silva 1998), and *m. flexor digitorum brevis superficialis* of the foot inserts with two tendons (Burton 2004). Additional morphological characters supporting Allocentroleniae can be found in Burton (1998, 2004), da Silva (1998), Duellman (2001), and Wiens *et al.* (2005). Molecular studies supporting the validity of this clade include Austin *et al.* (2002), Faivovich *et al.* (2005), Wiens *et al.* (2005), Frost *et al.* (2006), Grant *et al.* (2006), and Guayasamin *et al.* (2008a).

CONTENT: Centrolenidae Taylor 1951, and Allophrynidae Goin, Goin, & Zug 1978.

ETYMOLOGY: The name Allocentroleniae is derived from the genera *Allophryne* and *Centrolene*; the suffix *-iae* is added to denote the plural nature of the name. The name Allocentroleniae recognizes the sister relationships between Centrolenidae and Allophrynidae.

DISTRIBUTION: Tropical Mexico to Bolivia, plus Tobago, northeastern Argentina, and southeastern Brazil, with highest diversity in the northern Andes (Colombia and Ecuador).

COMMENTS: Phylogenetics studies including *Allophryne*, Centrolenidae, Hylidae and Leptodactylidae show total congruence in placing *Allophryne* as the sister taxon of Glassfrogs (Austin *et al.* 2002; Faivovich *et al.* 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Guayasamin *et al.* 2008a). Recently, Frost *et al.* (2006) merged Centrolenidae Taylor 1951, and Allophrynidae Goin, Goin, & Zug 1978, into a single family (i.e., Centrolenidae); this action intended to formalize the sister relationship between glassfrogs and *Allophryne ruthveni*, but has several problems. (a) It creates nomenclatural instability by shifting the ranks of taxa (fig. 9); in order to formalize the evolutionary affinity between glassfrogs and *Allophryne*, a more stable solution would be to create an intermediate rank or an unranked taxon. (b) It mingles taxa with clear morphological, behavioral, and genetic differences (see below). (c) It immediately disassociates decades of literature and the names of the merged family. The name Centrolenidae has been used exclusively for Glassfrogs since 1951, and Allophrynidae for *Allophryne ruthveni* since 1978. To exemplify this point, in Google Scholar, a search using the word Centroleninae produces seven findings, whereas a search using Centrolenidae produces 686 findings. In order to recognize and name the evolutionary proximity of Centrolenidae and Allophrynidae, we had two main alternative options: (i) creating an intermediate rank, and (ii) creating an unranked name. Given that the Superfamily rank is already in use (e.g., Hyloidea Rafinesque 1815; sensu Dubois 2005) and contains, among others, the families Centrolenidae and Allophrynidae, the only available option allowed by the ICZN that did not involve rank shifting (i.e., name instability) was to erect an unusual intermediate rank (e.g., Subsuperfamily). We see of little practical value the creation of an unusual intermediate rank given that such a rank would be of difficult interpretation for most scientists and non-scientists. We have decided, then, to erect an unranked name (Alloctrolenidae), which has the benefit of preserving the name and species content of Centrolenidae (glassfrogs) and Allophrynidae (*Allophryne ruthveni*), recognizing the evolutionary affinity of Centrolenidae and Allophrynidae, and avoiding rank shifts and unusual intermediate ranks, and thence facilitating communication and fulfilling the primary principle of zoological nomenclature (i.e., maintenance of name stability; ICZN 1999).

FAMILY: **Allophrynidae** Goin, Goin, & Zug 1978

PHYLOGENETIC DEFINITION: A clade consisting of *Allophryne ruthveni* Gaige 1926, and other species that share a more recent common ancestor with *A. ruthveni* than with *Centrolene geckoideum* Jiménez de la Espada 1872.

TYPE GENUS: *Allophryne* Gaige 1926.

DIAGNOSIS: Phenotypic characteristics present in *Allophryne ruthveni* and absent in centrolenid frogs include: eggs deposited in water, tibiale and fibulare not fused (Fabrezi & Langone 2000), dilated medial process on Metacarpal III absent, neopalatine absent, ventral transparency absent. Also, *Allophryne ruthveni* lacks intercalary elements (Fabrezi & Langone 2000), which are present in all glassfrogs (see Comments). Additional characteristics restricted to *Allophryne ruthveni* can be found in Lynch & Freeman (1966), Burton (1998, 2004), and Fabrezi & Langone (2000).

CONTENT: *Allophryne ruthveni* Gaige 1926.

SISTER TAXON: Centrolenidae Taylor 1951. Noble (1931) was the first to associate *Allophryne ruthveni* with centrolenid frogs. Morphological (Duellman 2001; Burton 2004; Wiens *et al.* 2005) and molecular (Austin *et al.* 2002; Faivovich *et al.* 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Guayasamin *et al.* 2008a) data corroborate the Allophrynidae + Centrolenidae clade.

ETYMOLOGY: The family name Allophrynidae is derived from its type genus *Allophryne*.

DISTRIBUTION: *Allophryne ruthveni* is known from the Guiana region of South America (Venezuela, Guyana, Surinam, French Guiana to north central Brazil) and central Brazil at elevations of 0–300 m (Langone & Segalla 1997; Caldwell & Hoogmoed 1998; Fig. 10).

COMMENTS: Savage (1973) considered *Allophryne ruthveni* to form a monotypic family (Allophrynidae), but neither described nor diagnosed the family. The first diagnosis of Allophrynidae is that of Goin *et al.* (1978). Frost *et al.* (2006) considered this taxon as a subfamily (Allophryninae); for reasons explained above, we do not follow their suggested taxonomy. *Allophryne ruthveni* lacks intercalary elements, but presents a

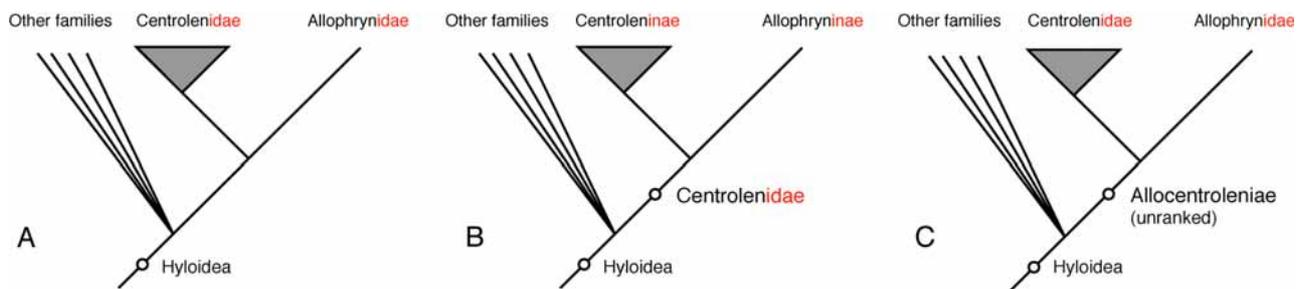


FIGURE 9. Use of unranked taxa as a mean to increase name stability. (A) Accepted relationships and taxonomy until 2006. (B) Proposal by Frost *et al.* (2006); note the change in names and species contents. (C) Recognition of Allocentroleniae as an unranked name; note that clade names and clade contents are as those used before 2006, and the Centrolenidae + Allophrynidae clade is recognized.



FIGURE 10. Distribution of Centrolenidae and Allophrynidae.

well-developed digital pad, short tendons of Mm. *extensores breves profundus*, a biaxial articulation between penultimate–terminal phalanges, and Mm. *extensores breves distalis* (Fabrezi & Langone 2000). These features could be either interpreted as remnants from a condition with the intercalary element present ancestrally but that is today lost, or as a first step before the reappearance of an intercalary element (Manzano *et al.* 2007).

GENUS: *Allophryne* Gaige 1926

PHYLOGENETIC DEFINITION: A clade nested within Allophrynidae that includes *Allophryne ruthveni* Gaige 1926.

TYPE SPECIES: *Allophryne ruthveni* Gaige 1926, by original designation.

DIAGNOSIS: Same as Allophrynidae.

CONTENT: *Allophryne ruthveni* Gaige 1926.

ETYMOLOGY: The name *Allophryne* is derived from the Greek words *allos*, meaning other, foreign, or strange, and *phryne*, meaning toad. *Allophryne* is feminine in gender.

DISTRIBUTION: Same as the family Allophrynidae (see above).

FAMILY: **Centrolenidae** Taylor 1951

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Centrolene geckoideum* Jiménez de la Espada 1872, *Centrolene tayrona* Ruiz-Carranza & Lynch 1991b, and *Hyalinobatrachium fleischmanni* (Boettger 1893).

TYPE GENUS: *Centrolene* Jiménez de la Espada 1872.

DIAGNOSIS: Characters shared by all species in Centrolenidae include: dilated medial process on Metacarpal III (Hayes & Starrett 1980); intercalary element between distal and penultimate phalanges (Taylor 1951); complete or partial fusion of tibiale and fibulare (Taylor 1951; Sanchiz & De la Riva 1993); eggs deposited out of water (Ruiz-Carranza & Lynch 1991a); ventral parietal peritoneum partially or completely transparent (Fig. 1A); and eyes directed forward at an angle of 45° relative to the axis of the body, a characteristic that may provide binocular vision. Some of the aforementioned traits are hypothesized to be synapomorphies for Glassfrogs, such as the presence of a dilated medial process on Metacarpal III (Hayes & Starrett 1980; Guayasamin & Trueb 2007), complete or partial fusion of tibiale and fibulare (Taylor 1951; Sanchiz & De la Riva 1993), eggs deposited out of water (Ruiz-Carranza & Lynch 1991a), and ventral parietal peritoneum partially or completely transparent. Additional putative synapomorphies include myological (Burton 1998, 2004; da Silva 1998; Señaris & Ayarzagüena 2005), osteological (Guayasamin & Trueb 2007), chromatic (Schwalm & McNulty 1980), and larval (Haas 2003) traits. The presence of a small medial process on the external surface of Metacarpal IV (see Guayasamin *et al.* 2006b:Fig. 15) could also represent a primary homology (*sensu* de Pinna 1991).

CONTENT (12 GENERA): *Celsiella* new genus; *Centrolene* Jiménez de la Espada 1872; *Chimerella* new genus; *Cochranella* Taylor 1951; *Espadarana* new genus; *Hyalinobatrachium* Ruiz-Carranza & Lynch 1991a; *Ikakogi* new genus; *Nymphargus* Cisneros-Heredia & McDiarmid 2007; *Rulyrana* new genus; *Sachatamia* new genus; *Teratohyla* Taylor 1951; *Vitreorana* new genus (Fig. 3).

SISTER TAXON: Allophrynidae Goin, Goin, & Zug 1978. Morphological (Burton 2004; Duellman 2001; Wiens *et al.* 2005) and molecular (Austin *et al.* 2002; Faivovich *et al.* 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Guayasamin *et al.* 2008a) evidence places Allophrynidae as the sister taxon of Centrolenidae. Noble (1931) first associated *Allophryne ruthveni* with centrolenids based on similarities of internal and external morphology.

ETYMOLOGY: The family name Centrolenidae is derived from its type genus *Centrolene*.

DISTRIBUTION: Tropical Central America, tropical Andes, Sierra Nevada de Santa Marta in Colombia, Cordillera de la Costa of Venezuela, Tobago, Guiana Shield, Amazon Basin, and Atlantic Forest of Brazil (Fig. 10); highest diversity in northern Andes.

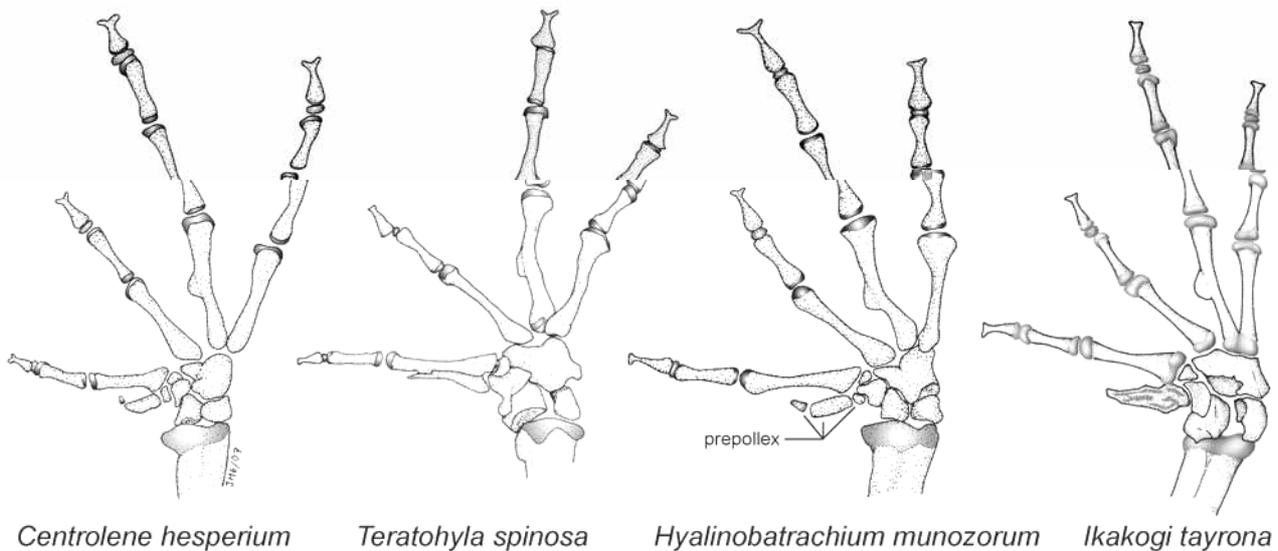


FIGURE 11. Size of prepollex relative to Metacarpal I (dorsal view). Note that in *Hyalinobatrachium* the prepollex has a length $\leq 50\%$ of the length of Metacarpal I. Also, note relative length of Fingers I and II. Species illustrated: *Centrolene hesperium*, FMNH 232502; *Teratohyla spinosa*, KU 32935; *Hyalinobatrachium munozorum*, KU 155497; *Ikakogi tayrona*, KU 169754.

COMMENTS: We use the family name Centrolenidae as originally intended by Taylor (1951). Frost *et al.* (2006) applied the name Centrolenidae to the clade that we define herein as Allocentroleninae. We consider our terminology to reflect the current understanding of evolutionary relationships, the phenotypic and genotypic differences between the two taxa, and, at the same time, maintain the historic association between the names Centrolenidae (*sensu* Taylor 1951) and Allophrynidae and their literature. The topologies inferred using the combined mitochondrial, combined nuclear, and complete datasets (Figs. 3, 8), consistently recovered a monophyletic Centrolenidae (Guayasamin *et al.* 2008a). The monophyly of Centrolenidae is further supported by morphological (Duellman 2001; Burton 2004; Wiens *et al.* 2005) and other molecular (Austin *et al.* 2002; Darst & Cannatella 2004; Faivovich *et al.* 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006) data. The placement of species in the family Centrolenidae is unambiguous because, as far as we know, this is the only Neotropical clade with a medial process on Metacarpal III (Guayasamin & Trueb 2007; Fig. 1C).

SUBFAMILY: **Centroleninae** Taylor 1951

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Centrolene geckoideum* Jiménez de la Espada 1872, and *Cochranella granulosa* Taylor 1949.

TYPE GENUS: *Centrolene* Jiménez de la Espada 1872.

SISTER TAXON: Ambiguous. Topologies present conflicting and unsupported resolution of the three early divergent branches of Centrolenidae (Figs. 3, 8). Two taxa are the possible sister taxon of Centroleninae, *Ikakogi* new genus, or Hyalinobatrachinae new subfamily.

DIAGNOSIS: Species in Centroleninae (except *Espadarana andina*, "*Cochranella*" *balionota*, *Sachatamia albomaculata*, and *S. illex*) have a crista medialis in the humerus (absent in all species in Hyalinobatrachinae; Fig. 13); *Ikakogi tayrona* has an extremely large crista medialis, which extends along the entire length of the humerus (Fig. 13). Another trait diagnostic of the subfamily Centroleninae is the presence of a relatively long prepollex (relative length $> 50\%$ of Metacarpal I), which is short ($< 50\%$ of Metacarpal I) in Hyalinobatrachinae new subfamily (Fig. 11); the prepollex of *Ikakogi tayrona* shows the same character state as species in Centroleninae (Fig. 11). More observations are necessary to confirm the validity of this trait.

A derived fighting behavior in which males dangle by their feet and grapple venter-to-venter (Fig. 12) has been observed in several species of Centroleninae (Duellman & Savitzky 1976; Bolívar *et al.* 1999;

Guayasamin & Barrio-Amorós 2005; Kubicki 2007) and we consider it a primary homology of the clade. The amplexus-like or “wrestling-on-leaves” fighting behavior is hypothesized to be primitive and restricted to Hyalinobatrachinae; this hypothesis differs from that proposed by Bolívar *et al.* (1999) because Hyalinobatrachinae includes two species (*Celsiella revocata* [Rivero 1985], *C. vozmedianoi*) that previously were part of the genus *Cochranella* *sensu* Ruiz-Carranza and Lynch (1991a). Most species in Centroleninae have lobed livers (tri-, tetra-, or pentalobed), green bones in life (white bones in *Nymphargus rosadus* [Ruiz-Carranza & Lynch 1997] and *Nymphargus anomalus* [Lynch & Duellman 1973]), and a lavender dorsum in preservative. Males usually call from the upper surfaces of leaves, and females of most species deposit their eggs on the upper surfaces of leaves; exceptions in which females place egg clutches on undersides of leaves include *Centrolene antioquiense*, *C. notostictum*, *C. peristictum*, *Cochranella spinosa*, and *Hyalinobatrachium eurygnathum* (MR pers. obs.; M. Bustamante, pers. comm.; Starrett 1960; Ruiz-Carranza & Lynch 1991b; Lutz 1947; respectively), whereas females of *Hyalinobatrachium uranoscopum* place egg clutches on the upper and undersides of leaves (C. Zank, pers. comm.). Humeral spines are present in several clades within Centroleninae, but they are completely absent in Hyalinobatrachinae. Additionally, we have observed the presence of a small medial process on the external surface of Metacarpal I (Fig. 11: *Teratohyla spinosa*) that seems to be absent in *Hyalinobatrachium*; the validity of this trait as a derived homology of Centroleninae needs to be assessed with more observations.



FIGURE 12. Derived fighting behavior between males of *Espadarana andina*. The illustrated character state is considered

Co G) C (Jiménez de la Espada 1872, *Chimerella* new genus, *Cochranella* Taylor 1951, *Espadarana* new genus, *Nymphargus*

Cisneros-Heredia & McDiarmid 2007, *Rulyrana* new genus, *Sachatamia* new genus, *Teratohyla* Taylor 1951, *Vitreorana* new genus. Centroleninae also contains Cochranellini new tribe, which includes seven of the aforementioned genera (*Chimerella*, *Cochranella*, *Espadarana*, *Rulyrana*, *Sachatamia*, *Teratohyla*, *Vitreorana*).

ETYMOLOGY: The subfamily name Centroleninae is derived from the genus *Centrolene*.

DISTRIBUTION: Tropical Central America, tropical Andes, Cordillera de la Costa of Venezuela, Guiana Shield, Amazon Basin, and Atlantic Forest.

COMMENTS: The clade Centroleninae is inferred with statistical support by the combined dataset (parsimony, ML, and Bayesian) and by the combined mitochondrial (Bayesian) and combined nuclear (Bayesian) datasets (Figs. 3, 8).

GENUS: ***Centrolene*** Jiménez de la Espada 1872

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Centrolene geckoideum* Jiménez de la Espada 1872 and *Centrolenella peristicta* Lynch & Duellman 1973.

TYPE SPECIES: *Centrolene geckoideum* Jiménez de la Espada 1872, by monotypy.

SISTER TAXON: The sister relationship of *Centrolene* Jiménez de la Espada 1872 and *Nymphargus* Cisneros-Heredia & McDiarmid 2007 is supported by mitochondrial dataset and the overall molecular dataset (Figs. 3, 8). However, combined nuclear genes support a topology with *Centrolene* + Cochranellini new taxon (Fig. 8). We favor the *Centrolene* + *Nymphargus* hypothesis because it results from a more complete analysis. Also, it seems that the topology obtained from the combined nuclear dataset mostly derives from the information contained in the gene POMC, which is the only nuclear gene that supports *Centrolene* + Cochranellini. The other nuclear genes either provide weak support for a *Centrolene* + *Nymphargus* clade (*c-myc*) or lack any resolution at this level (RAG1). Nevertheless, we recommend caution because the complete dataset is dominated by mtDNA data (Guayasamin *et al.* 2008a).

DIAGNOSIS: The following combination of characteristics is diagnostic of *Centrolene*: (1) humeral spines present in adult males of all species, except *Centrolene daidaleum* Ruiz-Carranza & Lynch 1991c and *C. savagei* Ruiz-Carranza & Lynch 1991c; (2) tri-, tetra-, or pentalobed liver, covered by a transparent hepatic peritoneum; (3) ventral parietal peritoneum white anteriorly and transparent/translucent posteriorly; (4) bones varying from pale to bright green in life; (5) dorsum lavender in preservative, with or without spots; (6) dorsum of males usually with spinules during breeding season (spinules not visible in *C. antioquiense*, *C. hybrida*); (7) nuptial pads conspicuous in males; (8) males usually call from the upper sides of leaves and females deposit egg masses on the upper sides of leaves along streams; *C. geckoideum* calls from behind waterfalls or near spray zones and deposits the eggs on rocks (Lynch *et al.* 1983; Rueda-Almonacid 1994; Grant *et al.* 1998), and *C. peristictum* calls and deposits eggs from the undersides of leaves (M. R. Bustamante, pers. comm.); *C. antioquiense* calls from the upper surfaces of leaves or branches and females deposit their eggs on the underside of leaves (M. Rada, pers. comm.); (9) quadratojugal articulating with maxilla. The presence of large humeral spines in the adult males of species in *Centrolene* (except in *Centrolene daidaleum* and *C. savagei*, which lack humeral spines) distinguishes this clade from most other genera (Fig. 13). The other two genera presenting this trait are *Espadarana* new genus and *Ikakogi* new genus. The monotypic *Ikakogi* has, in life, white bones, and is the only centrolenid species with a crista medialis that is almost as long as the humerus; also females guard egg clutches in *I. tayrona* (MR, pers. obs.). The morphological similarity between *Centrolene* and *Espadarana* is remarkable. At present, we are unaware of any single morphological character that would unambiguously differentiate species from the two clades; although species in *Centrolene* usually have enameled pericloacal warts, which are absent in *Espadarana* as far as we know. Also, most species in *Centrolene* lack teeth on the vomers (teeth present in *C. condor*, *C. daidaleum*, *C. geckoideum*, *C. savagei*, *C. solitaria*), whereas all species in *Espadarana* have vomerine teeth. Other clades contain some species with humeral spines, including *Nymphargus grandisonae*, *Chimerella mariaelenae*, *Cochranella litoralis*, and *Vitreorana gorzulae*; however, spines in these species are morphologically different from those of *Centrolene* and, likely, not homologous (Fig. 13).

CONTENT (23 SPECIES): *Centrolene altitudinale* (Rivero 1968), *C. antioquiense* (Noble 1920), *C. bacatum* Wild 1994, *C. buckleyi* (Boulenger 1882), *C. daidaleum* (Ruiz-Carranza & Lynch 1991c) new combination, *C. geckoideum* Jiménez de la Espada 1872, *C. hesperium* (Cadle & McDiarmid 1990), *C. hybrida* Ruiz-Carranza & Lynch 1991b, *C. muelleri* Duellman & Schulte 1993, *C. notostictum* Ruiz-Carranza & Lynch 1991b, *C. peristictum* (Lynch & Duellman 1973), *C. pipilatum* (Lynch & Duellman 1973), *C. savagei* (Ruiz-Carranza & Lynch 1991c) new combination, *C. venezuelense* (Rivero 1968). Based on morphology and geographic distribution, we tentatively place in *Centrolene* the following species: *C. condor* Cisneros-Heredia & Morales-Mite (2008), *C. gemmatum* (Flores 1985), *C. heloderma* (Duellman 1981), *C. lemniscatum* Duellman & Schulte 1993, *C. lynchi* (Duellman 1980), *C. paezorum* Ruiz-Carranza, Hernández-Camacho, & Ardila-Robayo 1986, *C. sanchezi* Ruiz-Carranza & Lynch 1991b, *C. scirtetes* (Duellman & Burrowes 1989), and *C. solitaria* (Ruiz-Carranza & Lynch 1991c) new combination. *Centrolene condor*, *C. heloderma*, and *C. lemniscatum* morphologically resemble *C. altitudinale* and *C. buckleyi* by having sloping snouts in lateral view, white labial stripes, and ulnar folds, among other characteristics. *Centrolene gemmatum*, *C. lynchi*, and *C. scirtetes* share several phenotypic traits with *C. pipilatum*; *Centrolene solitaria* is remarkably similar to *C. daidaleum* and *C. savagei*; and *C. paezorum* is almost indistinguishable from *C. geckoideum*.

ETYMOLOGY: The name *Centrolene* is probably derived from the Greek *kentron* = point or spur, and *olene* = elbow (McCranie & Wilson 2002), in reference to the conspicuous humeral spine that is present in adult males of the type species, *Centrolene geckoideum*. *Centrolene* is neuter in gender.

DISTRIBUTION: The genus *Centrolene* is endemic to the northern Andes, from the Cordillera de Mérida in Venezuela, across the Andes of Colombia and Ecuador, to the Cordillera de Huancabamba in northern Peru, at elevations of 1100–3500 m (Fig. 14).

COMMENTS: The genus *Centrolene* (*sensu* Ruiz-Carranza & Lynch 1991a) was characterized by a single morphological feature, the presence of a humeral spine in adult males. However, as suggested by Frost *et al.* (2006) and corroborated by this study, coding this character as the presence or absence of a humeral spine is overly simplistic. Several species (e.g., *Nymphargus armatus* [Ruiz-Carranza & Lynch 1996], “*Cochranella*” *balionota*, and *Nymphargus griffithsi* [Goin 1961]) have a conspicuously developed ventral humeral crest (Ruiz-Carranza & Lynch 1991a; Lynch & Ruiz-Carranza 1996), which is easily confused with a poorly developed humeral spine. Based on our hypothesis of centrolenid relationships, it is evident that the evolution of humeral spines is complex. At least five genera (*Chimerella*, *Centrolene*, *Cochranella*, *Espadarana*, *Vitreorana*) contain species with humeral spines; so this feature seems to have undergone multiple origins (or losses). A detailed consideration of patterns of morphological evolution among centrolenid frogs is beyond the scope of this paper and will be addressed in a subsequent study. A monophyletic *Centrolene* was inferred in analyses of the RAG1, *c-myc*, POMC, combined nuclear, and complete datasets.

GENUS: *Nymphargus* Cisneros-Heredia & McDiarmid 2007

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Cochranella cochranae* Goin 1961, and *Centrolenella bejaranoi* Cannatella 1980.

TYPE SPECIES: *Cochranella cochranae* Goin 1961.

SISTER TAXON: *Centrolene* Jiménez de la Espada 1872. See comments on the Sister Taxon section below *Centrolene*.

DIAGNOSIS: The most conspicuous trait shared by all species in *Nymphargus* is the reduced webbing between the outermost fingers (Fingers III and IV; Fig. 15). Additionally, the following character states are characteristic of *Nymphargus*: (1) humeral spines absent, except in males of *N. grandisonae*, which have a small spine; (2) tri- or tetralobed liver, covered by a transparent hepatic peritoneum; (3) ventral parietal peritoneum white anteriorly and transparent posteriorly; (4) bones green in life (white in *N. rosadus* and *N. anomalus*); (5) dorsum lavender in preservative, with or without spots; (6) dorsum of males usually with conspicuous spinules during breeding season; (7) Type-I nuptial pads conspicuous in reproductive males; (8) males call from the upper sides of leaves, females deposit egg masses on the upper sides of leaves along streams.

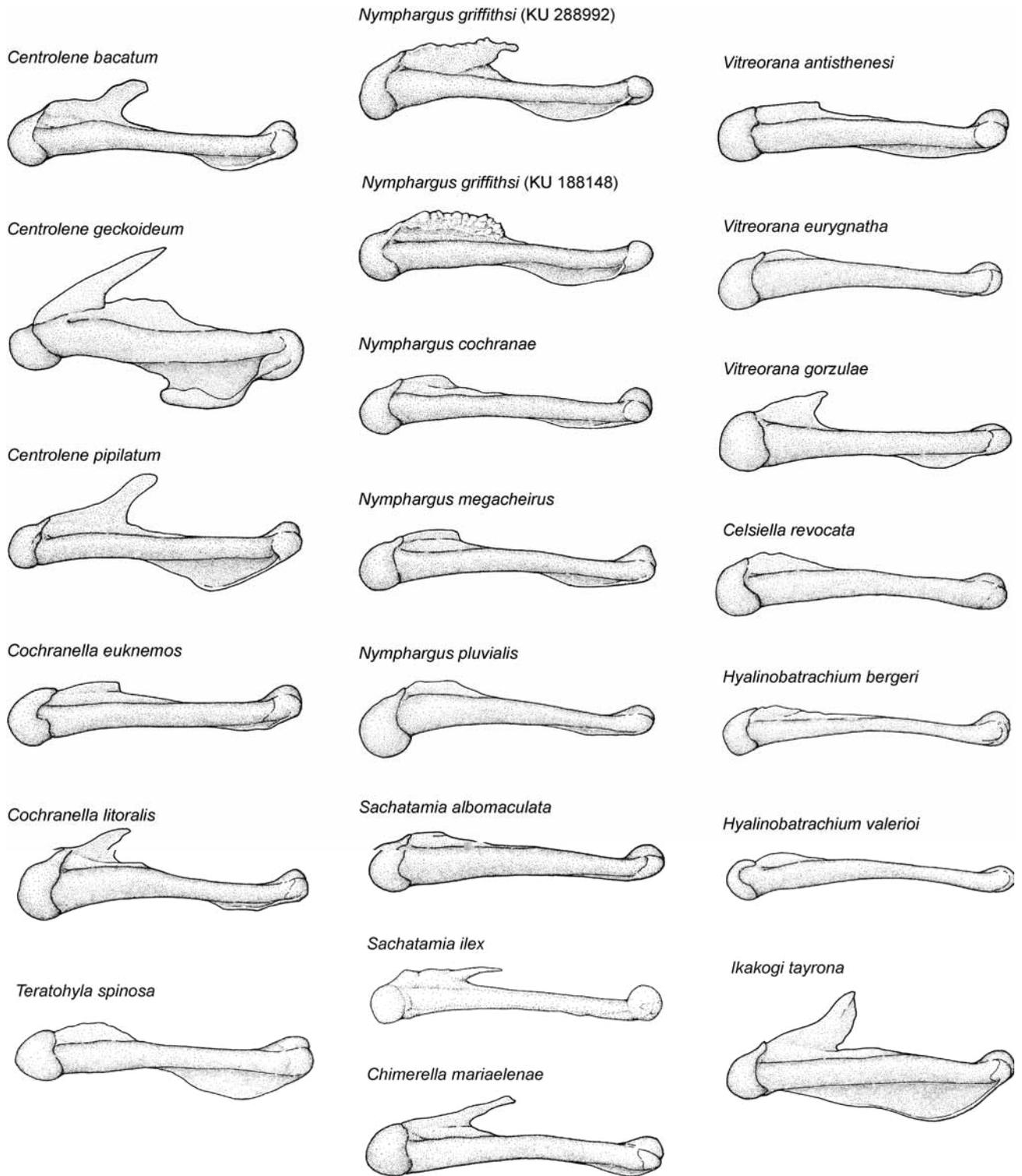


FIGURE 13. *Crista medialis*, *crista ventralis*, and humeral spines in centrolenid adult males. *Centrolene bacatum*, KU 170116; *C. geckoideum*, ICN 5598; *C. pipilatum*, KU 143286; *Cochranella euknemos*, KU 77534; *Cochranella litoralis*, QCAZ 27693; *Teratohyla spinosa*, KU 32935; *Nymphargus griffithsi*, KU 288992 188148; *N. cochranae*, KU 123218; *N. megacheirus*, KU 143271; *N. pluvialis*, KU 173488; *Sachatamia albomaculata*, KU 65185; *S. ilex*, LACM 72910; *Chimerella mariaelenae*, QCAZ 21252; *Vitreorana antisthenesi*, KU 167775; *V. eurygnatha*, KU 93225; *V. gorzulae*, UTA 52240; *Celsiella revocata*, MHNLS 13352; *Hyalinobatrachium bergeri*, KU 162256; *H. valerioi*, KU 178091; *Ikakogi tayrona*, KU 169754. Note that the *crista medialis* of *I. tayrona* is almost as long as the humerus.

Centrolene*Nymphargus*

FIGURE 14. DISTRIBUTION OF *CENTROLENE* AND *NYMPHARGUS*.

The genera *Celsiella*, *Rulyrana*, and *Sachatamia* include species morphologically similar to *Nymphargus*. However, species of *Celsiella* have a small prepollex (length < 50% of Metacarpal I; Fig. 11), and cream to gray dorsal coloration in preservative. Furthermore, *Celsiella* is restricted to the Cordillera de la Costa of Venezuela, whereas *Nymphargus* is endemic to the Andes. Species of *Rulyrana* and *Sachatamia* have moderate to extensive webbing between Fingers III and IV (basal or absent in *Nymphargus*; Fig. 15).

CONTENT (34 SPECIES): *Nymphargus bejaranoi* (Cannatella 1980), *N. cochranae* (Goin 1961), *N. garciae* (Ruiz-Carranza & Lynch 1995a), *N. grandisonae* (Cochran & Goin 1970) new combination, *N. griffithsi* (Goin 1961), *N. megacheirus* (Lynch & Duellman 1973), *N. mixomaculatus* (Guayasamin, Lehr, Rodríguez & Aguilar 2006a), *N. pluvialis* (Cannatella & Duellman 1982), *N. posadae* (Ruiz-Carranza & Lynch 1995a), *N. puyoensis* (Flores & McDiarmid 1989) new combination, *N. rosada* (Ruiz-Carranza & Lynch 1997), *N. siren* (Lynch & Duellman 1973), *N. vicenteruedai* Velásquez-Álvarez, Rada, Sánchez-Pacheco, & Acosta 2007, and *N. wileyi* (Guayasamin, Bustamante, Almeida-Reinoso & Funk 2006a). Species for which we lack molecular data, but that have a morphology that corresponds to the diagnosis (provided above) are tentatively placed in *Nymphargus*; these species are: *N. anomalus* (Lynch & Duellman 1973), *N. armatus* (Lynch & Ruiz-Carranza 1996), *N. buenaventura* (Cisneros-Heredia & Yáñez-Muñoz 2007), *N. cariticommatu*s (Wild 1994), *N. chami* (Ruiz-Carranza & Lynch 1995b), *N. chancas* (Duellman & Schulte 1993), *N. cristinae* (Ruiz-Carranza & Lynch 1995b), *N. ignotus* (Lynch 1990), *N. laurae* Cisneros-Heredia & McDiarmid 2007, *N. luminosus* (Ruiz-Carranza & Lynch 1995b), *N. luteopunctatus* (Ruiz-Carranza & Lynch 1996), *N. mariae* (Duellman & Toft 1979) new combination, *N. nephelophilus* (Ruiz-Carranza & Lynch 1991d), *N. ocellatus* (Boulenger, 1918) new combination, *N. oreonympha* (Ruiz-Carranza & Lynch 1991d), *N. phenax* (Cannatella & Duellman 1982), *N. prasinus* (Duellman 1981), *N. ruizi* (Lynch 1993), *N. spilotus* (Ruiz-Carranza & Lynch 1997), and *N. truebae* (Duellman 1976). As mentioned before, the placement of these species is tentative and should be tested with molecular data (Appendix I).

ETYMOLOGY: The name *Nymphargus* is formed from the Greek *nýmphae* in allusion to the nymphs, and *argus* in allusion to the mythological Greek Argus, nephew of the nymph *Io*, a giant with a hundred eyes, which became the ocelli in the peacock's tail. The name is masculine and alludes to the ocelli found on the dorsum of four species of the genus: *anomalus*, *cochranae*, *ignotus*, and *laurae* (Cisneros-Heredia & McDiarmid 2007).

DISTRIBUTION: *Nymphargus* is endemic to the Andes and Andean foothills in Colombia, Ecuador, Peru, and Bolivia. Most of the species are restricted to elevations above 1000 m, and only *N. cochranae*, *N. laurae*, and *N. puyoense* are found also at lower elevations on the Amazonian slopes of the Andes (Fig. 14).

COMMENTS: Ruiz-Carranza & Lynch (1991a, 1995a) created the *Cochranella ocellata* Group for species that have reduced webbing between Fingers III and IV, lobed livers, visceral and hepatic peritonea without white iridophores, and that lack humeral spines. Our phylogenetic analysis shows that most of the species included in the *ocellata* Group are part of a natural group. Also, the reduced webbing between Fingers III and IV is a synapomorphy within Centrolenidae, although not unambiguous (*Celsiella vozmediano* has the same character state). After a phenetic analysis of morphological characters, Cisneros-Heredia & McDiarmid (2007) rearranged the generic classification of Centrolenidae, placing most species of the *Cochranella ocellata* Group in a new genus, which they named *Nymphargus*. The taxon *Nymphargus sensu* Cisneros-Heredia & McDiarmid (2007) is paraphyletic and lacks the morphological cohesion of the *ocellata* Group *sensu* Ruiz-Carranza & Lynch (1991a, 1995a). For example, Cisneros-Heredia & McDiarmid (2007) excluded species (e.g., *C. ocellata*, *puyoensis*, *mariae*) that have all but one (color pattern) of the diagnostic characteristics that they listed for *Nymphargus*. The clade *Nymphargus*, as defined herein, is well supported by 12S, 16S, ND1, *c-myc*, POMC, RAG1, combined mitochondrial, combined nuclear, and complete datasets (Figs. 3, 8).

TRIBE: **Cochranellini** new tribe

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Cochranella granulosa* Taylor 1949, and *Centrolenella gorzulae* Ayarzagüena 1992.

TYPE GENUS: *Cochranella* Taylor 1949.

SISTER TAXON: The mitochondrial and complete datasets support a sister relationship between Cochranellini and a clade formed by *Centrolene* + *Nymphargus* (Figs. 3, 8). However, the nuclear topology supports a Cochranellini + *Centrolene* clade (Fig. 8). See comments under *Centrolene*.

DIAGNOSIS: The morphology and behavior within this clade are remarkably diverse. All species in Cochranellini have a moderate to extensive webbing between Fingers III and IV, a characteristic that differentiates them from species that have reduced webbing between Fingers III and IV (all in *Nymphargus* and most in *Centrolene*; Fig. 15). Additionally, most species in Cochranellini have lobed livers, green bones in life, and lavender dorsal coloration in preservative. The combination of these traits distinguishes most Cochranellini from species in Hyalinobatrachinae that have a bulbous liver, white bones (lobed liver and green bones in *Celsiella*), and a cream to gray dorsal coloration in preservative. Most species in Cochranellini differ from species in *Centrolene* by lacking prominent humeral spines; however, members of *Espadarana* have such spines in males and are almost indistinguishable from *Centrolene* (see comments under *Centrolene*).

CONTENT (7 GENERA): Cochranellini contains seven genera (as defined in this work): *Chimerella* new genus, *Cochranella* Taylor 1951, *Espadarana* new genus, *Rulyrana* new genus, *Sachatamia* new genus, *Teratohyla* Taylor 1951, *Vitreorana* new genus.

ETYMOLOGY: The name Cochranellini is derived from the genus *Cochranella*.

DISTRIBUTION: Tropical Central America, tropical Andes, Cordillera de la Costa of Venezuela, Guiana Shield, Amazon Basin, and Atlantic Forest.

COMMENTS: In the combined and nuclear topologies (Figs. 3, 8), relationships among genera in Cochranellini have low node support, perhaps as a result of a rapid radiation that has produced short internodes. Under the scenario of a rapid radiation, slow-evolving genes (i.e., nuclear genes) may present

stochastic lineage sorting of ancestral polymorphisms, whereas fast-evolving genes (i.e., mitochondrial genes) have a higher probability of coalescence and, consequently, a higher probability of accurately tracking a short internode (Moore 1995; Zink & Barrowclough 2008; and references therein). In the mitochondrial phylogeny presented in Figure 8, most of the relationships among genera in Cochranellini are resolved and have high node support.

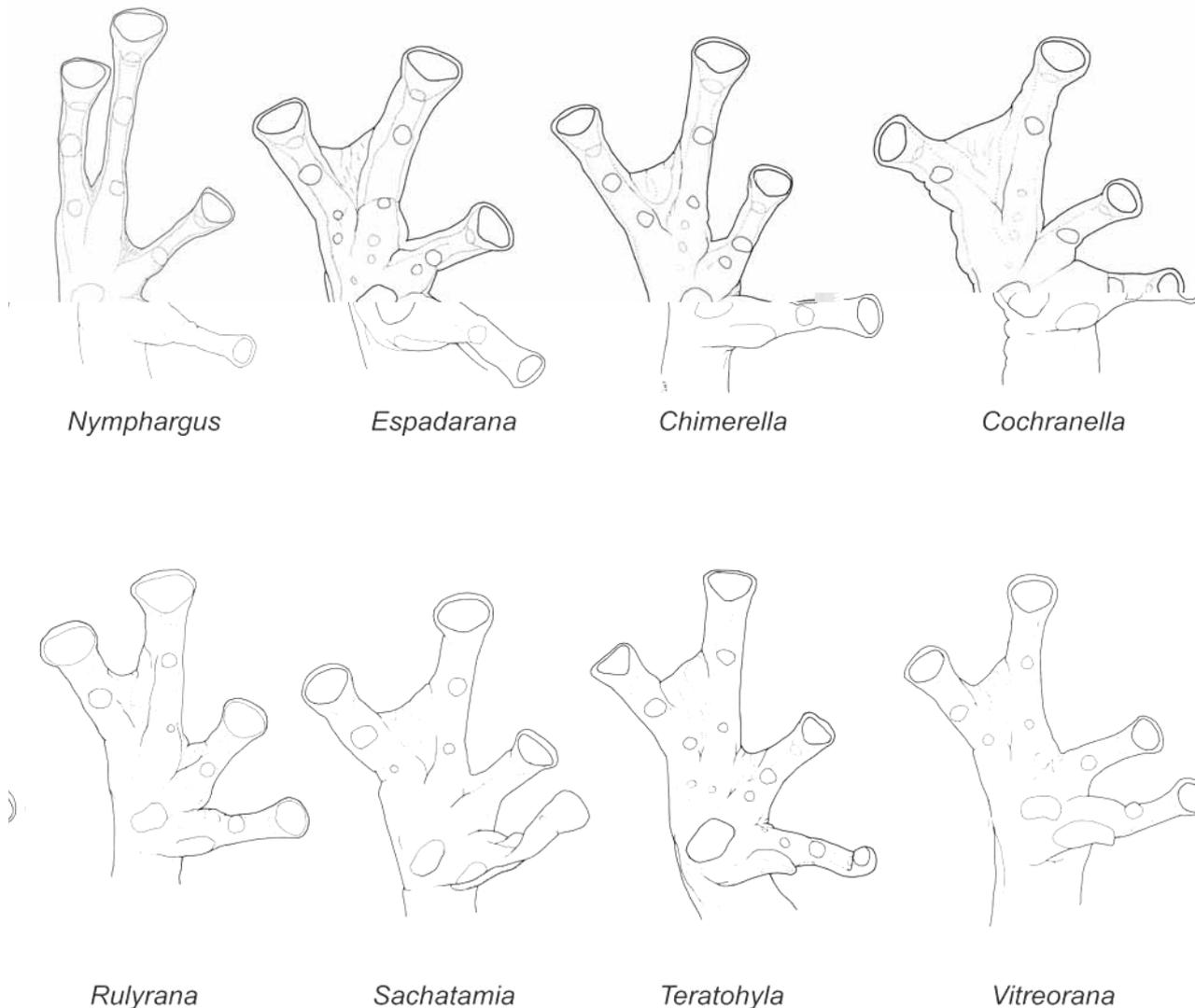


FIGURE 15. Differences in hand webbing (Fingers III and IV) between *Nymphargus* and genera within Cochranellini. The following species are illustrated: *Nymphargus posadae*, QCAZ 25090; *Espadarana prosoblepon*, KU 132462; *Chimerella mariaelena*, QCAZ 22363; *Cochranella resplendens*, KU 118053; *Rulyrana flavopunctata*, KU 121046; *Sachatamia albomaculata*, QCAZ 4325; *Teratohyla spinosa*, KU 164668; *Vitreorana ametarsia*, ICN 50847.

The ranked nature of the ICZN has the drawback that, when the commonly used ranks (e.g., family, subfamily, genus) are not available, naming clades requires the use of ranks that are rarely seen in amphibian taxonomic studies (i.e., tribe). An additional counterintuitive problem arises in this case because we name the tribe Cochranellini, but we do not name its sister clade (*Centrolene* + *Nymphargus*; Fig. 3). The reason for not naming *Centrolene* + *Nymphargus* is the lack of congruence between the topologies inferred from the complete dataset and the combined nuclear dataset (Figs. 3, 8). As explained in the Materials and Methods section, we decided *a priori* to name taxa only when there is congruence among genes as a mean to increase nomenclatural stability.

Creating the Tribe Cochranellini does not imply that we are required to erect tribes for the other glassfrogs not included in Cochranellini. The Principle of Coordination of the ICZN states that “A name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at all other ranks in the family group; all these taxa have the same type genus, and their names are formed from the stem of the name of the type genus with appropriate change of suffix. The name has the same authorship and date at every rank”. In other words, the Principle of Coordination only emphasizes that the name of any family-group taxon was already established when the first name of that family-group was formalized. For example, if we were to create a Superfamily for the Centrolenidae + Allophrynidae clade, because the first recognized name in the family-group is Centrolenidae (Taylor, 1951), the proper authorship for such a new superfamily would be Taylor (1951).

The other possible source of confusion is the Principle of Exhaustive Subsidiary Taxa, in which if a nonmandatory categorical level is used within any taxon, then it is used for all members of that taxon. For example, when creating the nonmandatory Tribe Cochranellini, we would need to erect at the same time the tribes Centrolenini, Nymphargini, and Hyalinobatrachini for the remaining glassfrogs (those not included in Cochranellini). However, the Principle of Exhaustive Subsidiary Taxa is not a rule of nomenclature (i.e., it is not in the ICZN); instead, it is an informal taxonomic convention (see de Queiroz and Gauthier 1992). We prefer to avoid having taxa with the same definition and the same species content, a redundancy that seems unnecessary; therefore, we have avoided, whenever possible, the erection of such taxa.

GENUS: *Chimerella* new genus

P

Andes and the Guiana Shield. The relationships of *C. mariaelenae* and other genera within Cochranellini do not get strong support in the topologies obtained from the complete and nuclear datasets (Figs. 3, 8). The phylogeny, however, does not support the Andes-Guiana Shield hypothesis. If the mitochondrial topology were correct, it would imply that the most recent common ancestor of the clade Cochranellini was similar (morphology, behavior) to species in *Chimerella* and *Vitreorana*.

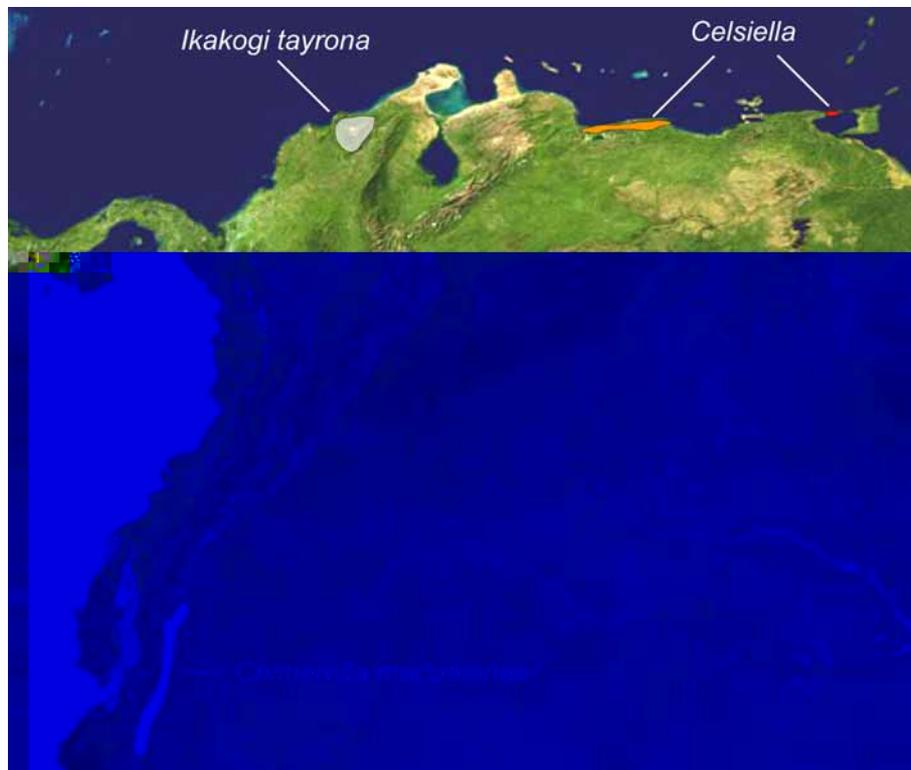


FIGURE 16. Distribution of *Celsiella*, *Chimerella*, and *Ikakogi*.

GENUS: *Cochranella* Taylor 1951

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Centrolenella granulosa* Taylor 1949, *Centrolene litorale* Ruiz-Carranza & Lynch 1996, and *Cochranella nola* Harvey 1996.

TYPE SPECIES: *Centrolenella granulosa* Taylor 1949.

SISTER TAXON: Uncertain (Figs. 3, 8). However, the topology inferred from the combined mitochondrial dataset supports a clade formed by *Cochranella* Taylor 1951 + *Espadarana* new genus.

DIAGNOSIS: This clade is diagnosed by the following combination of characters: (1) absence of humeral spines (small spine present in *C. litoralis*); (2) digestive tract white (translucent in *Cochranella nola*), lobed liver covered by a transparent hepatic peritoneum; (3) ventral parietal peritoneum white anteriorly and transparent posteriorly; (4) moderate to extensive webbing between Fingers III and IV; (5) bones green in life; (6) dorsum lavender in preservative, with or without spots; (7) dentigerous process of the vomer and vomerine teeth present (absent in *C. litoralis*); (8) males call from the upper surfaces of leaves, and females deposit eggs on the upper sides of leaves along streams; (9) quadratojugal articulating with maxilla. *Cochranella* is differentiated from *Rulyrana* by usually having white visceral peritoneum (translucent in *Rulyrana*). Three species of *Centrolene* (*C. daidaleum*, *C. savagei*, and *C. solitaria*) are remarkably similar to some species in *Cochranella* (*C. mache* Guayasamin & Bonaccorso 2004, *C. resplendens* [Lynch & Duellman 1973]); these species in *Centrolene* differ mainly by having a concentration of iridophores (resembling a line) that separates the upper and lower flanks of the body (absent in *Cochranella*). Also, they occur in different biogeographic

areas; all species of *Centrolene* are restricted to the tropical Andes, whereas *Cochranella mache* and *C. resplendens* are found only in lowlands (≤ 1000 m).

CONTENT (7 SPECIES): *Cochranella euknemos* (Savage & Starrett 1967), *C. granulosa* (Taylor 1949), *C. litoralis* (Ruiz-Carranza & Lynch 1996) new combination, *C. mache* Guayasamin & Bonaccorso 2004, and *C. nola* Harvey 1996. Additionally, based on morphology, we consider *C. phryxa* Aguayo & Harvey 2006, and *C. resplendens* (Lynch & Duellman 1973) as part of the clade *Cochranella*. These two species (*C. phryxa* and *C. resplendens*) share the following characters with *C. mache*: dermal folds with white tubercles on the arms and legs, snout gradually inclined in profile, and cloacal ornaments. This tentative placement needs to be tested with molecular data.

ETYMOLOGY: Taylor (1951) named *Cochranella* in honor of Doris M. Cochran, former curator at the Smithsonian Institution. Cochran's research focused primarily on the herpetofauna of the West Indies and South America, particularly Brazil and Colombia (Cochran 1955; Cochran & Goin 1970). The genus is feminine in gender.

DISTRIBUTION: The genus *Cochranella* is distributed in the lowlands and mountains at elevations below 1750 m in Central America (*Cochranella granulosa*, *C. euknemos*), the Pacific lowlands and cloud forests of Colombia (*C. euknemos*, *C. litoralis*) and Ecuador (*C. litoralis*, *C. mache*), the Amazonian slopes of the Andes of Bolivia (*C. nola*), and the Amazonian lowlands of Ecuador (*C. resplendens*), Peru (*C. resplendens*), and Bolivia (*C. phryxa*). See Figure 17.

COMMENTS: Most of the species that we place in *Cochranella* (*C. granulosa*, *C. euknemos*, *C. mache*, *C. resplendens*) used to be part of the *Cochranella granulosa* Group (*sensu* Ruiz-Carranza & Lynch 1991a, b). The monophyly of *Cochranella* is strongly supported by 12S, 16S, combined mitochondrial, combined nuclear, and complete datasets.

GENUS: ***Espadarana*** new genus

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Centrolenella andina* Rivero 1968, and *Hyla prosoblepon* Boettger 1892.

TYPE SPECIES: *Centrolenella andina* Rivero 1968.

SISTER TAXON: Uncertain (Figs. 3, 8). The topology inferred from the mitochondrial dataset supports a sister relationship between *Cochranella* Taylor 1951 and *Espadarana* new genus. The nuclear tree does not have significant node support for the relationships among genera within Cochranellini (Fig. 8).

DIAGNOSIS: *Espadarana* is diagnosable by the following combination of characters: (1) adult males with conspicuous humeral spines; (2) lobed liver covered by a transparent hepatic peritoneum, digestive tract translucent; (3) ventral parietal peritoneum white anteriorly and transparent posteriorly; (4) moderate webbing between Fingers III and IV; (5) bones green in life; (6) dorsum lavender in preservative, with or without spots; (7) dentigerous process of the vomer bearing teeth; (8) males call from the upper surfaces of leaves or branches, females deposit eggs on the upper sides of leaves over streams (*Espadarana prosoblepon* has been observed to deposit eggs on the upper and lower surfaces of leaves; MR pers. com.); (9) quadratojugal articulating with maxilla. The presence of conspicuous humeral spines in the adult males of species in *Espadarana* distinguishes this clade from most other centrolenids. The other two genera presenting this trait are *Centrolene* and the monotypic *Ikakogi* new genus. *Ikakogi tayrona* is the only centrolenid species in which females guard egg clutches (MR, pers. obs.); also, the bones of *I. tayrona* are white in life, and the humerus has an enlarged crista medialis (Fig. 13). Species in *Centrolene* usually have enameled pericloacal warts, which are absent in *Espadarana* as far as we know; also, most *Centrolene* lack teeth on the vomers (teeth present in *C. geckoideum*, *C. savagei*, *C. daidalea*, and *C. condor*), whereas all species in *Espadarana* have vomerine teeth; however, DNA data are needed for the unambiguous placement of species in either of these two clades. *Chimerella mariaelenae* and *Vitreorana gorzulae* have small humeral spines that are easily differentiated from the spines present in *Espadarana* (Figs. 6, 13).

CONTENT (3 SPECIES): *Espadarana andina* (Rivero 1968) new combination, *E. prosoblepon* (Boettger 1892) new combination, *E. callistomma* (Guayasamin & Trueb 2007) new combination.

ETYMOLOGY: The name *Espadarana* honors Marcos Jiménez de la Espada, a Spanish zoologist who was part of the Comisión Científica del Pacífico that explored America between 1862 and 1865. His work, *Vertebrados del Viaje al Pacífico Verificado de 1862 a 1865 por una Comisión de Naturalistas Enviada por el Gobierno Español – Batracios*, has been an indispensable reference for anyone interested on the amphibians of South America. Jay Savage, in the introduction of the facsimile reprint of *Vertebrados del Viaje al Pacífico* published by the Society for the Study of Amphibians and Reptiles, provides a detailed and insightful commentary regarding Jiménez de la Espada's trip to America and his return to Spain. Jiménez de la Espada described the first centrolenid frog, *Centrolene geckoideum* in 1872. In Spanish, the word *Espada* means sword, which we associate with the humeral spines present in the adult males of the species in this clade. *Espadarana* is a combination of the words *Espada* and *rana* (frog), and is feminine in gender.

DISTRIBUTION: Members of the genus *Espadarana* occur at elevations below 2500 m in the lowlands and mountains of Central America (*E. prosoblepon*), the Pacific lowlands of Colombia and Ecuador (*E. callistomma*, *E. prosoblepon*), and the cloud forests of the Andes in Colombia, Cordillera de Mérida, and Serranía del Perijá in Venezuela (*E. andina*). See Figure 17.

COMMENTS: Only species in *Centrolene*, *Espadarana*, and *Ikakogi* have pronounced humeral spines in adult males (i.e., *crista ventralis* expanded into a conspicuous spine). Other species have small (*Chimerella mariaelenae*, *Nymphargus grandisonae*, *V. gorzulae*), hidden (*Sachatamia illex*), or lack spines (*Celsiella*, *Hyalinobatrachium*, most species in *Nymphargus*). Some adult males of *Nymphargus griffithsi* have a *crista ventralis* expanded into a process that resembles a small spine; however, the common character state in this species is the absence of such process. The monophyly of *Espadarana* is strongly supported by 12S, 16S, ND1, POMC, combined mitochondrial, combined nuclear, and complete datasets.

GENUS: ***Rulyrana*** new genus

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Cochranella adiazeta* Ruiz-Carranza & Lynch 1991d, and *Centrolenella flavopunctata* Lynch & Duellman 1973.

TYPE SPECIES: *Centrolenella flavopunctata* Lynch & Duellman 1973.

SISTER TAXON: Uncertain (Figs. 3, 8). The topology inferred from the mitochondrial dataset supports a clade formed by *Rulyrana* new genus + *Teratohyla* Taylor 1951. The nuclear tree show a *Rulyrana* + *Sachatamia* clade, but with low support.

DIAGNOSIS: The following characteristics are diagnostic of *Rulyrana*: (1) humeral spines absent; (2) lobed liver covered by a transparent hepatic peritoneum, digestive tract translucent; (3) ventral parietal peritoneum white anteriorly and transparent posteriorly; (4) moderate to extensive webbing between Fingers III and IV; (5) bones green in life; (6) dorsum lavender in preservative, with or without spots; (7) dentigerous process of the vomer present, vomerine teeth usually present (present or absent in *R. spiculata* [Duellman 1976] and *R. flavopunctata*); (8) males call from the upper surfaces of leaves or rocks, females deposit eggs on the upper sides of leaves or rocks. The main characters to distinguish *Rulyrana* from other genera are the presence of moderate to extensive webbing between Fingers III and IV, ventral parietal peritoneum white anteriorly and transparent posteriorly, and the lack of humeral spines in adult males. The genus *Sachatamia* (see below), however, cannot be morphologically differentiated from *Rulyrana*. See comments.

CONTENT (8 SPECIES): *Rulyrana adiazeta* (Ruiz-Carranza & Lynch 1991d) new combination, *R. flavopunctata* (Lynch & Duellman 1973) new combination, *R. spiculata* (Duellman 1976) new combination, and *R. susatamai* (Ruiz-Carranza & Lynch 1995a) new combination. Additionally, based on morphology and geographic distribution, we tentatively place in *Rulyrana* the following species: *R. erminae* (Torres-Gastello, Suárez-Segovia, & Cisneros-Heredia 2007) new combination, *R. mcdiarmidi* (Cisneros-Heredia, Venegas, Rada & Schulte 2008) new combination, *R. saxiscandens* (Duellman & Schulte 1993) new combination, and *R. tangarana* (Duellman & Schulte 1993) new combination. *Rulyrana saxiscandens* and *R. tangarana* are morphologically identical to *R. spiculata*; *R. mcdiarmidi* is nearly identical to *R. flavopunctata*; whereas *R. erminea* has all the diagnostic traits of the genus (see above), including the absence of humeral spines in adult males (M. Medina, pers. comm.)

Cochranella



Espadarana



Rulyrana



Sachatamia



FIGURE 17. Distribution of *Cochranella*, *Espadarana*, *Rulyrana*, and *Sachatamia*.

ETYMOLOGY: *Rulyrana* is named in honor of Pedro Ruiz-Carranza and John D. Lynch, who have contributed enormously to the understanding of centrolenid diversity, biology, and evolution. The name *Rulyrana* comes from an arbitrary association of the two first letters of Ruiz and Lynch (Ruly) and the word *rana* (= frog). Additionally, *Ruly* happens to be the nickname of JMG's good friend and colleague Martín Bustamante, herein, we also recognize his work on amphibian conservation. The name *Rulyrana* is feminine in gender.

DISTRIBUTION: The genus *Rulyrana* is distributed on the Amazonian slopes of the Andes (*R. flavopunctata*, *R. spiculata*) in Ecuador and Peru, the western slopes of the Cordillera Oriental of the Andes in Colombia (*R. adiazeta*), and the eastern slopes of the Cordillera Central of the Andes in Colombia (*R. susatamai*). See Figure 17.

COMMENTS: We are unable to find discrete phenotypic differences between *Rulyrana* and *Sachatamia* new genus. Ideally, these two taxa would have been placed in a single genus, as suggested by the nuclear dataset (Fig. 8) and Bayesian analysis of the complete dataset (Fig. 3). However, the mitochondrial phylogeny indicates that *Rulyrana* + *Sachatamia* do not form a monophyletic group (Fig. 8). Given the incongruence among datasets, we prefer to recognize the two genera, each of which is inferred as monophyletic in all datasets (nuclear, mitochondrial, combined). If further work finds that *Rulyrana* + *Sachatamia* do form a natural group, it would be recommended to consider *Sachatamia* as a synonym of *Rulyrana*. At the moment, however, placement of species in either of these two genera requires the use of molecular data. The monophyly of the clade *Rulyrana* is well supported by 12S, RAG1, POMC, combined nuclear, combined mitochondrial, and complete datasets.

GENUS: *Sachatamia* new genus

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Centrolenella ilex* Savage 1967, and *Centrolenella albomaculata* Taylor 1949.

TYPE SPECIES: *Centrolenella albomaculata* Taylor 1949.

SISTER TAXON: Uncertain (Figs. 3, 8). The mitochondrial topology supports a clade formed by *Sachatamia* new genus + (*Rulyrana* new genus + *Teratohyla* Taylor 1951). The nuclear and complete datasets suggests a *Sachatamia* + *Rulyrana* clade, but with low node support.

DIAGNOSIS: The following combination of characteristics is diagnostic of *Sachatamia*: (1) humeral spines present (*S. ilex*) or absent (*S. albomaculata*, *S. punctulata* [Ruiz-Carranza & Lynch 1995a]); (2) lobed liver covered by a transparent hepatic peritoneum, digestive tract translucent; (3) ventral parietal peritoneum white anteriorly and transparent posteriorly; (4) moderate to extensive webbing between Fingers III and IV; (5) bones green in life; (6) dorsum lavender in preservative, with or without spots; (7) dentigerous process of the vomer present, bearing teeth; (8) males call from the upper surfaces of leaves or rocks, females deposit pigmented eggs on the upper sides of leaves or rocks; (9) quadratojugal articulating with maxilla. Although phenotypic characters distinguish *Sachatamia* from most centrolenid taxa, there are no discrete differences between this genus and *Rulyrana*; geographically, however, *Rulyrana* is found on the central and Amazonian slopes of the Andes, whereas *Sachatamia* occurs in Central America, the South American Choco, and the central Andes. DNA data are necessary to unambiguously allocate species in one of these two clades.

CONTENT (3 SPECIES): *Sachatamia albomaculata* (Taylor 1949) new combination, *S. ilex* (Savage 1967) new combination, *S. punctulata* (Ruiz-Carranza & Lynch 1995a) new combination.

ETYMOLOGY: The name *Sachatamia* comes from the Quichua words *sacha*, meaning "forest," and *tamia*, meaning "rain," and refers to the tropical rainforest occupied by the clade. *Sachatamia* is feminine in gender.

DISTRIBUTION: The genus *Sachatamia* is distributed in the rainforest at elevations below 1500 m in Central America (Honduras, Nicaragua, Costa Rica, Panama) and South America (Colombia, Ecuador). In South America, *Sachatamia ilex* and *S. albomaculata* occur in the Pacific lowlands, whereas *S. punctulata* is restricted to the eastern slopes of the Cordillera Central of the Colombian Andes. See Figure 17.

COMMENTS: The monophyly of *Sachatamia* is strongly supported by the 16S, ND1, combined mitochondrial, and complete datasets. See comments under *Rulyrana*.

GENUS: *Teratohyla* Taylor 1951

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Centrolenella spinosa* Taylor 1949, and *Hyla pulverata* Peters 1873.

TYPE SPECIES: *Centrolenella spinosa* Taylor 1949, by original designation.

SISTER TAXON: Uncertain (Figs. 3, 8). The results from the ML and Bayesian analysis of the mitochondrial dataset support a clade consisting of *Teratohyla* + *Rulyrana*. The nuclear topology shows *Teratohyla* as sister to a clade formed by *Chimerella* + *Espadarana* + *Cochranella* + *Rulyrana* + *Sachatamia* (Fig. 8), but with weak support.

DIAGNOSIS: The most conspicuous characteristics of *Teratohyla* are: (1) humeral spines absent; (2) liver covered by a transparent (*T. midas* [Lynch & Duellman 1973], *T. spinosa*) or white (*T. pulverata*, *T. amelie* [Cisneros-Heredia & Meza-Ramos 2007]) hepatic peritoneum, digestive tract translucent (*T. spinosa*) or white (*T. amelie*, *T. midas*, *T. pulverata*); (3) ventral parietal peritoneum white anteriorly and transparent posteriorly (*T. midas*, *T. spinosa*) or completely transparent (*T. amelie*, *T. pulverata*); (4) moderate to extensive webbing between Fingers III and IV; (5) bones pale to dark green in life; (6) dorsum creamy lavender to dark lavender in preservative, with or without spots; (7) dentigerous process of the vomer present, with or without teeth; (8) males call from the upper surfaces of leaves, females deposit eggs on the tips of leaves (*T. pulverata*, Savage [2002]) or along the margins of the undersides of leaves (*T. spinosa*, Starrett [1960]; Fig. 2: Type D); (9) prepollical spine protruding (*T. spinosa*) or not protruding (*T. amelie*, *T. midas*, *T. pulverata*). By having a ventral parietal peritoneum that is white anteriorly and transparent posteriorly, a liver that is covered by a transparent hepatic peritoneum, moderate to extensive hand webbing, and lacking humeral spines, *Teratohyla spinosa* and *T. midas* resemble species in *Sachatamia* and *Rulyrana*; however, *T. spinosa* is small (SVL < 21 mm) and has an evident prepollex spine that is clearly separated from Finger I, and *T. midas* has a white digestive tract. The two other species of the clade *Teratohyla*, *T. pulverata* and *T. amelie*, have a completely transparent ventral parietal peritoneum and a white hepatic and visceral peritonea, and can be confused with *Hyalinobatrachium*, *Vitreorana*, and *Chimerella*. Species in *Hyalinobatrachium* have white bones (except *H. taylori* and *H. mesai*, which have green bones; all species in *Teratohyla* have green bones) and dorsal cream coloration in preservative (lavender in *Teratohyla*); males of *Chimerella* present a small humeral spine (absent in *Teratohyla*), and species in *Vitreorana* (except *V. oyampiensis*) are restricted to the Cordillera de la Costa of Venezuela, Guiana Shield, and the Atlantic Forest (*Teratohyla* is restricted to Central America and the Pacific and Amazonian lowlands of South America, only with *T. midas* reaching French Guiana).

CONTENT (4 SPECIES): *Teratohyla amelie* (Cisneros-Heredia & Meza-Ramos 2007) new combination, *T. midas* (Lynch & Duellman 1973) new combination, *T. pulverata* (Peters 1873) new combination, and *T. spinosa* (Taylor 1949) new combination.

ETYMOLOGY: The name *Teratohyla* is derived from the Greek *teras*, meaning monster, marvel or wonder, and the word *Hyla*, traditionally associated to treefrogs. The origin of the frog name *Hyla* was recently clarified by Myers and Stothers (2006). The name is based on the mythological Greek boy Hylas. Although the boy's name is masculine, *Hyla* has been unambiguously treated as feminine by amphibian systematists.

DISTRIBUTION: *Teratohyla* occurs in the lowlands of Central America and in the Pacific and Amazonian lowlands of South America below 1000 m (Fig. 18).

COMMENTS: This clade is one of the few examples within Centrolenidae in which the vicariant barrier hypothesized to cause speciation is the uplift of the Andes. According to Hoorn (1995), the eastern cordillera formed a continuous range between 12.9 and 11.8 Ma; however, it probably became an important vicariant barrier to lowland species during the early Pliocene (5.3–3.6 Ma; Hooghiemstra et al., 2006). If this dating is correct, sister species in *Teratohyla* have been evolving independently for a long period of time. Despite this long isolation, the general morphology of sister species (*T. midas* + *T. spinosa*; *T. pulverata* + *T. amelie*) has been maintained (described in diagnosis above). Also, sister species still inhabit the lowlands (< 1000 m) of tropical rainforests on opposite sides of the Andes, suggesting that the niche has been conserved (see Peterson et al. 1999). The monophyly of *Teratohyla* is inferred with significant support from the mitochondrial (Bayesian), nuclear (Bayesian and ML), and complete (Bayesian, ML, and parsimony) datasets.

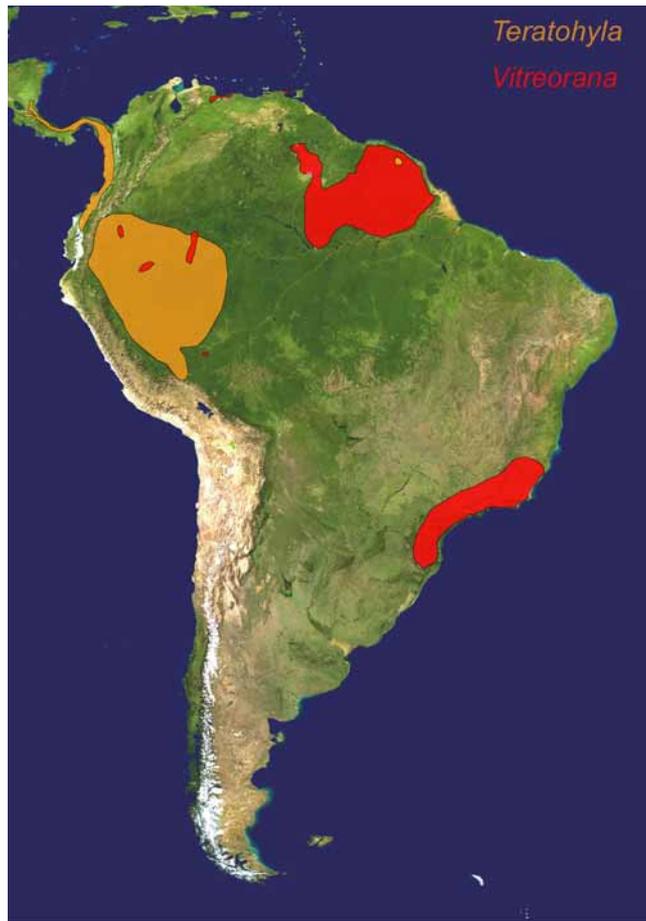


FIGURE 18. Distribution of *Teratohyla* and *Vitreorana*.

GENUS: *Vitreorana* new genus

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Centrolenella antisthenesi* Goin 1963, and *Centrolenella gorzulae* Ayarzagüena 1992.

TYPE SPECIES: *Centrolenella antisthenesi* Goin 1963.

SISTER TAXON: The sister clade of *Vitreorana* is not clearly established. The combined and nuclear datasets suggest (with low support) that *Vitreorana* is sister to a clade containing all the other genera in Cochranellini. The Bayesian mitochondrial phylogeny shows *Vitreorana* as sister to all genera in Cochranellini, except *Chimerella mariaelenae* (Fig. 8), with significant support.

DIAGNOSIS: The most conspicuous feature of *Vitreorana* is the presence of a white hepatic peritoneum covering the liver (or partially covering the liver in *V. oyampiensis* [Lescure 1975]); this trait is a synapomorphy at this level of the phylogeny (also present in *Hyalinobatrachium*, *Chimerella*, and some species of *Teratohyla*). Also, most species in *Vitreorana* have a white gastrointestinal peritoneum (opaque in *V. eurygnatha* [Lutz 1925]). The combination of these two traits distinguishes *Vitreorana* from most centrolenid clades, except *Hyalinobatrachium*, *Chimerella*, and two species of *Teratohyla*. Most species in *Hyalinobatrachium* have white bones (green in *H. mesai* and *H. taylori*), dorsal coloration in preservative cream, and deposit their eggs on the undersides of leaves, whereas all species in *Vitreorana* have green bones and dorsal coloration in preservative lavender, and most deposit their eggs on the upper surfaces of leaves, the only exception being *V. eurygnatha* and *V. uranoscopa*, which have been observed to deposit their eggs on either the upper- or the under-side of leaves (Lutz 1947; C. Zank, pers. comm.). Morphologically, *Chimerella mariaelenae* resembles *V. gorzulae*. Although the phenotypic similarity between these species suggests an evolutionary relatedness (Cisneros-Heredia & McDiarmid 2006a), none of the genes studied supports a *Chimerella* + *Vitreorana* clade. See comments under *Chimerella*. *Vitreorana* is differentiated from *Teratohyla*

mainly by geographic distribution: species in *Teratohyla* occur in the lowlands of Central America and in the Pacific and Amazonian lowlands of South America, whereas *Vitreorana* (except *V. oyampiensis*, distributed from the Guiana region across western Amazonia) is restricted to the Cordillera de la Costa of Venezuela, Guiana Shield, and the Atlantic Forest.

CONTENT (8 SPECIES): *Vitreorana antisthenesi* (Goin 1963) new combination, *V. castroviejoi* (Ayarzagüena & Señaris 1996) new combination, *V. eurygnatha* (Lutz 1925) new combination, *V. gorzulae* (Ayarzagüena 1992) new combination, *V. helenae* (Ayarzagüena 1992) new combination, *V. oyampiensis* (Lescure 1975) new combination, *Vitreorana parvula* (Boulenger 1895) new combination, *V. uranoscopa* (Müller 1924) new combination. One additional species, *Cochranella ritae* (Lutz 1952), known only from the description (holotype is lost), could have name priority over *Vitreorana oyampiensis*. The description of *C. ritae* matches the general characteristics of *V. oyampiensis* (SVL, dorsal color pattern), but there are traits that add uncertainty to the hypothesis that the two species may be, in fact, only one species. For example, Lutz (1952) emphasizes that *C. ritae* has “large spatulate disks like those of *Centrolene geckoideum*” and a “snout round, declivous in front...” In contrast, *Vitreorana oyampiensis* has narrow disks and a round head (Guayasamin *et al.* 2008b). Given these differences, and to avoid arbitrary decisions, we prefer to keep recognizing the two species until material from the type locality of *C. ritae* is available or the holotype is found.

ETYMOLOGY: *Vitreorana* is derived from the Latin *vitreum*, meaning “glass,” and the Latin *rana*, meaning “frog.” The name refers to the total or partial transparency of the venter of these frogs. *Vitreorana* is feminine in gender.

DISTRIBUTION: Members of *Vitreorana* occur at elevations below 1900 m in the Cordillera de la Costa of Venezuela (*V. antisthenesi*, *V. castroviejoi*), Guiana Shield (*V. gorzulae*, *V. helenae*, *V. oyampiensis*) and Amazonia of Colombia and Ecuador (*V. oyampiensis*), and in the Atlantic Forest of Brazil and Argentina (*V. eurygnatha*, *V. parvula*, *V. uranoscopa*). See Figure 18.

COMMENTS: Based on morphology and behavior, we place *Hyalinobatrachium parvulum*, and *H. uranoscopum* in the genus *Vitreorana*. *Vitreorana parvula* and *V. uranoscopa* are hypothesized to be close relatives of *V. eurygnatha*, for which the available molecular data support placement in *Vitreorana*. Characters that suggest a close evolutionary relationship of the three species from the Atlantic Forest include the presence of guanophores on the urinary bladder, dentate vomers, green bones in life, and eggs usually deposited on the upper surface of leaves. Based on the molecular phylogeny, a white urinary bladder has evolved only two times in Centrolenidae, once in the clade of the three Atlantic Forest Glassfrogs, and one more time in the Andean *Nymphargus grandisonae*. The monophyly of the clade formed by *V. eurygnatha*, *V. parvula*, and *V. uranoscopa* already was suggested by Ruiz-Carranza & Lynch (1991a), who placed these taxa in the *Hyalinobatrachium parvulum* species group. The monophyly of *Vitreorana* is strongly supported in the trees inferred from the 16S, combined mitochondrial, combined nuclear, and complete datasets.

SUBFAMILY: **Hyalinobatrachinae** new subfamily

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Hylella fleischmanni* Boettger 1893, and *Centrolenella revocata* Rivero 1985.

TYPE GENUS: *Hyalinobatrachium* Ruiz-Carranza & Lynch 1991a.

SISTER TAXON: Uncertain (Figs. 3, 8). At the base, the relationships of Centrolenidae are uncertain; therefore, further gene sampling is needed to resolve the relatedness among Centroleninae, Hyalinobatrachinae, and *Ikakogi tayrona*.

DIAGNOSIS: Traits that diagnose Hyalinobatrachinae include: (1) when fighting, males in Hyalinobatrachinae assume an amplexus-like position (Bolívar *et al.* 1999; Kubicki 2007) or wrestle until one of the males throws the other off the leaf by thrusts with the hind legs (Kubicki 2007); these fighting behaviors differ from those in Centroleninae (Fig. 12); (2) males in all species in *Hyalinobatrachium* (except *H. taylori* [Goin 1968], see Ayarzagüena 1992; Señaris & Ayarzagüena 2005) and at least one of the two species of *Celsiella* (*C. revocata*) usually call from the undersides of leaves (Ruiz-Carranza & Lynch 1998;

Señaris & Ayarzagüena 2005); (3) females of *Hyalinobatrachium* deposit their egg masses on the undersides of leaves (Ruiz-Carranza & Lynch 1998), *Celsiella revocata* deposits eggs on both the upper side and underside of leaves, whereas *C. vozmedianoi* (Ayarzagüena & Señaris 1996) deposits the eggs on the upper side of leaves (Señaris & Ayarzagüena 2005; Castroviejo-Fisher pers. obs.); (4) parental care (i.e., male guarding egg clutches placed on the same leaf) is primary homology of Hyalinobatrachinae, and has been observed in several species of *Hyalinobatrachium* (*H. fleischmanni*, *H. chirripoi*, *H. colymbiphylum*, *H. talamancae*, *H. valerioi*, *H. vireovittatum*; Kubicki 2007) and in *Celsiella vozmedianoi*; (5) complete fusion between the tibiale and fibulare (Figs. 1, 11) is present in all species of Hyalinobatrachinae; (6) reduced prepollex (relative length < 50% of Metacarpal I) is present in several species (*Celsiella revocata*, *C. vozmedianoi*, *Hyalinobatrachium crurifasciatum*, *H. durantii*, *H. iaspidiense*, *H. mondolfii*, *H. munozorum*, *H. orientale*, *H. talori*; Señaris & Ayarzagüena 2005; this work) of Hyalinobatrachinae and we consider this character state as an untested derived homology of the subfamily; (7) crista medialis of the humerus absent (present in most species in Centroleninae, except *Espadarana andina*, "*Cochranella*" *balionota*, *Sachatamia albomaculata*, and *S. ilex*; Fig. 13); *Ikakogi tayrona* has an extremely large crista medialis, which extends along the entire length of the humerus (Fig. 13).

CONTENT (2 GENERA): *Celsiella* new genus, and *Hyalinobatrachium* Ruiz-Carranza & Lynch 1991a, as modified in this work.

ETYMOLOGY: The subfamily name Hyalinobatrachinae is derived from the genus *Hyalinobatrachium*.

DISTRIBUTION: Representatives of Hyalinobatrachinae occur at elevations up to 2500 m in tropical Central America, the tropical Andes, the coastal mountains of Venezuela, Tobago, the upper Amazon Basin, and the Guiana Shield (Fig. 19).

COMMENTS: The behavior of species in Hyalinobatrachinae needs to be studied in more detail to understand the extent of its phylogenetic significance. With the data at hand, it seems that the ancestral condition for Centrolenidae is calling and depositing eggs on the upper surfaces of leaves. *Celsiella vozmedianoi* displays the ancestral condition of these behaviors; *C. revocata* is polymorphic, and species in *Hyalinobatrachium* show the derived states (i.e., call and deposit eggs on the underside of leaves). This apparent transitional pattern on the reproductive behavior of glassfrogs needs further investigation, with emphasis on species of the genus *Celsiella*. The monophyly of the subfamily Hyalinobatrachinae is strongly supported by 12S, 16S, combined mitochondrial, combined nuclear, and complete datasets.

GENUS: *Celsiella* new genus

PHYLOGENETIC DEFINITION: A clade stemming from the most recent common ancestor of *Cochranella vozmedianoi* Ayarzagüena & Señaris 1996, and *Centrolenella revocata* Rivero 1985.

TYPE SPECIES: *Centrolenella revocata* Rivero 1985.

SISTER TAXON: *Hyalinobatrachium* Ruiz-Carranza & Lynch 1991a, as modified in this work.

DIAGNOSIS: The genus *Celsiella* can be differentiated from most other centrolenid genera by the following characters: (1) humeral spines absent; (2) trilobed liver, covered by a clear hepatic peritoneum; (3) ventral parietal peritoneum white anteriorly and transparent posteriorly; (4) bones pale green or green in life; (5) dorsum mainly cream in preservative; (6) males lack conspicuous spinules on the dorsum; (7) nuptial pads inconspicuous; (8) vomer lacking dentigerous process and teeth; (9) males call from the upper side of leaves in *C. vozmedianoi*, and from the upper- or undersides of leaves in *C. revocata* (Señaris & Ayarzagüena 2005), females deposit eggs on the upper side of leaves along streams in *C. vozmedianoi*, and on the upper- or underside of leaves in *C. revocata* (Señaris & Ayarzagüena 2005); (10) tibiale and fibulare fused. Observations suggest that the two species in *Celsiella* probably provide parental care to their egg clutches (male guarding egg clutches placed on the same leaf); if this is confirmed, parental care would be a synapomorphy of the subfamily Hyalinobatrachinae. *Celsiella* is morphologically similar to the genera *Nymphargus*, *Rulyrana*, and *Sachatamia*. None of the species in these three genera is known to deposit eggs on the underside of leaves. Furthermore, *Celsiella* has a reduced prepollex (length < 50% of Metacarpal I), whereas *Nymphargus*, *Rulyrana*, and *Sachatamia* have a long prepollex (length > 50% of Metacarpal I).

Hyalinobatrachium, the sister group of *Celsiella*, has a drastically different morphology (i.e., venter completely transparent, white liver, white bones).

CONTENT (2 SPECIES): *Celsiella vozmedianoi* (Ayarzagüena & Señaris 1996) new combination, and *C. revocata* (Rivero 1985) new combination.

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(4) white bones in life (Savage 1967), green in *H. mesai* and *H. taylori*; (5) dorsal coloration in preservative white or cream (Savage 1967); (6) males lack conspicuous dorsal spinules during breeding season; (7) when present, nuptial pad small and restricted to the inner edge of Finger I in males (Type V of Cisneros-Heredia & McDiarmid 2007; Fig. 7); (8) dentigerous process of the vomer and vomerine teeth absent (Ruiz-Carranza & Lynch 1991a; Savage 1967); (9) males usually vocalize from the underside of leaves, and females deposit one layer of eggs on the underside of leaves (Ruiz-Carranza & Lynch 1998); and (11) complete fusion of tibiale and fibulare. Other potential derived homologies of *Hyalinobatrachium* are the possession of small nasal bones widely separated from one another (Barrera-Rodríguez 2000; Señaris & Ayarzagüena 2005; Cisneros-Heredia & McDiarmid 2006a; this work) and two exposed parietal fontanelles (Señaris & Ayarzagüena 2005; for definition see Guayasamin & Trueb 2007). Exposed parietal fontanelles are evident in *H. colymbiphyllum*, *H. crurifasciatum*, *H. durantei*, *H. esmeralda*, *H. fleischmanni*, *H. fragile*, *H. iaspidiense*, *H. mondolfii*, *H. orientale*, *H. talamancae*, and *H. taylori* (Señaris & Ayarzagüena 2005; this study). However, this character state is not unambiguous for *Hyalinobatrachium*; the parietal fontanelles are partially or completely covered by bone in *H. aureoguttatum*, *H. bergeri*, and *H. chirripoi*. Additionally, *Espadarana andina*, *Centrolene hesperium*, *Vitreorana eurygnatha*, and *V. uranoscopa* present a similar derived character state (i.e., exposed parietal fontanelles). *Hyalinobatrachium* can be easily differentiated from most Glassfrog genera by having a completely transparent ventral parietal peritoneum and lacking humeral spines, traits that are otherwise present only in *Vitreorana* and some *Teratohyla* species. *Teratohyla*, however, has green bones (white in most *Hyalinobatrachium*, except *H. taylori* and *H. mesai*) and call from the upper sides of leaves (under sides of leaves in *Hyalinobatrachium*). Species in *Vitreorana* have green bones in life (white in *Hyalinobatrachium*) and lavender color in preservative (cream in *Hyalinobatrachium*). Also, most species in *Vitreorana* and *Teratohyla* deposit their eggs on the upper surfaces of leaves, whereas all species in *Hyalinobatrachium* deposit their eggs on the underside of leaves.

CONTENT (28 SPECIES): *Hyalinobatrachium aureoguttatum* (Barrera-Rodríguez & Ruiz-Carranza 1989), *H. bergeri* (Cannatella 1980), *H. chirripoi* (Taylor 1958), *H. colymbiphyllum* (Taylor 1949), *H. crurifasciatum* Myers & Donnelly 1997, *H. durantei* (Rivero 1985), *H. eccentricum* Myers & Donnelly 2001, *H. esmeralda* Ruiz-Carranza & Lynch 1998, *H. fleischmanni* (Boettger 1893), *H. fragile* (Rivero 1985), *H. guairarepanense* Señaris 2001, *H. iaspidiense* (Ayarzagüena 1992), *H. ibama* Ruiz-Carranza & Lynch 1998, *H. ignioculus* Noonan & Bonett 2003, *H. lemur* Duellman & Schulte 1993, *H. mesai* Barrio-Amorós & Brewer-Carias 2008, *H. mondolfii* Señaris & Ayarzagüena 2001, *H. munozorum* (Lynch & Duellman 1973), *H. nouraguense* Lescure & Marty 2000, *H. orientale* (Rivero 1968), *H. orocostale* (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, & Vilà 2007, *H. taylori* (Goin 1968), *H. valerioi* (Dunn 1931), *H. vireovittatum* (Starrett & Savage 1973). Although placement of most species in the genus *Hyalinobatrachium* was based on molecular data, a few were included only on the basis of morphological and behavioral characteristics (Appendix I); given that *Hyalinobatrachium* is a well-defined clade (diagnosis), the assignment of these species into the genus is unambiguous.

ETYMOLOGY: The name *Hyalinobatrachium* is derived from the Greek *hyalos* = glass, and *batrachion* = frog, in reference to the translucent and fragile aspect of the species in the genus (Ruiz-Carranza & Lynch 1991a). *Hyalinobatrachium* is neuter in gender.

DISTRIBUTION: *Hyalinobatrachium* has a wide distribution that includes tropical Central America, the tropical Andes, the Cordillera de la Costa of Venezuela, Tobago, the upper Amazon Basin, and the Guiana Shield, at elevations between sea level and 2500 m (Fig. 19).

COMMENTS: The *fleischmanni* Group was first recognized by Savage (1967) and corresponds to the *Hyalinobatrachium fleischmanni sensu* Ruiz-Carranza and Lynch (1991a, 1998). These two authors recognized three species groups within the genus *Hyalinobatrachium* (i.e., *fleischmanni*, *pulveratum*, and *parvulum*). Our results strongly show that *Hyalinobatrachium sensu* Ruiz-Carranza & Lynch 1991a) is polyphyletic. However, the *H. fleischmanni* Group (*sensu* Ruiz-Carranza & Lynch 1998) is monophyletic and we restrict the name *Hyalinobatrachium* to it, in agreement with the proposal presented by Cisneros-Heredia

and McDiarmid (2007). As noted above, *Hyalinobatrachium* (*sensu stricto*) is distinct morphologically and behaviorally. However, several of the traits listed in the diagnosis occur in other clades. For example, many species in *Vitreorana* have a transparent ventral parietal peritoneum and a white bulbous or lobed liver. Other species also are known to call from the underside of leaves (*Celsiella revocata*, *Centrolene peristictum*) and deposit eggs (*Celsiella revocata*, *Centrolene antioquiense*, *C. peristictum*) on the underside of leaves (Señaris & Ayarzagüena 2005, MR pers. obs., M. R. Bustamante, pers. comm.). Other characters, such as the absence of humeral spines, dentigerous process of the vomer, and the complete fusion of the tibiale and fibulare are widespread in the family. *Hyalinobatrachium*, as defined in this work, is strongly supported by the combined mitochondrial and the complete datasets.

INCERTAE SEDIS WITHIN CENTROLENIDAE: *Ikakogi* new genus

PHYLOGENETIC DEFINITION: A clade consisting of *Centrolene tayrona* Ruiz-Carranza & Lynch 1991b, and other species that share a more recent common ancestor with *C. tayrona* than with *Centrolene geckoideum* Jiménez de la Espada 1872, *Centrolenella revocata* Rivero 1985, and *Centrolenella antisthenesi* Goin 1963.

TYPE SPECIES: *Centrolene tayrona* Ruiz-Carranza & Lynch 1991b.

DIAGNOSIS: The combination of the following characteristics differentiates this taxon from other genera: (1) humerus with a conspicuous humeral spines and an extremely large crista medialis, which extends along the entire length of the humerus (Fig. 13); (2) white bones in life; (3) ventral parietal peritoneum white anteriorly and transparent posteriorly, and (4) hepatic and visceral peritonea transparent. There are two unusual behaviors in *Ikakogi tayrona*. So far, it is the only known centrolenid species in which females guard eggs clutches (MR, pers. obs.). In all other species that have paternal care, males protect their offspring (McDiarmid 1978; Ruiz-Carranza & Lynch 1998; Señaris & Ayarzagüena 2005; and references therein). Additionally, *I. tayrona* is polymorphic for the egg deposition site, egg clutches have been found on the upper and lower surfaces of leaves (MR, pers. obs.). The combination of having white bones and a humerus with conspicuous humeral spine and extremely large crista medialis (Fig. 13) in adult males differentiates *Ikakogi* from all other species in Centrolenidae. *Ikakogi tayrona* shares with Centroleninae the presence of a long prepollex (prepollex length > 50% of Metacarpal I length).

CONTENT (1 SPECIES): *Ikakogi tayrona* (Ruiz-Carranza & Lynch 1991b).

ETYMOLOGY: The name *Ikakogi* makes reference to the Ika (or Ijka) and Kogi people, descendants of the Tayrona, who inhabit the Sierra Nevada de Santa Marta, Colombia.

DISTRIBUTION: *Ikakogi tayrona* inhabits the cloud forests of the Sierra Nevada de Santa Marta (Ruiz-Carranza & Lynch 1991b), a mountain range completely isolated from other Andean moist forests by lower-elevation dry forests and xeric shrub lands (Fig. 16).

COMMENTS: The phylogenetic position of *Ikakogi tayrona* (Figs. 3, 8) indicates that this species diverged early in the evolutionary history of Glassfrogs. Although its external morphology is similar to that of species in *Centrolene* and *Espadarana*, the behavior of *I. tayrona* is certainly unusual, as noted above. Two nuclear genes (POMC, RAG1) show a weak support for a *Nymphargus* + *Ikakogi* clade; however, all the other genes were unable to resolve the placement of *I. tayrona*. Data from more loci are necessary to establish the phylogenetic position of *I. tayrona*; until then, we consider this species as *incertae sedis* within Centrolenidae.

Discussion

Centrolenidae, Allophrynidae, and Neobatrachia

The phylogenetic position of Centrolenidae within the diversity of Neobatrachia has been debated but not resolved with confidence either by molecular studies (Austin *et al.* 2002; Biju & Bossuyt 2003; Darst & Cannatella 2004; Faivovich *et al.* 2005; Wiens *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Roelants *et al.* 2007) or by phenotypic data (Jiménez de la Espada 1872; Noble 1931; Taylor 1951; Lynch 1973; Ford & Cannatella 1993; Duellman & Trueb 1994; Rueda-Almonacid 1994; Duellman 2001; Haas 2003; Burton

2004; Wiens *et al.* 2005). We attempted to address this issue in a previous study (Guayasamin *et al.* 2008a) using molecular data, and obtained results supporting an Allophrynidae + Centrolenidae clade. Herein, we propose the unranked taxon Allocentroleniae for the Centrolenidae + Allophrynidae clade, which was considered a family (i.e., Centrolenidae) by Frost *et al.* (2006). Our arrangement has the virtue of maintaining the names that have been used in recent decades (i.e., Centrolenidae, Allophrynidae). When naming clades under the rules of the ICZN (1999) or any other system, taxonomists should promote name stability. In a ranked system such as the ICZN, there are multiple available ranks above the genus and below the superfamily (Article 35.1; ICZN); however, only few of these ranks are commonly used by systematists. As mentioned before, we had the option of erecting an intermediate rank (e.g., Subsuperfamily) to recognize the Centrolenidae + Allophrynidae clade, but such a rank, we think, would have created more confusion. Instead, we favored a simpler alternative, creating an unranked taxon. It is clear that, if we want to avoid constant rank shifting to accommodate the need of formalizing new ranks, the Linnaean system needs modification. There are only a limited number of ranks to name all the diversity of life. Unranked names solve that problem (see Cantino & de Queiroz 2007, and references therein).

The relationships of Allocentroleniae and other anurans remain uncertain. Although some studies suggest Leptodactylidae or Leiuperidae as the sister taxon of Allocentroleniae (Frost *et al.* 2006; Guayasamin *et al.* 2008a), it is evident that more nuclear loci will be necessary to clarify the relationships within Hyloidea.

The new taxonomy

There is consensus among biologists that taxonomic classifications should reflect evolutionary history and relationships between organisms. However, it is difficult to imagine a classification system that could capture all the complexity of the processes involved in the evolution of life. This is true even at the most basic level of taxonomy—there is no consensus in how to define taxonomic categories (e.g., Henning 1966; Avise & Johns 1999; ICZN 1999; Cantino & de Queiroz 2007). For example, Hennig (1966) proposed that supraspecific groups that have equivalent age should have the same Linnaean rank, allowing for evolutionary significant comparisons among all organisms. As currently used, most Linnaean ranks are not comparable because groups having the same rank usually are not the same age, a fact that tends to confuse people not familiar with systematics. However, in most of the cases, including the classification presented herein, the commonly used Linnaean ranks do reflect information related to the phenotypic distinctiveness of taxa, their distribution, and/or ecology. At the moment, we see that reaching a new consensus for naming ranks is problematic, and prefer to maintain the traditional system (i.e., ICZN), with some modifications suggested in the PhyloCode (e.g., phylogenetic definitions), and the criteria listed above (see Criteria for taxon naming section).

One could argue that a disadvantage of our classification is the number of new genera described. Since Jiménez de la Espada described the first Glassfrog in 1872, six genera have been recognized (*Centrolene*, *Centrolenella*, *Cochranella*, *Hyalinobatrachium*, *Nymphargus*, and *Teratohyla*), and our proposal adds seven new genera. Nevertheless, the recognition of these new genera is a necessary step to establish a taxonomy where supraspecific taxa are monophyletic and can be, in most cases, diagnosed using morphology and behavior.

We have attempted to provide a scheme whereby genera are presented as natural groups that have statistical support and phenotypically diagnosable. We have argued before that the main goal of our taxonomy is to deliver a stable classification that reflects evolutionary relationships. Also, we have prioritized the morphological diagnoses of genera to the detriment of, for example, the relative age of clades (e.g., *Hyalinobatrachium* is much older genus than *Espadarana*, and therefore, not comparable). Other examples related to our desire to provide stable and diagnosable clades include our decision to recognize *Celsiella* as a separate genus (i.e., excluded from *Hyalinobatrachium*) and to split the tribe Cochranellini into seven genera, five of them new. It is clear that a classification with only four genera *Centrolene*, *Cochranella* (= Cochranellini), *Hyalinobatrachium* (= Hyalinobatrachinae), and *Nymphargus* would have been less of shock for those used to the current taxonomy of centrolenids. Our arrangement, however, has several benefits. It recognizes two fully diagnosable clades (i.e., *Hyalinobatrachium* and *Celsiella*) and makes this relationship

explicit by naming it (i.e., Hyalinobatrachinae). The phenotypic disparity within Cochranellini is even more dramatic. Species in Cochranellini show such an amalgam of phenotypes that assigning this clade to the genus rank would make species placement futile. Therefore, we preferred to navigate the tree towards the tips to find stable clades that could be diagnosed at the cost of creating new names. On the other hand, the new taxonomy transmits evolutionary, morphological, behavioral, and biogeographical information that, from all perspectives, is beneficial to biologists and non-biologists.

We could not resolve the phylogenetic position of the new genus *Ikakogi*; hence, we treated it as *incertae sedis*. There is agreement between the mitochondrial and nuclear datasets in suggesting that *I. tayrona* is an early divergent species within Centrolenidae (Fig. 8). Given that the Sierra Nevada de Santa Marta seems to be an older geological formation than the Andes (Tschanz *et al.* 1974), it is not surprising that old lineages are found in the area. Additionally, the small size and isolation of the Sierra Nevada from other cloud forests offers an explanation for the occurrence of only one species in the clade (i.e., lack of possibilities for dispersal and speciation).

Generic placement of species. The mechanics of taxonomy require the use of the binomen (genus and species). Therefore, users of this (or any) taxonomy are accepting, explicitly or implicitly, a hypothesis of relationships given by the genus. Despite our efforts, we could not assign with enough confidence around 16% of the described species of Glassfrogs (Appendix I) because molecular data were not available and phenotypic traits were ambiguous. We imagine that other taxonomists will encounter similar difficulties when describing new species based solely on morphological characters. However, investigators always can tentatively assign species to a genus, and their hypothesis will be re-evaluated as more data become available. Alternately, sequencing short fragments of DNA would allow assigning species to clades with high confidence (Wiens *et al.* 2005). Cases in which we are uncertain about the generic placement of a particular species are listed in Appendix I. Individuals working with centrolenid frogs are invited to follow the system presented in Appendix I, in which phylogenetic uncertainty is clearly labeled. We consider it preferable to recognize those species that have equivocal phylogenetic placement to reduce the chance of erroneous evolutionary interpretations of their ecology, morphology, or behavior.

Unresolved Clades. Throughout the Results section, we have noted that the relationships among some clades, especially at the genus level, are unresolved or resolved with low support (e.g., genera within Cochranellini). Polytomies and poorly supported clades can result from several evolutionary processes, the quality of the data and the way in which it is analyzed, and deviations between gene trees and species trees. For example, rapid radiations in which a single common ancestor gives rise to multiple distinct lineages at the same time produce hard polytomies, meaning that the polytomy reflects the true evolutionary relationships among the lineages. On the other hand, rapid but successive branching of lineages can produce soft polytomies, where the inferred internodes are short and poorly supported; in this case, adding data should allow recovering the dichotomous branching pattern. In other cases, poor resolution is a function of the quality of the data, which may prove to not be variable enough to resolve the topology with confidence. Finally, gene phylogeny can differ from the species phylogeny as a result of undetected gene duplication (i.e., hidden paralogy), lineage sorting of multiple alleles, and horizontal gene transfer or gene conversion.

There is accumulating evidence indicating that the radiation of Hyloidea corresponds to a rapid and ancient event (e.g., Darst & Cannatella 2004; Wiens *et al.* 2005; Roelants *et al.* 2007, Guayasamin *et al.* 2008a). We speculate that this could also be the case in some clades of Centrolenidae that likely radiated in parallel with the uplift of the Andes.

In principle, the relationships underlying soft polytomies can be resolved by adding data. However, the type and amount of data necessary to solve these problems are uncertain, and currently the subject of an intense debate among phylogeneticists (e.g., Whitfield & Lockhart 2007; Philippe & Telford 2006; Gatesy *et al.* 2007). Expressed sequence tags, genome-level characters, large genome comparisons, and sequence of more than 20 genes have been proposed as ways to improve phylogenetic accuracy (e.g., Rokas *et al.* 2003;

Boore 2006; Philippe & Telford 2006; Whitfield & Lockhart 2007; Gatesy *et al.* 2007). However, to solve relationships of recent radiations, mitochondrial genes are most likely to provide correct topologies because their shorter coalescence time (Zink & Barrowclough 2008).

Conclusions

We formalize the evolutionary proximity of Centrolenidae and Allophrynidae with the name Allocentroleniinae. This arrangement maintains the validity and species content of the two families, avoiding nomenclatural instability (Fig. 9).

The proposed taxonomy of Glassfrogs (Fig. 3) is our attempt to formalize the recent findings presented in a previous study (Guayasamin *et al.* 2008a). Our taxonomy drastically differs from previous arrangements, which relied on few phenotypic traits that have been shown to be homoplastic (Guayasamin *et al.* 2008a); therefore, in most of the cases, previous classifications recognized para- or polyphyletic groups. A limitation of our proposal is that is based on an incomplete taxon sampling (54% of the recognized Glassfrogs). Although we provide diagnoses based on phenotypic traits, there are several cases in which the allocation of species is ambiguous when molecular data are lacking (Appendix I). We encourage researchers interested in the centrolenids frogs to focus their efforts on these species. Another unanticipated result that deserves further investigation is the evolutionary relationship of *Ikakogi tayrona* and other Glassfrogs. The data at hand suggest that *I. tayrona* is the representative of a clade that is as old as the subfamilies Hyalinobatrachinae and Centroleniinae. If this hypothesis were confirmed, studying the morphology and behavior of *I. tayrona* would be of great importance for understanding the evolution of traits and biogeography of Glassfrogs. Finally, we stress that ranks, and particularly genera, herein proposed are not comparable evolutionary units (a problem shared by most classifications) unless they are sister to each other or have approximately the same age.

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APPENDIX I. Current and new generic taxonomy of Glassfrogs (Centrolenidae). The current taxonomy follows the classification proposed by Ruiz-Carranza & Lynch (1991a), with the addition of *Nymphargus* Cisneros-Heredia & McDiarmid 2007. In the new taxonomy, placement of species is based on molecular data. *Species for which no molecular data were available, but that have morphological and/or behavioral characteristics that allow a tentative generic placement. **Species that we consider *Incertae sedis* within Centroleninae because molecular data are not available, and morphological and behavioral characters do not provide unambiguous evidence on their generic placement; for these species, we suggest to maintain the generic names provided in the current taxonomy (*sensu* Ruiz-Carranza & Lynch 1991a), adding quotation to denote their uncertain phylogenetic position and to differentiate them from monophyletic clades. Molecular data is necessary for establishing the exact phylogenetic relationships of species.

SPECIES	AUTHOR	ORIGINAL GENUS	CURRENT TAXONOMY	NEW TAXONOMY
<i>acanthidiocephala</i>	Ruiz-Carranza & Lynch 1989	<i>Centrolenella</i>	<i>Centrolene acanthidiocephalum</i>	** " <i>Centrolene</i> " <i>acanthidiocephalum</i>
<i>adenocheira</i>	Harvey & Noonan 2005	<i>Cochranella</i>	<i>Cochranella adenocheira</i>	** " <i>Cochranella</i> " <i>adenocheira</i>
<i>adiazeta</i>	Ruiz-Carranza & Lynch 1991d	<i>Cochranella</i>	<i>Cochranella adiazeta</i>	<i>Rulyrana adiazeta</i>
<i>albomaculata</i>	Taylor 1949	<i>Centrolenella</i>	<i>Cochranella albomaculata</i>	<i>Sachatamia albomaculata</i>
<i>altitudinalis</i>	Rivero 1968	<i>Centrolenella</i>	<i>Centrolene altitudinale</i>	<i>Centrolene altitudinale</i>
<i>amelie</i>	Cisneros-Heredia & Meza-Ramos 2007	<i>Cochranella</i>	<i>Cochranella amelie</i>	<i>Teratohyla amelie</i>
<i>andina</i>	Rivero 1968	<i>Centrolenella</i>	<i>Centrolene andinum</i>	<i>Espadarana andina</i>
<i>anomala</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Nymphargus anomalus</i>	* <i>Nymphargus anomalus</i>
<i>antioquiensis</i>	Noble 1920	<i>Centrolenella</i>	<i>Centrolene antioquiense</i>	<i>Centrolene antioquiense</i>
<i>antisthenesi</i>	Goin 1963	<i>Centrolenella</i>	<i>Hyalinobatrachium antisthenesi</i>	<i>Vitreorana antisthenesi</i>
<i>armata</i>	Lynch & Ruiz-Carranza 1996	<i>Cochranella</i>	<i>Nymphargus armatus</i>	* <i>Nymphargus armatus</i>
<i>audax</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Centrolene audax</i>	** " <i>Centrolene</i> " <i>audax</i>
<i>aureoguttata</i>	Barrera-Rodríguez & Ruiz-Carranza 1989	<i>Centrolenella</i>	<i>Hyalinobatrachium aureoguttatum</i>	<i>Hyalinobatrachium aureoguttatum</i>
<i>azulae</i>	Flores & McDiarmid 1989	<i>Centrolenella</i>	<i>Centrolene azulae</i>	** " <i>Centrolene</i> " <i>azulae</i>
<i>bacatum</i>	Wild 1994	<i>Centrolene</i>	<i>Centrolene bacatum</i>	<i>Centrolene bacatum</i>
<i>balionota</i>	Duellman 1981	<i>Centrolenella</i>	<i>Cochranella balionota</i>	** " <i>Cochranella</i> " <i>balionota</i>
<i>ballux</i>	Duellman & Burrowes 1989	<i>Centrolenella</i>	<i>Centrolene ballux</i>	** " <i>Centrolene</i> " <i>ballux</i>
<i>bejaranoi</i>	Cannatella 1980	<i>Centrolenella</i>	<i>Nymphargus bejaranoi</i>	<i>Nymphargus bejaranoi</i>
<i>bergeri</i>	Cannatella 1980	<i>Centrolenella</i>	<i>Hyalinobatrachium bergeri</i>	<i>Hyalinobatrachium bergeri</i>
<i>buckleyi</i>	Boulenger 1882	<i>Hylella</i>	<i>Centrolene buckleyi</i>	<i>Centrolene buckleyi</i>
<i>buckleyi venezuelensis</i>	Rivero 1968	<i>Centrolenella</i>	<i>Centrolene venezuelense</i>	<i>Centrolene venezuelense</i>
<i>buenaventura</i>	Cisneros-Heredia & Yáñez-Muñoz 2007	<i>Cochranella</i>	<i>Nymphargus buenaventura</i>	* <i>Nymphargus buenaventura</i>

SPECIES	AUTHOR	ORIGINAL GENUS	CURRENT TAXONOMY	NEW TAXONOMY
<i>callistommum</i>	Guayasamin & Trueb 2007	<i>Centrolene</i>	<i>Centrolene callistommum</i>	<i>Espadarana callistomma</i>
<i>cariticommatata</i>	Wild 1994	<i>Cochranella</i>	<i>Nymphargus cariticommatatus</i>	* <i>Nymphargus cariticommatatus</i>
<i>castroviejoi</i>	Ayarzagüena & Señaris 1996	<i>Cochranella</i>	<i>Cochranella castroviejoi</i>	<i>Vitreorana castroviejoi</i>
<i>chami</i>	Ruiz-Carranza & Lynch 1995b	<i>Cochranella</i>	<i>Nymphargus chami</i>	* <i>Nymphargus chami</i>
<i>chancas</i>	Duellman & Schulte 1993	<i>Cochranella</i>	<i>Nymphargus chancas</i>	* <i>Nymphargus chancas</i>
<i>chirripoi</i>	Taylor 1958	<i>Cochranella</i>	<i>Hyalinobatrachium chirripoi</i>	<i>Hyalinobatrachium chirripoi</i>
<i>cochranae</i>	Goin 1961	<i>Cochranella</i>	<i>Nymphargus cochranae</i>	<i>Nymphargus cochranae</i>
<i>colymbiphyllum</i>	Taylor 1949	<i>Centrolenella</i>	<i>Hyalinobatrachium colymbiphyllum</i>	<i>Hyalinobatrachium colymbiphyllum</i>
<i>condor</i>	Cisneros-Hereida & Morales-Mite 2008	<i>Centrolene</i>	<i>Centrolene condor</i>	* <i>Centrolene condor</i>
<i>cristinae</i>	Ruiz-Carranza & Lynch 1995b	<i>Cochranella</i>	<i>Nymphargus cristinae</i>	* <i>Nymphargus cristinae</i>
<i>croceopodes</i>	Duellman & Schulte 1993	<i>Cochranella</i>	<i>Cochranella croceopodes</i>	** “ <i>Cochranella</i> ” <i>croceopodes</i>
<i>crurifasciatum</i>	Myers & Donnelly 1997	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium crurifasciatum</i>	<i>Hyalinobatrachium crurifasciatum</i>
<i>daidalea</i>	Ruiz-Carranza & Lynch 1991c	<i>Cochranella</i>	<i>Cochranella daidalea</i>	<i>Centrolene daidaleum</i>
<i>duidaeana</i>	Ayarzagüena 1992	<i>Centrolenella</i>	<i>Cochranella duidaeana</i>	** “ <i>Cochranella</i> ” <i>duidaeana</i>
<i>duranti</i>	Rivero 1985	<i>Centrolenella</i>	<i>Hyalinobatrachium durantei</i>	<i>Hyalinobatrachium durantei</i>
<i>durrellorum</i>	Cisneros-Heredia 2007	<i>Centrolene</i>	<i>Centrolene durrellorum</i>	** “ <i>Centrolene</i> ” <i>durrellorum</i>
<i>eccentricum</i>	Myers & Donnelly 2001	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium eccentricum</i>	<i>Hyalinobatrachium eccentricum</i>
<i>erminea</i>	Torres-Gastello, Suárez-Segovia, & Cisneros-Heredia 2007	<i>Cochranella</i>	<i>Cochranella erminea</i>	* <i>Rulyrana erminea</i>
<i>esmeralda</i>	Ruiz-Carranza & Lynch 1998	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium esmeralda</i>	* <i>Hyalinobatrachium esmeralda</i>
<i>euhystrix</i>	Cadle & McDiarmid 1990	<i>Centrolenella</i>	<i>Cochranella euhystrix</i>	** “ <i>Cochranella</i> ” <i>euhystrix</i>
<i>euknemos</i>	Savage & Starrett 1967	<i>Centrolenella</i>	<i>Cochranella euknemos</i>	<i>Cochranella euknemos</i>
<i>eurygnatha</i>	Lutz 1925	<i>Hyla</i>	<i>Hyalinobatrachium eurygnathum</i>	<i>Vitreorana eurygnatha</i>
<i>fernandoi</i>	Duellman & Schulte 1993	<i>Centrolene</i>	<i>Centrolene fernandoi</i>	** “ <i>Centrolene</i> ” <i>fernandoi</i>
<i>flavopunctata</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Cochranella flavopunctata</i>	<i>Rulyrana flavopunctata</i>

SPECIES	AUTHOR	ORIGINAL GENUS	CURRENT TAXONOMY	NEW TAXONOMY
<i>fleischmanni</i>	Boettger 1893	<i>Hylella</i>	<i>Hyalinobatrachium fleischmanni</i>	<i>Hyalinobatrachium fleischmanni</i>
<i>fragilis</i>	Rivero 1985	<i>Centrolenella</i>	<i>Hyalinobatrachium fragile</i>	<i>Hyalinobatrachium fragile</i>
<i>garciae</i>	Ruiz-Carranza & Lynch 1995a	<i>Cochranella</i>	<i>Nymphargus garciae</i>	<i>Nymphargus garciae</i>
<i>geckoideum</i>	Jiménez de la Espada 1872	<i>Centrolene</i>	<i>Centrolene geckoideum</i>	<i>Centrolene geckoideum</i>
<i>geijskesi</i>	Goin 1966	<i>Centrolenella</i>	<i>Cochranella geijskesi</i>	** " <i>Cochranella</i> " <i>geijskesi</i>
<i>gemmata</i>	Flores 1985	<i>Centrolenella</i>	<i>Centrolene gemmatum</i>	* <i>Centrolene gemmatum</i>
<i>gorzulae</i>	Ayarzagüena 1992	<i>Centrolenella</i>	<i>Centrolene gorzulai</i>	<i>Vitreorana gorzulae</i>
<i>grandisonae</i>	Cochran & Goin 1970	<i>Centrolenella</i>	<i>Centrolene grandisonae</i>	<i>Nymphargus grandisonae</i>
<i>granulosa</i>	Taylor 1949	<i>Centrolenella</i>	<i>Cochranella granulosa</i>	<i>Cochranella granulosa</i>
<i>griffithsi</i>	Goin 1961	<i>Cochranella</i>	<i>Nymphargus griffithsi</i>	<i>Nymphargus griffithsi</i>
<i>guairarepanensis</i>	Señaris 2001	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium guairarepanensis</i>	* <i>Hyalinobatrachium guairarepanense</i>
<i>guanacarum</i>	Ruiz-Carranza & Lynch 1995c	<i>Centrolene</i>	<i>Centrolene guanacarum</i>	** " <i>Centrolene</i> " <i>guanacarum</i>
<i>helenae</i>	Ayarzagüena 1992	<i>Centrolenella</i>	<i>Cochranella helenae</i>	<i>Vitreorana helenae</i>
<i>heloderma</i>	Duellman 1981	<i>Centrolenella</i>	<i>Centrolene heloderma</i>	* <i>Centrolene heloderma</i>
<i>hesperia</i>	Cadle & McDiarmid 1990	<i>Centrolenella</i>	<i>Centrolene hesperium</i>	<i>Centrolene hesperium</i>
<i>huilense</i>	Ruiz-Carranza & Lynch 1995c	<i>Centrolene</i>	<i>Centrolene huilense</i>	** " <i>Centrolene</i> " <i>huilense</i>
<i>hybrida</i>	Ruiz-Carranza & Lynch 1991b	<i>Centrolene</i>	<i>Centrolene hybrida</i>	<i>Centrolene hybrida</i>
<i>iaspidiensis</i>	Ayarzagüena 1992	<i>Centrolenella</i>	<i>Hyalinobatrachium iaspidiense</i>	<i>Hyalinobatrachium iaspidiense</i>
<i>ibama</i>	Ruiz-Carranza & Lynch 1998	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium ibama</i>	<i>Hyalinobatrachium ibama</i>
<i>ignioculus</i>	Noonan & Bonett 2003	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium ignioculus</i>	<i>Hyalinobatrachium ignioculus</i>
<i>ignota</i>	Lynch 1990	<i>Centrolenella</i>	<i>Nymphargus ignotus</i>	* <i>Nymphargus ignotus</i>
<i>ilex</i>	Savage 1967	<i>Centrolenella</i>	<i>Centrolene ilex</i>	<i>Sachatamia ilex</i>
<i>laurae</i>	Cisneros-Heredia & McDiarmid 2007	<i>Nymphargus</i>	<i>Nymphargus laurae</i>	* <i>Nymphargus laurae</i>
<i>lemniscatum</i>	Duellman & Schulte 1993	<i>Centrolene</i>	<i>Centrolene lemniscatum</i>	* <i>Centrolene lemniscatum</i>
<i>lemur</i>	Duellman & Schulte 1993	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium lemur</i>	* <i>Hyalinobatrachium lemur</i>
<i>litoralis</i>	Ruiz-Carranza & Lynch 1996	<i>Centrolene</i>	<i>Centrolene litorale</i>	<i>Cochranella litoralis</i>
<i>luminosa</i>	Ruiz-Carranza & Lynch 1995b	<i>Cochranella</i>	<i>Nymphargus luminosa</i>	* <i>Nymphargus luminosus</i>

SPECIES	AUTHOR	ORIGINAL GENUS	CURRENT TAXONOMY	NEW TAXONOMY
<i>luteopunctata</i>	Ruiz-Carranza & Lynch 1996	<i>Cochranella</i>	<i>Nymphargus luteopunctatus</i>	* <i>Nymphargus luteopunctatus</i>
<i>lynchi</i>	Duellman 1980	<i>Centrolenella</i>	<i>Centrolene lynchi</i>	* <i>Centrolene lynchi</i>
<i>mache</i>	Guayasamin & Bonaccorso 2004	<i>Cochranella</i>	<i>Cochranella mache</i>	<i>Cochranella mache</i>
<i>mariae</i>	Duellman & Toft 1979	<i>Centrolenella</i>	<i>Centrolene mariae</i>	* <i>Nymphargus mariae</i>
<i>mariaelena</i>	Cisneros-Heredia & McDiarmid 2006	<i>Centrolene</i>	<i>Centrolene mariaelena</i>	<i>Chimerella mariaelena</i>
<i>mcdiarmidi</i>	Cisneros-Heredia, Venegas, Rada & Schulte 2008	<i>Cochranella</i>	<i>Cochranella mcdiarmidi</i>	* <i>Rulyrana mcdiarmidi</i>
<i>medemi</i>	Cochran & Goin 1970	<i>Centrolenella</i>	<i>Centrolene medemi</i>	** “ <i>Centrolene</i> ” <i>medemi</i>
<i>megacheira</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Nymphargus megacheirus</i>	<i>Nymphargus megacheirus</i>
<i>megista</i>	Rivero 1985	<i>Centrolenella</i>	<i>Cochranella megista</i>	** “ <i>Cochranella</i> ” <i>megista</i>
<i>mesai</i>	Barrio-Amorós & Brewer-Carías 2008	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium mesai</i>	* <i>Hyalinobatrachium mesai</i>
<i>midas</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Cochranella midas</i>	<i>Teratohyla midas</i>
<i>mixomaculata</i>	Guayasamin, Lehr, Rodriguez & Aguilar 2006b	<i>Cochranella</i>	<i>Nymphargus mixomaculatus</i>	<i>Nymphargus mixomaculatus</i>
<i>mondolfii</i>	Señaris & Ayarzagüena 2001	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium mondolfii</i>	<i>Hyalinobatrachium mondolfii</i>
<i>muelleri</i>	Duellman & Schulte 1993	<i>Centrolene</i>	<i>Centrolene muelleri</i>	* <i>Centrolene muelleri</i>
<i>munozorum</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Hyalinobatrachium munozorum</i>	<i>Hyalinobatrachium munozorum</i>
<i>nephelophila</i>	Ruiz-Carranza & Lynch 1991d	<i>Cochranella</i>	<i>Nymphargus nephelophila</i>	* <i>Nymphargus nephelophilus</i>
<i>nola</i>	Harvey 1996	<i>Cochranella</i>	<i>Cochranella nola</i>	<i>Cochranella nola</i>
<i>notostictum</i>	Ruiz-Carranza & Lynch 1991b	<i>Centrolene</i>	<i>Centrolene notostictum</i>	<i>Centrolene notostictum</i>
<i>nouraguensis</i>	Lescure & Marty 2000	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium nouraguensis</i>	<i>Hyalinobatrachium nouraguense</i>
<i>ocellata</i>	Boulenger 1918	<i>Hylella</i>	<i>Cochranella ocellata</i>	* <i>Nymphargus ocellatus</i>
<i>orejuela</i>	Duellman & Burrowes 1989	<i>Centrolenella</i>	<i>Cochranella orejuela</i>	** “ <i>Cochranella</i> ” <i>orejuela</i>
<i>oreonympha</i>	Ruiz-Carranza & Lynch 1991d	<i>Cochranella</i>	<i>Nymphargus oreonympha</i>	* <i>Nymphargus oreonympha</i>
<i>orientalis</i>	Rivero 1968	<i>Centrolenella</i>	<i>Hyalinobatrachium orientale</i>	<i>Hyalinobatrachium orientale</i>
<i>orocostalis</i>	Rivero 1968	<i>Centrolenella</i>	<i>Hyalinobatrachium orocostalis</i>	<i>Hyalinobatrachium orocostale</i>
<i>oyampiensis</i>	Lescure 1975	<i>Cochranella</i>	<i>Cochranella oyampiensis</i>	<i>Vitreorana oyampiensis</i>

SPECIES	AUTHOR	ORIGINAL GENUS	CURRENT TAXONOMY	NEW TAXONOMY
<i>paezorum</i>	Ruiz-Carranza Hernández-Camacho & Ardila-Robayo 1986	<i>Centrolene</i>	<i>Centrolene paezorum</i>	* <i>Centrolene paezorum</i>
<i>pallida</i>	Rivero 1985	<i>Centrolenella</i>	<i>Hyalinobatrachium pallidum</i>	<i>Hyalinobatrachium pallidum</i>
<i>parvula</i>	Boulenger 1895	<i>Hylella</i>	<i>Hyalinobatrachium parvulum</i>	* <i>Vitreorana parvula</i>
<i>pellucida</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Hyalinobatrachium pellucidum</i>	<i>Hyalinobatrachium pellucidum</i>
<i>peristicta</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Centrolene peristictum</i>	<i>Centrolene peristictum</i>
<i>petrophilum</i>	Ruiz-Carranza & Lynch 1991b	<i>Centrolene</i>	<i>Centrolene petrophilum</i>	** " <i>Centrolene</i> " <i>petrophilum</i>
<i>phenax</i>	Cannatella & Duellman 1982	<i>Centrolenella</i>	<i>Nymphargus phenax</i>	* <i>Nymphargus phenax</i>
<i>phryxa</i>	Aguayo & Harvey 2006	<i>Cochranella</i>	<i>Cochranella phryxa</i>	* <i>Cochranella phryxa</i>
<i>pipilata</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Centrolene pipilatum</i>	<i>Centrolene pipilatum</i>
<i>pluvialis</i>	Cannatella & Duellman 1982	<i>Centrolenella</i>	<i>Nymphargus pluvialis</i>	<i>Nymphargus pluvialis</i>
<i>posadae</i>	Ruiz-Carranza & Lynch 1995a	<i>Cochranella</i>	<i>Nymphargus posadae</i>	<i>Nymphargus posadae</i>
<i>prasina</i>	Duellman 1981	<i>Centrolenella</i>	<i>Nymphargus prasinus</i>	* <i>Nymphargus prasinus</i>
<i>prosolepon</i>	Boettger 1892	<i>Hyla</i>	<i>Centrolene prosolepon</i>	<i>Espadarana prosolepon</i>
<i>pulverata</i>	Peters 1873	<i>Hyla</i>	<i>Hyalinobatrachium pulveratum</i>	<i>Teratohyla pulverata</i>
<i>punctulata</i>	Ruiz-Carranza & Lynch 1995a	<i>Cochranella</i>	<i>Cochranella punctulata</i>	<i>Sachatamia punctulata</i>
<i>puyoensis</i>	Flores & McDiarmid 1989	<i>Centrolenella</i>	<i>Cochranella puyoensis</i>	<i>Nymphargus puyoensis</i>
<i>quindianum</i>	Ruiz-Carranza & Lynch 1995c	<i>Centrolene</i>	<i>Centrolene quindianum</i>	** " <i>Centrolene</i> " <i>quindianum</i>
<i>ramirezi</i>	Ruiz-Carranza & Lynch 1991c	<i>Cochranella</i>	<i>Cochranella ramirezi</i>	** " <i>Cochranella</i> " <i>ramirezi</i>
<i>resplendens</i>	Lynch & Duellman 1973	<i>Centrolenella</i>	<i>Cochranella resplendens</i>	* <i>Cochranella resplendens</i>
<i>revocata</i>	Rivero 1985	<i>Centrolenella</i>	<i>Cochranella revocata</i>	<i>Celsiella revocata</i>
<i>ritae</i>	Lutz 1952	<i>Centrolene</i>	<i>Cochranella ritae</i>	** " <i>Cochranella</i> " <i>ritae</i>
<i>riveroi</i>	Ayarzagüena 1992	<i>Centrolenella</i>	<i>Cochranella riveroi</i>	** " <i>Cochranella</i> " <i>riveroi</i>
<i>robledoi</i>	Ruiz-Carranza & Lynch 1995c	<i>Centrolene</i>	<i>Centrolene robledoi</i>	** " <i>Centrolene</i> " <i>robledoi</i>
<i>rosada</i>	Ruiz-Carranza & Lynch 1997	<i>Cochranella</i>	<i>Nymphargus rosada</i>	<i>Nymphargus rosadus</i>
<i>ruedai</i>	Ruiz-Carranza & Lynch 1998	<i>Hyalinobatrachium</i>	<i>Hyalinobatrachium ruedai</i>	* <i>Hyalinobatrachium ruedai</i>
<i>ruizi</i>	Lynch 1993	<i>Cochranella</i>	<i>Nymphargus ruizi</i>	* <i>Nymphargus ruizi</i>
<i>sanchezi</i>	Ruiz-Carranza & Lynch 1991b	<i>Centrolene</i>	<i>Centrolene sanchezi</i>	* <i>Centrolene sanchezi</i>
<i>savagei</i>	Ruiz-Carranza & Lynch 1991c	<i>Cochranella</i>	<i>Cochranella savagei</i>	<i>Centrolene savagei</i>

SPECIES	AUTHOR	ORIGINAL GENUS	CURRENT TAXONOMY	NEW TAXONOMY
<i>saxiscandens</i>				

APPENDIX II. Specimens examined.

Allophryne: *ruthveni*, KU 166713, 167756.

Celsiella: *revocata*, MHNLS 13352, 17319 (topotypes); *vozmedianoi*, MHNLS 13355 (holotype), 16427, 16430, 17877 (topotypes).

Centrolene: *altitudinale* MHNLS 17194, 17225 (topotypes); *antioquiense* ICN 19649, *bacatum*, KU 202807–12 (paratypes), 170116; *buckleyi*, KU 118006, 148429–30, 155481, 155483, 155485, 164505, 164509–11, 164513, 164515, QCAZ 22388, 26031–32; *fernandoi*, KU 211771–75 (paratypes); *geckoideum*, MNCN 1596 (holotype); KU 164490, 164492, ICN 5598; *gemmatum*, MCZ A-104074, A-104077; *guanacarium*, ICN 11685; *heloderma*, KU 164714–15; *hesperium*, FMNH 232502; *lemniscatus*, KU 217300 (holotype); *lynchi*, KU 164692–99 (paratypes); *muelleri*, KU 217301 (holotype); *paezorum*, ICN 11866 (holotype); *peristicum*, KU 118051–52; *pipilatum*, KU 143279–82, 143286 (paratypes); *scirtetes*, KU 202720 (holotype); *sanchezi*, ICN 24294 (paratype); *solitaria*, ICN 24298 (holotype); *venezuelense* ULABG 2096–9.

"*Centrolene*": *audax*, KU 143290, 143292 (paratypes); *ballux*, KU 164725–27; *huilense*, KU 169720–47; *quindianum*, ICN 24920.

Chimerella: *mariaelenae*, QCAZ 21252, 22363, 31729.

Cochranella: *euknemos*, KU 77534; *granulosa* SMF 78562, 82896; *litoralis*, ICN 13821, QCAZ 27693; *mache*, QCAZ 22412 (holotype), 31327; *nola* MNCN 42682; *resplendens*, KU 118053 (holotype);

"*Cochranella*": *balionota*, KU 164703–11 (paratypes), ICN 13106; *duidaena* MHNLS 12000 (holotype); *megista*, ICN 17243; *riveroi*, MBUCV 6190 (holotype); *xanthoheridia*, ICN 27757.

Espadarana: *andina*, MHNLS 16485–92 (topotypes); *callistomma*, QCAZ 28555–57 (paratypes), 28803; *prosoblepon*, SMF 3756 (holotype), KU 291165–75, 132462.

Hyalinobatrachium: *aureoguttatum*, QCAZ 32069–70; *bergeri*, KU 162256; *chirripoi*, KU 36866–70 (paratypes); *colymbiphylllum*, KU 103819; *crurifasciatum* MBUCV 6828 (paratype); *duranti*, MHNLS 16493; *eccentricum* EBRG 3049 (holotype); *fleischmanni*, SMF 3760 (holotype), QCAZ 32107; *fragile*, MHNLS 17161 (topotype); *guairarepanensis* MHNLS 13731 (holotype); *iaspidiense*, EBD 28803 (holotype); *ibama*, ICN 50091–92; *ignioculus*, UTA 51658 (paratype), UTACV A51660; *lemur*, KU 211769 (paratype); *mondolfii* MHNLS 12710 (holotype); *munozorum*, KU 155497; *nouraguense*, MNHNP 1999-8604 (holotype); *orientale*, KU 167371; *orocostale* MHNLS 15108–9 (paratopotypes); *pallidum* MHNLS 17238 (topotype); *pellucidum*, KU 143298 (holotype); *petersi* BM 1902-5-27-24 (holotype); *tatayoi* MHNLS 17174 (holotype); *taylori* BMNH 1939.1.1.65 (holotype); *uranoscopum*, KU 74310–11, 93229–30; *valerioi*, KU 178091.

Ikakogi: *tayrona*, KU 169750–52, 169754.

Nymphargus: *anomalus*, KU KU 143299 (holotype); *armatus*, ICN 25000; *bejaranoi*, KU 182370–71 (paratypes); *cariticommatus*, KU 202806 (holotype), 202805 (paratype); *chancas*, KU 211778 (holotype); *cristinae*, ICN 18649; *cochranae*, BM 1912-11-1-68 (holotype), KU 121033–35, 123218, QCAZ 31113; *grandisonae*, BM 1910-7-11-68 (holotype); KU 164686–690; *griffithsi*, BM 1940-2-20-4 (holotype), 1940-2-20-3 (paratype); KU 142649, 164519–76, 173116, 288992, 188148; *ignotus*, KU 209763–65 (paratypes); *megacheirus*, KU 143246–71 (paratypes); *mixomaculatus*, MHNMS 18653 (holotype); *pluvialis*, KU 173488; *ocellatus*, KU 197030; *posadae*, QCAZ 25090; *phenax*, KU 162264, 162266–67 (paratypes); *pluvialis*, KU 173225–27 (paratypes); *posadae* QCAZ 25090, 26022–23; *prasinus*, KU 169691–92 (paratypes); *siren*, KU 146611–23 (paratypes); *truebae*, KU 162269–80 (paratypes); *wileyi*, QCAZ 26029 (paratype).

Sachatamia: *albomaculata*, KU 65185, QCAZ 4325; *ilex*, ICN 10625–29, 10630, 10631–32, KU 116464, LACM 72910.

Teratohyla: cf. *amelie* MNCN 44212, MHNCP 5646; *midas*, KU 123219; *pulverata*, QCAZ 32066, 32224; *spinosa*, KU 164668, 32935.

Rulyrana: *flavopunctata*, QCAZ 32265, KU 121046; *spiculata*, KU 162283 (paratype); *saxiscandens*, KU 211800–01 (paratypes); *tangarana*, KU 21777 (paratype).

Vitreorana: *antisthenesi*, MNHLS 17909, KU 167775; *castroviejo* 13356 (holotype); *eurygnatha*, KU 93225; *gorzulae* MNHLS 11221 (holotype), MHNLS 17267 (holotype of *Centrolene lema*), 17142 (topotypes); UTA 52240; *helenae* MNHLS 9431 (holotype); *oyampiensis*, MNHN 1973.1673 (holotype), MNHN 1973.1674, MNHN 2003.1598, MCZ A-96522 (holotype of *C. ametarsia*), ICN 50846–47, KU 175216, DFCH-USFQ D162, QCAZ 16652, 22709, 28138, RMNH 37670, 37673–74; *parvula* BM 88-2-7-3 (lectotype).

APPENDIX III. Indented classification summarizing the new arrangement. Species that are considered as *incertae sedis* at the generic level (all within Centroleninae) are listed in Appendix I. Note that equivalence in rank does not mean that clades are comparable evolutionary units, unless they are sister to each other.

Unranked taxon: Allocentroleninae

Family: Allophrynidae

Genus: *Allophryne*

Family: Centrolenidae

incertae sedis: *Ikakogi tayrona*

Subfamily: Centroleninae

Genus: *Centrolene*

Genus: *Nymphargus*

Tribe: Cochranellini

Genus: *Chimerella*

Genus: *Cochranella*

Genus: *Espadarana*

Genus: *Rulyrana*

Genus: *Sachatamia*

Genus: *Teratohyla*

Genus: *Vitreorana*

Subfamily: Hyalinobatrachinae

Genus: *Celsiella*

Genus: *Hyalinobatrachium*

Appendix IV. Species diversity within Centrolenidae. All recognized species are illustrated, except “*Cochranella*” *ritae* (Lutz 1952), “*Cochranella*” *riveroi* (Ayarzagüena 1992), *Hyalinobatrachium esmeralda* Ruiz-Carranza and Lynch 1998, *H. guairarepanense* Señaris 2001, and *Vitreorana parvula* (Boulenger 1895). Species name is followed by sex, museum number, locality, species SVL, and author of the photograph.



Celsiella revocata. Male, MHNLS 13351. Venezuela: Estado Aragua: Colonia Tovar, Río Tuy (10°23' N, 67°17' W; 1800 m). Species SVL = 21.8–25.2 mm. Photo by JA.



Celsiella vozmedianoi. Female, MHNLS 17877. Venezuela: Estado Sucre: Península de Paria, Cerro Humo (10°42' N, 62°37' W; 800 m). Species SVL= 26.2–28.4 mm. Photo by JMG.



Celsiella vozmedianoi. Female, MHNLS 17877. Venezuela: Estado Sucre: Península de Paria, Cerro Humo (10°42' N, 62°37' W; 800 m). Species SVL= 26.2–28.4 mm. Photo by JMG.



Centrolene altitudinale. Male, CLBA 06-MER-015. Venezuela: Estado Mérida: San Luis: Finca el Cedral, Quebrada Caño Seco, 1900 m. Species SVL= 21.5–24.5 mm. Photo by C. Barrio-Amorós.



Centrolene antioquiense. Male, ICN (not cataloged). Colombia: Departamento Tolima: Municipio Falán: Vereda El Llano, Finca La Llera, 1800 m. Species SVL= 20.5–22.5 mm. Photo by M. Rivera.



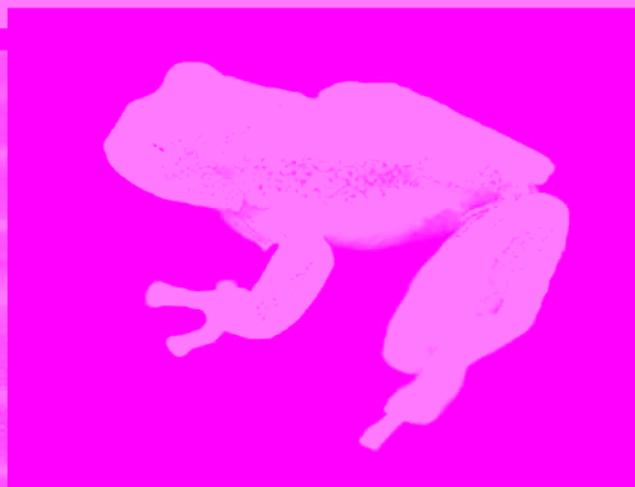
Centrolene bacatum. Male, QCAZ 26056. Ecuador: Provincia Napo: Yanayacu Biological Station, 2000 m. Species SVL= 19.4–21.8 mm. Photo by M. R. Bustamante.



Centrolene buckleyi. Male, not collected. Ecuador, Provincia Pichincha, Reserva Las Galarias, 2080 m. Species SVL= 25.0–34.7 mm. Photo by Tim Krynak.



Centrolene buckleyi. Male, not collected. Ecuador, Provincia Cotopaxi, Sigchos, ca. 3000 m. Species SVL= 25.0–34.7 mm. Photo by L. A. Coloma.



Centrolene condor. Male, OCAZ 37279, holotype. Ecuador, Zamora-Chinchipec, Destacamento militar Cóndor Mirador, 1750–1850 m. Species SVL= 27.6 mm. Photo modified from Cisneros-Heredia & Morales-Mite (2008).



Centrolene daidaleum. Male, MUJ 5918. Colombia, Departamento Boyacá, Municipio Arcabuco, Vereda Peña Blanca, Alto Las Chapas, 2750 m. Species SVL= 20.0–24.1 mm. Photos by MR.



Centrolene daidaleum. Male, MUJ 5918. Colombia, Departamento Boyacá, Municipio Arcabuco, Vereda Peña Blanca, Alto Las Chapas, 2750 m. Species SVL= 20.0–24.1 mm. Photos by MR.



Centrolene geckoideum. Male, KU 164490. Ecuador, Provincia Pichincha, 9 km SE of Tandyapa, 2160 m. Species SVL= 61.8–80.7 mm. Photos by W. E. Duellman.



Centrolene gemmatum. Male, MCZ A-104077, paratype. Ecuador: Provincia Cotopaxi: San Francisco de las Pampas just NW of junction of Rio Las Juritas and Rio Toachi, 1500 m. Species SVL= 23.3–24.9 mm. Photos by JMG.



Centrolene heloderma. Male, KU 164715, holotype. Ecuador: Provincia Pichincha: Quebrada Zapadores, 5 km ESE of Chiriboga, 2010 m. Species SVL= 26.8–32.3 mm. Photo by W. E. Duellman.



Centrolene hesperium. Male, USNM 292586, paratype. Peru: Departamento Cajamarca: 2.5 km (airline) NE of Monte Seco, Río Zaña, 1800 m. Species SVL= 23.0–28.8 mm. Photo by JMG.



Centrolene hybrida. Male, MUJ 5467. Colombia: Departamento Boyacá: Municipio Garagoa: Vereda Ciénago-Balvanera, Reserva Natural El Secreto, Quebrada Las Palmitas, 2100 m. Species SVL= 20.0–23.1 mm. Photos by MR.





Centrolene lemniscatum. Female, not collected, Peru: Departamento San Martín. Species SVL= 27.0 mm. Photo by P. Venegas.



Centrolene lynchi. Male, KU 164691, holotype. Ecuador: Provincia Pichincha: 4 km northeast (by road) of Dos Ríos, 1140 m. Species SVL= 23.5–26.4 mm. Photo by W. E. Duellman.



Centrolene muelleri. Male, not collected. Peru: Región San Martín. Species SVL= 23.5 mm. Photos by P. Venegas.



Centrolene notostictum. Male, MUJ 5471. Colombia: Departamento Norte de Santander: Municipio La Playa de Alem: Vereda Piritama, Quebrada Piritama, 1800 m. Species SVL = 19.4–24.9 mm. Photo by S. Sánchez-L.



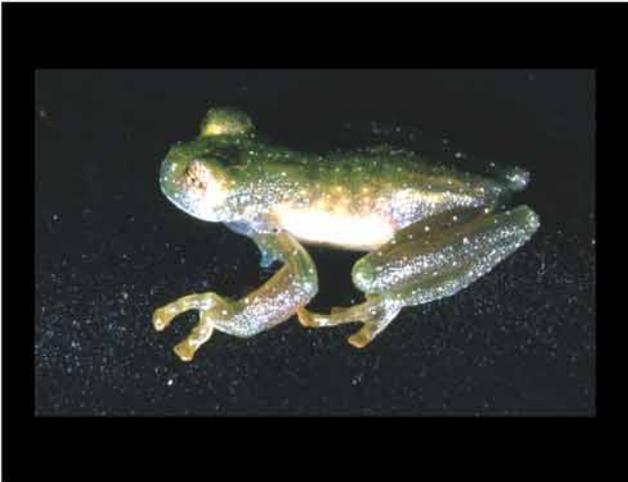
Centrolene cf. paezorum. Juvenile male, MAR 840. Colombia: Departamento del Tolima: Municipio Rancesvalles: Vereda San Marcos: Finca El Carmen, Quebrada El Carmen, 2200 m. Species SVL= 44.5 mm. Photo by M. Rivera-Correa.



Centrolene peristictum. Male guarding eggs, QCAZ 22313. Ecuador: Provincia Pichincha: Mindo Biological Reserve, 1600 m. Species SVL= 18.7–20.6 mm. Photo by M. R. Bustamante.



Centrolene peristictum. Male, QCAZ 22314. Ecuador: Provincia Pichincha: Mindo Biological Reserve, 1600 m. Species SVL= 18.7–20.6 mm. Photo by JMG.



Centrolene pipilatum. Male, KU 143278, holotype. Ecuador: Provincia Napo: 16.5 km NNE of Santa Rosa on Quito–Lago Agrio road. Species SVL= 19.5–22.9 mm. Photo by W. E. Duellman.



Centrolene sanchezi. Male, ICN 24294. Colombia: Departamento Caquetá: Municipio Florencia: 3.1 km (by road) from Cumbre Alto Gabinete, 2190 m. Species SVL= 18.9–20.7 mm. Photo by JMG.



Centrolene savagei. Male, not cataloged. Colombia: Departamento Tolima: Municipio de Falan: creed near Cabecera Municipal, 1100 m. Species SVL= 19.8–23.9 mm. Photo by M. Arredondo.



Centrolene savagei. Male, ICN 24927. Colombia: Departamento Quindío: Municipio Filandia: Vereda El Roble: Quebrada La Popa, 2000 m. Species SVL= 19.8–23.9 mm. Photo by JMG.



Centrolene scirtetes. Male, KU 202720, holotype. Ecuador: Provincia Pichincha: 1.4 km (by road) SW of Tandayapa, 1820 m. Species SVL= 24.4–26.1 mm. Photo by M. R. Bustamante.



Centrolene solitaria. Male, ICN 24298, holotype. Colombia: Departamento Caquetá: Vereda Tarqui, 39.3 km NW of Florencia, 1410 m. Species SVL= 19.3 mm. Photo by JMG.



Centrolene venezuelense. Male, not collected, Venezuela: Estado Mérida: Motús Alta, 2800 m. Species SVL = 23.4–33.8 mm. Photo by C. Barrio-Amorós.



“Centrolene” acanthidiocephalum. Male, ICN 11071. Colombia: Departamento Santander: Municipio Charalá: Virolín, cabeceras del Río Luisito, 1750 m. Species SVL = 30.0–32.7 mm. Photo by JMG.



“Centrolene” audax. Male, KU 164500. Ecuador: Provincia Napo: 2 km SSW of Río Reventador, 1700 m. Species SVL= 21.6–28.8 mm. Photo by W. E. Duellman.



“Centrolene” audax. Male, KU178018. Ecuador: Provincia Napo: Río Salado, 1 km upstream of Río Coca, 1420 m. Species SVL= 21.6–28.8 mm. Photo by JMG.



"Centrolene" azulae. Female, USNM 195988, holotype. Peru: Provincia Leoncio Prado: about 3.3 km (by Tingo María–Pucallpa Rd.) W of Funda Nuevo Mundo, Cordillera Azul. SVL = 27.5 mm. Photo by JMG.



"Centrolene" ballux. Male, KU 164725. Ecuador: Provincia Pichincha: 14 km W of Chiriboga, 1960 m. Species SVL = 19.2–23.3 mm. Photo by W. E. Duellman.



"Centrolene" durrellorum. Male, DFCH-USFQ D131, holotype. Ecuador: Provincia Zamora-Chinchipec: tributary of Río Jambue (ca. 04°03'S, 78°56'W; 1150 m). Species SVL = 25.7–26.1 mm. Photo from Cisneros-Heredia (2007).



"Centrolene" fernandoi. Male, KU 211770, holotype. Peru: San Martín: 7 km NE of San Juan de Pacaysapa, 1080 m. Species SVL = 22.5–26.4 mm. Photo by W. E. Duellman.



"Centrolene" guanacarum. Male, KU 169697. Colombia: Departamento Huila: 3 km SW of San Agustín, Paramo Arriápolón, 1750 m. Species SVL = 20.6–22.3 mm. Photo by W. E. Duellman.



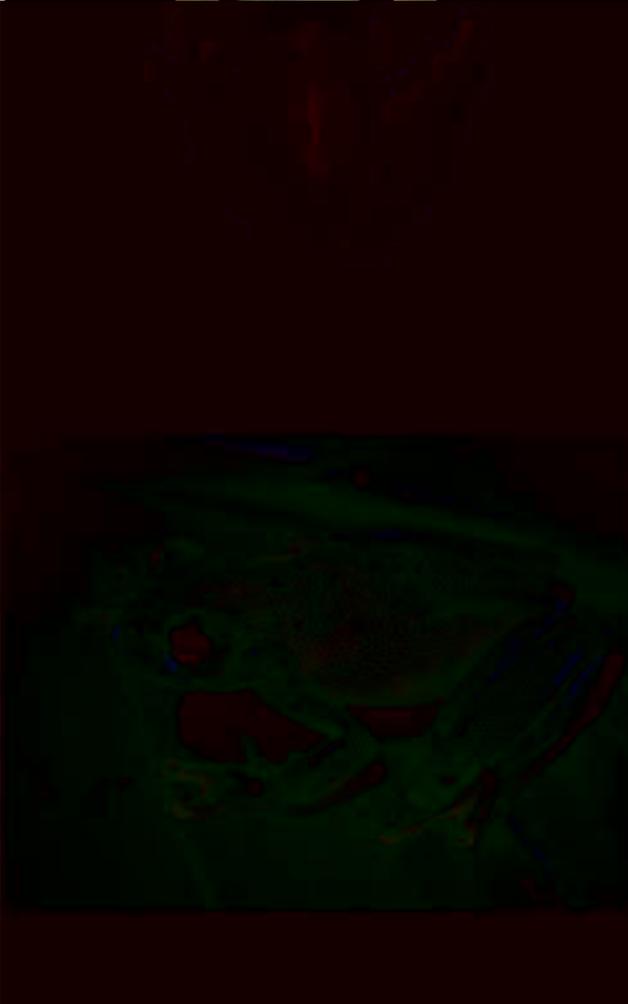
"Centrolene" huilense. Male, ICN 7454, paratype. Colombia: Departamento Huila: 7.4 km NW of Isnos. Species SVL = 23.6–26.7 mm. Photo by JMG.

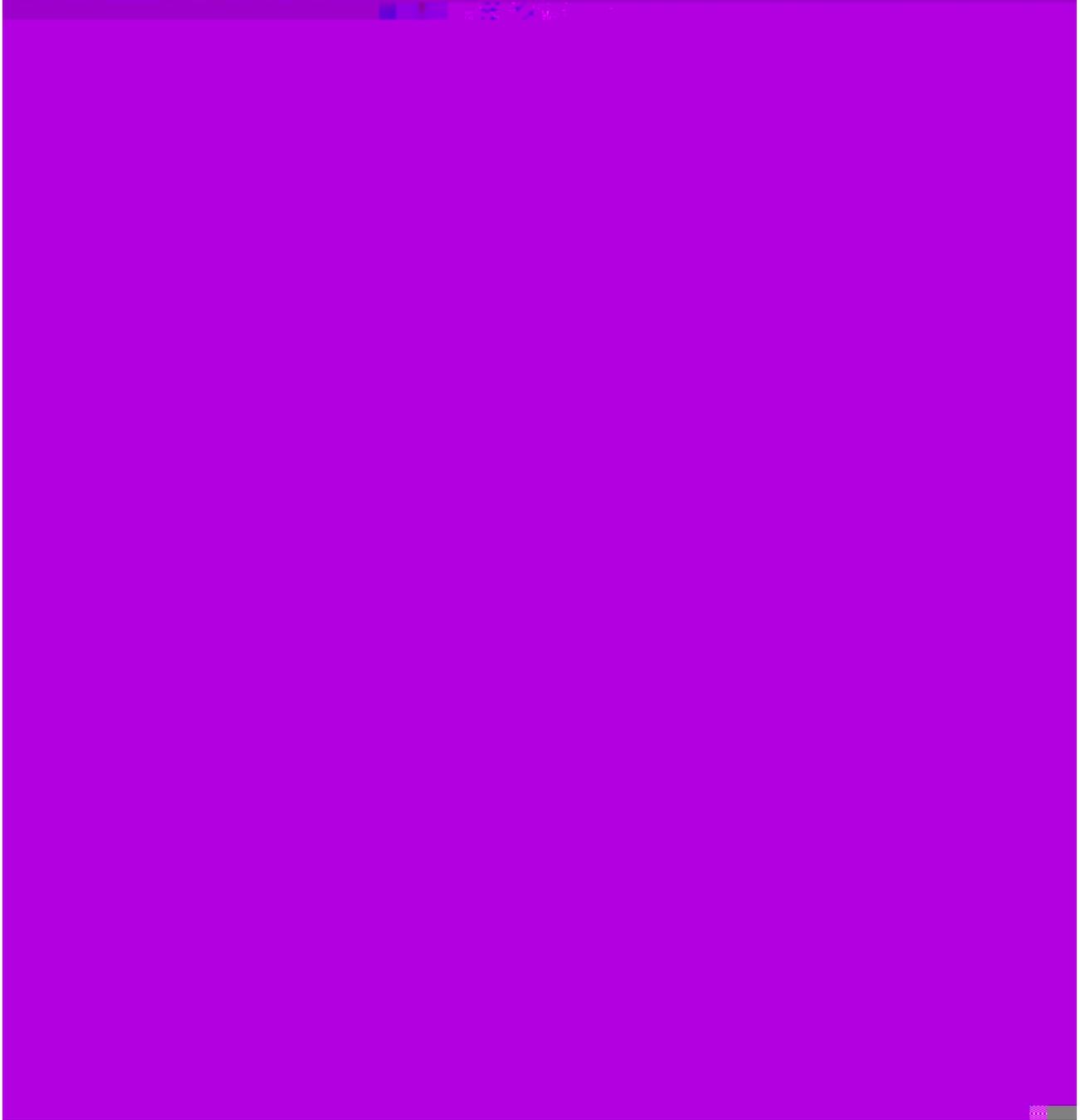


Centrolene medemi. Female, KU 164493. Ecuador: Provincia Napo: 2 km SSW of junction between Río Reventador and Baeza-Lumbaqui road. Species SVL = 25.5–44.3 mm. Photo by W. E. Duellman.



Chimerella mariaelenae. Male, QCAZ 31729. Ecuador: Provincia Tungurahua: Río Negro, 1423 m. Species SVL = 17.9–19.7 mm. Photos by M. R. Bustamante.







"Cochranella" balionota. Male, KU 164702. Ecuador: Provincia Pichincha: 3.5 km NE of Mindo, 1340 m. Species SVL = 20.1–21.8 mm. Photo by W. E. Duellman.



"Cochranella" croceopodes. Female, KU 211804, holotype. Peru: Provincia San Martín: 23.2 km NE of Tarapoto, 800 m. SVL = 24.7–24.8 mm. Photo by W. E. Duellman.



"Cochranella" duidaeana. Male, MHNSL 12000. Venezuela: Estado Amazonas: Cerro Duida, cumbre Sur (03°19' N, 60°53' W, 2410 m). Species SVL = 24.5–25.1 mm. Photo by J. Ayarzagüena.



"Cochranella" erminea. Male, MHNC 7247. Peru: Provincia Satipo: Distrito Mazamari: Valle de Tsiriari, Catarata Arco Iris. Species SVL = 24.7–24.8 mm. Photo by M. Medina.



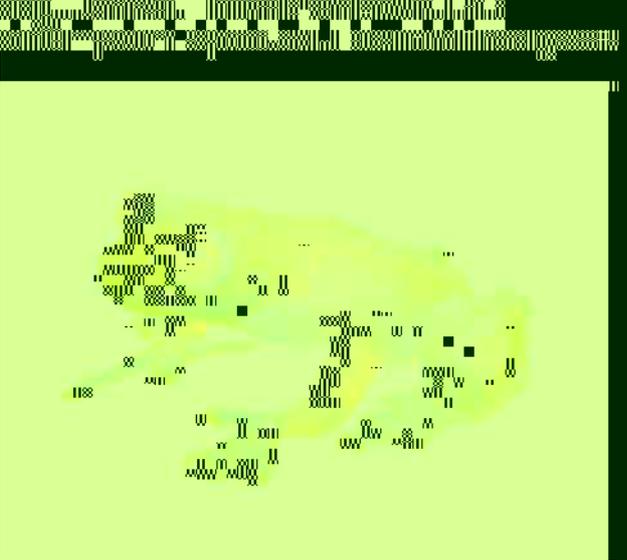
"Cochranella" erminea. Male, MHNC 7247. Peru: Provincia Satipo: Distrito Mazamari: Valle de Tsiriari, Catarata Arco Iris, ca. 600 m. Species SVL = 23.6 mm. Photo by M. Medina.



"Cochranella" euhystrix. Male, USNM 292587, paratype. Peru: Cajamarca: about 2.5 km (airline) NE of Monte Seco, 1800 m. Species SVL = 28.5–33.6 mm. Photo by JMG.



"Cochranella" geijskesi Female RMNH





Espadarana andina. Male, MHNLS 16491. Venezuela: Estado de Mérida: Quebrada Azul, on the La Azulita–El Hato road. Species SVL = 21.5–27.6 mm. Photos by JMG.



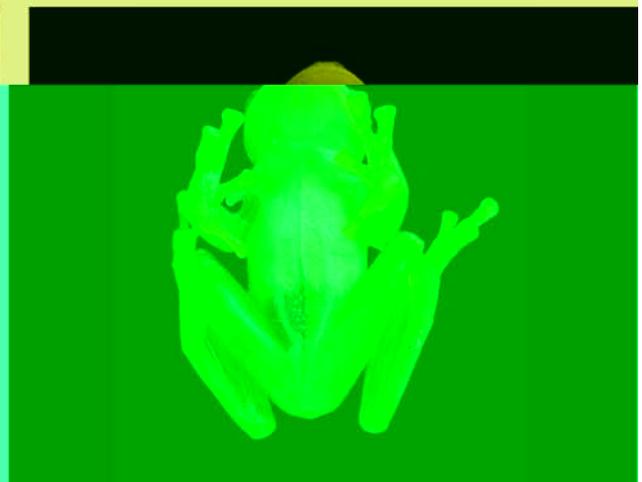
Espadarana andina. Male, uncatologued. Colombia: Departamento Santander: Municipio Charala: Virolin, Finca La Argentina, 1700 m. Species SVL = 21.5–27.6 mm. Photo by MR.



Espadarana callistomma. Male, QCAZ 32055, Ecuador: Provincia Esmeraldas: stream affluent of Río Durango, 284 m. Species SVL = 26.7–31.8 mm. Photos by M. R. Bustamante.



Espadarana prosoblepon. Male, QCAZ 31982. Ecuador: Provincia Santo Domingo de los Tsáchilas: 3.4 km NE on the Dos Ríos–Chiriboga road, 1270 m. Species SVL = 21.0–31.0 mm. Photo by M. R. Bustamante.







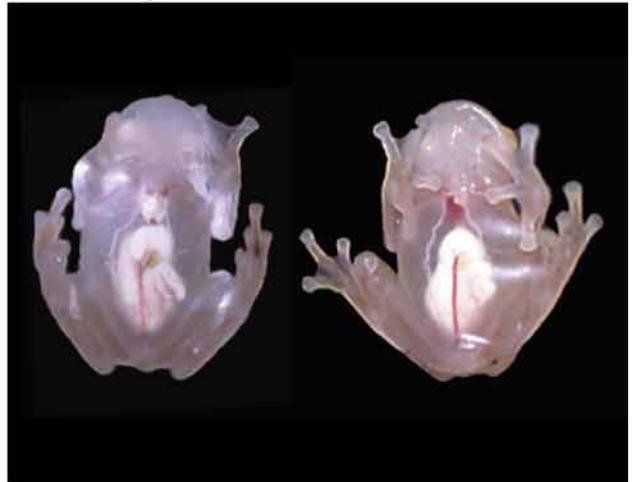
Hyalinobatrachium colymbiphillum. Underdetermined sex, not collected. Costa Rica. Species SVL = 23.0–29.0 mm. Photo by R. Puschendorf.



Hyalinobatrachium colymbiphillum. Underdetermined sex, not collected. Costa Rica: Puntarenas: Rincón de Osa: Quebrada Aguas Buenas, 10 m. Species SVL = 23.0–29.0 mm. Photo by B. Kubicki.



Hyalinobatrachium crurifasciatum. Male, MHNLS 17328. Venezuela: Estado Bolívar: Auyan-tepui, ascent to Auyan-tepui from Uruyen, 1005 m. Species SVL = 19.0–24.0 mm. Photo by SCF.



Hyalinobatrachium crurifasciatum. Males, MHNLS 16477 (left), 16475 (right). Venezuela: Estado Bolívar: La Escalera, 900 m. SVL = 19.0–24.0 mm. Photos by JMG.



Hyalinobatrachium durante. Male, MHNLS 17166. Venezuela: Merida: Chorotal (08°40'21.8" N, 71°24'44.3" W; 1964 m). Species SVL = 21.1–24.6 mm. Photos by SCF.





Hyalinobatrachium eccentricum. Male, MHNLS 17335. Venezuela: Bolívar: Auyan-tepui, stream between Campamento Oso and ascent to the top of Auyan-tepui, 2000 m. Species SVL = 26.6–22.9 mm. Photo by SCF.



Hyalinobatrachium fleischmanni. Egg clutch on under side of leaf, KU 68369. Costa Rica: Cartágo: Tapanti, 1200 m. Species SVL = 19.0–32.0 mm. Photo by W. E. Duellman.



Hyalinobatrachium fleischmanni. Male, QCAZ 37308. Ecuador: Provincia Esmeraldas: Caimito, 47 m. Species SVL = 19.0–32.0 mm. Photo by S. R. Ron



Hyalinobatrachium fleischmanni. Male, QCAZ 32107. Ecuador: Provincia Esmeraldas: 2 km E on San Francisco–Durango road, 77 m. Species SVL = 19.0–32 mm. Photo by M. R. Bustamante.



Hyalinobatrachium fragile. Males, MIZA 280 (left) and MIZA 279 (right). Venezuela: Estado Aragua: road Maracay-Choroní, Los Cerritos, 1 Km from La Planta and 9 Km from Puerto Colombia. Species SVL = 18.9–24.5 mm. Photos by J. Valera-Leal.





Hyalinobatrachium iaspidiense. Male, SMNS 12247. Guyana: Upper Demerara–Berbice Distrit: Mabura Hill Forest Reserve, Maiko creek (05°09'19.30" N, 58°41'58.96" W; 60 m). Species SVL = 19.8–22.7 mm. Photos by Raffael Ernst.



Hyalinobatrachium ibama. Undetermined sex, MAR 502. Colombia: Departamento Norte de Santander: Municipio La Playa de Belem: Quebrada Piritama, 1800 m. Species SVL = 19.9–23.5 mm. Photo by S. Sánchez.



Hyalinobatrachium ignioculus. Male, MHNSL 17327. Venezuela: Bolívar: Auyan-tepui, Campamento Uayaraca, ascent to Auyan-tepui from Uruyen (05°41'06" N, 62°31'32" W, 1005 m). Species SVL = 20.8–23.0 mm. Photo by SCF.

Hyalinobatrachium lemur. Male, KU 211768, holotype SVL = 20.4 mm. Peru: Provincia Lamas: 7 km (by road) NE of San Juan de Pacaysapa, 1080 m. Species SVL = 20.4–21.3 mm. Photo by W. E. Duellman.



Hyalinobatrachium mondolfii. Male, SMNS 12255. Guayana: Mabura Hill Forest Reserve, Maiko creek (05°09'19.30" N, 58°41'58.96" W, 60 m). Species SVL = 20.3–22.5 mm. Photos by Raffael Ernst.



Hyalinobatrachium munozorum. Male, paratype, KU 123225. Ecuador: Provincia Sucumbios: Santa Cecilia, 340 m. Species SVL = 18.8–20.7 mm. Photo by W. E. Duellman.

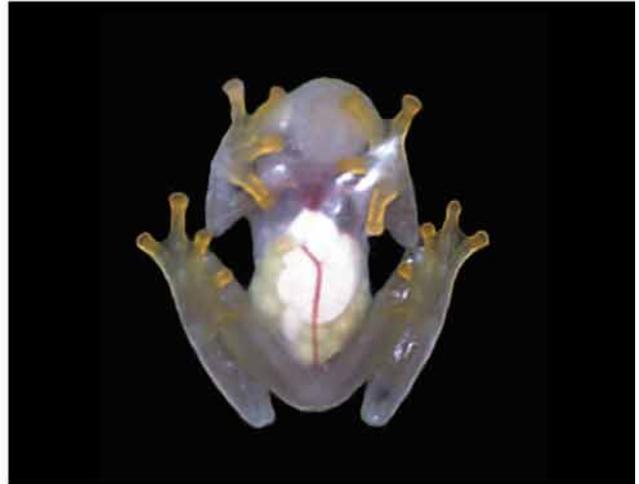


Hyalinobatrachium mesai. Male, EBRG 4644, SVL = 20 mm, holotype. Venezuela: Bolivar: Sarisariñama-tepui, 420 m. Photo by M. Moffett, courtesy of C. Barrio-Amorós.





Hyalinobatrachium orientale. Male, MHNLS 13354. Venezuela: Estado Sucre: Península de Paria, Cerro Humo (10°42' N, 62°37' W; 800 m). Species SVL = 19.8–23.6 mm. Photo by JA.



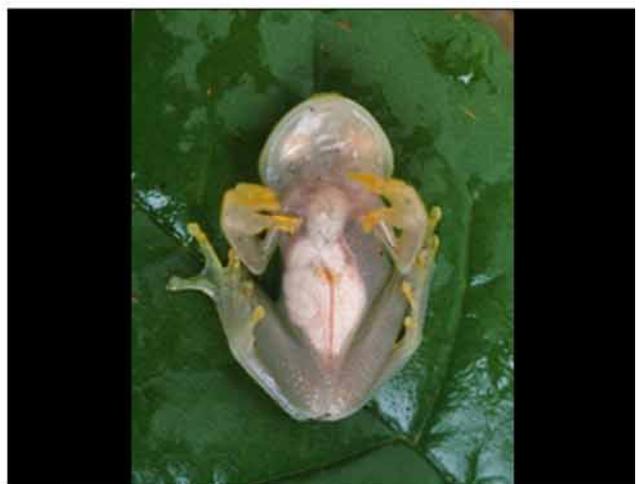
Hyalinobatrachium orientale. Female, MHNLS 16445. Venezuela: Estado Sucre: Península de Paria, Cerro Humo (10°41' N, 61°37' W; 850 m). Species SVL = 19.8–23.6 mm. Photo by JMG.



Hyalinobatrachium orocostale. Male, MHNLS 17247. Venezuela: Estado Guárico: Cordillera del Interior, Hacienda Picachito, Cerro Platillón (09°51'23" N, 67°30'09.1" W; 1200–1500 m). Species SVL = 19.7–20.5 mm. Photos by SCF.



Hyalinobatrachium pallidum. Male, MHNLS 17238. Venezuela: Estado Táchira. Between Sábana Grande and La Grita, Quebrada Guacharaquita (08°10'02.8" N, 71°58'44.2" W; 1600–1700 m). Species SVL = 21.9–22.4 mm. Photos by SCF.





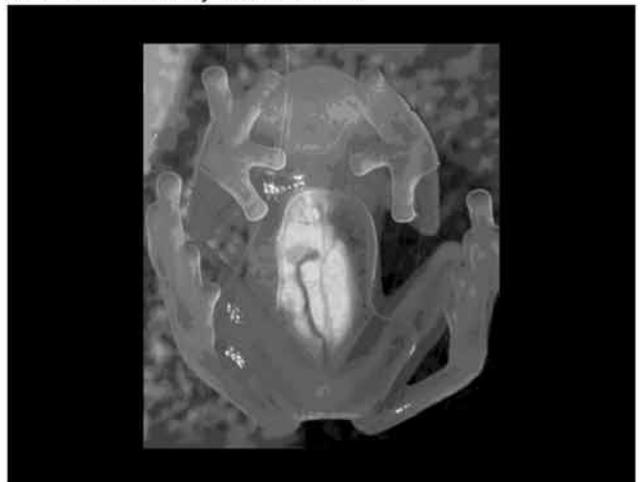
Hyalinobatrachium pellucidum. Female, KU 143298, holotype. Ecuador: Provincia Sucumbios: Río Azuela, 1740 m. Species SVL = 22.0 mm. Photo by W. E. Duellman.



Hyalinobatrachium pellucidum. Male, not cataloged. Ecuador: Provincia Morona Santiago: Quebrada Napinaza, Km 6.8 on the Limón–Macas road, 990 m. Species SVL = 22.0 mm. Photo by L. A. Coloma.



Hyalinobatrachium ruedai. Male, USFQ-DFCH 735. Ecuador: Provincia Napo: vicinities of Tena, 500 m. Species SVL = 20.2–22.6 mm. Photos from Cisneros-Heredia and McDiarmid (2006).



Hyalinobatrachium talamancae. Male guarding eggs, not collected, Costa Rica: Limón: Fila-Asuncion, 475 m. Species SVL = 22.0–27.0 mm. Photo by B. Kubicki.



Hyalinobatrachium talamancae. Not collected, undetermined sex. Costa Rica: Limón: Guayacán, 500 m. Species SVL = 22.0–27.0 mm. Photo by B. Kubicki.



Hyalinobatrachium tatayoi. Male (MHNLS 17174, left) and female (MHNLS 17182, right). Venezuela: Estado Zulia: stream near Tokuko (09°50'30.6" N, 72°49'13.6" W; 301 m). Species SVL = 21.5–22.4 mm. Photo by SCF.



Hyalinobatrachium taylori. Male, AG 212. Venezuela: Estado Bolívar: Río Cuyuni. Species SVL = 17.9–21.5 mm. Photos by C. Barrio-Amorós.



Hyalinobatrachium valerioi. Not collected, undetermined sex. Costa Rica: Provincia Limón: Guayacán, 400 m. Species SVL = 19.5–26.0 mm. Photo by B. Kubicki.

Hyalinobatrachium valerioi. Female, LAC 1407. Ecuador: Provincia Pichincha: 5 km W of La Florida. Species SVL = 19.5–26.0 mm. Photo by L. A. Coloma.



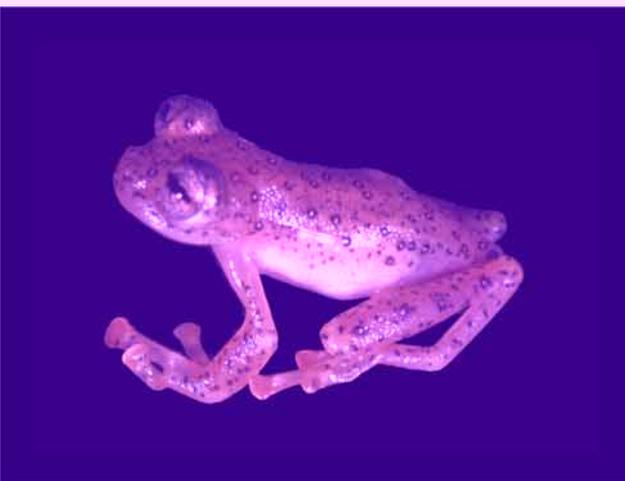
Hyalinobatrachium vireovittatum. Undetermined sex, not collected. Costa Rica: Provincia Puntarenas: near Quepos, 350 m. Species SVL = 21.5–25.0 mm. Photo by B. Kubicki.



Hyalinobatrachium vireovittatum. Undetermined sex, not collected. Costa Rica: Provincia Puntarenas: Fila Chonta, 300 m. Species SVL = 21.5–25.0 mm. Photo by B. Kubicki.



Ikakogi tayrona. Male, MAR 545. Colombia: Departamento Magdalena: Municipio Santa Marta: San Lorenzo. Species SVL = 28.2–30.8 mm. Photo by S. Sánchez.



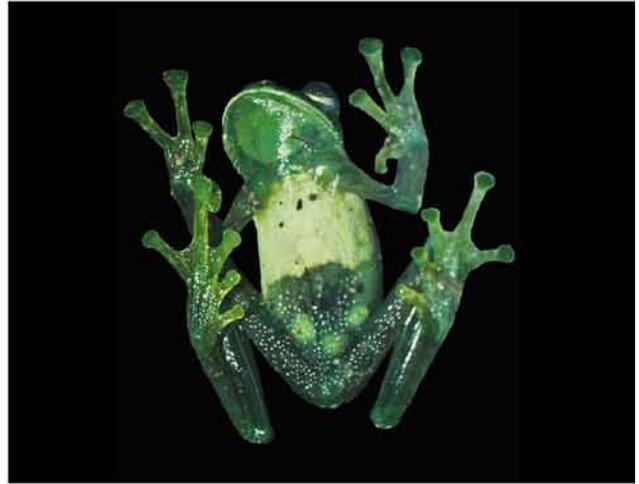
Nymphargus anomalus. Male, KU 143299, holotype. Ecuador: Provincia Sucumbios: Río Azuela, 1740 m, Quito–Lago Agrio road. Species SVL = 24.1 mm. Photo by W. E. Duellman.



Nymphargus armatus. Male, ICN 25000. Colombia: Departamento Valle del Cauca: Vereda Las Amarillas: km 19 on the El Cairo–Boquerón road, 2160 m. Species SVL = 23.3–24.8 mm. Photo by JMG.



Nymphargus bejaranoi. Male, not collected. Bolivia: Departamento La Paz: Parque Nacional Madidi: Santa Cruz de Valle Ameno (14°38'24"S, 68°31'39"W; 1800 m. Species SVL = 23.8–24.4 mm. Photo by I. de la Riva.



Nymphargus bejaranoi. Female, not collected. Bolivia: Departamento Cochabamba: Provincia Chapare: road to Tablasmontes (17°07'S, 65°56'W; 2400 m. Species SVL = 23.8–24.4 mm. Photo by I. de la Riva.



Nymphargus buenaventura. Undetermined sex. Ecuador: Provincia El Oro: Reserva Buenaventura, 1200 m. Species SVL = 20.9–22.4 mm. Photo by M. Yáñez.



Nymphargus cariticommatus. Male, DHMECN 2429. Ecuador: Provincia Zamora Chinchipe: Reserva Tapichalaca. Species SVL = 23.5–25.7 mm. Photo by M. Yáñez.



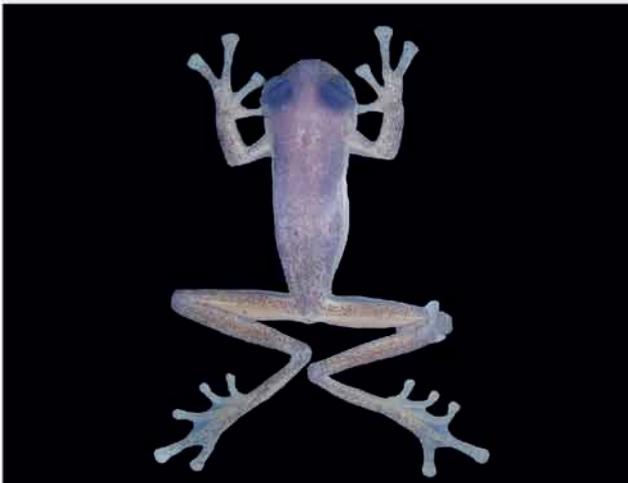
Nymphargus chami. Undetermined sex, not collected. Colombia: Departamento Antioquia: Municipio Amalfi. Species SVL = 30.5–37.6 mm. Photo by J. C. Arredondo.



Nymphargus chancas. Male, KU 211778, holotype. SVL = 24.9 mm. Peru: Provincia Lamas: Abra Tangarana, 7 km (by road) NE of San Juan de Pacaysapa (06°12' S, 76°44' W; 1080 m). Species SVL = 27.9 mm. Photo by JMG.



Nymphargus cochranae. Female, QCAZ 31113. Ecuador: Volcán Sumaco, Pacto Sumaco, 1500 m. Species SVL = 24.0–30.3 mm. Photos by L. A. Coloma.



Nymphargus cristinae. Male, ICN 18649. Colombia: Departamento Antioquia: Municipio Urrao: Río Encarnación, Quebrada La Clara, 2330 m. Species SVL = 26.0–29.7 mm. Photo by JMG.



Nymphargus garciae. Male, KU 164658. Ecuador: Provincia Napo: 11 km ESE Papallacta, 2660 m. Species SVL = 25.1–28.4 mm. Photo by W. E. Duellman.



Nymphargus grandisonae. Male, QCAZ 30790. Ecuador: Provincia Pichincha: 1.4 km SW of Tandayapa, 1820 m. Species SVL = 25.1–30.7 mm. Photo by JMG.



Nymphargus grandisonae. Female, QCAZ 32282. Ecuador: Provincia Cotopaxi: San Francisco de Las Pampas, ca. 1600 m. Species SVL = 25.1–30.7 mm. Photo by M. R. Bustamante.



Nymphargus griffithsi. Male (QCAZ 29525, left) and female (QCAZ 29528, right). Ecuador: Provincia Pichincha: Km 16 on the San Juan de Chillogallo–Chiriboga road. Species SVL = 19.9–26.6 mm. Photos by JMG.



Nymphargus ignotus. Male, ICN 14750. Colombia: Departamento Valle del Cauca: Farallones de Cali, Peñas Blancas, ca. 6 km SE of Pichindé by road, 1900 m. Species SVL = 20.8–23.0 mm. Photo by JMG.



Nymphargus laurae. Male, USNM 288453. SVL = 19.9 mm. Ecuador: Provincia Orellana: Volcán Sumaco, Loreto, Upper Río Napo, ca. 500 m. Photo from Cisneros-Heredia & McDiarmid (2007).



Nymphargus luteopunctatus. Male, ICN 20747, holotype. Colombia: Departamento Cauca: Municipio El Tambo: Vereda La Playa: Río San Joaquín, 1200 m. Species SVL = 33.1 mm. Photo by JMG.



Nymphargus mariae. Female, KU 174713, holotype. Peru: Serranía de Sira, ca. 1550 m. Species SVL = 30.0 mm. Photo by JMG.



Nymphargus megacheirus. Male, KU 143245, holotype. Ecuador: Provincia Napo: stream 16.5 km NNE of Santa Rosa. 1700 m. Species SVL = 27.1–32.8 mm. Photo by W. E. Duellman.



Nymphargus mixomaculatus. Male, MHNSM 18653. Peru: Provincia Huánuco: Caserio Carpish de Mayobamba. 2625 m. Species SVL = 22.8–26.3 mm. Photo by E. Lehr.



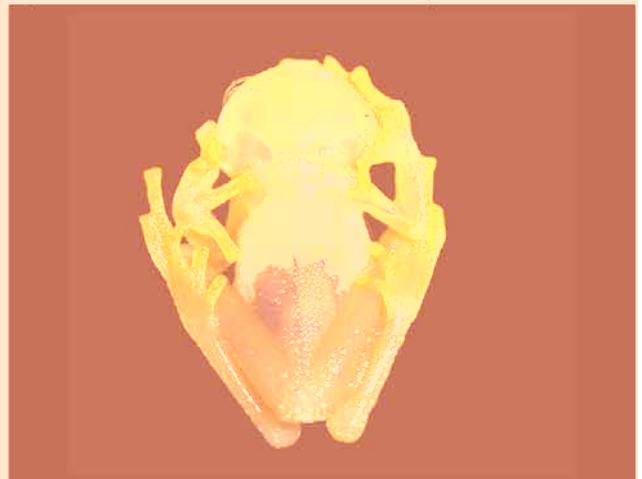
Nymphargus nephelophilus. Male, ICN 24296, paratype. Colombia: Departamento Caquetá: Municipio Florencia. 46 km N of Florencia by road. 1600 m. Species SVL = 22.6–24.1 mm. Photo by JMG.



Nymphargus oreonympha. Male, ICN 20770, paratype. Colombia: Departamento Caquetá: Municipio Florencia. 31–38.6 km E of Alto Gabinete. 2040 m. Species SVL = 24.0–26.4 mm. Photo by JMG.



Nymphargus ocellatus. Undetermined sex, GCI 363. Peru: Provincia Oxapampa: Chacos (UTM E461580–N8826212, 1977 m). Species SVL = 21.0–29.0 mm. Photos by G. Chavez.





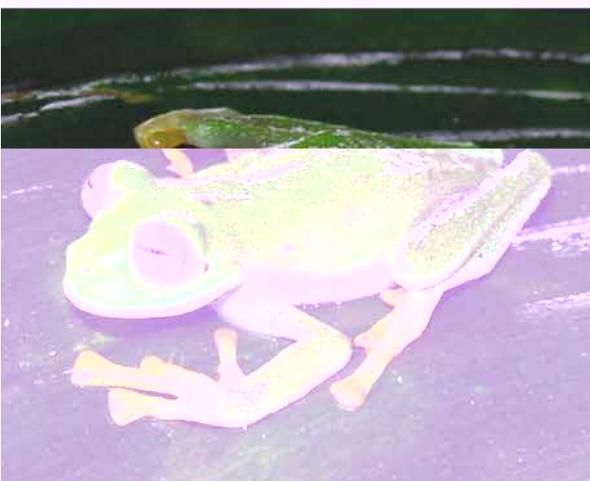
Nymphargus phenax. Male, IDLR 5004. Peru: Provincia Ayacucho: La Mar: km 2.2 on the Toccate–San Antonio road (12°59'15.4" S, 73°39'18.5" W; 2250 m). Species SVL = 20.2–22.1 mm. Photo by J. M. Padial.



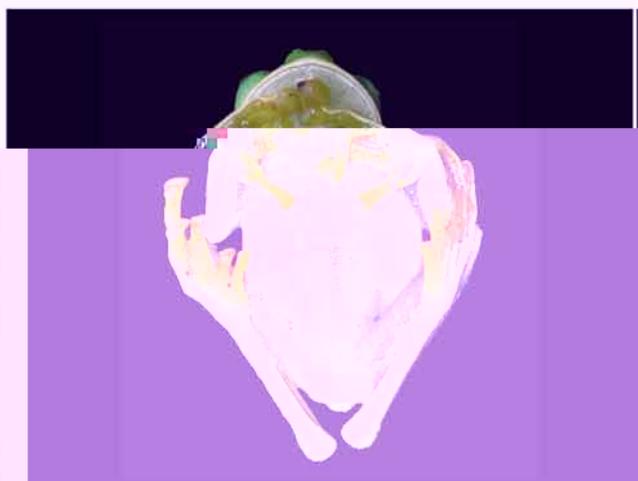
Nymphargus phenax. Male, KU 162267, holotype. SVL = 20.2–22.1 mm. Peru: Ayacucho: Tutumbaro, Río Piene (73°55' W, 12°42' S; 1840 m). Species SVL = 20.2–22.1 mm. Photo by JMG.



Nymphargus pluvialis. Female, MHNC 6756. SVL = 24.9–26.5 mm. Peru: Cusco: Provincia La Convencion: Distrito Santa Teresa: Hidroelectrica de Machupicchu (13°09'23.3" S, 72°34'50.1" W; 1649 m). Species SVL = 24.9–26.5 mm. Photos by J. C. Chaparro.



Nymphargus posadae. Male, OCAZ 25090. Ecuador: Provincia Napo: Yanayacu Biological Station, 2100 m. Species SVL = 30.2–34.1 mm. Photos by M. R. Bustamante.





Nymphargus prasinus. Male, KU 169693. Colombia: Municipio Calima, 1.5 km W Lago Calima, 1230 m. Species SVL = 32.8–34.5 mm. Photo by W. E. Duellman.



Nymphargus puyoensis. Female, QCAZ 37923. Ecuador: Provincia Pastaza: stream tributary of Río Lliquino. Species SVL = 21.2–30.0 mm. Photo by M. R. Bustamante.



Nymphargus rosada. Male. Colombia: Departamento Tolima: Municipio Falan: Vereda El Llano: Finca la Lulera, 800 m. Species SVL = 24.1–28.3 mm. Photo by M. Rivera.



Nymphargus rosada. Male, MAR 613. Colombia: Departamento Tolima: Municipio Ortega: Vereda Corazón de Peralonso: Quebrada La Ondina, 1800 m. Species SVL = 24.1–28.3 mm. Photo by MR.



Nymphargus ruizi. Male (ICN 26032, left) and female (ICN 26037, right). Colombia: Departamento Cauca: Parque Nacional Munchique, km 33 NNW of Uribe, Quebrada Sopladero, 2190 m. Species SVL = 24.3–29.5 mm. Photo by JMG.





Nymphargus siren. Male, KU 143293. Ecuador: Provincia Napo: 6.5 km NW de Santa Rosa, 1700 m. Species SVL = 19.8–23.3 mm. Photo by W. E. Duellman.



Nymphargus siren. Male, QCAZ 37971. Ecuador: Provincia Napo: Yanayacu Biological Station, 2100 m. Species SVL = 19.8–23.3 mm. Photo by JMG.



Nymphargus solitus. Male, ICN 35158. Colombia: Departamento Caldas: Municipio Samaná: Sitio El Estadero, 1850 m. Species SVL = 25.3–28.5 mm. Photo by JMG.



Nymphargus trichae. Undetermined sex, not collected. Peru: Region Cusco: Valle Cosñipata. Species SVL = 22.6–24.8 mm. Photo by A. Catenazzi.



Nymphargus vicenteruedai. Male, paratype. Colombia: Departamento de Santander: Santuario de Fauna y Flora Guantotá-Alto Río Fonce, Quebrada Aguas Claras, 2690 m. Species SVL = 23.3–27.8 mm. Photo by MR.



Nymphargus wileyi. Male, QCAZ 37972. Ecuador: Provincia Napo: Yanayacu Biological Station, 2100 m. Species SVL = 23.3–27.1 mm. Photo by JMG.



Rulyrana adiazeta. Male, MUJ 5919. Colombia: Departamento Santander. Municipio de Charalá: Corregimiento Virofín: Vereda el Reloj, 1770 m. Species SVL = 22.5–28.8 mm. Photo by MR.



Rulyrana flavopunctata. Male, KU 123224. Ecuador: Provincia Sucumbíos: Bermejo No. 4, 15 km ENE Lumbaqui, 720 m. Species SVL = 20.6–25.7 mm. Photo by W. E. Duellman.



Rulyrana flavopunctata. Undertermined sex, SC 17462. Ecuador: Morona Santiago: Río Napinaza. Species SVL = 20.6–25.7 mm. Photo by L. A. Coloma.



Rulyrana saxiscandens. Males (KU 211779, holotype, left; KU 211780, paratype, right). Peru: Provincia San Martín: Cataratas Ahaushiyacu, 730 m. Species SVL = 20.8–23.2 mm. Photos by W. E. Duellman.





Rulyrana spiculata. Undetermined sex, not collected. Peru: Region Cusco: Valle Cosñipata. Species SVL = 21.7–27.7 mm. Photo by A. Catenazzi.



Rulyrana spiculata. Female, MHNSM 24869. Peru: Provincia Satipo: Distrito Llaylla: Vista Alegre (11°24'32.3''S, 74°39'1''W, 1340m). Species SVL = 21.7–27.7 mm. Photo by K. Siu.



Rulyrana susatamai. Male, MUJ 3537. Colombia: Departamento Tolima: Municipio Ibagué: Vereda El Totumo: Finca la Magnolia, Quebrada El Cural, 1050 m. Species SVL = 22.3–25.6 mm. Photo by MR.



Rulyrana tangarana. Male, KU 211776, holotype. Peru: Provincia Lamas: 7 km (by road) NE of San Juan de Pacaysapa, 1080 m. Species SVL = 22.5–23.3 mm. Photo by W. E. Duellman.



Sachatamia albomaculata. Undetermined sex (SC 19621, left; SC 19622, right). Ecuador: Provincia Imbabura: near Lita, ca. 500 m. Species SVL = 20.5–32.0 mm. Photos by L. A. Coloma.





Sachatamia ilex. Male, not collected. Panama: El Valle. Species SVL = 26.3–34.0 mm. Photo by D. B. Fenolio.



Sachatamia punctulata. Male, ICN (not cataloged). Colombia: Departamento Tolima: Municipio Falán: Río Cuamo, 450 m. Species SVL = 24.5–27.3 mm. Photo by M. Rivera.



Teratohyla ameliae. Male, QCAZ 37920. Ecuador: Pastaza: Stream tributary of the Río Lliquino, 350 m. Species SVL = 18.1–18.3 mm. Photos by M. R. Bustamante.



Teratohyla midas. Female, QCAZ 28134. Ecuador: Provincia Sucumbios: Cuyabeno, Puerto Bolívar, 240 m.



Teratohyla midas. Undetermined sex, not collected. Ecuador: Amazon basin. Species SVL = 19.0–26.8 mm.

Species SVL = 19.0–26.8 mm. Photo by M. R. Bustamante. Photo by M. R. Bustamante.



Teratohyla pulverata. Male, QCAZ 32066. Ecuador: Provincia Esmeraldas: Durango, ca. 70 m. Species SVL = 22.0–33.0 mm. Photos by M. R. Bustamante.



Teratohyla spinosa. Undermated sex, not collected. Costa Rica: Reserva Guayacán, 500 m. Species SVL = 17.8–23.0 mm. Photo by B. Kubicki.



Teratohyla spinosa. Male, not collected. Species SVL = 17.8–23.0 mm. Costa Rica: Río Palmas. Photo by P. Janzen.



Vitreorana antisthenesi. Male (left) and female (right), not collected. Venezuela: Estado Aragua: Estación Biológica Rancho Grande, 1000 m. Species SVL = 21.4–27.0 mm. Photos by JMG.





Vitreorana castroviejoii. Male, MHNLS 13356. Venezuela: Estado Sucre: Península de Paria, Cerro El Humo. Species SVL = 21.5–25.1 mm. Photo by JA.



Vitreorana castroviejoii. Male, MHNLS 16446. Venezuela: Estado Sucre: Península de Paria (10°41'32" N 61°57'44" W; 580 m). Species SVL = 21.5–25.1 mm. Photo by JMG.



Vitreorana eurygnatha. Undermined sex, not collected. Brazil: Minas Gerais: Parque Estadual Nova Baden. Species SVL = 17.9–24.0 mm. Photos by M. Sacramento.

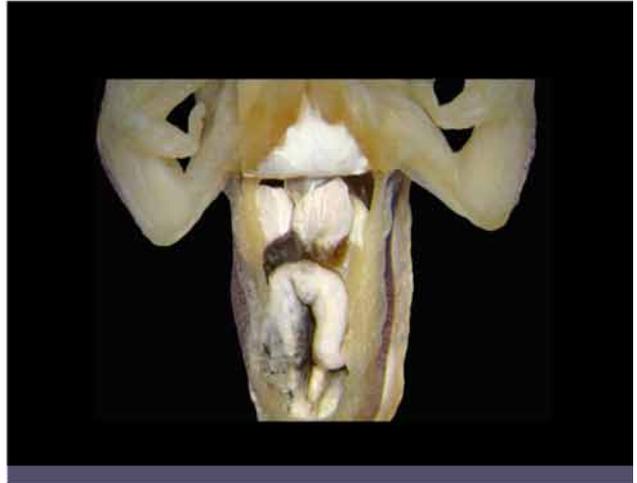


Vitreorana gorzulai. Male, MHNLS 17325. Venezuela: Bolívar: Auyan-tepui, Campamento Uayaraca, ascent to Auyan-tepui from Uruyen (05°41'06" N, 62°31'32" W, 1005 m). Species SVL = 19.0–22.5 mm. Photos by SCF.





Vitreorana helenae. Male, IRSNB 13980. Guyana: Kaieteur National Park. Species SVL = 19.2–20.4 mm. Photos by P. J. R. Kok.



Vitreorana oyampiensis. Male, QCAZ 16652. Ecuador: Provincia Napo: Estación Científica Yasuni PUCE, 240 m. Species SVL = 17.0–24.0 mm. Photo by C. D. D.



Vitreorana oyampiensis. Male, MB (Michel Blanc) 292. French Guiana: Aya / Trinité. Species SVL = 17.0–24.0 mm. Photo by M. Blanc.

