UNIVERSIDAD REGIONAL AMAZÓNICA IKIAM
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Evolution of the coloration of glass frogs (Anura: Centrolenidae) and its relationship with altitudinal gradients in the Neotropic

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CONTENIDO DEL DOCUMENTO

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ÍNDICE GENERAL

ÍNDICE DE FIGURAS

ÍNDICE DE APENDICES

RESUMEN

Los Andes juegan un papel importante en la evolución de la flora y fauna de América del Sur. La familia Centrolenidae (Anura) comprende más de 156 especies con alta diversidad y endemismo en los Andes. La presente contribución investiga la historia biogeográfica de esta familia utilizando filogenética molecular y datación, para determinar el papel del levantamiento andino en la diversificación de la coloración dorsalde las especies en la región Neotropical. Para la reconstrucción filogenética, usamos datos de los patrones de coloración de 120 especies de ranas de cristal y secuencias de genes nucleares (c-myc, POMC y RAG-1) y genes mitocondriales (12S, 16S y ND1). Además, se utilizó información sobre las distribuciones altitudinales para la reconstrucción de áreas ancestrales entre los linajes. Encontramos que el ascenso de los Andes del Norte está relacionado con los procesos de diversificación de los linajes durante los últimos 10 millones de años, lo que promueve la evolución de los patrones cromáticos en el gradiente altitudinal. Biogeográficamente, las tierras altas albergan la mayor cantidad de características cromáticas, tanto en vida como en preservado. Nuestro estudio demuestra la importancia de los eventos de formación de montañas como impulsores de una rápida diversificación de los linajes y de los patrones de evolución del color de la familia Centrolenidae en el Neotrópico.

Palabras clave: Biogeografía – Coloración – Centrolenidae – Evolución – Neotrópico

ABSTRACT

The Andes played an important role in the flora and fauna evolution of South America. The Andes played an important role in flora and fauna evolution of South America. The Centrolenidae family comprises more than 156 species with high diversity and endemism in the Andes. Herein, we investigate the biogeographic history of this family using molecular phylogenetics and dating, to determine the role of the Andean uplift in the diversification of dorsal color patterns of species in the Neotropical region. For phylogenetic reconstruction, we used data on the coloration patterns of 120 glass frog species and sequences of nuclear genes (c-myc, POMC, and RAG-1) and mitochondrial genes (12S, 16S, and ND1). In addition, information on elevational distributions was used for biogeographical reconstruction across ancestral areas among lineages. We found that the rise of the Northern Andes is strongly associated with lineage diversification processes during the last 10 million years, promoting the evolution of color patterns in the altitudinal gradient. Biogeographically, highlands harbor the greatest number of chromatic characteristics, both in life and in preservation. Our study demonstrates the importance of mountain orogeny as driver of rapid lineage diversification and color evolution patterns in the family Centrolenidae in the Neotropics.

Key words: Biogeography - Coloration - Centrolenidae - Elevational shifts - Evolution - Neotropics - Systematic

INTRODUCTION

Coloration is one of the most important characteristics for animals as an antipredator strategy, since it can function to reduce the detection of predators (crypsis) or as part of a warning signal to discourage predators (aposematism). In particular, understanding the evolutionary history of populations that vary widely in the traits of these antipredatory signals are critical for formulating predictions and assumptions about the forces that are likely to constrain or facilitate the evolution of hese traits (Wang & Shaffer, 2008). For this reason, several studies have been developed on these coloration characteristics in various taxa, including amphibians. Amphibians are one of the most abundant and diverse groups of vertebrates in Neotropic (Vasconcelos *et al.*, 2019). This bioregion includes tropical and subtropical forests from Latin America and the Caribbean. This terrestrial ecozone corresponds to one of the most important in the world, since it harbor more than half of all species on the planet (Myers *et al.*, 2000; Cayuela & Cerda, 2012) and near to 49% of amphibian species (Cortes-Gómez *et al.*, 2014). This great diversity is due to climatic heterogeneity and the geological history of the region (Hartshorn, 2002; Cayuela & Cerda, 2012). Therefore, the wide variety of species is reflected in a diversity of morphological and ecological traits, wich serve a variety of functions including camouflage and warning coloration and influence aspects or behavior such as mate recognition and mate choice (Endler, 1980, 1984; Reynolds & Fitzpatrick, 2007; Mills & Patterson, 2009). Wherein, the variation in the coloration and texture of the skin of amphibians have ecological importance that makes pigment patterns potential targets for multiple evolutionary forces (sexual selection and natural selection) (Endler, 1980, 1984; Mills & Patterson, 2009; Willink, 2013).

One of the groups most studied and appreciated for their beauty are the species of the Centrolenidae family, characterized mostly by their ventral transparency, which allows us to see their internal organs, which is why they are called “glass frogs”. This family constitutes a monophyletic taxon that contains around 156 species (Frost, 2022) classified into 12 genera (Guayasamin *et al.*, 2020). Glass frogs are distributed throughout tropical America, from southern Mexico, Central America, Bolivia, Venezuela, the Guiana Shield and the northern part of the Amazon basin (Cisneros-Heredia & McDiarmid, 2007; Guayasamin *et al.*, 2009, 2020; Cardozo-Urdaneta & Señaris, 2012). Due to its wide distribution, it has a wide altitudinal range that reaches up to 3,500 meters above sea level, inhabiting various ecosystems such as riverbanks, understory, canopy of evergreen and semi-deciduous forests, tropical forests, cloud forests and moorland habitats (Cisneros-Heredia & McDiarmid, 2007; Guayasamin *et al.*, 2020).

Glass frogs are considered as cryptic species, since they have a color pattern that is not very contrasting with their background, which allows them to blend in with the environment, reducing the probability of being detected by predators. Recent studies show that the green coloration in Centrolenidae is attributed to two reasons: (I) to the particular spatial arrangement of the dermal chromatophore unit (DCU) in their skins and (II) to the presence of the pigment biliverdin (Starrett & Savage, 1973; Taboada *et al.*, 2020). On the one hand, the species that have a predominance of DCUs turn lavender or blue when preserved in alcohol, while the species that have biliverdin turn cream or white (Cisneros-Heredia & McDiarmid, 2007). These morphological characteristics of coloration fulfill camouflage functions (Salazar Gómez, 2014; Barrionuevo, 2017; Barnett *et al.*, 2020; Taboada *et al.*, 2020). Therefore, the dorsal green coloration in anurans has reflective properties similar to those of photosynthetic leaves, since they reflect light in the near infrared region (700 to 900 nm) similar to plants, allowing them to camouflage as an anti-predatory mechanism (Cisneros-Heredia & McDiarmid, 2007; Barnett *et al.*, 2020). It is worth mentioning that studies suggest that these characteristics appeared in the ancestor of the clade, that is, they are subject to ancestral evolutionary forces along the lineages and therefore to its biographical history (Barnett *et al.*, 2020). Historical biogeographic evidence suggests that glass frogs originated in South America, where their most recent ancestor occupied mid-elevation mountains (1000–2000m), with recent colonizations towards Central America, occupying lower and higher elevations

(Hutter, Guayasamin, & Wiens, 2013; Guayasamin *et al.*, 2020). However, near 70% of the Centrolenidae species are found in the Andes (Guayasamin *et al.*, 2009; Hutter *et al.*, 2013). This accumulation of species in the Andes is attributed to the relationship between the age of formation of the Northern Andes (~10 Myr) (Stern, 2004; Hoorn *et al.*, 2010; Chaves, Weir, & Smith, 2011) and the high diversification rates of glass frogs (Hutter, Lambert, & Wiens, 2017).

However, there is no study that relates the evolutionary dorsal color patterns in glass frogs, through phylogenetic analysis in the context of biogeographic questions. It can be pointed out that understanding the origin and intraspecific variation in coloration is fundamental to understanding its evolutionary history, and complement the knowledge about its phylogenetic relationships, as fundamental components of diversification in Neotropical ecosystems. For this reason, the present contribution investigated the evolutionary patterns of the chromatic characteristics in life and preserved glass frogs and their possible relationship with the altitude in the Neotropical region, considering: (I) How the coloration patterns evolved in species along an altitudinal gradient? (II) Does the diversification of lineages and the evolution of color in glass frogs have a biogeographic relationship with the orogeny of the Andes Mountains?

MATERIAL AND METHODS

COLOR DATA COLLECTION AND ANALYSIS

We documented information of dorsal color patterns (in life and preserved), from published photographs of 120 species of the Centrolenidae family, and 15 species of the outgroup assessed in scientific articles with the original taxonomic descriptions (e.g. Duellman & Schulte, 1993; Ruiz-Carranza & Lynch, 1997, 1998; Señaris & Ayarzaguena, 2005), taxonomic or systematic revisions (e.g. Cisneros-Heredia & McDiarmid, 2007; Guayasamin et al., 2020), and online catalogues (BIOWEB (https://bioweb.bio/faunaweb/amphibiaweb/, AmphibiaWeb (https://amphibiaweb.org/). To complete the information of coloration in preserved species, we reviewed 32 species from the herpetological division of Instituto Nacional de Biodiversidad (DHMECN) and the Museo de Zoología, Universidad San Francisco de Quito (ZSFQ) (Appendix 1).

For each of the photographs obtained (173 photos), we measured standard RGB values using Adobe Color CC web application (https://color.adobe.com/). We chose three regions of the photograph that represented the color present on the dorsum (Fig. 1). We did this manually to secure that the RGB measurements were obtained from the pixels have adequate lighting (e.g., no shadows or flash glare) to ensure that the color measured matched the general perception of color and was not an artefact of the photography (Fig. 1). All data were extracted by the same person (M.J.S.C). Given that the photographs we used differed in lighting, quality and angle parameters, the slight differences in RGB values are probably the result of the lack of photograph standardisation, rather than representing biologically meaningful variation. For this reason, once the three RGB measurements were obtained for each species, an average of each dimension (Red, Green and Blue) was made for performed an analysis of groups of K-means of the RGB values obtained from 124 photographs in life (109 from centrolenids and 15 from outgroup) and 49 photographs in preserved (41 from centrolenids and 8 from outgroup) (Fig. 1, Table S1) using the statistical package in R v4.1.0 (R Core Team, 2021). This analysis finds color categories within the data and assigns each point to one of these categories (Table S1). This reclassification is more objective than manually assigning color categories to each color and is more conservative than using RGB values from non-standardized photographs (Medina *et al.*, 2020b,a).

In addition to the background color in life and preserved, glass frogs are also distinguished by spot patterns, classified in 6 states: spots/circular dots and or stripe, flecks, ocelli, false ocelli, reticulations and "combinated", following the distinctive marks made by Cisneros-Heredia & McDiarmid, 2007 (Appendix 2). The circular dots and spots are very similar, so were classified as a single state considering that both are formed by aggregations of generally elevated chromatophores (Cisneros-Heredia & McDiarmid, 2007). In addition, the distinctive mark “punctuations” described by Cisneros-Heredia & McDiarmid, 2007, were not used for classification because not all the taxonomic description refers to this type of mark and generally it is not visible to eye. In addition, the "combinated" state refers to species that have more than one type of spot pattern. On the other hand, the color of marks was classified in 5 states: Black/Brown, Yellow/Orange, Red, Blue/Green and “combinated” based on the color reflecting by the chromatophore types (melanophores, xanthophores and iridophores) (Appendix 2). Iridophores are defined as cellular pigments that reflect light giving bright blue and green colors, xanthophores contain yellow, red and orange pigments and melanophores contain black and brown colors (Taylor & Bagnara, 1972; Bagnara, Frost, & Matsumoto, 1978). The "combinated" classification refers to the presence of two or more colors come from two or more types of chromatophore, such as ocelli that have melanophores and xanthophores (Cisneros-Heredia & McDiarmid, 2007) or the species than have more than one spot pattern.

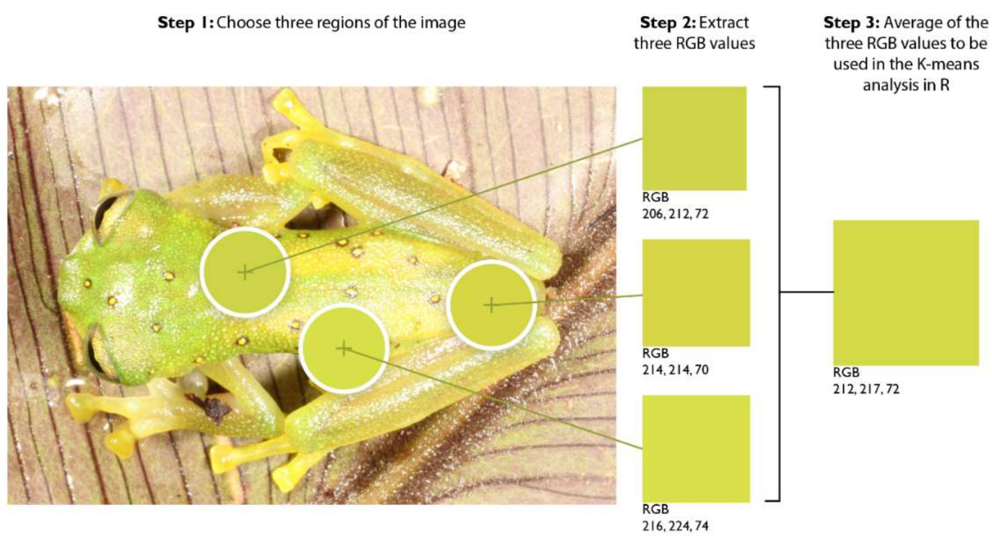

Figura 1. Diagram with the steps to obtain the RGB values of the dorsal coloration in life and preserved using Adobe Color CC. Step 1. Load the image on the web page and choose three regions of the image (no shadows or flash glare). Step 2. Extraction of three RGB values and finally, Step 3. Average of the three RGB values for color reclassification with K-means in R.

Finally, for the distinctive preserved marks we classified as "light", "dark" and "both", based on 32 species reviewed in ZSFQ and DHEMCN, taxonomic descriptions and available preserved photographs (32 photographs). The "light" mark corresponds to areas with light pigments, generally white or cream produced by iridophores or xanthophores. In the case of iridophores, as they contain purines, guanine, hypoxanthine and adenine (Taylor & Bagnara, 1972; Bagnara *et al.*, 1978; Hoffman & Blouin, 2000), this doesn't dissolve in the preservative liquid, so white or cream marks remain. While the xanthophores, contain carotenois, pteridines and flavins (Taylor & Bagnara, 1972; Hoffman & Blouin, 2000), are destroyed in the preservative liquid and the marks in life (yellow or orange) are completely lost in preservation, leaving a cream or white area without chromatophores (Bagnara, 1966; Cisneros-Heredia & McDiarmid, 2007). While the "dark" mark corresponds to black or lavender marks (produced by melanophores) and "both" to the presence of the two marks described above (Appendix 2).

TAXON AND GENE SAMPLING

A molecular database was compiled for 120 species of the Centrolenidae family, excluding those species with uncertain identifications (cf. (= *confer*), aff. (= *affinis*) or sp. (= *species*)). Therefore, the sample included the representatives of all the genera that have molecular and morphological information described. We used Allophrynidae (3 spp), and species belonging to families within Hyloidea (12 spp) as external groups (Table S2).

Sequences were downloaded from the NCBI GenBank database of the specimens. We included relatively rapidly evolving mitochondrial loci for the resolution of recent divergences, as well as slower evolving nuclear loci for relationships between older clades. The genes chosen for this analysis are: mitochondrial 12S rRNA (12S), 16S rRNA (16S), subunit 1 of NADH dehydrogenase (ND1), portions of the nuclear proto-oncogene cellular myelocytomatosis (c-myc), the proopiomelanocortin A gene (POMC) and the Recombination activating gene 1 (RAG-1) (Table S2).

PHYLOGENETIC RECONSTRUCTION AND ANALYSIS

Sequences were edited, consensed and aligned with Geneious Prime v.2020.0.5 software (Kearse *et al.*, 2012). Alignments were reviewed and edited manually to trim regions with high proportion of missing data at the edges. We used Mesquite v.3.61 software (Maddison & Maddison, 2019) to create the concatenated matrix of all the genes (12S, 16S, ND1, c-myc, POMC and RAG-1). Since our combined data set comprises three mitochondrial genes (12S, 16S and ND1) and three nuclear genes (c-myc, POMC and RAG-1) we search a nucleotide substitution model in a partitioned matrix. The model of molecular evolution was determined in jModelTest2 v.1.6 (Darriba *et al.*, 2012) in CIPRES Science Gateway V.3.3 (Miller, Pfeiffer, & Schwartz, 2010) using the Akaike Information Criterion (AIC). Our final matrix was configured with GTR + I + G model for all the partitions.

Phylogenetic analysis with all genes were performed using a maximum likelihood (ML) algorithm and a Bayesian analysis (BA) in CIPRES Science Gateway V.3.3. ML analyzes were performed with Garli v2.0 [Genetic Algorithm for Rapid Likelihood Inference; (Zwickl, 2006)] configuring a total of 10 runs to reduce the probability of inferring a suboptimal probability solution. Node support was evaluated using 1000 bootstrap. BA analyzes were performed in MrBayes v.3.2.2 (Ronquist & Huelsenbeck, 2003), using three runs of the Monte Carlo Markov Chain (MCMC) algorithm for 20 million generations each, with four heated chains (0.2 heating parameter). Trees were sampled every 20000 generations, with burning of 25% of the total trees. To evaluate the effective sample size of the three independent uncorrelated runs, we used the statistical number of effectively independent draws from the posterior (ESS>200), visualized with Tracer v.1.6. (Rambaut, 2014).

ESTIMATION OF THE DIVERGENCE TIME AND ALTITUDINAL RECONSTRUCTION

Divergence times of Centrolenidae were estimated using BEAST v.2.6.6 (Bouckaert *et al.*, 2014). We used a single secondary calibration point using age estimated from Hutter et al., 2013; Guayasamin et al., 2020. We used median age of Centrolenidae

(Mean = 33.4 Myr; Sigma = 6). Analyses were run for 100 million generations, with parameter sampling every 10,000 generations. We used a relaxed clock lognormal linked across all partitions and a Calibrated Yule speciation process for the tree prior. The GTR + I + G evolutionary model was selected, given that it is the closes model to those calculated in jModelTest2 v.1.6 (Darriba *et al.*, 2012). The results on convergence and effective sample size (ESS) were evaluated using Tracer v.1.6. (Rambaut *et al.*, 2014).

We also reconstructed the ancestral areas for the altitudinal distribution using RASP v.3.0 (Yu *et al.*, 2015), with the statistical method of dispersion-vicariance (S-DIVA). We used the minimum and maximum altitude of each species collected from the IUCN Red List database (https://www.iucnredlist.org/) for amphibians, and by Castroviejo-Fisher et al., 2014; Guayasamin et al., 2020. The species were classified according to the coding of Castroviejo-Fisher *et al.*, 2014, in "lowlands" between 0–900m a.s.l, "highlands" between 800–3500m a.s.l and "continuous" from lowlands to highlands (0–3500m a.s.l) (Appendix 3).

RESULTS

PHYLOGENETIC ANALYSES

The evolutionary relationship resulted in a total of 4166 base pairs of (887bp 12S, 858bp 16S, 961bp ND1, 403bp c-myc, 601bp POMC and 456bp RAG-1). Maximum-likelihood and Bayesian searches produced topologically similar trees with consistently high bootstrap values and posterior probabilities in *Celsiella* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009; *Hyalinobatrachium* Ruiz-Carranza & Lynch, 1991; *Centrolene* Jiménez de la Espada, 1872; *Nymphargus* Cisneros-Heredia & McDiarmid, 2007; *Cochranella* Taylor, 1951; *Espadarana* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009; *Rulyrana* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009; *Sachatamia* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009 and *Teratohyla* Taylor, 1951 (Fig. S1). Within Centrolenidae, the BA showed a highly supported sister relationship with Allophrynidae as sister group to Centrolenidae (PP = 1.0; Fig. S1). The phylogenetic relationships retrieved here for Centrolenidae are mostly congruent with previous phylogenetic studies (Guayasamin *et al.*, 2008, 2009, 2020; Caramaschi *et al.*, 2013; Castroviejo-Fisher *et al.*, 2014), we consider the resulting BA tree topology to be a reasonable estimate. The topology resulting from the MrBAYES analysis (Fig. S1) was also congruent with the BEAST analysis (Fig. S2).

MOLECULAR DATING ANALYSES

Relationships between centrolenids species estimated in BEAST strongly supported common ancestry for the Centrolenidae (PP = 1; Fig. S2). Our Results suggest that the split between Allophrynidae and Centrolenidae occurred about 54.52 Ma (95% HPD: 41.57–69.47) in the Paleogene period in late Eocene (Fig. S3). The family Centrolenidae start to diversify in the Paleogene period in late Oligocene, about 33.59 Ma (95% HPD: 27.98–39.24) (Fig. S3). All currently recognized genera within the Centrolenidae appeared during the Miocene. Most of the current species of Allocentroleniae (Centrolenidae + Allophrynidae) originated during the Neogene (Fig. S3). Moreover, our divergence time estimates coincide with recent estimations for the glass frogs in which the clades diverged during the late Miocene to Oligocene (Guayasamin *et al.*, 2020).

COLOR CLUSTERING AND ALTITUDINAL RECONSTRUCTION

The three dimensions assessed (Red, Green, Blue) results in 6 cluster categories of color in life using all the sampled colors in Centrolenid and in outgroup species (Fig. S4 A and B). Noticed that the K-means analysis didn't find color cluster categories for the unique RGB measurements (grayish green, cream, lavender and black) (Table S1). We end up with 10 color categories in life, each of these categories has an associated coordinate in tree-dimensional RGB space: Brown (105, 83, 34), Yellowish-green (148, 154, 15), Green (58, 77, 21), Olive green (96, 122, 21), Grayish green (124, 140, 112), Bluish green (142, 153, 74), Cream (236, 205, 120), Lavender (166, 119, 91), Black (20, 25, 5) and Yellow (198, 199, 74) (Table S1). On the other hand, we calculated 4 color categories in preserved (Fig S4 C and D), excluding the unique RGB value for the white. Having 5 categories of color in preserved: Brown (149, 123, 104), Cream (209, 185, 157), Lavender (82, 66, 70), Gray (156, 154, 175) and White (235, 223, 199) (Table S1). With this color classification and the RASP results we map the chromatic characteristics in life and preserved.

Our RASP results in altitude changes scattered throughout the phylogeny of glass frogs, in turn, mapping the coloration in living specimens shows that there is a wide variation in the combinations of shades of green. On the one hand, according to the reconstructed ancestral elevation, the most common recent ancestor of Centrolenidae inhabited lowlands (0–900 m) (Fig. 2), and higher elevation habitats were colonized more recently (Fig. 2A and C). The most recent common ancestor of Hyalinobatrachinae (*Celsiella* and *Hyalinobatrachium*) and Cochranellini (*Chimerella* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009, *Cochranella*, *Espadarana*, *Rulyrana*, *Sachatamia*, *Teratohyla* and *Vitreorana* Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada & Vilà, 2009), occupied the lowlands and the highlands, that is, the species of both tribes occupy a wide range of elevations (Appendix 3). Whereas *Centrolene* + *Nymphargus* is inferred as restricted to evolve and diversificate at highlands (Fig. 2, Appendix 3). This biogeographic character is maintained through the radiation of these two genera except for three terminal changes, two in *Nymphargus* (*N. laurae* Cisneros-Heredia & McDiarmid, 2007 and *N. mariae* Duellman & Toft, 1979) and one in *Centrolene* (*C. charapita* Twomey, Delia, & Castroviejo-Fisher, 2014) (Fig. 2, Appendix 3). These results are consistent with those found by Castroviejo-Fisher et al., 2014. On the other hand, we can see that the green color is a character derived from Centrolenidae, as it is present in sister clade species (Fig. S5) and it is an ancestral character among members of the family Centrolenidae (Fig. 2, S5). At the same time, preserved coloration (Fig. 2, S6) mapped on the phylogeny reveal that the ancestral coloration in glass frogs is brown and cream. This brown coloration was totally lost during the Allocentroleniae divergence (54.52 Ma) and when the gray color appeared. From here, the lineages that we currently know for the family Centrolenidae diverged (33.59 Ma) and other colors with green tones in life appeared and the lavender color in preservation (Fig. 2, S5, S6).

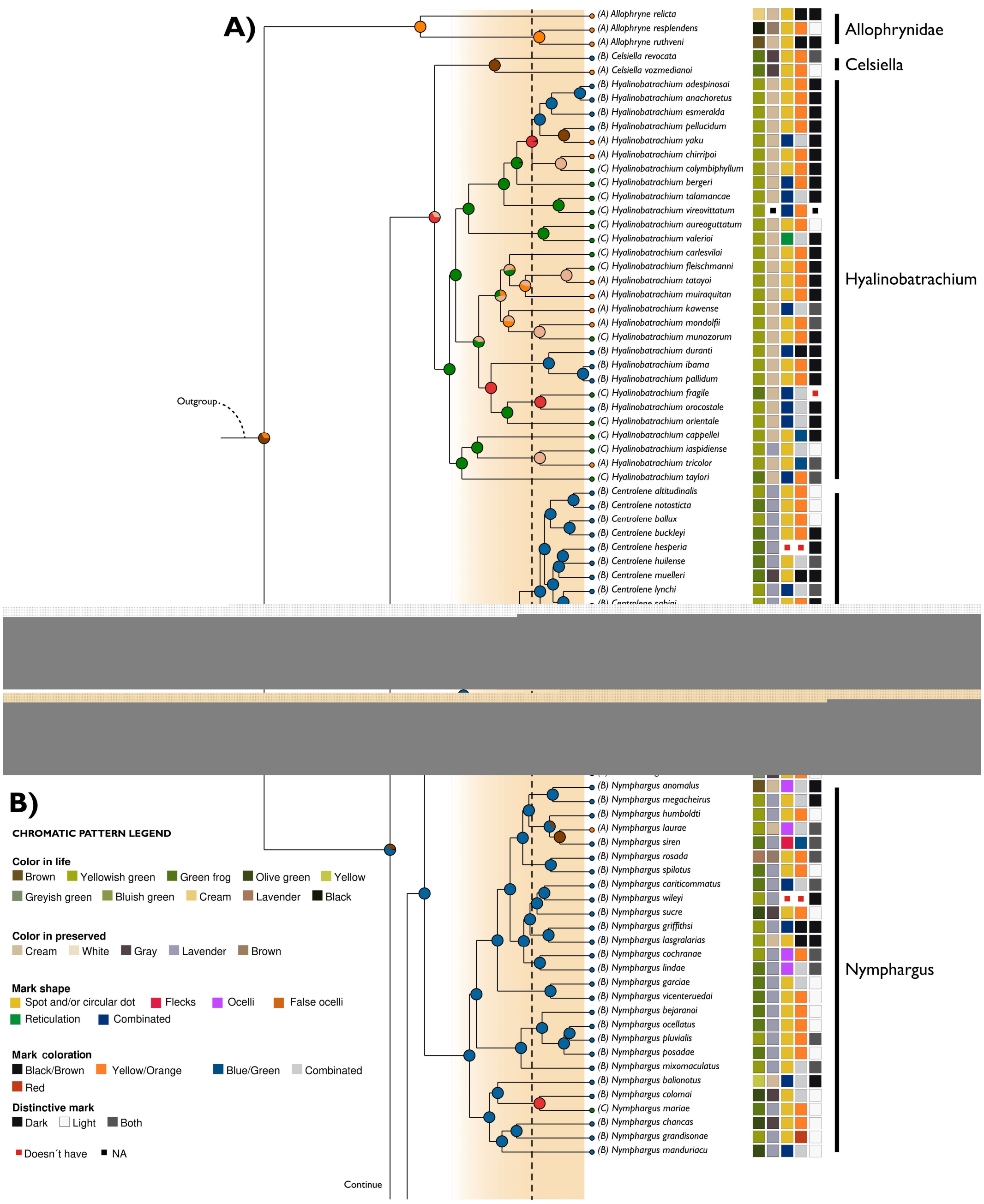

Figura 2. Ancestral elevation distributions for Allocentroleniae reconstructed by S-DIVA analysis. a) Altitudinal ancestral areas mapped along the phylogeny of glass frogs. The pie charts at the inner nodes represent the marginal probabilities for each ancestral altitude. The vertical yellow column indicates the Neogene time span. The vertical dotted line indicates the rise of the Northern Andes (10 Ma). The matrix of squares on the right side indicates the patterns of coloration in life and preserved of each of the species, from left to right in the matrix: 1) coloration in life, 2) coloration in preserved, 3) mark shape, 4) marks coloration in life and 5) distinctive mark in preserved. b) Color coding according to the K-means analysis of the chromatic characteristics in life and preserved. c) Dispersión and density of the divergence time of nodes along their altitudinal ranges for Centrolenidae estimated by S-DIVA analysis: lowlands 0–900 (A), highlands 800–3500 (B), and continuous 0–3500 (C).

The green color and yellowish green are the most predominant in living glass frogs (Fig. 2), both occupying the highlands (800–3500m) and also present in lower quantities in the lowlands (0–900m) (Fig. 2 and S7). While the rest of the colors (olive green, grayish green, bluish green, lavender and yellow) are characters that have evolved in the last ~20 Ma in glass frogs (Fig. S5). In addition, some of these colors in glass frogs are specific within an altitudinal range, such as brown, grayish green and lavender are present only in highlands or on the contrary, occupy the entire altitude range (0–3500) as the bluish green (Fig. 2, S7). While, the lavender coloration in preservative is present in all the species of the Centrolenidae family at high elevations (800–3500), except for some species in the genus *Hyalinobatrachium* (only *H. iaspidiense* Ayarzaguena, 1992 is lavender), which is characterized by having a cream coloration. It should be noted that the cream coloration is an ancestral chromatic characteristic that reappeared within the Centroleninae, specifically within the genus *Nymphargus* and within Cochranellini, occupying high and low elevations (Fig. 2, S7).

While, the ancestral character of the mark shape is the presence of spot, circular dots and/or stripe. This character is present throughout the phylogeny and mainly occupies the highlands (Fig. 2, S7). It should be noted that the rest of the mapped characters have recently evolved within the phylogeny, an exception of the flecks, that is present in ancestors far from Allocentroleniae but doesn't correspond to an ancestral character (Fig. S8). The ocelli and false ocelli correspond to polyphyletic characters, present in highlands in the genus *Nymphargus* for the case of ocelli and lowlands to higlands for false ocelli present in the *Nymphargus* and *Espadarana* clade.

Also, the ancestral color of the marks corresponds to the black color present in the most distant ancestors of Allocentroleniae and in some species of the Centrolenidae family, maily distributed to the higlands (Fig. 2, S7). Since the divergence of the Allocentroleninae, the color yellow produced form the presence of cell pigments xanthopohores appeared and is the most predominant in the markings towards the highlands (Fig. 2, S7). The color red produced for the same cell pigment apper more recently (14 Ma) in only one specie (*Nymphargus grandisonae* Cochran & Goin, 1970). Then blue/green colors markings appear related mainly to lowlands/highlands, whereas "combined" colors are restricted to highlands (Fig. S7, S9). In addition, when mapping the distinctive marks in preserved specimens, we found that the ancestral character is the dark marks, and the light and "both" characters evolved from the divergence of the Allocentroleniae lineages (Fig. S10). It should be noted that the light and "both" distintive mark are present mainly at high elevations, while dark distinctive mark is present in the same proportion in highlands and from lowlands to highlands (Fig. 2, S7).

DISCUSSION

COLOR EVOLUTION AND ALTITUDINAL DISTRIBUTION

The chromatic characteristics of glass frogs are a factor that influences the camouflage of the species as part of anti-predator mechanisms, preventing detection and/or recognition by matching the background, disrupting edges, or mimicking particular background features (crypsis) (Stevens & Merilaita, 2009; Salazar Gómez, 2014; Barrionuevo, 2017; Barnett *et al.*, 2020; Taboada *et al.*, 2020). In turn, these characteristics can help understand natural selection and its evolutionary processes (such as speciation along elevational gradients) that influence the diversification of lineages and evolution of color patterns of glass frogs as a camouflage strategy (Merilaita & Lind, 2005; Stevens & Merilaita, 2009; Guayasamin *et al.*, 2020; Taboada *et al.*, 2020).

Our biogeographical results show that most species of *Centrolene*, *Nymphargus*, *Teratohyla*, *Vitreorana* and some *Hyalinobatrachium* subclades retain their ancestral elevation range despite their ancient origin (e.g., 95% HPD: 22.85–33.21 Ma *Centrolene* + *Nymphargus* and 95% HPD: 18.43–27.72 Ma *Vitreorana* (Fig. 2 and S3)). The restricted elevational distribution can be explained by the fact that the taxa must be closely related to the ancestral habitats, that is, there is a phylogenetic niche conservatism (Hutter *et al.*, 2013; Castroviejo-Fisher *et al.*, 2014; Guayasamin *et al.*, 2020). In contrast, clades with generalist elevation lineages (Hyalinobatrachinae and Cochranellini) have colonized new biogeographical areas. The highlands (800–3500m) host the largest number of chromatic features mapped in this study (Fig. S7). This diversity of chromatic characteristics present at high elevations coincides with the richness of species present at intermediate elevations in the tropical Andes (1000–2000m) (Hutter *et al.*, 2013, 2017; Armesto & Señaris, 2017). This means that the orogeny of the Andes mountain range has allowed the species to preserve their ancestral ecological niche and have few elevation changes, that is, the clades tend to radiate within the same climatic and altitudinal regimes (Guayasamin *et al.*, 2020). This can be seen in the *Centrolene* and *Nymphargus* clades (Fig. 2). However, the importance of species with wide elevational ranges, such as the *Hyalinobatrachium* clade, cannot be ignored. This is the only ones that have within their entire clade (with the exception of *H. iaspidiense*), the presence of the biliverdin pigment in preserved cream coloration. The ecological role and the physiological basis that the serpin present in the biliverdin pigment has been reported to be important on the modulation of reflectance properties (Schwalm & McNulty, 1980; Taboada *et al.*, 2020). We consider this chromatic characteristic as a factor that influenced the adaptability of these species present in wide elevation ranges (0–3500m). Therefore, it cannot be ruled out that the success of the *Hyalinobatrachium* clade in the diffusion of the Neotropics could have been related, at least to some extent, to the presence of the pigment biliverdin, which will possibly an adaptation to extreme temperature, humidity and radiation conditions at altitudes above 2,500 m.a.s.l. (Schwalm & McNulty, 1980; Cadavid, Valencia, & Gómez, 2005; Armesto & Señaris, 2017).

The lavender color assessed in preserved specimens has been evolving over time and is present in other green species outside the Centrolenidae family, such as within Hylidae (e.g., *Isthmohyla calypsa* Lips, 1996; *Boana nympha* Faivovich, Moravec, Cisneros-Heredia, and Köhler, 2006; *Agalychnis buckleyi* Boulenger, 1882 (Duellman, 1969); *Litoria rubrops* Kraus & Allison, 2004, *Ecnomiohyla miliaria* Cope, 1886 (Savage & Heyer, 1969)) and Rhacophoridae (e.g., *Rhacophorus reinwardtii* Schlegel, 1844 (Onn & Grismer, 2010)). Therefore, the lavender color character is polyphyletic, since it is a common character that was acquired independently. However, unlike the families Hylidae and Rhacophoridae, within Centrolenidae the preserved lavender color is present in all genera of the family except for the clade *Hyalinobatrachium* (Fig. 2). On the other hand, the cream color is a paraphyletic character that is shared with the sister ancestor of Centrolenidae (Allophrynidae). In turn, the preserved cream color is evident in other species outside of Allocentroleninae, such as

Craugastoridae (e.g., *Pristimantis galdi* Jiménez de la Espada, 1870) and Hylidae (e.g., *Hyloscirtus colymba* Dunn, 1931 (Duellman, 1970) and *Osteocephalus cabrerai* Cochran & Goin, 1970 (Jungfer, 2010)) (Fig. S6; Appendix 2). With these results we can infer that the presence of the pigment biliverdin in the dermis of the anurans is present independently over time (Taboada *et al.*, 2020) and, within the Centrolenidae family it appeared recently in the clade *Hyalinobatrachium* (23.67 Ma) and other recently evolved species <17Ma (*Cochranella guayasamini* Twomey, Delia & Castroviejo-Fisher, 2014*; Nymphargus lasgralarias* Hutter & Guayasamin, 2012*; N. laurae; Teratohyla pulverata* Peters, 1873 and *Vitreorana franciscana* Santana, Barros, Pontes & Feio, 2015) (Fig. S6). Whereas, the arrangement of the DCU is present in the most recent common ancestor and in most of its descendants.

However, there are other species that are not within the rule of cream or lavender in preserved, for example *Nymphargus rosada* Ruiz-Carranza & Lynch, 1997 is lavender in life and brown in preserved. In turn, there are species that are grayish in preserved with greenish reflections (*Centrolene venezuelense* Rivero, 1968), or cream (*Celsiella revocata* Rivero, 1985; *Chimerella corleone* Twomey, Delia & Castroviejo-Fisher, 2014; *Cochranella erminea* Torres-Gastello, Suárez-Segovia & Cisneros-Heredia, 2007 and *Teratohyla adenocheira* Harvey & Noonan, 2005) or brown (*Centrolene muelleri* Duellman & Schulte, 1993) or are totally gray (*Sachatamia orejuela* Duellman & Burrowes, 1989). Due to these variations, the morphology and dermal structure of glass frogs may involve a structural and/or chemical composition that allows obtaining preserved colors other than cream and lavender. But sometimes, this dorsal color pattern can also vary due to erroneous methodological problems during the conservation process. For example, species within the prosoblepon group that have been in preservatives for a long time or exposed to light, the lavender color commonly changes to brown (Starrett & Savage, 1973).

In addition, it should be mentioned that the distribution of the species was organized only in reference to the elevation, which can accommodate several climatic floors and therefore different physical and biological characteristics that may influence the camouflage mechanisms, and therefore the coloration patterns. We must add that the information on the coloration patterns, as well as their distinctive markings in glass frogs, obtained from the literature are commonly not explicitly mentioned in taxonomic descriptions. However, in most cases, they are easily identifiable from good quality photographs. Despite this, the limitations of this approach are that (I) old taxonomic papers have limitations on color descriptions, and (II) available photographs may not be informative due low quality or at worst cases, not be available.

DIVERGENCE OF LINEAGES AND ONTOGENY OF THE ANDES

The diversification of the lineages that we know today within the Centrolenidae family during the last 10-5 Ma, coincides with the last phase of the Andes uplift, when the mountain chain increased an altitude of 3000 m in a relatively short period of time (Hoorn *et al.*, 2010; Chaves *et al.*, 2011; Ceccarelli *et al.*, 2016). In spite that Andes Mountain is considered as an ecological barrier, we found that some species conserve their ancestral areas of distribution, thus also maintaining the greatest number of chromatic characteristics within the same altitudinal range (e.g., *Centrolene* and *Nymphargus*) (Fig. 2). Nevertheless, there is evidence indicating that there are clades that evolved in response to different altitudinal ranges, causing the divergence of the distribution, niches (Guayasamin *et al.*, 2020) (e.g., Hyalinobatrachidae and Cochranellini) and of chromatic characteristics, as occurs in the presence of the biliverdin (Taboada *et al.*, 2020) (Fig. 2). The diversification of Centrolenidae is a continuous process that has been operating for the last 50 Ma (Hoorn *et al.*, 2010; Castroviejo-Fisher *et al.*, 2014). For this reason, the chromatic characteristics evolved over time among lineages and their distribution on different altitudinal ranges.

CONCLUSION

This study has a great contribution for understanding the evolution of color patterns and the biogeography of Centrolenidae, as fundamental components of diversification in the ecosystems of the Neotropics. We provide evidence for the link between Andean uplift and glassfrog diversification along with their chromatic characteristics and elevational gradients. Changes in coloration in species of the family Centrolenidae occurs repeatedly as independent events, i.e. biliverdin pigment, or as dependent events, as the case of dermal chromatophore units (DCUs). Due to the importance of these chromatic characteristics for camouflage, it was found that they are related to the distribution of species in altitudinal gradients. *Centrolene* and *Nymphargus*, which occupy a montane elevational range (800–3500m), are commonly lavender in preservation. While *Hyalinobatrachium*, wich are in vast majority cream in preserved, occupy lowlands to highlands (0–3500). Being the highlands (800–3500), the altitudinal range that harbor the wider number of chromatic characteristics. Therefore, our results highlight the importance of the Andes uplift in the evolution and diversification of the lineages of the Centrolenidae family, as well as in the evolution of the chromatic characteristics.

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APPENDIX

Appendix 1. Dataset of glass frogs reviewed from the Instituto Nacional de Biodiversidad (DHMECN) and the Museo de Zoología, Universidad San Francisco de Quito (ZSFQ).

Genus	Specie	Catalog Number	Country	Province
Centrolene	*buckleyi*	INABIO 868-893	Ecuador	Sucumbíos
Centrolene	*condor*	INABIO 6796, 12049	Ecuador	Zamora Chinchipe
Centrolene	*geckoidea*	INABIO 900	Ecuador	Carchi
Centrolene	*lynchi*	INABIO 11650	Ecuador	Pichincha
Centrolene	*peristicta*	INABIO 3538	Ecuador	Imbabura
Centrolene	*peristicta*	INABIO 7067, 10319	Ecuador	Pichincha
Centrolene	*pipilata*	INABIO 11722	Ecuador	Zamora Chinchipe
Chimerella	*mariaelenae*	ZSFQ 437-704	Ecuador	Napo
Cochranella	*litoralis*	INABIO 3198	Ecuador	Esmeraldas
Cochranella	*mache*	INABIO 3560, 2611	Ecuador	Esmeraldas
Cochranella	*resplendens*	INABIO 8243-8244, 10480	Ecuador	Sucumbíos
Cochranella	*resplendens*	INABIO 11240, 13007, 13528-13530	Ecuador	Zamora Chinchipe
Espadarana	*audax*	ZSFQ 382-386	Ecuador	Napo
Espadarana	*callistomma*	INABIO 3229-3235	Ecuador	Esmeraldas
Espadarana	*durrellorum*	INABIO 895-898	Ecuador	Napo
Espadarana	*durrellorum*	INABIO 6793-6796	Ecuador	Sucumbíos
Espadarana	*durrellorum*	INABIO 11306-11307	Ecuador	Zamora Chinchipe
Espadarana	*prosoblepon*	ZSFQ 1282-1289	Ecuador	Carchi
Hyalinobatrachium	*aureoguttatum*	INABIO 3221-3225	Ecuador	Esmeraldas
Hyalinobatrachium	*fleischmanni*	INABIO 2602	Ecuador	Pichincha
Hyalinobatrachium	*fleischmanni*	INABIO 2588-2600	Ecuador	Esmeraldas
Hyalinobatrachium	*fleischmanni*	INABIO 14582-14583	Ecuador	El Oro
Hyalinobatrachium	*munozorum*	INABIO 5568, 9825-9826	Ecuador	Orellana
Hyalinobatrachium	*munozorum*	INABIO 7118	Ecuador	Pastaza
Hyalinobatrachium	*pellucidum*	ZSFQ 592-593	Ecuador	Napo
Hyalinobatrachium	*pellucidum*	INABIO 9244	Ecuador	Napo
Hyalinobatrachium	*pellucidum*	INABIO 11305, 11095	Ecuador	Zamora Chinchipe
Hyalinobatrachium	*valerioi*	ZSFQ 537	Ecuador	Imbabura
Nymphargus	*balionotus*	INABIO 865	Ecuador	Carchi
Nymphargus	*cochranae*	ZSFQ 1150-1151	Ecuador	Zamora Chinchipe
Nymphargus	*grandisonae*	INABIO 10317	Ecuador	Pichincha
Nymphargus	*griffithsi*	INABIO 4163-4165	Ecuador	Pichincha
Nymphargus	*laurae*	INABIO 15383-15384	Ecuador	Napo
Nymphargus	*mariae*	ZSFQ 1322	Ecuador	Pastaza
Nymphargus	*posadae*	ZSFQ 819-820	Ecuador	Napo
Nymphargus	*siren*	ZSFQ 833	Ecuador	Napo
Sachatamia	*ilex*	INABIO 9319-9320, 9620-9627	Ecuador	Pichincha
Sachatamia	*ilex*	INABIO 11977-11980	Ecuador	Esmeraldas

Teratohyla	*amelie*	INABIO 4372, 11298	Ecuador	Pastaza
Teratohyla	*amelie*	INABIO 3591	Ecuador	Zamora Chinchipe
Teratohyla	*midas*	DFCH 0272	Ecuador	Orellana
Teratohyla	*spinosa*	INABIO 3226	Ecuador	Esmeraldas
Teratohyla	*spinosa*	INABIO 3227	Ecuador	Carchi
Teratohyla	*spinosa*	INABIO 3228	Ecuador	Napo

Appendix 2. Dataset of coloration in life and preserved for glass frogs used in this study. The green columns correspond to the chromatic characteristics in life: dorsal coloration, mark shape and marks coloration. Orange columns correspond to the dorsal coloration and distinctive marks in preserved.

Gene	Specie	Life			Preserved		Source
		Dorsal coloration	**Mark shape**	**Marks coloration**	**Dorsal coloration**	**Distinctive mark**	
Celsiella	*revocata*	Green	Spot, circular dots and/or stripe	Yellow	Gray	Both	Señaris et al., 2005
	vozmedianoi	Green	Spot, circular dots and/or stripe	Yellow	Gray	Light	Señaris et al., 2005
Centrolene	*altitudinalis*	Yellowish green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Guayasamin et al., 2006; Rivero 1868
	antioquiensis	Yellowish green	Spot, circular dots and/or stripe	Yellow	Lavender	Both	Rivera-Correa 2010
	ballux	Yellowish green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Guayasamin et al., 2020
	buckleyi	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Dark	Guayasamin et al., 2020
	charapita	Green	Combinated	Combinated	Lavender	Light	Guayasamin et al., 2020
	condor	Green	Fleck	Yellow	Lavender	Both	Guayasamin et al., 2020
	daidalea	Green	Spot, circular dots and/or stripe	Yellow	NA	NA	Rojas-Runnjaic et al., 2011
	geckoidea	Greyish green	Spot, circular dots and/or stripe	Yellow	Gray	Light	Guayasamin et al., 2020

Centrolene	*heloderma*	Yellowish green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Guayasamin et al., 2020
	hesperia	Green	Doesn't have marks	Doesn't have marks	Lavender	Light	Cadle et al., 1990
	huilense	Green	Spot, circular dots and/or stripe	Combinated	Lavender	Both	Guayasamin et al., 2020
	hybrida	Green	Spot, circular dots and/or stripe	Yellow	Lavender	NA	AmphibiaWeb 2009 Centrolene hybrida <https://amphibiaweb.org/species/1728> University of California, Berkeley, CA, USA. Accessed Jan 10, 2022; Guayasamin et al., 2006
	lynchi	Yellowish green	Combinated	Combinated	Lavender	Both	Guayasamin et al., 2020
	muelleri	Green	Spot, circular dots and/or stripe	Black/brown	Gray	Dark	Duellman, 1993; Guayasamin et al., 2006
	notosticta	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Guayasamin et al., 2006
	peristicta	Yellowish green	Spot, circular dots and/or stripe	Combinated	Lavender	Both	Guayasamin et al., 2020
	pipilata	Olive green	Combinated	Combinated	Lavender	Both	Guayasamin et al., 2020
	sabini	Yellowish green	Spot, circular dots and/or stripe	Yellow	Lavender	Dark	Catenazzi et al., 2012
	sanchezi	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Guayasamin et al., 2020
	savagei	Green	Spot, circular dots and/or stripe	Combinated	Lavender	Both	Vargas et al., 2017

Centrolene	*venezuelense*	Green	Spot, circular dots and/or stripe	Yellow	Lavender	NA	Rivero, 1968; Señaris et al., 2005
Chimerella	*corleone*	Yellowish green	Spot, circular dots and/or stripe	Yellow	Gray	Both	Guayasamin et al., 2020; Twomey et al., 2014
	mariaelenae	Yellowish green	Fleck	Black/brown	Lavender	Dark	Guayasamin et al., 2020
Cochranella	*erminea*	Olive green	Spot, circular dots and/or stripe	Combinated	Gray	Dark	Torre-Gastello et al., 2007
	euknemos	Bluish green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Molina-Zuluaga et al., 2017; Savage et al., 1967
	granulosa	Bluish green	Spot, circular dots and/or stripe	Combinated	Lavender	Dark	Guayasamin et al., 2020
	guayasamini	Yellowish green	Fleck	Blue/green	Cream	Dark	Twomey et al., 2014
	litoralis	Yellow	Spot, circular dots and/or stripe	Black/brown	Lavender	Dark	Guayasamin et al., 2020
	mache	Bluish green	Spot, circular dots and/or stripe	Yellow	Lavender	Both	Guayasamin et al., 2020
	nola	Green	Fleck	Yellow	Gray	Dark	Harvey 1996; Lujan et al., 2014
	resplendens	Green	Spot, circular dots and/or stripe	Blue/green	Lavender	Light	Guayasamin et al., 2020

Espadarana	*andina*	Yellowish green	Spot, circular dots and/or stripe	Blue/green	Lavender	Dark	Rivero 1968
	audax	Green	Spot, circular dots and/or stripe	Red/yellow/ Orange	Lavender	Light	Guayasamin et al., 2020
	callistomma	Olive green	Doesn't have marks	Doesn't have marks	Lavender	Doesn't have marks	Guayasamin et al., 2020
	durrellorum	Green	Doesn't have marks	Doesn't have marks	Lavender	Dark	Guayasamin et al., 2020
	prosoblepon	Green	Spot, circular dots and/or stripe	Black/brown	Lavender	Dark	Guayasamin et al., 2020
	prosoblepon	Green	False ocelli	Blue/green	Lavender	Light	Guayasamin et al., 2020
Hyalinobatrachium	*adespinosai*	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Guayasamin et al., 2020
	anachoretus	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Twomey et al., 2014
	aureoguttatum	Greenish yellow	Spot, circular dots and/or stripe	Yellow	Cream	Light	Guayasamin et al., 2020
	bergeri	Yellowish green	Combinated	Yellow	Cream	Dark	Cannatella, 1980
	cappellei	Yellowish green	Spot, circular dots and/or stripe	Blue/green	Cream	Dark	Castroviejo et al., 2011
	carlesvilai	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Castroviejo et al., 2009
	chirripoi	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Guayasamin et al., 2020

Hyalinobatrachium	*colymbiphyllum*	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Taylor 1949
	duranti	Yellowish green	Combinated	Black/brown	Cream	Dark	Señaris et al., 2005
	esmeralda	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Ruiz-Carranza et al., 1998
	fleischmanni	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Guayasamin et al., 2020
	fragile	Green	Combinated	Combinated	Crema	NA	Señaris et al., 2005
	iaspidiense	Yellowish green	Spot, circular dots and/or stripe	Combinated	Lavender	Light	Guayasamin et al., 2020
	ibama	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Ruiz-Carranza et al., 1998
	kawense	Yellowish green	Combinated	Combinated	Cream	Both	Castroviejo et al., 2011
	mondolfii	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Both	Castroviejo et al., 2011
	muiraquitan	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Araújo de Oliveira et al., 2017
	munozorum	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Guayasamin et al., 2020
	orientale	Yellowish green	Combinated	Combinated	Cream	Dark	Señaris et al., 2005
	orocostale	Yellowish green	Combinated	Combinated	Cream	Dark	Castroviejo et al., 2008

Hyalinobatrachium	*pallidum*	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Señaris et al., 2005
	pellucidum	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Guayasamin et al., 2020
	talamancae	Yellowish green	Combinated	Combinated	Cream	Dark	Starrett & Savage. 1973
	tatayoi	Yellowish green	Spot, circular dots and/or stripe	Yellow	Cream	Dark	Castroviejo-Fisher et al., 2007
	taylori	Green	Combinated	Yellow	Cream	Both	Castroviejo et al., 2011
	tricolor	Yellowish green	Spot, circular dots and/or stripe	Blue/green	Cream	Both	Castroviejo et al., 2011
	valerioi	Yellowish green	Reticulation	Combinated	Cream	Dark	Guayasamin et al., 2020
	vireovittatum	Yellowish green	Combinated	Yellow	NA	NA	Starrett & Savage., 1973
	yaku	Yellowish green	Combinated	Combinated	Cream	Dark	Guayasamin et al., 2020
Ikakogi	*tayrona*	Green	Fleck	Combinated	Lavender	Dark	Pérez-Gonzales et al., 2018; Rada et al., 2019
Nymphargus	*anomalus*	Brown	Ocelli	Combinated	Cream	Dark	Guayasamin et al., 2020
	balionotus	Yellow	Combinated	Combinated	Cream	Dark	Guayasamin et al., 2020
	bejaranoi	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Cannatella, 1980
	cariticommatus	Green	Combinated	Combinated	Lavender	Both	Guayasamin et al., 2020

Nymphargus	*chancas*	Olive green	Spot, circular dots and/or stripe	Yellow	Gray	Light	Duellman et al., 1993
	cochranae	Yellowish green	Ocelli	Red	Lavender	Both	Guayasamin et al., 2020
	colomai	Olive green	Spot, circular dots and/or stripe	Combinated	Gray	Light	Guayasamin et al., 2020
	garciae	Green	Spot, circular dots and/or stripe	Combinated	Lavender	Light	Guayasamin et al., 2020
	grandisonae	Yellowish green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Guayasamin et al., 2020
	griffithsi	Yellowish green	Fleck	Black/brown	Lavender	Dark	Guayasamin et al., 2020
	humboldti	Yellowish green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Guayasamin et al., 2020
	lasgralarias	Yellowish green	Spot, circular dots and/or stripe	Black/brown	Cream	Dark	Guayasamin et al., 2020
	laurae	Yellowish green	Ocelli	Combinated	Cream	Both	Sánchez-Carvajal et al., 2021
	lindae	Green	Ocelli	Combinated	Lavender	Both	Guayasamin et al., 2020
	manduriacu	Olive green	Combinated	Combinated	Lavender	Light	Guayasamin et al., 2020
	mariae	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Guayasamin et al., 2020
	megacheirus	Yellowish green	Spot, circular dots and/or stripe	Combinated	Lavender	Dark	Guayasamin et al., 2020

Nymphargus	*mixomaculatus*	Yellowish green	Spot, circular dots and/or stripe	Combinated	Lavender	Both	Guayasamin, Lehr et al., 2006
	ocellatus	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	AmphibiaWeb 2009 Nymphargus ocellatus <https://amphibiaweb.org/species/1779> University of California, Berkeley, CA, USA. Accessed Jan 10, 2022.
	pluvialis	Yellowish green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Cannatella et al., 1982
	posadae	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Both	Guayasamin et al., 2020
	rosada	Dark lavender	Spot, circular dots and/or stripe	Yellow	Brown	Light	Rada et al., 2017
	siren	Green	False ocelli	Blue/green	Lavender	Both	Guayasamin et al., 2020
	spilotus	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Ruiz-Carranza et al., 1997
	sucre	Olive green	Spot, circular dots and/or stripe	Yellow	Gray	Light	Guayasamin et al., 2020
	vicenteruedai	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Velásquez-Álvarez et al., 2007
	wileyi	Yellowish green	Doesn't have marks	Doesn't have marks	Lavender	Dark	Guayasamin et al., 2020
Rulyrana	*adiazeta*	Green frog	NA	NA	NA	NA	AmphibiaWeb 2009 Rulyrana adiazeta <https://amphibiaweb.org/species/1749> University of California, Berkeley, CA, USA. Accessed Jan 10, 2022.
	flavopunctata	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Both	Guayasamin et al., 2020

Rulyrana	*mcdiarmidi*	Olive green	Spot, circular dots and/or stripe	Yellow	Lavender	Both	Guayasamin et al., 2020
	saxiscandens	Green	Fleck	Black/brown	Gray	Dark	Duellman et al, 1993; Twomey et al., 2014
	spiculata	Green	Spot, circular dots and/or stripe	Yellow	Lavender	NA	Duellman 1976
	susatamai	Green	Spot, circular dots and/or stripe	Yellow	NA	NA	AmphibiaWeb 2009 Rulyrana susatamai <https://amphibiaweb.org/species/1800> University of California, Berkeley, CA, USA. Accessed Jan 10, 2022.
Sachatamia	*albomaculata*	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Guayasamin et al., 2020
	electrops	Yellowish green	Combinated	Combinated	Lavender	Both	Rada, Jeckel et al., 2017b
	ilex	Green	Fleck	Black/brown	Lavender	Dark	Guayasamin et al., 2020
	orejuela	Olive green	Fleck	Black/brown	Gray	Dark	Guayasamin et al., 2020
	punctulata	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Rojas-Morales et al., 2014
Teratohyla	*adenocheira*	Green	Spot, circular dots and/or stripe	Yellow	Gray	Light	Harvey et al., 2005
	amelie	Bluish green	Doesn't have marks	Doesn't have marks	Lavender	Dark	Cisneros & Mesa 2007; Guayasamin et al., 2020
	midas	Yellowish green	Spot, circular dots and/or stripe	Yellow	Lavender	Dark	Guayasamin et al., 2020
	pulverata	Green	Spot, circular dots and/or stripe	Yellow	Cream	Light	Guayasamin et al., 2020

Teratohyla	*spinosa*	Yellowish green	Fleck	Black/brown	Lavender	Dark	Guayasamin et al., 2020
Vitreorana	*antisthenesi*	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Señaris et al., 2005
	castroviejoi	Olive green	Spot, circular dots and/or stripe	Yellow	Lavender	Light	Señaris et al., 2005
	eurygnatha	Green	Fleck	Black/brown	Lavender	NA	Heyer et al., 1990
	franciscana	Yellowish green	Fleck	Black/brown	Cream	Dark	Santana et al., 2015
	gorzulae	Green	Spot, circular dots and/or stripe	Yellow	Lavender	Dark	Castroviejo et al., 2009
	helenae	Yellowish green	Fleck	Blue/green	Lavender	Dark	Señaris et al., 2005
	ritae	Yellowish green	Spot, circular dots and/or stripe	Blue/green	Lavender	Dark	Guayasamin et al., 2020
	uranoscopa	Green	Combinated	Combinated	Lavender	Light	Heyer et al., 1990
OutGroup							
Allophrynidae: Allophryne	*relicta*	Cream	Spot, circular dots and/or stripe	Black/Brown	Cream	Dark	Caramaschi et al., 2013
	resplendens	Black	Spot, circular dots and/or stripe	Yellow	Brown	Light	Castroviejo-Fisher et al., 2012
	ruthveni	Brown	Spot, circular dots and/or stripe	Black/Brown	Cream	Dark	Castroviejo-Fisher et al., 2012; Gaige, 1926

Craugastoridae: Pristimantis	*cruentus*	Brown	Spot, circular dots and/or stripe	Combinated	Brown	Dark	Kohler, 2011
	galdi	Green frog	Spot, circular dots and/or stripe	Black/brown	Cream	Dark	Lynch et al., 1990
Hemiphractidae: Gastrotheca	*dendronastes*	Brown	Doesn't have marks	Doesn't have marks	Brown	Dark	Chasiluisa et al., 2018
	longipes	Green frog	Doesn't have marks	Doesn't have marks	White	Doesn't have marks	Almendáriz et al., 2005
Hylidae: Hyloscirtus	*colymba*	Yellowish green	Fleck	Black/brown	Cream	Dark	Duellman, 1970
	lindae	Brown	Doesn't have marks	Doesn't have marks	Gray	Dark	Coloma et al., 2019
Hylidae: Pseudis	*cardosoi*	Green frog	Spot, circular dots and/or stripe	Black/brown	Gray	Dark	AmphibiaWeb 2010 Pseudis cardosoi <https://amphibiaweb.org/species/6093> University of California, Berkeley, CA, USA. Accessed Jan 10, 2022.
	limellum	Brown	Spot, circular dots and/or stripe	Black/brown	Brown	Dark	AmphibiaWeb 2018 Lysapsus limellum: Uruguay harlequin frog <https://amphibiaweb.org/species/5222> University of California, Berkeley, CA, USA. Accessed Jan 10, 2022.

Hylidae: Scinax	*funereus*	Olive green	Spot, circular dots and/or stripe	Black/brown	Brown	Dark	Duellman 1971; Ron, S. R. y Read, M. 2020. Scinax funereus En: Ron, S. R., Merino-Viteri, A. Ortiz, D. A. (Eds). Anfibios del Ecuador. Version 2021.0. Museo de Zoología, Pontificia Universidad Católica del Ecuador. https://bioweb.bio/faunaweb/amphibiaweb/FichaEspecie/Scinax%20funereus, acceso lunes, 10 de Enero de 2022
	sugillatus	Brown	Spot, circular dots and/or stripe	Black/brown	Brown	Dark	Duellman 1973; Ron, S. R., Read. M. y Pazmiño-Armijos, G. 2019. Scinax sugillatus En: Ron, S. R., Merino-Viteri, A. Ortiz, D. A. (Eds). Anfibios del Ecuador. Version 2021.0. Museo de Zoología, Pontificia Universidad Católica del Ecuador.https://bioweb.bio/faunaweb/amphibiaweb/FichaEspecie/Scinax%20sugillatus, acceso lunes, 10 de Enero de 2022
Hylidae: Osteocephalus	*cabrerai*	Yellowish green	Spot, circular dots and/or stripe	Black/brown	Cream	Dark	Jungfer, 2010; Read, M. y Ron, S. R. 2018. Osteocephalus cabrerai En: Ron, S. R., Merino-Viteri, A. Ortiz, D. A. (Eds). Anfibios del Ecuador. Version 2021.0. Museo de Zoología, Pontificia Universidad Católica del Ecuador. https://bioweb.bio/faunaweb/amphibiaweb/FichaEspecie/Osteocephalus%20cabrerai, acceso lunes, 10 de Enero de 2022
	festae	Brown	Spot, circular dots and/or stripe	Black/brown	Brown	Dark	Jungfer 2010

Appendix 3. Altitudinal data (minimum and maximum) and altitudinal codes for RASP analyses.

Species	Altitude Min	Altitude Max	Altitudinal code
Celsiella revocata	1200	1800	B
Celsiella vozmedianoi	150	800	A
Centrolene altitudinalis	1900	2400	B
Centrolene antioquiensis	1730	2450	B
Centrolene ballux	1700	2340	B
Centrolene buckleyi	2100	3300	B
Centrolene charapita	664	1219	C
Centrolene condor	1737	2960	B
Centrolene daidalea	800	2060	B
Centrolene geckoidea	1750	2500	B
Centrolene heloderma	1850	2575	B
Centrolene hesperia	1500	1800	B
Centrolene huilense	2000	2190	B
Centrolene hybrida	1410	2020	B
Centrolene lynchi	1140	2075	B
Centrolene muelleri	1140	1875	B
Centrolene notostictum	1600	2440	B
Centrolene peristicta	1380	1900	B
Centrolene pipilata	1300	1910	B
Centrolene sabini	2750	2800	B
Centrolene sanchezi	1800	2350	B
Centrolene savagei	1400	2410	B
Centrolene venezuelense	2100	3051	B

Species	Altitude Min	Altitude Max	Altitudinal code
Chimerella corleone	610	–	A
Chimerella mariaelenae	813	1820	B
Cochranella erminea	300	870	A
Cochranella euknemos	90	1650	C
Cochranella granulosa	30	1500	C
Cochranella guayasamini	517	1120	C
Cochranella litoralis	100	260	A
Cochranella mache	38	1030	C
Cochranella nola	500	1750	C
Cochranella resplendens	190	1100	C
Espadarana andina	505	2500	C
Espadarana audax	800	1900	B
Espadarana callistomma	20	500	A
Espadarana durrellorum	403	1150	C
Espadarana prosoblepon	20	1935	C
Hyalinobatrachium adespinosai	1795	–	B
Hyalinobatrachium anachoretus	2000	2050	B
Hyalinobatrachium aureoguttatum	45	1570	C
Hyalinobatrachium bergeri	300	2000	C
Hyalinobatrachium cappellei	10	2000	C
Hyalinobatrachium carlesvilai	300	1200	C
Hyalinobatrachium chirripoi	0	600	A
Hyalinobatrachium colymbiphyllum	50	1800	C

Species	Altitude Min	Altitude Max	Altitudinal code
Hyalinobatrachium duranti	1800	2400	B
Hyalinobatrachium esmeralda	1600	1650	B
Hyalinobatrachium fleischmanni	10	1680	C
Hyalinobatrachium fragile	100	1400	C
Hyalinobatrachium iaspidiense	10	1000	C
Hyalinobatrachium ibama	1600	2050	B
Hyalinobatrachium kawense	1	100	A
Hyalinobatrachium mondolfii	15	270	A
Hyalinobatrachium muiraquitan	–	–	
Hyalinobatrachium munozorum	200	1840	C
Hyalinobatrachium orientale	190	1200	C
Hyalinobatrachium orocostale	1200	1500	B
Hyalinobatrachium pallidum	1132	2250	B
Hyalinobatrachium pellucidum	1000	1740	B
Hyalinobatrachium talamancae	400	1116	C
Hyalinobatrachium tatayoi	230	512	A
Hyalinobatrachium taylori	30	1850	C
Hyalinobatrachium tricolor	10	100	A
Hyalinobatrachium valerioi	10	1500	C
Hyalinobatrachium vireovittatum	630	1100	C
Hyalinobatrachium yaku	300	360	A
Ikakogi tayrona	980	1790	B
Nymphargus anomalus	1668	1770	B
Nymphargus balionotus	889	1523	B
Nymphargus bejaranoi	1600	2400	B
Nymphargus cariticommatus	2200	2700	B
Nymphargus chancas	1080	1200	B
Nymphargus colomai	1200	–	B

Species	Altitude Min	Altitude Max	Altitudinal code
Nymphargus cochranae	1100	1600	B
Nymphargus garciae	1900	2700	B
Nymphargus grandisonae	1140	2710	B
Nymphargus griffithsi	1340	2600	B
Nymphargus humboldti	1770	2400	B
Nymphargus lasgralarias	1400	2600	B
Nymphargus laurae	500	–	A
Nymphargus lindae	1200	–	B
Nymphargus manduriacu	1215	1242	B
Nymphargus mariae	400	1050	C
Nymphargus megacheirus	1300	1750	B
Nymphargus mixomaculatus	2625	2750	B
Nymphargus ocellatus	1200	1700	B
Nymphargus pluvialis	1820	2250	B
Nymphargus posadae	1100	2800	B
Nymphargus rosada	1100	2000	B
Nymphargus siren	1410	2000	B
Nymphargus spilotus	1850	1940	B
Nymphargus sucre	2140	2160	B
Nymphargus vicenteruedai	2650	2700	B
Nymphargus wileyi	2100	–	B
Rulyrana adiazeta	1030	2060	B
Rulyrana flavopunctata	300	1710	C
Rulyrana mcdiarmidi	1150	1500	B
Rulyrana saxiscandens	800	1000	B
Rulyrana spiculata	1200	1700	B
Rulyrana susatamai	400	1650	C
Sachatamia albomaculata	50	1500	C

Species	Altitude Min	Altitude Max	Altitudinal code
Sachatamia electrops	980	1630	B
Sachatamia ilex	50	1420	C
Sachatamia orejuela	500	1250	C
Sachatamia punctulata	500	930	A
Teratohyla adenocheira	30	380	A
Teratohyla amelie	350	1037	C
Teratohyla midas	190	930	A
Teratohyla pulverata	2	960	A
Teratohyla spinosa	2	800	A
Vitreorana antisthenesi	110	1300	C
Vitreorana castroviejoi	580	800	A
Vitreorana eurygnatha	50	1750	C
Vitreorana franciscana	850	–	A
Vitreorana gorzulae	450	1900	C
Vitreorana helenae	440	990	C
Vitreorana ritae	10	400	A
Vitreorana uranoscopa	532	1337	C
OutGroup			
Allophryne relicta	90	–	A
Allophryne resplendens	90	120	A
Allophryne ruthveni	2	300	A
Gastrotheca dendronastes	1230	1700	C
Gastrotheca longipes	–	500	A
Hyloscirtus colymba	600	1400	C
Hyloscirtus lindae	2000	2500	B
Osteocephalus cabrerai	250	700	A
Osteocephalus festae	1000	2200	B
Pristimantis cruentus	40	1800	C
Pristimantis galdi	1000	2900	B
Pseudis cardosoi	700	1100	C
Pseudis limellum	100	200	A
Scinax funereus	70	100	A
Scinax sugillatus	20	500	A

SUPPORTING INFORMATION

Figure S1. Optimal maximum likelihood tree (log likelihood = -63762.98), showing the phylogenetic relationships among 120 species of Centrolenidae and 15 outgroup taxa. Values above nodes are posterior probabilities resulting from Bayesian phylogenetic analyses (values < 0.50 not shown, black circles = 1). Numbers bellow nodes correspond to non-parametric bootstraps (values < 0.70 not shown, black circles = 1).

Figure S2. Maximum clade credibility chronogram from Bayesian analyses with clade posterior probabilities

Figure S3. Maximum clade credibility chronogram from BEAST analyses with 95% high posterior densities indicated by blue bars and median age in nodes.

Figure S4. Colour groups from the analysis of RGB values in life (A and B) and preserved (C and D). The larger circles correspond to the centroids of the calculated color groups and the color of the group. The smaller transparent circles represent the raw measured values. Principal component analysis was performed on the RGB coordinates to generate the two plotted axes.

Figure S5. Mapping the coloration in life in the chronogram obtained by BEAST

Figure S6. Mapping the coloration in preserved in the chronogram obtained by BEAST

Figure S7. Number of species of Centrolenidae distributed according to the chromatic character in life and preserved. Color in life (A), Color in preserved (B), Mark shape in life (C), Marks coloration in life (D) and Distintive marks in preserved (E); based on elevational distribution: lowlands 0–900 (black), highlands 800–3500 (grey), and continuous 0–3500 (white).

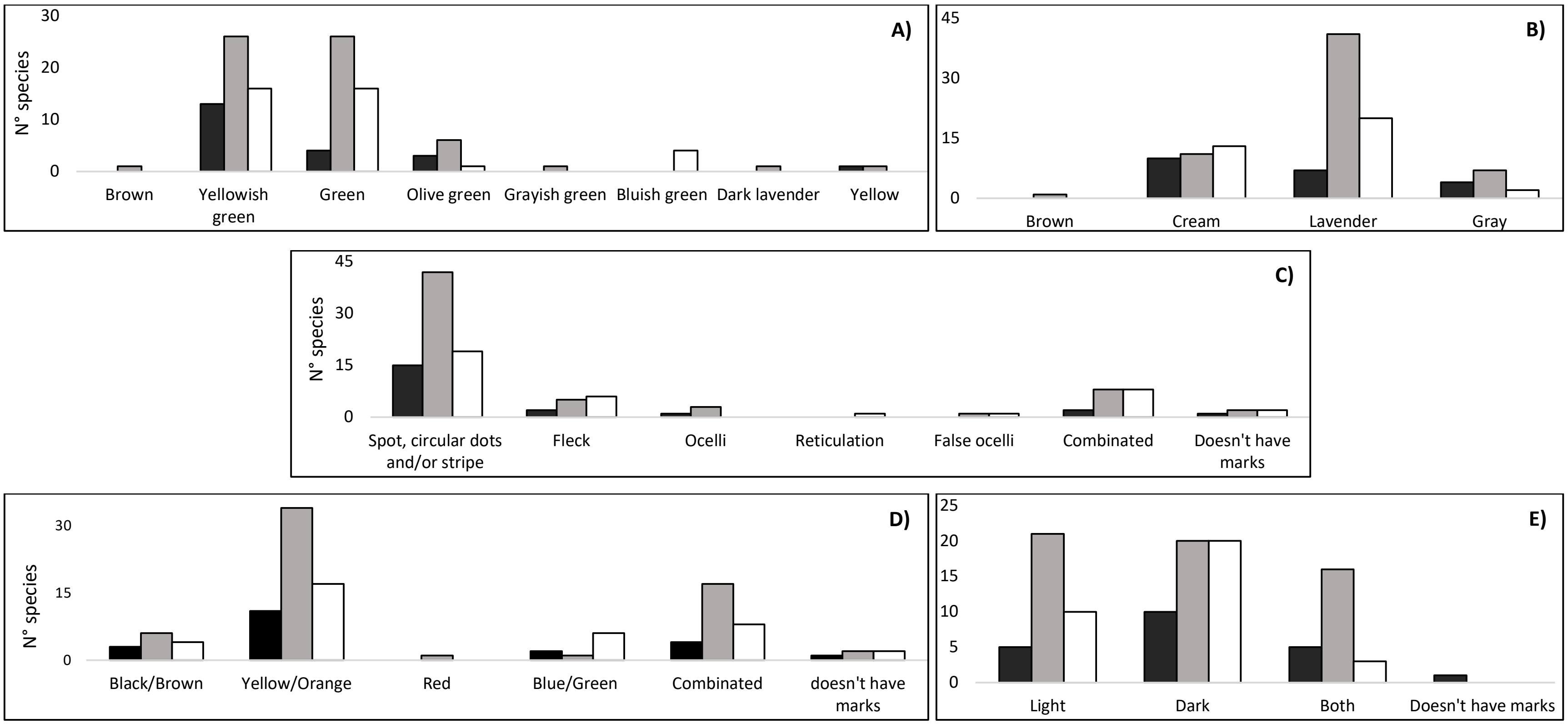

Figure S8. Mapping the mark shape in life in the chronogram obtained by BEAST

Figure S9. Mapping the marks coloration in life in the chronogram obtained by BEAST

Figure S10. Mapping the distinctive mark in preserved in the chronogram obtained by BEAST

Table S1. Species names and GenBank accession numbers for the specimens included in this study.

Genus and species	Voucher	12S	16S	ND1	c-myc	POMC	RAG-1
Celsiella revocata	MHNLS 17319	EU663379	EU663019	EU663113	EU663281	EU663204	EU663479
Celsiella vozmedianoi	MHNLS 17877, 17318	EU663385	EU663025	EU663163	EU663324	EU663247	EU663531
Centrolene altitudinalis	MHNLS 17194	EU663333	EU662974	EU663070	EU663249	EU663165	EU663433
Centrolene antioquiensis	NRPS 014	EU663336	EU662977	EU663073	EU663251	EU663167	EU663436
Centrolene ballux	QCAZ 40182	—	JX126954	—	—	—	—
Centrolene ballux	QCAZ 40196	KF639754	—	HG764783	—	—	—
Centrolene buckleyi	KU 178031	EU663338	EU662979	EU663075	EU663253	EU663169	—
Centrolene charapita	MHNC 13933 (AJC 2733)	KM068247	KM068256	—	—	—	—
Centrolene condor	QCAZ 44896	KF639755	JX126955	JX187513	—	—	—
Centrolene daidalea	MHUA 3271, MHNLS 18890	EU663366	EU663007	EU663101	EU663272	—	EU663465
Centrolene geckoidea	KU 178015	EU663341	EU662982	EU663077	—	—	EU663440
Centrolene heloderma	QCAZ 40200	KF639757	JX126956	JX187509	—	—	—
Centrolene hesperia	MHNSM 25802	EU663345	EU662986	EU663081	EU663258	KF639777	EU663444
Centrolene huilense	QCAZ 37230, 45905	—	JX126959	JX187510	—	—	—
Centrolene hybrida	MAR 347	EU663346	EU662987	EU663082	EU663259	EU663175	EU663445
Centrolene lynchi	QCAZ 40191–92	KF639758	JX126957	JX187508	—	—	—
Centrolene muelleri	PV001 (Pablo Venegas)	KF639759	JX126958	HG764785	KF534458	KF639778	—
Centrolene notosticta	MAR 510	EU663351	EU662992	EU663087	EU663264	EU663180	EU663450
Centrolene peristicta	QCAZ 22312	EU663352	EU662993	EU663088	EU663266	EU663181	EU663451
Centrolene pipilata	KU 178154	EU663353	EU662994	EU663089	KF534459	KF639779	EU663452
Centrolene sabini	MUSM 28018	—	JX126960	JX187511	—	—	—
Centrolene sanchezi	QCAZ 22728	EU663337	EU662978	EU663074	EU663252	EU663168	EU663437
Centrolene savagei	MHUA 4094	EU663380	EU663020	EU663114	EU663282	EU663205	EU663480
Centrolene venezuelense	EBRG 5244	—	—	—	—	EU663186	—

Centrolene venezuelense	MHNLS 16497	EU663360	EU663001	—	—	—	EU663459
Chimerella corleone	CORDIBI 10466	—	KM068276	—	—	—	—
Chimerella mariaelenae	QCAZ 31729	EU663350	EU662991	EU663086	EU663263	EU663179	EU663449
Cochranella erminea	MHNC 7247	KF639762	KF534360	HG764786	KF534460	KF639780	—
Cochranella euknemos	CH 5109	EU663367	EU663008	EU663102	KF534461	EU663193	EU663466
Cochranella granulosa	CH 5121	—	EU663010	—	—	—	—
Cochranella granulosa	USNM 559082	EU663370	—	—	EU663274	EU663195	EU663469
Cochranella guayasamini	MHNC 13930	KM068250	KM068259	—	—	—	—
Cochranella litoralis	QCAZ 27693	EU663349	EU662990	EU663085	EU663262	EU663178	EU663448
Cochranella mache	QCAZ 27747	EU663373	EU663013	EU663107	EU663277	EU663198	EU663472
Cochranella nola	CBG 1096	EU663381	EU663021	EU663115	EU663283	EU663206	EU663481
Cochranella resplendens	QCAZ 38088	KF639763	KF534361	HG764787	—	—	—
Espadarana andina	JMG 366	EU663335	EU662976	EU663072	EU663250	EU663166	EU663435
Espadarana audax	QCAZ 23910	MT225173	MT225187	MT225131	—	—	—
Espadarana callistomma	QCAZ 28555	EU663340	EU662981	EU663076	EU663255	EU663171	EU663439
Espadarana durrellorum	QCAZ 47909	—	KF534356	HG764784	—	—	—
Espadarana durrellorum	QCAZ 27832	KF639756	—	—	—	—	—
Espadarana prosoblepon	MVZ 149741	—	—	AY819466	AY819170	AY819085	—
Espadarana prosoblepon	UCR 17102	EU663354	EU662995	—	—	—	EU663453
Hyalinobatrachium adespinosai	ZSFQ 1648	—	MN604036.1	—	—	—	—
Hyalinobatrachium anachoretus	CORBIDI 10472	KM068254	KM068300	—	—	—	—
Hyalinobatrachium aureoguttatum	QCAZ 32105	EU663391	EU663032	EU663124	EU663288	EU663214	EU663491
Hyalinobatrachium bergeri	MHNC 5676; MNCN/ADN 5547	EU663392	EU663033	EU663125	EU663289	EU663215	EU663492l
Hyalinobatrachium cappellei	MHNLS 16475, 17125	EU663401	EU663040	EU663132	EU663297	EU663222	EU663499
Hyalinobatrachium carlesvilai	CBG 1099	EU663388	EU663030	EU663122	EU663291	EU663212	EU663489i
Hyalinobatrachium chirripoi	UCR 17424	EU663398	EU663037	EU663129	EU663294	EU663219	EU663496

Hyalinobatrachium colymbiphyllum	UCR 17423	EU663400	EU663039	EU663131	EU663296	EU663221	EU663498
Hyalinobatrachium duranti	MHNLS 16493, 17164	EU663402	EU663041	EU663133	EU663298	EU663223	EU663500
Hyalinobatrachium esmeralda	LSB 384	—	KP149361	—	—	—	—
Hyalinobatrachium fleischmanni	USNM 559092	EU663406	EU663045	EU663137	EU663300	EU663225	EU663504
Hyalinobatrachium fragile	MHNLS 17161	EU663407	EU447286	EU663138	EU663301	EU663226	EU663505
Hyalinobatrachium iaspidiense	MHNLS 17126, MTD 48145	EU663408	EU663047	EU663139	EU663302	—	EU663506
Hyalinobatrachium ibama	MAR 503	EU663409	EU663048	EU663140	EU663303	EU663227	EU663507
Hyalinobatrachium kawense	MNHN 2011.0119, MTD 48144	EU663387	EU663029	EU663121	EU663329	EU663211	EU663488
Hyalinobatrachium mondolfii	MHNLS 17119	EU663411	EU663050	EU663142	EU663305	EU663229	EU663509
Hyalinobatrachium muiraquitan	LZA 841	—	KY310571	—	—	—	—
Hyalinobatrachium munozorum	QCAZ 31056	EU663395	EU663034	EU663126	KF534464	EU663216	EU663493
Hyalinobatrachium orientale	MHNLS 17878, 17117	EU663413	EU447289	EU663144	EU663306	EU663230	EU663511
Hyalinobatrachium orocostale	MHNLS 17247	EU663414	EU447284	EU663145	EU663307	EU663231	EU663512
Hyalinobatrachium pallidum	MHNLS 17881, 17238	EU663415	EU663052	EU663146	EU663292	EU663217	EU663513
Hyalinobatrachium pellucidum	QCAZ 29438	EU663397	EU663036	EU663128	EU663293	EU663218	EU663495
Hyalinobatrachium talamancae	CH 5330	EU663418	EU663054	EU663149	EU663313	EU663233	EU663516
Hyalinobatrachium tatayoi	MHNLS 17174	EU663419	EU663055	EU663150	EU663310	EU663234	EU663517
Hyalinobatrachium taylori	MHNLS 17141	EU663420	EU663056	EU663151	EU663311	EU663235	EU663518
Hyalinobatrachium tricolor	MNCN 44828	—	—	HG764789	—	—	—
Hyalinobatrachium tricolor	MNHN 2011.0116	EU663386	EU663027	—	EU663328	—	EU663486
Hyalinobatrachium valerioi	UCR 17418	EU663421	EU663058	EU663152	EU663312	EU663236	EU663519
Hyalinobatrachium vireovittatum	CH 6443	—	KF604303	—	—	—	—
Hyalinobatrachium yaku	MZUTI 5001	MF002067	MF002065.1	MF002063	—	—	—
Ikakogi tayrona	MAR 544	EU663356	EU662997	EU663091	EU663330	EU663183	EU663455
Nymphargus anomalus	QCAZ 41312	—	KF534364	HG764790	—	—	—
Nymphargus anomalus	QCAZ 45703	KF639766	—	—	—	—	—

Nymphargus balionotus	JMG0796	MH746563	MH746537	—	—	—	—
Nymphargus bejaranoi	CBG 1488	EU663422	EU663059	EU663155	EU663314	EU663239	EU663522
Nymphargus cariticommatus	MRy 544	MH746581	MH746555	MT225140	—	—	—
Nymphargus chancas	CORBIDI 10471	—	KM068277	—	—	—	—
Nymphargus cochranae	QCAZ 31113	EU663425	EU663061	EU663156	EU663317	EU663240	EU663523
Nymphargus colomai	QCAZ 41590	KF639767	KF534365	HG764791	—	—	—
Nymphargus garciae	KU 20801	AY326022	AY326022	—	—	—	—
Nymphargus grandisonae	QCAZ 22310	EU663344	EU662985	EU663080	EU663257	EU663174	EU663443
Nymphargus griffithsi	QCAZ 24825	MT232661	MT232431	MT238202	—	—	—
Nymphargus humboldti	QCAZ 45713	MH746587	—	MT225155	—	—	—
Nymphargus lasgralarias	QCAZ 31768	EU663426	EU663062	EU663157	EU663318	EU663241	EU663524
Nymphargus laurae	DHMECN 15383	MZ820691	MZ831508	—	—	—	—
Nymphargus lindae	QCAZ 41572	MH746582	MH746556	MT225137	—	—	—
Nymphargus manduriacu	JMG0615	MH746582	MH746556	—	—	—	
Nymphargus mariae	QCAZ 37927, DFCH-USFQ D285	KF639771	KF534368	HG764793	—	—	EU663478
Nymphargus megacheirus	KU 143272	EU663427	EU663063	EU663158	EU663319	EU663242	EU663525
Nymphargus mixomaculatus	MTD 45200	KF639768	EU663064	EU663159	EU663320	EU663243	EU663526
Nymphargus ocellatus	GCI 363	KF639769	KF534366	HG764792	KF534465	KF639784	KF639787
Nymphargus pluvialis	KU 173224	EU663428	EU663065	EU663160	EU663321	EU663244	EU663527
Nymphargus posadae	QCAZ 25090	—	KF534367	—	—	—	—
Nymphargus posadae	QCAZ 26023	KF639770	—	—	—	—	EU663528
Nymphargus rosada	MHUA 4308	EU663429	EU663066	EU663161	EU663322	EU663245	EU663529
Nymphargus siren	KU 179171	EU663430	EU663067	EU663162	EU663323	EU663246	EU663530
Nymphargus spilotus	JD060	MH746590	MH746561	—	—	—	—
Nymphargus sucre	MZUTI 1422	MH746579	MH746553	MT225158	—	—	—
Nymphargus vicenteruedai	AAV 119	EU663424	EU663058	EU663154	EU663316	EU663238	EU663521l

Nymphargus wileyi	QCAZ 27435	EU663431	EU663068	EU663164	EU663325	EU663248	EU663532
Rulyrana adiazeta	MAR 483	EU663361	EU663002	EU663096	EU663268	EU663187	EU663460
Rulyrana flavopunctata	QCAZ 32265	EU663368	EU663009	EU663103	EU663273	EU663194	EU663467
Rulyrana mcdiarmidi	MZUTI 45	—	MT232432	—	—	—	—
Rulyrana mcdiarmidi	QCAZ 26545	MT225183	—	MT225163	—	—	—
Rulyrana saxiscandens	MNCN/ADN 51737	KF639772	KF534369	—	—	—	—
Rulyrana spiculata	MHNSM 24867	EU663382	EU663022	EU663116	EU663284	EU663207	EU663482
Rulyrana susatamai	MAR 337	EU663384	EU663024	EU663118	EU663286	EU663209	EU663484
Sachatamia albomaculata	USNM 534151	EU663362	EU663003	EU663097	EU663270	EU663188	EU663461
Sachatamia electrops	MHUA:A 9715	KY611461.1	KY611462.1	—	—	—	—
Sachatamia ilex	UCR 16861	EU663347	EU662988	EU663083	EU663260	EU663176	EU663446
Sachatamia orejuela	QCAZ 45993	KF639773	KF534371	HG764794	—	—	—
Sachatamia punctulata	MHUA 4071	EU663378	EU663018	EU663112	EU663280	EU663203	EU663477
Teratohyla adenocheira	LSUMZ H-17409	KF639774	—	HG764795	KF534466	KF639785	KF639788
Teratohyla adenocheira	LSUMZ H-17463	—	KF534372	—	—	—	—
Teratohyla amelie	MHNC 5646 / MNCN ADN 20619	EU663365	EU663005	EU663099	EU663327	EU663190	EU663463
Teratohyla midas	KHJ005	EU663374	EU663014	EU663108	EU663278	EU663199	EU663473l
Teratohyla pulverata	USNM 538588	EU663416	EU663053	EU663147	EU663308	EU663232	EU6635145
Teratohyla spinosa	USNM 538863	EU663383	EU663023	EU663117	EU663285	EU663208	EU663483
Vitreorana antisthenesi	MHNLS 17909	EU663390	EU663031	EU663123	EU663287	EU663213	EU663490
Vitreorana castroviejoi	MHNLS 16446	EU663363	EU663004	EU663098	EU663271	EU663189	EU663462
Vitreorana eurygnatha	CFBH 5729	AY843595	AY843595	EU663135	—	—	AY844383
Vitreorana franciscana	MZUFV9970	—	—	—	—	KR921744	—
Vitreorana gorzulae	MHNLS 16036	EU663343	EU662984	EU663079	EU663256	EU663173	EU663442
Vitreorana helenae	MHNLS 17139	EU663372	EU663012	EU663106	EU663276	EU663197	EU663471
Vitreorana ritae	MB 165	—	EU663017	—	—	—	—

Vitreorana ritae	MB 292	EU663377	—	EU663111	EU663326	EU663202	EU663476
Vitreorana uranoscopa	CFBHT13096	—	KU495614	—	—	—	MH988358
Vitreorana uranoscopa	CFBH7610	KY202833	—	—	—	—	—
Vitreorana uranoscopa	MTR 15819	—	—	—	—	JX298142	—
OutGroup							
Allophryne relicta	CFBH 29209	KF582053	KF582053	—	—	—	—
Allophryne resplendens	MZUNAP-01-605	JQ436697	JQ436698	—	—	—	—
Allophryne ruthveni	MAD 1852	AY819328	—	AY819458	AY819162	AY819077	—
Allophryne ruthveni	MAD 1857	—	EU662973	—	—	—	EU663432
Gastrotheca dendronastes	KU 181203	DQ679239	DQ679389	DQ679348	—	—	—
Gastrotheca longipes	USNM 258905	DQ679248	DQ679396	DQ679356	—	DQ679324	DQ679288
Hyloscirtus colymba	SIUC H-7079	AY843620	AY843620	KF794113	—	—	AY844410
Hyloscirtus colymba	SIUC H-6926	—	—	—	—	AY819157	—
Hyloscirtus lindae	QCAZ 45342	JX155824	JX155851	—	—	—	—
Osteocephalus cabrerai	JPC 13178/LSUMZ H-13720	AY843705	AY843705	—	—	—	AY844481
Osteocephalus cabrerai	KHJ F082	—	—	KF002199	—	—	—
Osteocephalus cabrerai	QCAZ 28231	—	—	—	—	JX875762	—
Osteocephalus festae	QCAZ 41039	—	—	HQ600614	—	JX875790	—
Osteocephalus festae	CORBIDI 1965	JX847064	—	—	—	—	—
Pristimantis cruentus	No voucher	EF493697	EF493697	—	—	—	—
Pristimantis cruentus	MVZ 203826	—	—	FJ882747	—	—	—
Pristimantis cruentus	AJC 0524	—	—	—	—	—	JQ025181
Pristimantis galdi	QCAZ 32368	EU186670	EU186671	—	—	—	EU186746
Pseudis cardosoi	CHUNB 42610	EF152997	EF152997	—	—	—	—
Pseudis limellum	MNRJ:34076	MK293749	MK293749	—	—	—	—
Pseudis limellum	MACN 38645	—	—	—	—	—	AY844477

Scinax funereus	QCAZ43799	MH662466	MH66248	MH662533	—	—	—
Scinax sugillatus	KU 217735	AY819392	—	AY819524	AY819227	AY819142	—

Table S2. Reclassification of the color in life and preserved with cluster analysis using RGB values. Meaning of the variables: Rl, Gl and Bl are the average RGB values of the three measured in life; R cl, G cl, and B cl are the RGB coordinates of the cluster in life; Rp, Gp and Bp are the average RGB values of the three measured in preserved and finally R cp, G cp and B cp are the RGB coordinates of the cluster in preserved.

Genus	Specie	Color in life	Rl	Gl	Bl	Cluster life	R cl	G cl	B cl	Color in preserved	Rp	Gp	Bp	Cluster preserved	R cp	G cp	B cp
Centrolene	*altitudinalis*	yellowish green	75	123	23	6	147	154	15	Lavender	170	173	191	4	82	66	70
Centrolene	*antioquiensis*	yellowish green	49	115	2	6	147	154	15	Lavender	137	124	166	4	82	66	70
Centrolene	*ballux*	yellowish green	115	107	2	6	147	154	15	Lavender	143	149	186	4	82	66	70
Centrolene	*buckleyi*	green	137	140	32	2	58	77	21	Lavender	149	160	191	4	82	66	70
Centrolene	*charapita*	green	50	64	29	2	58	77	21	Lavender	81	79	89	4	82	66	70
Centrolene	*condor*	green	86	115	52	2	58	77	21	Lavender	173	157	160	4	82	66	70
Centrolene	*daidalea*	green	65	117	53	2	58	77	21	Lavender	161	160	185	4	82	66	70
Centrolene	*geckoidea*	greyish green	124	140	112	—	124	140	112	Lavender	140	112	120	4	82	66	70
Centrolene	*heloderma*	yellowish green	73	85	42	6	147	154	15	Gray	140	133	94	1	156	154	175
Centrolene	*hesperia*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*huilense*	yellowish green	112	140	11	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*hybrida*	green	91	140	17	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*lynchi*	green	97	122	53	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*muelleri*	green	109	140	62	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*notosticta*	green	124	133	37	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA

Centrolene	*peristicta*	yellowish green	89	138	0	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*pipilata*	olive green	91	97	30	3	96	122	21	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*sabini*	yellowish green	61	138	10	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*sanchezi*	green	56	64	1	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*savagei*	green	46	89	3	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Centrolene	*venezuelense*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Celsiella	*revocata*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Celsiella	*vozmedianoi*	green	50	81	22	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Chimerella	*corleone*	yellowish green	169	191	4	6	147	154	15	Gray	191	179	117	1	156	154	175
Chimerella	*mariaelenae*	yellowish green	56	84	38	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Cochranella	*erminea*	yellowish green	94	89	4	6	147	154	15	Gray	92	83	73	1	156	154	175
Cochranella	*euknemos*	olive green	112	115	20	3	96	122	21	Cream	191	181	163	3	209	185	154
Cochranella	*granulosa*	bluish green	76	110	23	1	144	156	69	NA	NA	NA	NA	NA	NA	NA	NA
Cochranella	*guayasamini*	bluish green	99	166	123	1	144	156	69	NA	NA	NA	NA	NA	NA	NA	NA
Cochranella	*litoralis*	green	112	145	60	2	58	77	21	Lavender	166	135	124	4	82	66	70
Cochranella	*mache*	yellowish green	63	69	28	6	147	154	15	Lavender	166	141	133	4	82	66	70
Cochranella	*nola*	bluish green	160	172	105	1	144	156	69	NA	NA	NA	NA	NA	NA	NA	NA
Cochranella	*resplendens*	yellow	166	138	4	4	196	199	71	NA	NA	NA	NA	NA	NA	NA	NA
Espadarana	*andina*	green	66	83	15	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA

Espadarana	*audax*	yellowish green	125	143	26	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Espadarana	*callistomma*	green	144	141	30	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Espadarana	*durrellorum*	olive green	111	115	6	3	96	122	21	NA	NA	NA	NA	NA	NA	NA	NA
Espadarana	*prosoblepon*	green	28	64	2	2	58	77	21	Lavender	125	96	113	4	82	66	70
Espadarana	*prosoblepon*	green	111	122	4	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*adespinosai*	yellowish green	162	166	63	6	147	154	15	Cream	174	157	61	3	209	185	154
Hyalinobatrachium	*anachoretus*	yellowish green	123	140	59	6	147	154	15	Cream	151	124	101	3	209	185	154
Hyalinobatrachium	*aureoguttatum*	yellowish green	217	207	39	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*bergeri*	yellowish green	140	119	11	6	147	154	15	Cream	242	231	196	3	209	185	154
Hyalinobatrachium	*cappellei*	yellowish green	168	191	84	6	147	154	15	Cream	144	125	86	3	209	185	154
Hyalinobatrachium	*carlesvilai*	yellowish green	160	166	3	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*chirripoi*	yellowish green	191	179	4	6	147	154	15	Cream	217	172	132	3	209	185	154
Hyalinobatrachium	*colymbiphyllum*	yellowish green	185	194	53	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*duranti*	yellowish green	139	158	30	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*esmeralda*	yellowish green	178	209	51	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*fleischmanni*	yellowish green	140	131	3	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*fragile*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Hyalinobatrachium	*iaspidiense*	yellowish green	143	166	63	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*ibama*	yellowish green	167	208	9	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*kawense*	yellowish green	119	166	86	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*mondolfii*	yellowish green	181	191	101	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*muiraquitan*	yellowish green	140	133	28	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*munozorum*	yellowish green	162	166	55	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*orientale*	yellowish green	137	140	50	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*orocostale*	yellowish green	189	186	91	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*pallidum*	yellowish green	162	166	68	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*pellucidum*	yellowish green	112	115	25	6	147	154	15	Cream	225	203	180	3	209	185	154
Hyalinobatrachium	*talamancae*	yellowish green	140	131	4	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*tatayoi*	yellowish green	166	158	46	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*taylori*	green	51	89	45	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*tricolor*	yellowish green	132	191	90	6	147	154	15	Cream	200	171	131	3	209	185	154
Hyalinobatrachium	*valerioi*	yellowish green	132	166	10	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA

Hyalinobatrachium	*vireovittatum*	yellowish green	198	217	59	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Hyalinobatrachium	*yaku*	yellowish green	162	166	60	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Ikakogi	*tayrona*	green	86	114	22	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*anomalus*	brown	217	161	59	5	105	83	34	Cream	196	179	160	3	209	185	154
Nymphargus	*balionotus*	yellow	251	236	75	4	196	199	71	Lavender	102	100	86	4	82	66	70
Nymphargus	*bejaranoi*	green	104	120	32	2	58	77	21	Cream	224	193	177	3	209	185	154
Nymphargus	*cariticommatus*	green	150	156	63	2	58	77	21	Gray	189	181	174	1	156	154	175
Nymphargus	*chancas*	olive green	217	174	137	3	96	122	21	Cream	205	180	156	3	209	185	154
Nymphargus	*cochranae*	yellowish green	196	217	41	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*colomai*	olive green	140	133	31	3	96	122	21	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*garciae*	green	98	121	0	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*grandisonae*	yellowish green	186	191	44	6	147	154	15	Lavender	157	158	156	4	82	66	70
Nymphargus	*griffithsi*	yellowish green	135	166	23	6	147	154	15	Lavender	162	161	194	4	82	66	70
Nymphargus	*humboldti*	yellowish green	178	191	78	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*lasgralarias*	yellowish green	149	166	18	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*laurae*	yellowish green	212	217	72	6	147	154	15	Lavender	154	140	145	4	82	66	70
Nymphargus	*lindae*	green	111	115	2	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*manduriacu*	olive green	154	149	94	3	96	122	21	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*mariae*	green	112	115	26	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA

Nymphargus	*megacheirus*	yellowish green	131	140	58	6	147	154	15	Lavender	83	53	66	4	82	66	70
Nymphargus	*mixomaculatus*	yellowish green	137	140	55	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*ocellatus*	green	162	166	45	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*pluvialis*	yellowish green	122	156	15	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*posadae*	green	60	131	2	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*rosada*	lavender	166	119	91	—	166	119	91	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*siren*	green	115	107	2	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*spilotus*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*sucre*	olive green	178	157	69	3	96	122	21	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*vicenteruedai*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Nymphargus	*wileyi*	yellowish green	168	199	66	6	147	154	15	Lavender	191	152	143	4	82	66	70
Allophryne	*ruthveni*	brown	95	72	26	5	105	83	34	Cream	214	187	123	3	209	185	154
Allophryne	*relicta*	cream	236	205	120	—	236	205	120	Cream	246	211	154	3	209	185	154
Allophryne	*resplendens*	black	20	25	5	—	20	25	5	Brown	70	49	40	2	149	123	104
Gastrotheca	*dendronastes*	brown	89	61	54	5	105	83	34	Brown	115	83	64	2	149	123	104
Gastrotheca	*longipes*	green	115	100	29	2	58	77	21	White	235	223	199	—	235	223	199
Hyloscirtus	*colymba*	yellowish green	93	127	38	6	147	154	15	Gray	86	87	79	1	156	154	175
Hyloscirtus	*lindae*	brown	89	64	49	5	105	83	34	NA	NA	NA	NA	NA	NA	NA	NA
Osteocephalus	*cabrerai*	yellowish green	191	196	80	6	147	154	15	Brown	145	117	75	2	149	123	104
Osteocephalus	*festae*	brown	139	84	20	5	105	83	34	Cream	172	137	97	3	209	185	154
Pristimantis	*cruentus*	brown	140	97	59	5	105	83	34	NA	NA	NA	NA	NA	NA	NA	NA

Pristimantis	*galdi*	green	81	87	18	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Pseudis	*cardosoi*	green	50	70	35	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Pseudis	*limellum*	brown	68	79	32	5	105	83	34	NA	NA	NA	NA	NA	NA	NA	NA
Scinax	*funereus*	olive green	89	83	35	3	96	122	21	NA	NA	NA	NA	NA	NA	NA	NA
Scinax	*sugillatus*	brown	69	41	30	5	105	83	34	NA	NA	NA	NA	NA	NA	NA	NA
Rulyrana	*adiazeta*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Rulyrana	*flavopunctata*	green	160	166	3	2	58	77	21	Lavender	118	105	120	4	82	66	70
Rulyrana	*mcdiarmidi*	olive green	65	54	22	3	96	122	21	Lavender	95	70	92	4	82	66	70
Rulyrana	*saxiscandens*	green	43	68	24	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Rulyrana	*spiculata*	green	90	115	52	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Rulyrana	*susatamai*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Sachatamia	*albomaculata*	green	66	83	5	2	58	77	21	Lavender	64	39	50	4	82	66	70
Sachatamia	*electrops*	yellowish green	149	154	72	6	147	154	15	Lavender	135	97	113	4	82	66	70
Sachatamia	*ilex*	green	146	166	73	2	58	77	21	Lavender	86	65	89	4	82	66	70
Sachatamia	*orejuela*	olive green	140	133	94	3	96	122	21	Gray	54	52	64	1	156	154	175
Sachatamia	*punctulata*	green	70	115	23	2	58	77	21	Lavender	56	31	53	4	82	66	70
Teratohyla	*adenocheira*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Teratohyla	*amelie*	bluish green	137	140	28	1	144	156	69	NA	NA	NA	NA	NA	NA	NA	NA
Teratohyla	*midas*	yellowish green	162	166	60	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Teratohyla	*pulverata*	green	69	81	1	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Teratohyla	*spinosa*	yellowish green	104	115	18	6	147	154	15	Lavender	159	120	111	4	82	66	70
Vitreorana	*antisthenesi*	green	51	83	23	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Vitreorana	*castroviejoi*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Vitreorana	*eurygnatha*	green	116	137	10	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Vitreorana	*franciscana*	yellowish green	140	126	53	6	147	154	15	NA	NA	NA	NA	NA	NA	NA	NA
Vitreorana	*gorzulae*	green	76	89	30	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA
Vitreorana	*helenae*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vitreorana	*ritae*	yellowish green	169	162	5	6	147	154	15	Lavender	191	160	142	4	82	66	70
Vitreorana	*uranoscopa*	green	83	133	14	2	58	77	21	NA	NA	NA	NA	NA	NA	NA	NA