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Research Article

A new genus of terraranas (Anura: Brachycephaloidea) from northern South America, with a systematic review of *Tachiramantis*

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Since the systematics of Terrarana frogs was overhauled in 2008, five new genera have been named, including *Tachiramantis* from the Venezuelan Coastal Range and adjacent parts of the Cordillera Oriental of Colombia and the Sierra de Perijá along the Venezuela–Colombia border. The discovery of *Tachiramantis* raises questions about the relationships of several species of *Pristimantis* in the nearby Sierra Nevada de Santa Marta previously hypothesized to be closely related to species now referred to *Tachiramantis*. To test the monophyly of *Tachiramantis* and the relationships among its species, we generated DNA sequences for 42 individuals, and, given the variable placement of *Tachiramantis* in previous studies, analysed them with DNA sequences from GenBank representing 25 genera of terraranas. In total, the final matrix included DNA sequences from 414 terminals, which we analysed using tree-alignment under the parsimony optimality criterion. To identify morphological synapomorphies and diagnostic characters, we also examined cranial osteology and axial skeleton morphology. Our analyses corroborated both the placement of *Tachiramantis* far from *Pristimantis* in Craugastoridae and the monophyly of *Tachiramantis*. We also found that six species currently referred to *Pristimantis*, all endemic to the Sierra Nevada de Santa Marta, comprise the sister clade of *Tachiramantis*. This highly endemic clade is both well-supported by molecular data and diagnosed from *Tachiramantis* by seven morphological synapomorphies, leading us to recognize it as a new genus.

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Key words: Craugastoridae, morphology, northern Andes of Colombia, phylogeny, *Pristimantis*, taxonomy

Introduction

The terrestrially breeding frogs of the clade Brachycephaloidea Günther, 1858 (terraranas) comprise 1,225 species distributed from the south-western USA through Mexico and the West Indies south to northern Argentina (Frost, 2022). The monophyly of Brachycephaloidea is corroborated by both DNA sequences (e.g., Frost et al., 2006; Hedges et al., 2008; Heinicke et al., 2009; Padial et al., 2014; Pyron & Wiens, 2011) and seven putative morphological synapomorphies in the urogenital and vascular systems (Taboada et al., 2013). Also, phenotypic characters, including direct developmental and T-shaped terminal phalanges (Heinicke et al., 2009; Lynch, 1971) help diagnose Brachycephaloidea.

In the nearly 15 years since Hedges et al. (2008) overhauled the taxonomy of terraranas, molecular phylogenetic analyses have continued to hone our understanding of the radiation of these frogs (e.g., Hedges et al., 2008; Heinicke et al., 2009; Padial et al., 2014; Pyron & Wiens, 2011). The improved knowledge of phylogeny has been reflected in taxonomic changes, including both family-level rearrangements and the description of the genera *Ceuthomantis* Heinicke et al., 2009,

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Tachiramantis Heinicke et al., 2015, *Microkayla* De la Riva et al., 2018, *Qosqophryne* Catenazzi et al., 2020, and *Bahius* Dubois et al., 2021.

Tachiramantis was named to accommodate three species, *Tachiramantis douglasi* (Lynch, 1996), *Tachiramantis lentiginosus* (Rivero, 1982), and *Tachiramantis prolixodiscus* (Lynch, 1978), originally described as part of *Eleutherodactylus* and later transferred to *Pristimantis* Jiménez de la Espada, 1870 but found on the basis of molecular phylogenetic analyses to be more closely related to *Psychophrynella*, *Holoaden* Miranda-Ribeiro, 1920, *Bryophryne* Hedges et al., 2008, *Noblella* Barbour, 1930, and *Barycholos* Heyer, 1969 than to *Pristimantis* (Heinicke et al., 2015). *Tachiramantis* is distributed on both sides of the Táchira Depression in the Cordillera de Mérida of Venezuela and adjacent parts of the Cordillera Oriental of Colombia, as well as the Sierra de Perijá along the Venezuela–Colombia border. Subsequently, *Pristimantis lassoalcalai* Barrio-Amorós et al., 2010, distributed in the Serranía de Perijá in Venezuela with possible distribution in Colombia (Barrio-Amorós et al., 2010; Rojas-Runjaic et al., 2020), was found to be the sister species of *T. douglasi* + *T. lentiginosus* and transferred to *Tachiramantis* by Rojas-Runjaic et al. (2020).

Heinicke et al. (2015) considered the exact phylogenetic position of *Tachiramantis* to be ambiguous but tentatively included it in Craugastoridae (which then included Strabomantidae). Later, Heinicke et al. (2018) found *Tachiramantis* to be the sister group of *Craugastor* Cope, 1862 + *Haddadus* Hedges et al., 2008 and restricted Craugastoridae to these three genera. Jetz and Pyron (2018) and Dubois et al. (2021) did not include any of the *Tachiramantis* species in their phylogenetic analyses, because they employed the sequences analysed previously by Pyron and Wiens (2011).

The discovery of *Tachiramantis* raises questions about the relationships of several other species currently referred to *Pristimantis*, a genus of more than 500 species, approximately two-thirds of which have not been included in quantitative phylogenetic analyses. For example, Lynch (1996, 2003a) hypothesized that two of the species currently referred to *Tachiramantis* (*T. douglasi* and *T. prolixodiscus*) might be closely related to two *Pristimantis* species from the Sierra Nevada de Santa Marta (SNSM) in northern Colombia (*T. douglasi* with *P. galdi* and *T. prolixodiscus* with *P. tayrona* Lynch, 1996, 2003a), and several more potential close relatives have yet to be included in phylogenetic analyses. In this study, we use nuclear and mitochondrial gene sequences to test the monophyly and relationships of *Tachiramantis*. On the basis of our results, we describe a new genus of Craugastoridae and transfer two additional species from *Pristimantis* to *Tachiramantis*, while also providing a corrected and expanded morphological characterization of *Tachiramantis*.

Material and methods

Taxon sampling

In order to examine the phylogenetic relationships of *Tachiramantis*, we obtained tissue samples from specimens of the northern Cordillera Oriental, Serranía de Perijá, and adjacent portions of the Táchira depression in Colombia, where the genus has been reported to occur previously (Heinicke et al., 2015), and we also included species from the Sierra Nevada de Santa Marta (SNSM) in northern Colombia (Supplemental Table S1). We generated DNA sequences for 42 individuals representing 10 named species of *Tachiramantis* and *Pristimantis* and one undescribed species (Supplemental Table S1). Field numbers are reported for specimens not yet deposited in permanent collections, including JDL (John Douglas Lynch), JJS (Jhon Jairo Sarria), PAG (Pedro A Galvis), and TG (Taran Grant). Tissues collected by us were preserved in 95% ethanol following euthanization using 1% benzocaine; specimens were subsequently preserved in 10% formalin and stored in 70% ethanol. Tissues and specimens will be deposited in the collection of amphibians from the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (ICN). Given the variable placement of *Tachiramantis* (Heinicke et al., 2015, 2018), we also included sequences from GenBank representing all 25 genera of terraranas for which DNA sequences are available, as well as 35 non-brachycephaloid genera. We chose terminals from GenBank on the basis of their phylogenetic proximity and number of sequences available, with all chosen terminals having sequences of mitochondrially encoded 16S rRNA (see below). In total, the final matrix includes DNA sequences from 414 terminals.

Distribution and natural history

We used ArcMap 10.4 (ESRI, 2012) to generate maps for the species referred to *Tachiramantis* and the new genus described herein (Fig. 1). These maps include only the specimens used in our phylogenetic analysis and ICN specimens examined by us. Observations of the natural history of species of the new genus were obtained from Rueda-Solano and Vargas-Salinas (2010), Rueda-Solano et al. (2016), and expeditions to the SNSM by one of us (LARS) between 2008 and 2020.

Character sampling

DNA sequences. Gene names and symbols follow Yates et al. (2017), except *H1*, which is used herein to refer to

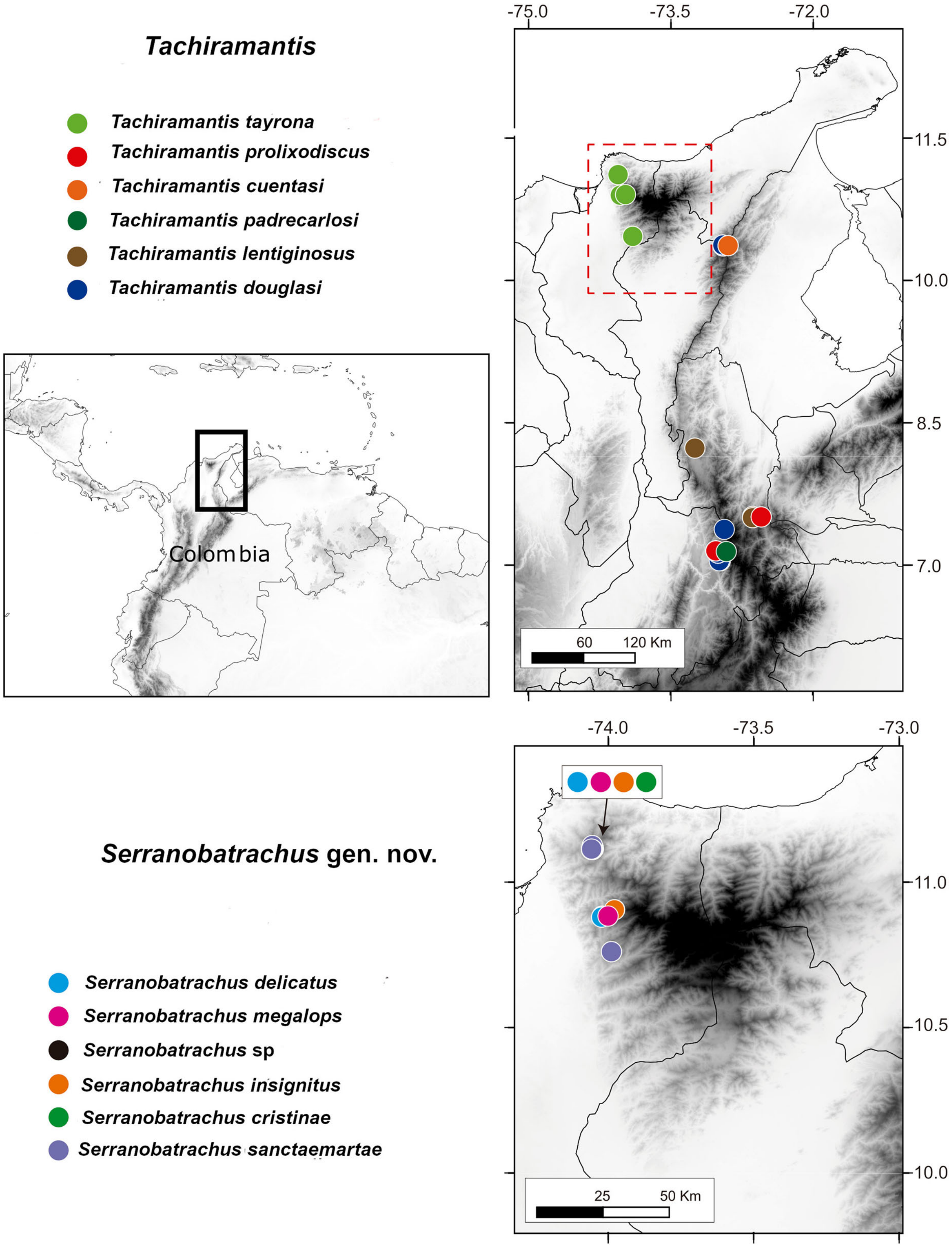

Fig. 1. Geographic distribution of *Tachiramantis* (above) and *Serranobatrachus* gen. nov. (below). The circles represent the localities from which we obtained tissue samples from specimens of the northern Cordillera Oriental, Serranía de Perijá, adjacent portions of the Táchira depression, and the Sierra Nevada de Santa Marta.

the mitochondrial H strand transcription unit 1 that includes mitochondrially encoded 12S rRNA (*MT-RNR1*), mitochondrially encoded 16S rRNA (*MT-RNR2*), and the intervening tRNA valine (*MT-TV*). The following fragments were sequenced for the present work (see also Supplemental Tables S1, S2; primers and corresponding citations are listed in Supplemental Table S3): *H1* (476–2527 bp); mitochondrially encoded cytochrome *c* oxidase I (*MT-CO1*, 480–654 bp); H3.5 histone (*H3F3C*, 285–328 bp), propiomelanocortin (*POMC*, 499–567 bp), recombination-activating 1 (*RAG1*, 471–630 bp), siah E3 ubiquitin protein ligase 1 (*SIAH1*, 397 bp), and tyrosinase (*TYR*, 356–531 bp); RNA, 28S ribosomal 1 (*RNA28S*, 843 bp).

In addition to data generated in this study, we included data for those markers and the following additional ones from GenBank (Supplemental Table S2): mitochondrially encoded cytochrome *b* (*MT-CYB*, 394–895 bp), *MT RNR2*, mitochondrially encoded NADH:ubiquinone oxidoreductase core subunit 1 (*MT-ND1*) and the intervening mitochondrially encoded tRNA-Leu (*MT TL*, 834–1435 bp), mitochondrially encoded NADH:ubiquinone oxidoreductase core subunit 2 (*MT-ND2*) and tRNAs (*MT-ND2*, 1452–1473 bp), two exons of MYC proto-oncogene, bHLH transcription factor (*MYC* 2, 302 bp; *MYC* 2 and 3, 408–1233 bp); C-X-C motif chemokine receptor 4 (*CXCR4*, 637–676 bp); solute carrier family 8 member A1 (*SLC8A1*, 1240–1276 bp), solute carrier family 8 member A3 (*SLC8A3*, 1043–1123 bp), a different fragment of *RAG1* than we sequenced (428–1354 bp), and rhodopsin (*RHO*, 316 bp). When museum voucher information was not available either from GenBank data or the respective publications, we used the identifiers provided by the original authors or the last name of the first author of the publication. In total, we included 18 molecular markers.

González-Durán et al. (2017) noted that the *H1* sequences published by Pinto-Sánchez et al. (2012) lack several stretches of DNA that are present in all other sequences available on GenBank and the sequences generated by them, indicating that portions of the sequences had been deleted prior to GenBank accession. As such, we followed González-Durán et al. (2017) in delimiting blocks of homologous portions of these genes to accommodate these incomplete sequences in our analyses.

DNA extraction, amplification, and sequencing. Total DNA was extracted from liver or thigh muscle preserved in 95% ethanol using standard phenol–chloroform extraction protocols (Sambrook et al., 1989) or DNeasy (QIAGEN, Valencia, CA) isolation kit. Amplification was carried out in a 25 µl reaction using the Thermo Scientific PCR Master Mix (2X) (Thermo Fisher Scientific Inc., USA). For the amplifications, the PCR program included an initial denaturing step of 30 s at 96 °C, followed by 35 (mitochondrial gene fragments) or 45 (nuclear gene fragments) cycles of amplification (96 °C for 30 s; 48–54 °C for 30 s; 60 °C for 60 s), with a final extension step at 60 °C for 7 min (Lyra et al., 2017). For low-yielding samples, the annealing temperature was lowered to 46 °C. PCR amplification products were cleaned using the Agencourt AMPure XP DNA Purification and Cleanup kit (Beckman Coulter Genomics, Brea, CA, USA), and sequenced by a third party (Macrogen Inc, Seoul, Korea), using fluorescent-dye labelled terminators (ABI Prism Big Dye Terminators v. 1.1 cycle sequencing kits; Applied Biosystems, Foster City, CA, USA) with an ABI 3730XL (Applied Biosystems, Foster City, CA, USA). All samples were sequenced in both directions to check for potential errors. Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software Sequencher 5.2.3. (Gene Codes, Ann Arbor, MI, USA). Complete sequences were edited using Geneious v.6.1.6 (Kearse et al., 2012).

Molecular phylogenetic analysis

We employed the optimality criterion of phylogenetic parsimony (Kluge, 2001), a non-parametric, non-statistical method of historical inference that selects as optimal the hypotheses of cladistic and patristic relationships that maximize explanatory power by hypothesizing the fewest causal events required to explain the data (Grant & Kluge, 2008; Kluge & Grant, 2006). We employed tree-alignment (e.g., Sankoff, 1975; Varón & Wheeler, 2012, 2013; Wheeler, 1996) in POY 5.1.1 (W. C. Wheeler et al., 2015), which tests hypotheses of nucleotide homology dynamically by optimizing unaligned DNA sequences directly onto alternative topologies (Grant & Kluge, 2008; Kluge & Grant, 2006; Padial et al., 2014; Wheeler et al., 2006). In this approach, the optimal alignment is selected objectively according to the same optimality criterion used to select the optimal topology (Wheeler, 1996, 2003a).

Computationally intensive analyses were performed on the high-performance computing cluster Ace, which consists of 12 quad-socket AMD Opteron 6376 16-core 2.3 GHz CPU, 16 MB cache, 6.4 GT/s compute nodes (=768 cores total), eight with 128 GB RAM DDR3 1600 MHz (16 × 8 Gb), two with 256 GB (16 × 16 GB), and two with 512 GB (32 × 16 GB), and QDR 4X InfiniBand (32 Gb/s) networking.

Analyses included the following steps. First, using the standard direct optimization algorithm (Wheeler, 1996), we ran three 72 h searches using 240–304 CPUs (total of 61,016 CPU-hours) and the command 'search', which implements a driven search composed of random addition sequence Wagner builds, Subtree Pruning and Regrafting (SPR) and Tree Bisection and Reconnection (TBR) branch swapping (RAS + swapping; Goloboff, 1996), Parsimony Ratcheting (Nixon, 1999), and Tree Fusing (Goloboff, 1996), storing the shortest trees from each independent run and performing a final round of Tree Fusing on the pooled trees. To accelerate searches, equal-length fragments were constrained to be prealigned in the first two runs, and that constraint was removed in the third analysis. Next, we performed 2000 rounds of Tree Fusing of the optimal trees from the three driven searches, also using the standard direct optimization algorithm and all fragments treated as unaligned. We then used the exact iterative pass algorithm (Wheeler, 2003b) to calculate the cost of the optimal trees identified in the previous analyses and generate the matrix version of the tree-alignment (i.e., the implied alignment; Wheeler, 2003a) of the optimal tree. All of the aforementioned analyses applied equal costs to substitutions and indels. Finally, to search for additional optimal trees, we performed an aggressive search of the implied alignment in TNT v.1.5 (Goloboff et al., 2008; Goloboff & Catalano, 2016; equal costs for all transformations, gaps treated as fifth state), stopping when the stable consensus was reached five times (tnt command: xmult = replications 10 rss css xss ratchet 10 drift 10 fuse 5 consense 5).

We estimated clade support (*sensu* Grant & Kluge, 2008) using the Goodman-Bremer measure (Bremer, 1988; Goodman et al., 1982; Grant & Kluge, 2008) calculated using the implied alignment and the parameters specified in the bremer.run macro (for details see Goloboff et al. (2008); macro available at ww.lillo.org.ar/phylogeny/tnt) in TNT v.1.5 (Goloboff et al., 2008; Goloboff & Catalano, 2016). As in any heuristic analysis, the resulting GB values should be interpreted as approximations. In addition to the effects of more exhaustive tree searches, shorter suboptimal trees could be found by calculating the optimal tree-alignment for each visited topology; however, the time requirements would be prohibitive, and GB values derived from implied alignments have been found to be less inflated than those calculated using a MAFFT (Katoh, 2005; Katoh & Standley, 2014) similarity-alignment (Padial et al., 2014).

We calculated uncorrected pairwise genetic distances (p-distances) among specimens of the new genus and *Tachiramantis* in Geneious Prime 2020.1.1 (Biomatters Inc., San Diego, CA, USA). For this analysis, a 499 bp fragment of *MT-RNR2* shared by almost all specimens was aligned using MAFFT (Katoh et al., 2005). We excluded terminals that did not contain the complete sequence of the selected fragment.

Morphological data

To identify morphological synapomorphies and diagnostic characters for *Tachiramantis*, we examined both external morphology, using the terminology of Lynch and Duellman (1997) and Duellman and Lehr (2009), and internal morphology (cranial osteology and axial skeleton) using the osteological terminology of Duellman and Trueb (1994), González-Durán et al. (2017), Guayasamin (2004), Lynch (1971, 1997, 2000, 2001), and Trueb (1993).

External and internal morphology was compared by direct examination of specimens in the ICN and MZUSP (Museu de Zoologia da Universidade de São Paulo) amphibian collections, including 113 specimens examined for external morphology and 44 for cranial and axial skeletal characters (Appendix 1). We also compared the observed variation to published accounts for species groups of *Pristimantis* and other genera of Brachycephaloidea (Ardila-Robayo, 1979; González-Durán et al., 2017; Guayasamin, 2004; Heinicke et al., 2018; Lynch, 1971, 1976, 1996, 2000, 2001).

We studied the following external characters: texture of skin of dorsum and venter; dorsolateral folds, tympanic membrane, vocal slits; vomerine odontophores; discs on fingers and toes; supernumerary plantar tubercles; relative length of fingers I and II (determined by adpressing finger I to finger II), relative lengths of toes III and V (assessed by pressing these two toes against toe IV). Abbreviations are as follows: snout–vent length (SVL); interorbital distance (IOD). Fingers are numbered preaxially to postaxially from I to IV. Although this is not consistent with the hypothesis that digit I of other tetrapods was lost in amphibians, it agrees with common usage in Terrarana taxonomy (e.g., González-Durán et al., 2016). We also studied one internal character: testis colour.

We studied the following characters of the skull: orientation of the alary processes of the premaxillae; relationship of the nasals; relationship between the nasals and frontoparietals (sphenethmoid visible or not visible dorsally); relationship of frontoparietals and prootics; occurrence and morphology of cranial crest; lengths of the zygomatic and otic rami of the squamosal; ornamentation along the dorsal edge of the zygomatic and otic rami of the squamosal; shape of the dentigerous process of the vomer; length of the dentigerous process of the vomer; orientation of the post-choanal process of the vomer; lengths of the palatines; length of the cultriform process of the parasphenoid;

length of the sphenethmoid (ventral view); and length of the alary process of the hyoid. We included one character of the axial skeleton: relationship of the sacrum and presacral vertebra VIII.

To identify putative morphological synapomorphies, we constructed a character matrix in Mesquite v. 3.61 (Maddison & Maddison, 2019) and optimized the characters on the optimal topology under Fitch optimization (Fitch, 1971).

Results

Molecular phylogenetic analyses

The driven searches performed 1418 RAS + TBR, 1955 rounds of Tree-Fusing, and 344 rounds of Ratcheting. Following additional Tree-Fusing, iterative pass optimization, and searching of the implied alignment, 361 most parsimonious trees of 81,713 steps were obtained. The entire topology of the strict consensus of all most parsimonious trees is presented in Supplemental Fig. S1.

Our analyses corroborated the monophyly of all brachycephaloid genera except *Pristimantis* (see below), as well as that of Brachycephaloidea (GB = 60), Brachycephalidae (GB = 59), Eleutherodactylidae (GB = 77), and Strabomantidae (GB = 29). Craugastoridae is not monophyletic due to the position of *Haddadus*, with *Ceuthomantis* + *Haddadus* recovered as sister to Eleutherodactylidae (i.e., *Ceuthomantis* [Ceuthomantidae] is not recovered as sister group to the remainder of Brachycephaloidea, as in Heinicke et al., 2018).

The differences among the most parsimonious trees involve the internal relationships among specimens of '*Pristimantis*' *cristinae* (Lynch & Ruiz-Carranza, 1985), '*P.*' *megalops* (Ruthven, 1917), '*P.*' *sanctaemartae* (Ruthven, 1917), '*P.*' *tayrona* (Lynch & Ruiz-Carranza, 1985), *P. lancinii* (Donoso-Barros, 1965), *P. vanadise* (La Marca, 1984), and *T. douglasi* (Supplemental Fig. S1), among species in the clade containing *Oreobates choristolemma* (Harvey & Sheehy, 2005), *O. granulosus* (Boulenger, 1903), and *O. sanderi* (Padial et al., 2005), and among species in the clade containing *O. lundbergi* (Lehr, 2005), *O. pereger* (Lynch, 1975), *O. remotus* (Teixeira et al., 2012), and *O. saxatilis* (Duellman, 1990) + *O. quixensis* (Jiménez de la Espada, 1872; Supplemental Fig. S1).

Our analyses corroborated both the placement of *Tachiramantis* far from *Pristimantis* in Craugastoridae and its monophyly (GB = 26), albeit with the inclusion of *Pristimantis cuentasi* (Lynch, 2003b) as the sister of *T. lentiginosus* (Rivero, 1984) + *T. padrecarlosi* (Mueses-Cisneros, 2006; Supplemental Fig. S1) and *P. tayrona* as sister to all other species of *Tachiramantis*. We also found that *Pristimantis carmelitae* (Ruthven, 1922), *P. cristinae*, *P. delicatus* (Ruthven, 1917), *P. insignitus* (Ruthven, 1917), *P. megalops*, and *P. sanctaemartae* – all endemic to the SNSM (Fig. 1) – comprise the sister clade of *Tachiramantis*, thereby further refuting the monophyly of *Pristimantis* (Supplemental Fig. S1). This clade is both well-supported by molecular data (GB = 31) and, as described below (Systematic account), diagnosed from *Tachiramantis* by seven morphological synapomorphies, including six in the skull and one in the axial skeleton, as well as differences in external morphology, leading us to propose a new genus for this clade (Fig. 2).

Systematic account

Order Anura Oppel, 1811
Superfamily Brachycephaloidea Günther, 1858
Family Craugastoridae Hedges et al., 2008
Genus ***Serranobatrachus* gen. nov.**

Type species.

***Eleutherodactylus insignitus Ruthven*, 1917**

Etymology. The genus name is formed by combining the word *serrano*, the local name used to refer to people from the Sierra Nevada de Santa Marta, and the Greek *batrachos* or *batrakheios*, meaning frog, in reference to the endemism of these frogs to this geological formation. The name is masculine.

Diagnosis. Medium to large terraranas (adult female SVL from 28 mm in *S. delicatus* to 63 mm in *S. cristinae*, $\bar{x} = 42$ mm. $n = 76$), adult males smaller than females (adult male SVL from 19 mm in *S. megalops* to 43 mm in *S. cristinae*, $\bar{x} = 32$ mm, $n = 93$); head narrow (37–41% SVL), snout short (*S. carmelitae*, *S. delicatus*, *S. megalops*, *S. insignitus*) or long (*S. sanctaemartae* and *S. ruthveni*); lips weakly flared in adult females; IOD usually broader than upper eyelid (adult females 102–110%, $n = 33$), except in *S. cristinae* and *S. ruthveni* with IOD narrower than upper eyelid (adult females 88.9–94.7%, $n = 19$). Skin of dorsum shagreen (*S. cristinae*, *S. delicatus*, *S. megalops*, and *S. sanctaemartae*) or smooth with low, flat warts (*S. carmelitae*, *S. insignitus*, and *S. ruthveni*); dorsolateral folds reaching level of sacral vertebra (*S. cristinae* and *S. ruthveni*), confined to anterior half of body (*S. carmelitae*, *S. delicatus*, and *S. sanctaemartae*) or absent (*S. insignitus* and *S. megalops*). Skin of venter usually areolate (skin of belly textured but not areolate or completely smooth in

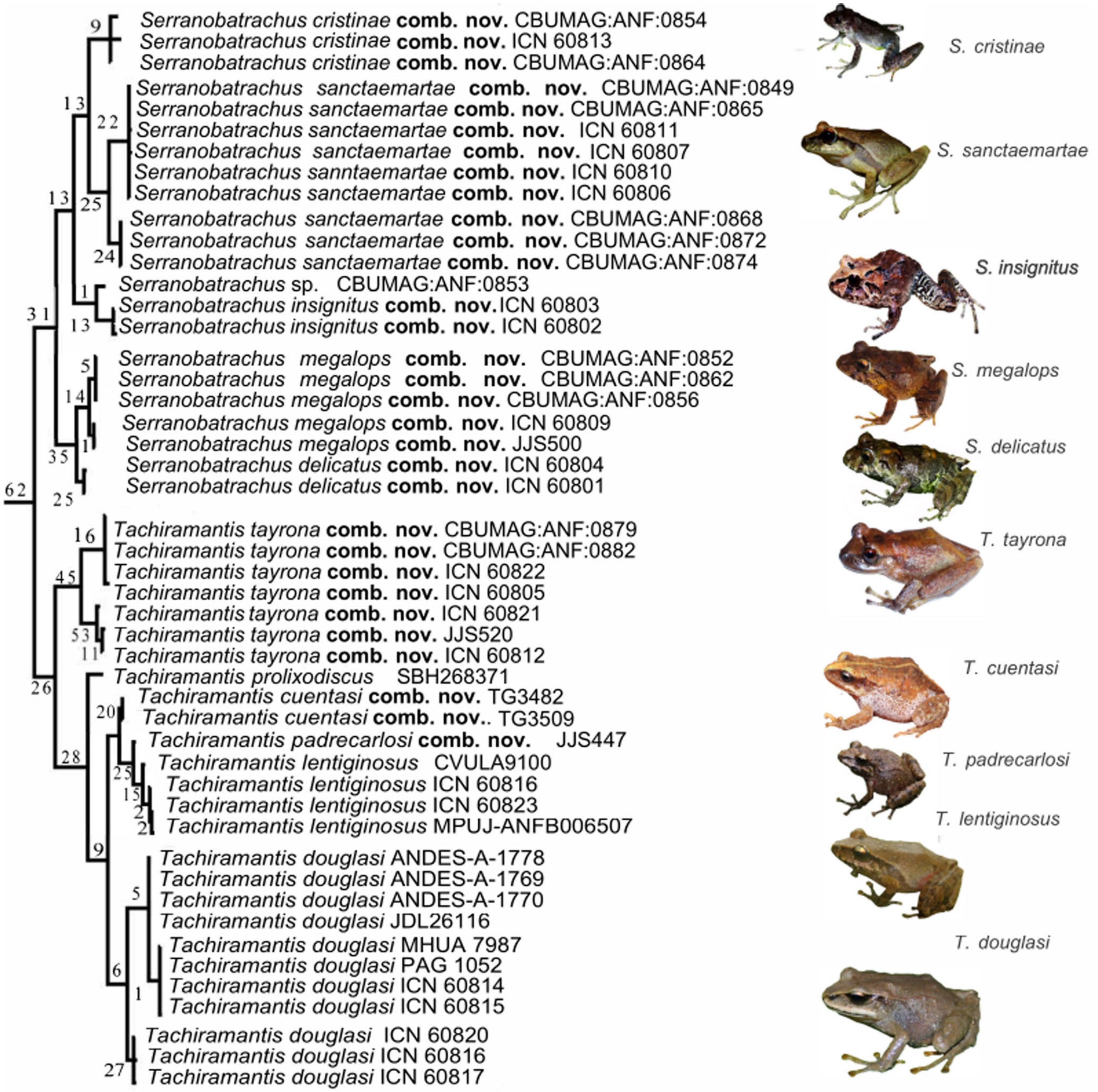

Fig. 2. Phylogenetic relationships of *Serranobatrachus* gen. nov. and *Tachiramantis*. The tree is a portion of the strict consensus of 361 most parsimonious trees (MPTs; 81713 steps) showing minimum branch-lengths (derived from one of the MPTs) and all supported nodes labelled with Goodman-Bremer values. Photos by Luis Alberto Rueda-Solano and Marco Rada.

S. carmelitae); vomerine odontophores large, triangular in outline; dentigerous processes reaching palatines posteriorly; vocal slits present in adult males (absent in *S. carmelitae* and *S. insignitus*); nuptial pads present on finger I of adult males (absent in *S. insignitus*, *S. ruthveni*, and *S. sanctaemartae*); tympanic membrane differentiated and tympanic annulus visible externally. Discs on fingers and toes expanded (narrow in *S. carmelitae*, *S. megalops*, and *S. ruthveni*); fingers and toes with lateral keels (absent in *S. carmelitae*); supernumerary plantar tubercles absent (small tubercle present at base of toes II–IV in *S. cristinae* and *S. sanctaemartae*); heel with tubercles or tarsus with fold; toe III longer than toe V (*S. carmelitae*, *S. delicatus*, *S. megalops*, *S. insignitus*, and *S. ruthveni*) or toe V longer than toe III, with toe V not extending beyond the penultimate subarticular tubercle of toe IV (*S. cristinae* and *S. sanctaemartae*). Apical supplementary elements of *m. intermandibularis* broad, in contact medially. Testes white in adult males (Fig. 4B). Alary process of premaxilla terminating in inverted V-shape and directed posterodorsad; otic ramus of squamosal shorter than zygomatic ramus and separated from posterolateral portion of prootic. Crests present on frontoparietals (Fig. 7A). Sphenethmoid long, reaching or surpassing the anterior edge of the nasals in fully developed adults. Sacrum and presacral vertebra VIII fused (Fig. 7C).

Content. Seven species: *Serranobatrachus carmelitae* (Ruthven, 1922) **new combination**; *S. cristinae* (Lynch & Ruiz-Carranza, 1985) **new combination**; *S. delicatus* (Lynch & Ruiz-Carranza, 1985) **new combination**; *S. insignitus* (Ruthven, 1917) **new combination**; *S. megalops* (Ruthven, 1917) **new combination**; *S. ruthveni* (Lynch & Ruiz-Carranza, 1985) **new combination**; *S. sanctaemartae* (Ruthven, 1917) **new combination** (Fig. 2).

Comparisons to other genera. *Serranobatrachus* is most readily distinguished from other terraranas on the basis of finger and toe lengths. Finger I being shorter than finger II differentiates *Serranobatrachus* from *Brachycephalus* Fitzinger, 1826, *Craugastor* (except some members of the *C. mexicanus* and *C. rhodopis* species series), *Strabomantis* Peters, 1863, and *Oreobates*. In *Serranobatrachus carmelitae*, *S. delicatus*, *S. megalops*, *S. insignitus*, and *S. ruthveni*, toe III is longer than toe V, a condition shared with *Adelophryne* Hoogmoed & Lescure, 1984, *Barycholos*, *Brachycephalus*, *Dischidodactylus* Lynch, 1979, *Euparkerella*, *Haddadus*, *Ischnocnema* Reinhardt & Lütken, 1862, *Oreobates*, *Phyzelaphryne* Heyer, 1977, and *Strabomantis*. Although toe V is longer than toe III in *S. cristinae* and *S. sanctaemartae*, toe V does not extend beyond the penultimate subarticular tubercle on toe IV, which is also seen in *Ceuthomantis*, a few species of *Craugastor* (viz. *Cr. alfredi* [Boulenger, 1898], *Cr. bocourti* [Brocchi, 1877], *Cr. decoratus* [Taylor, 1942], *C. glaucus* [Lynch, 1967], *Cr. guerreroensis* [Lynch, 1967], *Cr. megalotympanum* [Shannon & Werler, 1955], *Cr. polymniae* [Campbell et al., 1989], *C. silvicola* [Lynch, 1967], *Cr. spatulatus* [Smith, 1939], *Cr. stuarti* [Lynch, 1967], *Cr. taylori* [Lynch, 1966], *Cr. xucanebi* [Stuart, 1941], and *Cr. yucatanensis* [Lynch, 1965]), the *Eleutherodactylus* (*Pelorius*) *ruthae* species series, several *Pristimantis* species groups (viz. the *P. conspicillatus*, *P. ridens*, and *P. devillei* species groups), *Tachiramantis*, and *Yunganastes* (except in *Y. fraudator* [Lynch & McDiarmid, 1987]).

Remarks. Although DNA sequences are unavailable for *S. carmelitae* and *S. ruthveni*, we refer them to *Serranobatrachus* on the basis of the seven skeletal synapomorphies shared with the other species of this clade. Lynch and Ruiz-Carranza (1985) stated that *S. carmelitae* and *S. sanctaemartae* lack cranial crests; however, we observed low cranial crests in these two species (e.g., *S. carmelitae*: ICN 741–42, 8234, 8236; *S. sanctaemartae*: ICN 740, 13042, 13050), as in all other species referred to *Serranobatrachus*.

Scoring the lengths of fingers I and II and toes III and V requires caution, because lengths can vary due to preservation artefacts, and only straight digits of well-preserved specimens should be used for these comparisons. Additionally, Duellman and Lehr (2009) observed that ontogenetic changes in relative finger lengths occur in at least some species in which juveniles have finger I shorter than finger II and adults have finger I longer than finger II (e.g., *Hypodactylus lucida* [Cannatella, 1984]), although we have not observed any ontogenetic differences in the specimens we examined. To compare the length of fingers I and II we recommend adpressing the digits so that finger I lies immediately adjacent to finger II according to Duellman and Lehr (2009). To determine the relative lengths of toes III and V, we recommend adpressing toes III and V against toe IV.

The results of our phylogenetic analysis and genetic distances suggest the existence of an additional species, referred to in the trees as *Serranobatrachus* sp. (Fig. 2, Supplemental Fig. S1; Supporting Information Table S4). Genetic distances between species were 4.8–14.9% and between most conspecifics were 0.2–1.4%, the exception being *S. sanctaemartae* (Supporting Information Supplemental Table S4). In *S. sanctaemartae*, pairwise distances were 3.5–12%, suggesting that it comprises a complex of species. We suspect that the different lineages of *S. sanctaemartae* are probably associated with the polymorphism described by Ruthven (1917) and Lynch and Ruiz-Carranza (1985). Additional evidence is required to determine if the distances and phylogenetic structure refer to genetically structured conspecific populations or different species.

Distribution and natural history. *Serranobatrachus* gen. nov. is endemic to the cloud forest and páramo of the northern, eastern, and western flanks of the SNSM at 1,100–3,900 m above sea level (a.s.l.). The SNSM is an isolated mountain that reaches 5,775 m a.s.l. The dry months are between December and February and those with the highest rainfall are September and October (Jiménez, 1992).

Serranobatrachus carmelitae (Fig. 3A) is a common, nocturnal frog at 1,524–2,200 m a.s.l. found beneath

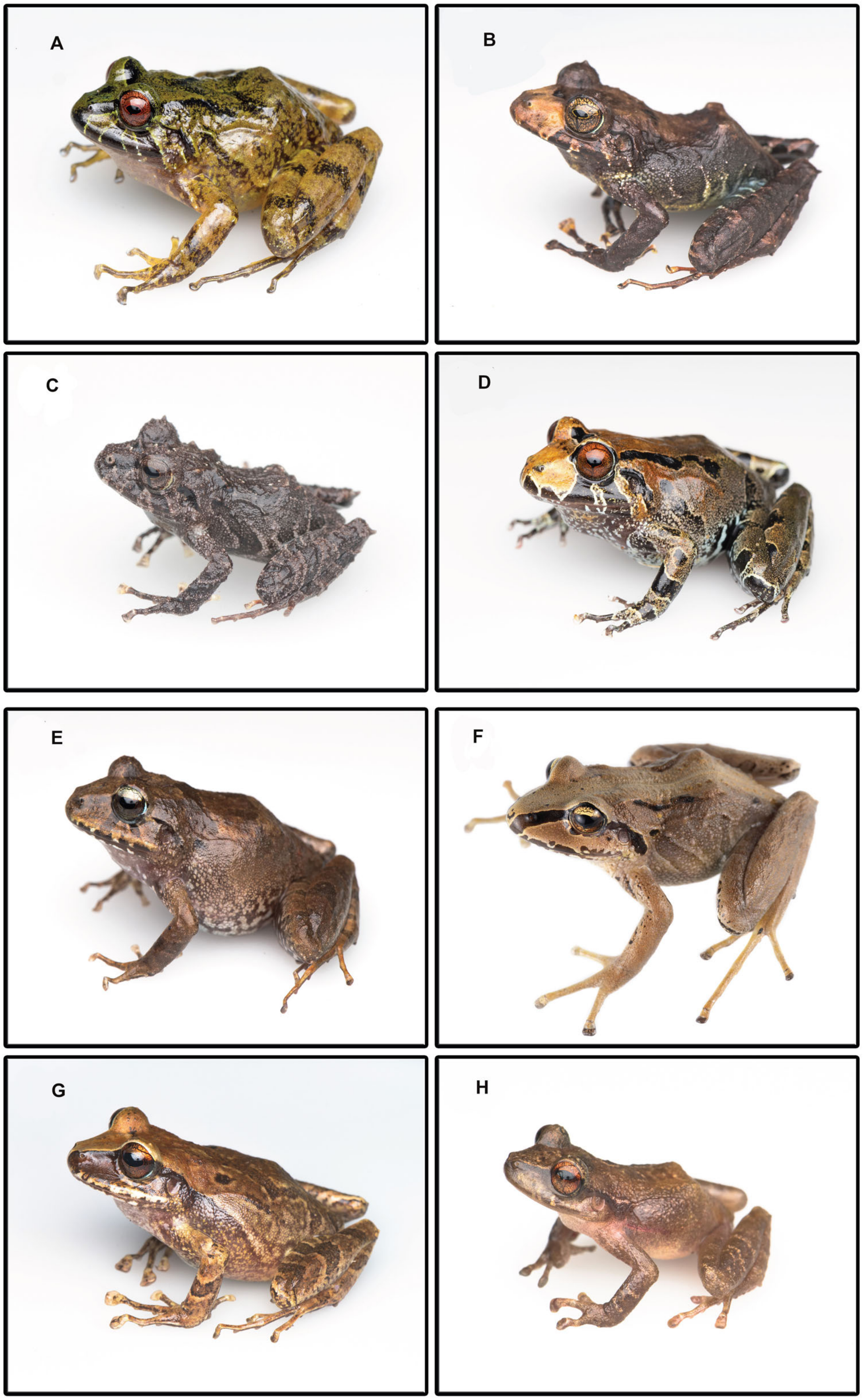

Fig. 3. Described species of *Serranobatrachus* gen. nov. and *Tachiramantis* from the Sierra Nevada de Santa Marta, Colombia. (A) *Serranobatrachus carmelitae*, (B) *Serranobatrachus cristinae*, (C) *Serranobatrachus delicatus*, (D) *Serranobatrachus insignitus*, (E) *Serranobatrachus megalops*, (F) *Serranobatrachus ruthveni*, (G) *Serranobatrachus sanctaemartae*, (H) *Tachiramantis tayrona*. Photo Giovanni Chaves-Portilla (A-E,G,H) and Jaime Culebras (F).

Table 1. Microhabitat use and time of activity in the frogs of the genera *Serranobatrachus* and *Tachiramantis.*

Specie	Microhabitat use	Time of activity
Serranobatrachus carmelitae	Low vegetation/leaf litter	Nocturnal
Serranobatrachus cristinae	Phytotelma/leaf litter	Nocturnal
Serranobatrachus delicatus	Low vegetation less than 80 cm high/leaf litter	Nocturnal
Serranobatrachus insignitus	Forest floor/leaf litter	Nocturnal
Serranobatrachus megalops	Low vegetation/leaf litter	Diurnal/Nocturnal
Serranobatrachus ruthveni	Forest floor	Nocturnal
Serranobatrachus sanctaemartae	Arboreal vegetation within 0–4.0 m of the ground	Nocturnal
Tachiramantis cuentasi	Arboreal vegetation within 0–2.0 m of the ground	Nocturnal
Tachiramantis douglasi	Low vegetation/leaf litter	Nocturnal
Tachiramantis lentiginosus	Arboreal vegetation	Nocturnal
Tachiramantis padrecarlosi	Low vegetation	Nocturnal
Tachiramantis prolixodiscus	Associate with bromeliads	Nocturnal
Tachiramantis tayrona	Associate with bromeliads/low vegetation	Nocturnal

rocks, moss, and leaf litter along mountain streams in cloud forest (Table 1). *Serranobatrachus cristinae* (Fig. 3B) is an uncommon, nocturnal frog found on phytotelmata, forest-floor plants, and leaf litter between 1,500–2,600 m a.s.l. (Rueda et al., 2016). This species has been observed during times of heavy rainfall and dry season. *Serranobatrachus delicatus* (Fig. 3C) is a frog known from elevations from 1500–3500 m a.s.l. within the páramo ecotone (like *Pristimantis cristinae* in Rueda-Solano & Vargas-Salinas, 2010) where it is active at night on the forest floor and on the leaves, branches, and stems of shrubs. Males call (a single 'click') at heights less than 70 cm above the ground (Table 1). *Serranobatrachus insignitus* (Fig. 3D) is a rare species found in cloud forest at 1,500–2,600 m a.s.l. This species is nocturnal and terrestrial, occurring in leaf litter and fallen trunks of the cloud forest (Rueda et al., 2016). A few individuals were also observed in intervened areas. *Serranobatrachus megalops* (Fig. 3E) is currently known at 1,300–2,500 m a.s.l. This is a very abundant species; although few individuals were also observed in degraded habitats, specimens have been found under rocks and in low vegetation during the day and night (Rueda et al., 2016), but vocalization peaks at night (Table 1). Calling males (calls with a single 'click') and gravid females were observed during the two climatic seasons of the year. *Serranobatrachus ruthveni* (Fig. 3F) is known at elevations from 1,800–3,900 m a.s.l. (Rueda-Solano & Vargas-Salinas, 2010). This species is nocturnal and terrestrial, being found under rocks, inside terrestrial cavities, and under logs of cloud forest and paramos (Rueda et al., 2016). *Serranobatrachus sanctaemartae* (Fig. 3G) is known at elevations of 1,100–2,600 m a.s.l. and is active at night on arboreal vegetation (Table 1). Choruses can be heard throughout the year, even during the driest periods (Rueda et al., 2016). Males have been heard calling during the dry season on vegetation growing near streams, but in the rainy season they call some distance (~20 m) from water courses inside the forest. Gravid females have been observed during the two climatic seasons of the year (Table 1).

Conservation. Species of *Serranobatrachus* are endemic to the SNSM and distributed within the Parque Nacional Natural Sierra Nevada de Santa Marta, considered the most irreplaceable protected area in the world (Le Saout et al., 2013). The SNSM boasts an amazing variety of ecosystems, including dry and wet tropical forests, sub-Andean and Andean forests, moors, and zones with perpetual snow cover, and extends from sea level to snow-capped peaks in a straight-line distance of less than 40 km (Dechner & Diazgranados, 2007; Rueda-Solano et al., 2016). However, over the past 50 years, the primary forest of the SNSM has decreased significantly (Dechner & Diazgranados, 2007). Some consider that 70–85% of its original coverage could already have been lost (Fundación Pro-Sierra Nevada de Santa Marta, 1991).

Serranobatrachus species are vulnerable to habitat destruction or changes in the landscape (Roach et al., 2020), climate change, and emerging diseases (e.g., chytridiomycosis), with several species of *Serranobatrachus* reported to be infected with *Batrachochytrium dendrobatidis* (Flechas et al., 2017). These factors contribute to four species of *Serranobatrachus* being in the Endangered (EN) category: *S. carmelitae*, *S. cristinae*, *S. delicatus*, and *S. ruthveni*, and the rest in the Near Threatened (NT) category: *S. insignitus*, *S. megalops*, and S. *sanctaemartae* by the IUCN Red List of Threatened (IUCN, 2020).

Order Anura Oppel, 1811
Superfamily Brachycephaloidea Günther, 1858
Family Craugastoridae Hedges et al., 2008
Tachiramantis Heinicke, Barrio-Amoros &
Hedges, 2015

Type species.

***Eleutherodactylus prolixodiscus* Lynch, 1978**

Diagnosis. Small to medium terraranas (adult females SVL from 22 mm in *T. douglasi* to 31 mm in *T. cuentasi*, $\bar{x} = 27$ mm, $n = 77$); moderate sexual size dimorphism (adult males SVL from 15 mm in *T. tayrona* to 30 mm in *T. cuentasi*, $\bar{x} = 22$ mm, $n = 50$); head narrow (32–40% SVL); head as long as wide, snout long (*T. cuentasi*, *T. douglasi*, and *T. lentiginosus*) or short (*T. prolixodiscus* and *T. tayrona*); tubercle or papilla present on tip of snout in *T. prolixodiscus* and *T. tayrona*; lips moderately flared, most obvious in adult females in *T. prolixodiscus* and *T. tayrona*; IOD narrower than upper eyelid (adult females 54.9–71.8%, $n = 46$); cranial crests of frontoparietals absent, except in *T. douglasi* (Fig. 7B). Short dorsolateral folds present, evident along the body up to the sacrum in *T. cuentasi*, *T. douglasi*, *T. lentiginosus*, and *T. padrecarlosi;* dorsal folds absent in *T. prolixodiscus* and *T. tayrona*; skin of venter areolate.

Vomerine odontophores triangular in outline; dentigerous process not reaching palatines posteriorly (except in *T. douglasi*, *T. padrecarlosi*, and *T. tayrona*); vocal slits present; males with nuptial pads on finger I (absent in *T. padrecarlosi*). Tympanic membrane differentiated and tympanic annulus visible externally. Discs on fingers and toes expanded; finger I shorter than finger II; fingers bearing lateral keels; numerous low supernumerary plantar tubercles present; toe V longer than toe III, with toe V reaching penultimate subarticular tubercle on toe III in *T. tayrona*. In profile, length of otic ramus of squamosal longer than zygomatic ramus. Sphenethmoid not reaching postchoanal process of vomer. Apical supplementary element of *m. intermandibularis* absent, except in *T. tayrona*. Presacral vertebra VIII and sacrum free (fused in *T. douglasi*). Testes of adult males black. *Tachiramantis douglasi*, *T. padrecarlosi*, and *T. lentiginosus* have dirty-white spots surrounded by black in the groin and on the hidden surfaces of the hind limbs.

Content. Seven species: *Tachiramantis cuentasi* (Lynch, 2003b) **new combination**; *T. douglasi* (Lynch, 1996); *T. lentiginosus* (Rivero, 1982); *T. lassoalcalai* (Barrio-Amorós et al., 2010); *T. padrecarlosi* (Mueses-Cisneros, 2006) **new combination**; *T. prolixodiscus* (Lynch, 1978); and *T. tayrona* (Lynch & Ruiz-Carranza, 1985) **new combination** (Fig. 2).

Remarks. In addition to the molecular evidence included in their phylogenetic analyses, Heinicke et al. (2015) reported morphological evidence that further supports recognition of *Tachiramantis*. Specifically, they considered the large, strongly developed vomers almost fully surrounding the choanae in *T. douglasi*, *T. lentiginosus*, and *T. prolixodiscus* to be a synapomorphy of *Tachiramantis*, and we also observed this morphology in *T. padrecarlosi* and *T. tayrona*. However, although Heinicke et al. (2015: 157) defined this character in terms of 'vomer size', it is actually related to the orientation of the post-choanal process of the vomer. That is, in *Tachiramantis* the post-choanal process is directed anterodorsad, which is what causes the choana to be almost entirely surrounded.

Heinicke et al. (2015) also reported frontoparietal–prootic fusion as a synapomorphy of *Tachiramantis*, scoring this character for *Tachiramantis* on the basis of one individual of *T. prolixodiscus* via high-resolution X-ray computed tomography (CT) and data on *T. douglasi* from the literature (Lynch, 1996); osteological information was (and is still) not available for *T. lentiginosus*. We examined the cranial morphology of a cleared and stained specimen of *T. prolixodiscus* (ICN 15163) and observed that these bones are not fused, although they are in *T. douglasi* (ICN 15526–15528). Given the variation within *Tachiramantis* and lack of information on the cranial morphology of *T. cuentasi*, *T. lentiginosus*, *T. padrecarlosi*, and *T. tayrona*, the optimization of frontoparietal–prootic fusion as a synapomorphy for *Tachiramantis* is unclear at this time.

Tachiramantis tayrona was initially referred to the *Eleutherodactylus lacrimosus* assemblage of the former *Eleutherodactylus unistrigatus* group by Lynch and Ruiz-Carranza (1985), subsequently recognized by Hedges et al. (2008) and Padial et al. (2014) as the *Pristimantis lacrimosus* group composed mostly of species that inhabit bromeliads. The monophyly of the *P. lacrimosus* species group was refuted by Pinto-Sánchez et al. (2012) and Rivera-Correa et al. (2017) and ultimately resolved by González-Durán et al. (2017) with the erection of the *P. boulengeri* species group, also mostly composed of species inhabiting bromeliads (at least occasionally).

According to our phylogenetic results, pairwise genetic distances, and morphological analysis, *T. tayrona* comprises more than one species, with pairwise genetic distances between putative conspecifics of 0.2–11.7%. Lynch and Ruiz-Carranza (1985) reported geographic variation in body size in the description of *T. tayrona*, and we suggest that the type series of *T. tayrona* probably comprises at least two species. Genetic distances also suggest species complexes within *T. douglasi*, for which intraspecific genetic distances varied from 0.2 to 7.9% (Supplemental Table S4).

In this study *Tachiramantis* is delimited by three putative synapomorphies. (1) Post-choanal process of vomer directed anterodorsad (modified from Heinicke et al., 2015; (2) palatines short (distance between

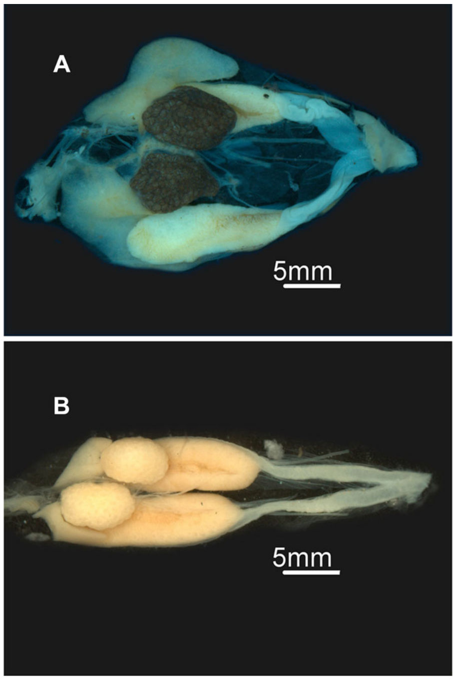

Fig. 4. Testes. (A) *Tachiramantis prolixodiscus* (ICN 15158), black testes. (B) *Serranobatrachus sanctamartae* (ICN 8244), white testes.

palatines equal to or greater than half the palatine length); (3) testes black in adult males (Fig. 4A).

Distribution and natural history. *Tachiramantis* is distributed from the northern Cordillera Oriental in Santander and Norte de Santander Departments to the northern and western slopes of the SNSM, in Colombia, in the Serranía de Perijá, Colombia and Venezuela, and in Cordillera de Merida in Táchira State, Venezuela, according to our samples from the ICN collection and data from literature. *Tachiramantis cuentasi* is known from the type locality in the Serranía de Perijá, Casa de Cristal at 2,900 m a.s.l. (Lynch, 2003b). The species has been observed at night on vegetation below 2 m from the ground (Lynch, 2003b). *Tachiramantis douglasi* occurs on the two flanks of the northern part of the Cordillera Oriental at elevations of 1,400–2,600 m a.s.l. (Arroyo et al., 2008). This is a common, nocturnal species, but males have been heard calling during the day as well (Arroyo et al., 2008). Reproduction in this species appears to be seasonal, with no vocalizations heard at the beginning of dry season and most adult males found in the rainy season (Arroyo et al., 2008). *Tachiramantis lentiginosus* is known from eastern flank of Cordillera Oriental, the eastern slopes of the Serranía de Perijá, and in Táchira Venezuela at elevations between 600 and 2,700 m a.s.l. (Barrio-Amorós et al., 2019). *Tachiramantis padrecarlosi* is only known from the type locality, cloud forest of the western flank of Cordillera Oriental, municipalities of Floridablanca and Tona at elevations of 1,750–1,950 m a.s.l. Frogs have been collected at night on vegetation below 2 m (Mueses-Cisneros, 2006). *Tachiramantis prolixodiscus* is known from the northern part of the Cordillera Oriental and the Serranía de Perijá along the Colombia–Venezuela border at elevations of 1,800–2,700 m a.s.l. The specimens have been found in bromeliads, and males have been heard calling at night (Arroyo et al., 2008; Table 1). *Tachiramantis tayrona* (Fig. 3H) is known from the northern and western flanks of the SNSM, in the sector of Serranía de San Lorenzo and Serranía Cebolleta, at elevations of 980–2,700 m a.s.l. Calling is restricted to bromeliads, and most males have been observed there (Rueda et al., 2016). We found adult males sitting on clutches of $9-14$ eggs ($\bar{x}=10$ eggs, SD $=1.69$, $n=7$) on phytotelmata. Males care for multiple clutches in the same place inside the bromeliad. Males have been heard calling during the rainy season of the year. The call is constituted by several clicks. Clutches have been observed exclusively in the rainy season. *Tachiramantis* aff. *tayrona* specimens collected in the sector of San Pedro de la Sierra and Santa Clara villages at elevations of 1,400 m a.s.l. were observed in bromeliads, but males have also been observed calling in ravines along the road. Specimens were captured under rocks and within low vegetation (Table 1). Although individuals of *T. prolixodiscus* have been found using bromeliads as a microhabitat (Arroyo et al., 2008; Lynch, 1978), evidence of reproduction in bromeliads has so far only been found in *T. tayrona*.

Conservation. *Tachiramantis douglasi*, *T. lentiginosus*, *T. prolixodiscus*, and *T. tayrona* are distributed within several protected areas in Colombia: Área Natural Única los Estoraques, Estación Experimental El Rasgón, and Parque Nacional Natural Sierra Nevada de Santa Marta. Secondary forest is the dominant vegetation coverage in these areas, with fragmented and deforested zones due to agricultural development. Distribution within protected areas is not sufficient for their conservation status given the presence of annual and perennial non-timber crops, livestock farming and ranching, and human settlements in their range (IUCN, 2020). There are two species in the Vulnerable (VU) category: *T. douglasi* and *T. lassoalcalai*, and one in the Endangered (EN) category: *T. lentiginosus* (IUCN, 2020).

Discussion

Hypothesis of phylogenetic relationships outside Brachycephaloidea

Insofar as our primary objectives were to test the monophyly and phylogenetic placement of *Tachiramantis* within Brachycephaloidea, we designed our sampling outside Brachycephaloidea to include representatives of most families in Nobleobatrachia (*sensu* Frost et al., 2006) as outgroups, but we did not sample those families densely. As such, our sample is not adequate to comprise a strong test of the relationships outside Brachycephaloidea. Nevertheless, below we summarize the relationships and compare them with previous findings (Fig. 5).

Australobatrachia, represented by *Calyptocephalella gayi* (Duméril & Bibron, 1841; Calyptocephallelidae) and *Philoria sphagnicolus* (Moore, 1958; Limnodynastidae), is not monophyletic, with *Sooglossus thomasseti* (Boulenger, 1909; Sooglossidae) sister to *P. sphagnicolus*. Previous studies have found Sooglossidae to be more closely related to Australobatrachia, with both groups together with Nobleobatrachia forming Hyloides (Frost et al., 2006), or the sister group of Ranoidea (Feng et al., 2017; Frazão et al., 2015; Pyron, 2014; Roelants et al., 2007; Wiens, 2007, 2011) or Ranoides + (Australobatrachia + Nobleobatrachia) (Pyron & Wiens, 2011). Note that the position of Sooglossidae violates the monophyly of Hyloides *sensu* Frost et al. (2006). Hyloidea, as defined by Pyron and Wiens (2011), is equivalent to Nobleobatrachia of Frost et al. (2006), which we employ to enable use of the superfamily rank within this clade (e.g., Brachycephaloidea and Dendrobatoidea).

Within Nobleobatrachia, our analysis corroborated the monophyly of Dendrobatoidea, Brachycephaloidea, Bufonidae, and Hemiphractidae, all of which were represented by more than one genus in our analysis (Fig. 5). Alsodidae, Hylidae, and Leptodactylidae, also represented by more than one genus, were not found to be monophyletic (Fig. 5). As in Grant et al. (2017), our representative of Leiuperinae, *Physalaemus cuvieri* (Fitzinger, 1826), is sister to Bufonidae. We recover Brachycephaloidea as the sister group of Hemiphractidae (Fig. 5), corroborating the monophyly of Orthobatrachia (Heinicke et al., 2009).

Phylogenetic relationships among genera of Brachycephaloidea

Our results regarding the relationships among the genera of Craugastoridae and Strabomantidae both agree and disagree with recent studies (Fig. 6). We recovered *Holoaden* and *Euparkerella* Griffiths, 1959 as sister taxa (Fig. 6) and corroborated the relationship *Bryophryne* (*Bahius* (*Barycholos* + *Noblella*)) (Canedo & Haddad, 2012; Pyron, 2014; Fig. 6F, G). Motta et al. (2021) recovered a different topology: (*Euparkerella* + *Holoaden*) (*Bahius* (*Barycholos* + *Noblella*)), while Dubois et al. (2021) found *Bahius*, *Barycholos*, and *Phyllonastes* Heyer, 1977 to form a trichotomy in a polytomy with *Bryophryne*, *Noblella* + *Microkayla*, and *Holoaden* + *Euparkerella*. Our data support the monophyly of Pristimantinae, with *Pristimantis* and *Yunganastes* Padial et al., 2007 as sister groups and *Phrynopus* Peters, 1873 as sister to *Lynchius* Hedges et al., 2008 + *Oreobates* Jiménez de la Espada, 1872, relationships that were also supported by Padial et al. (2014: Fig. 6E), Pyron (2014: Fig. 6F), Heinicke et al. (2015: Fig. 6D), González-Durán et al. (2017: Fig. 6C), and Motta et al. (2021).

Serranobatrachus gen. nov

In their study of the 'eleutherodactyline' frogs of the SNSM, Lynch and Ruiz-Carranza (1985) provided descriptions of three new species and a synopsis of six additional species. These authors proposed that the affinities of species from the SNSM are either to species found in the northern Andes of Colombia or with other Santa Marta montane species. These nine species were then placed in two different groups within *Eleutherodactylus* (the '*fitzingeri*' and '*unistrigatus*' groups) by Lynch and Ruiz-Carranza (1985), albeit with hesitation due to the presumed plesiomorphy of the character states they studied ('S' condition of the m. adductor mandibulae and unfused frontoparietals and prootics) in the SNSM taxa. Regarding the interpretation of plesiomorphy of the two-character states, this is due to the fact that these authors based their character polarization on use of a 'strict outgroup' method, whereby any and all states found in the outgroup are excluded as uninformative of relationships within the ingroup (Lynch, 1997). On the basis of our results, all of the 'eleutherodactyline' frogs of the SNSM are closely related, being placed in *Serranobatrachus* gen. nov. and *Tachiramantis* (*T. tayrona* and *Tachiramantis* sp.).

Six of the putative synapomorphies are found in the skull and one in the axial skeleton, as follows: (1) Alary process of premaxilla terminating in inverted V-shape and (2) directed posterodorsad. (3) Otic ramus of squamosal shorter than zygomatic ramus and (4) separated from posterolateral portion of prootic. (5) Crests present on frontoparietals. (6) Sphenethmoid long, reaching or surpassing the anterior edge of the nasals in fully developed adults. (7) Sacrum and presacral VIII fused (Fig. 7).

The alary process of the premaxilla is directed anterodorsad, dorsad, or posterodorsad in anurans (Lynch, 1971). Lynch and Ruiz-Carranza (1985) described the alary process for some of the SNSM species as slightly posterodorsad. Nevertheless, we found that the inclination of the alary process is significant enough to be described as

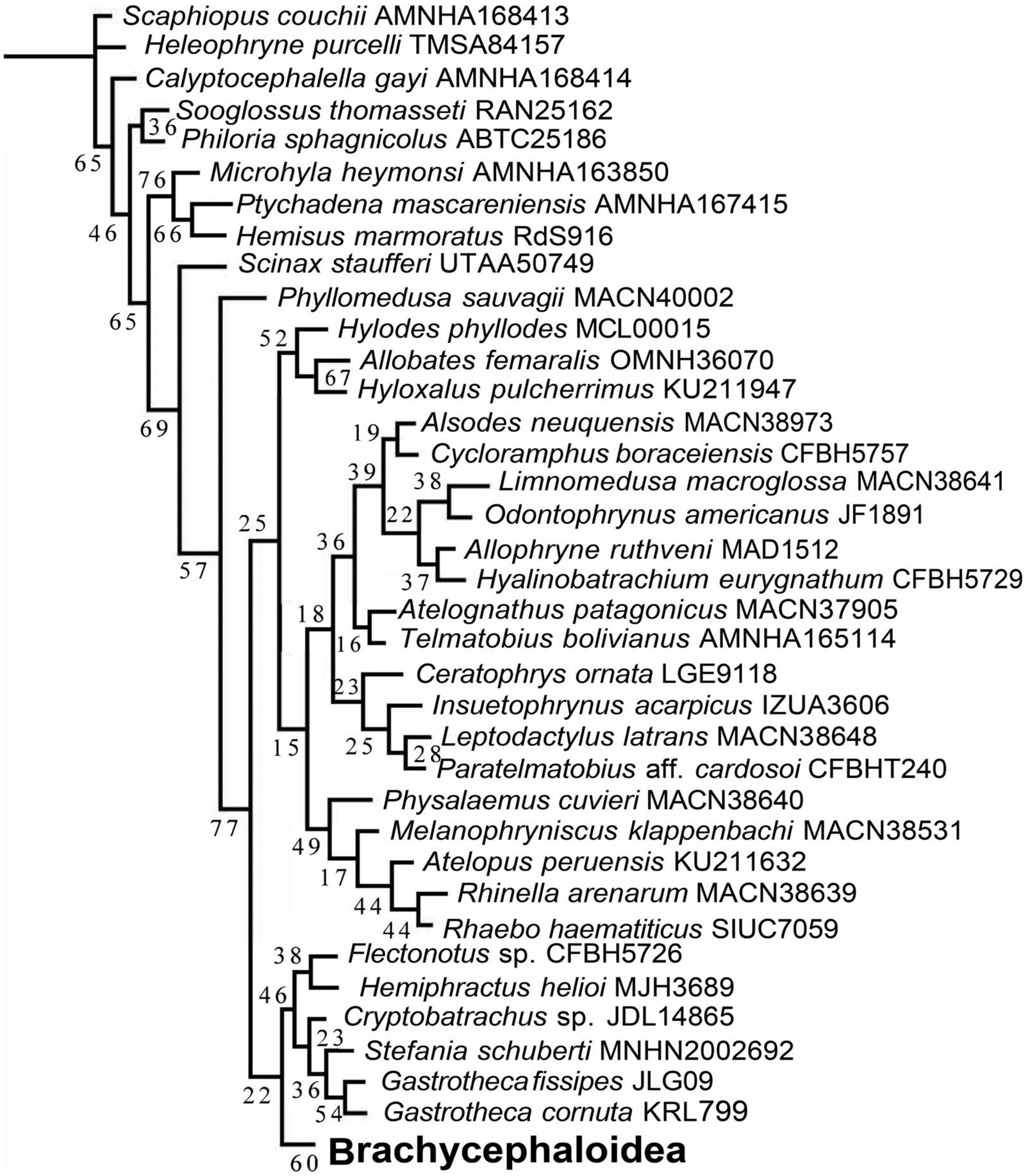

Fig. 5. Optimal hypothesis of relationships of Nobleobatrachia showing Brachycephaloidea as monophyletic. Hemiphractidae is recovered as the sister group of Brachycephaloidea. The tree is the strict consensus of 361 most parsimonious trees (MPTs; 81713 steps) showing minimum branch-lengths (derived from one of the MPTs) and all supported nodes labelled with Goodman-Bremer values.

posterodorsal in all specimens of *Serranobatrachus* gen. nov we examined (viz. *S. carmelitae*, *S. cristinae*, *S. delicatus*, *S. insignitus*, *S. megalops*, *S. ruthveni*, and *S. sanctamartae*). Optimization of the orientation of the alary process indicates it has evolved at least once in *Strabomantis* (*S. sulcatus*) and in *Serranobatrachus* gen. nov, and in *Pristimantis* at least twice when observed in *P. buckleyi* (Boulenger, 1882) and in *P. cryophilius* (Lynch, 1979). *Pristimantis buckley* is placed in the reformulated *Pristimantis devillei* species group by Padial et al. (2014) while *P. cryophilius* according to Padial et al. (2014) is not assignable to any *Pristimantis* species group.

The length of the otic ramus of the squamosal, which is shorter than the zygomatic ramus, is another character shared by the species of *Serranobatrachus* gen. nov. However, care must be taken with this character, because the otic and zygomatic rami vary greatly and can form a series of complex morphological transformations. The optimization of this character showed that otic ramus of the squamosal shorter than zygomatic ramus has at least three independent origins in terraranas, in the *Serranobatrachus* gen. nov in *Craugastor fitzingeri* (Schmidt, 1857), *C. longirostris* (Boulenger, 1898), and in *Strabomantis sulcatus* (Cope, 1874).

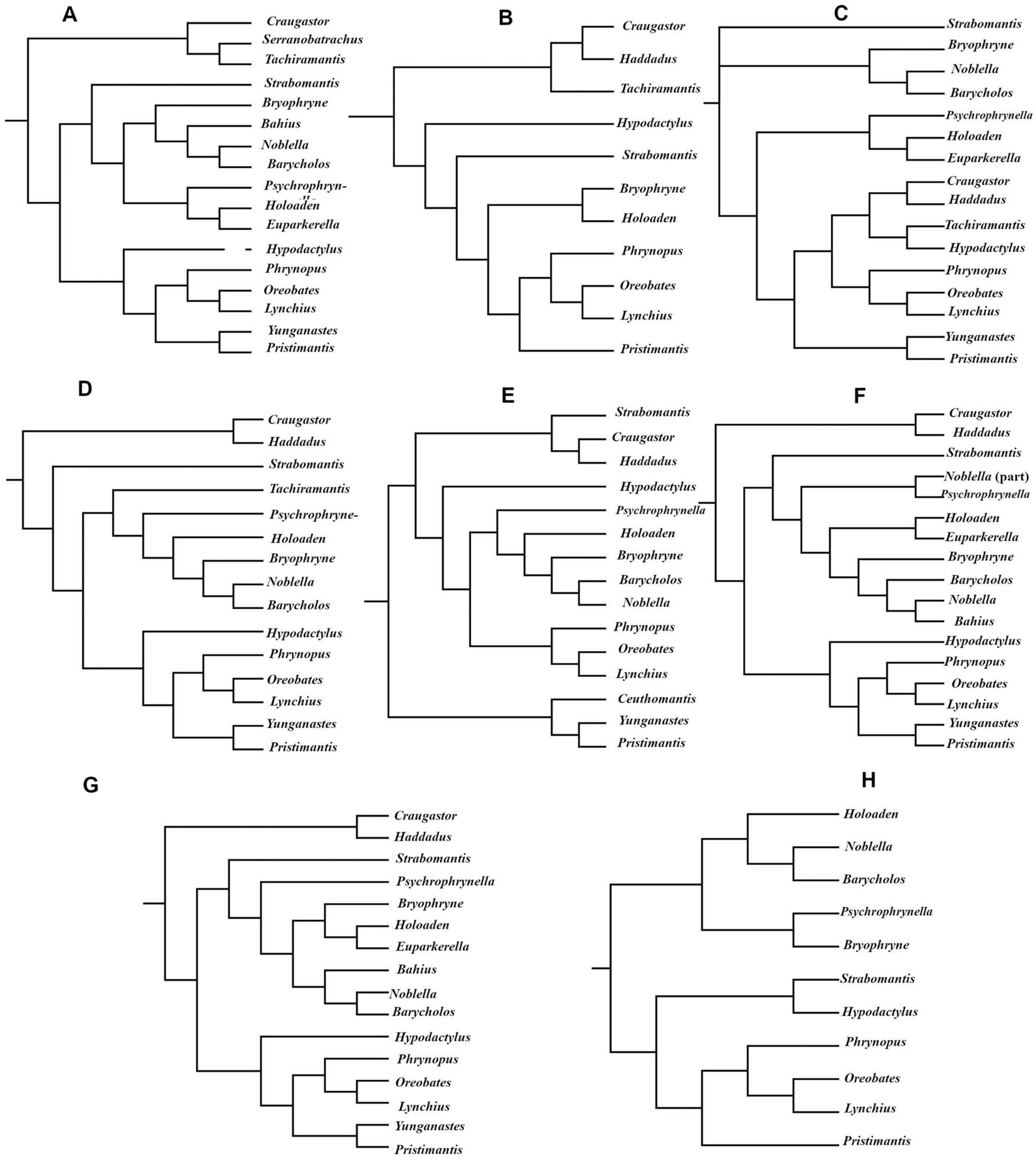

Fig. 6. Recent hypotheses of phylogenetic relationships among genera of Brachycephaloidea. (A) Tree alignment, phylogenetic parsimony, this study. (B) Similarity alignment, maximum likelihood, Heinicke et al. (2018). (C) Tree alignment, phylogenetic parsimony, González-Durán et al. (2017). (D) Similarity alignment, maximum likelihood, Heinicke et al. (2015). (E) Tree alignment, phylogenetic parsimony, Padial et al. (2014). (F) similarity alignment, maximum likelihood, Pyron (2014). (G) Similarity alignment, maximum likelihood, Canedo & Haddad (2012). (H) Similarity alignment, maximum likelihood, Hedges et al. (2008).

Within Brachycephaloidea, cranial crests are recognized as comprising an upturned lateral margin of the frontoparietals (Lynch 1975, 1995). This structure has been classified as prominent, massive, or low. Here we focus only on the absence or presence of cranial crests and not the variation in their morphology, such as width, height, and position. Although the phylogeny is incomplete, the optimization shows that a cranial crest

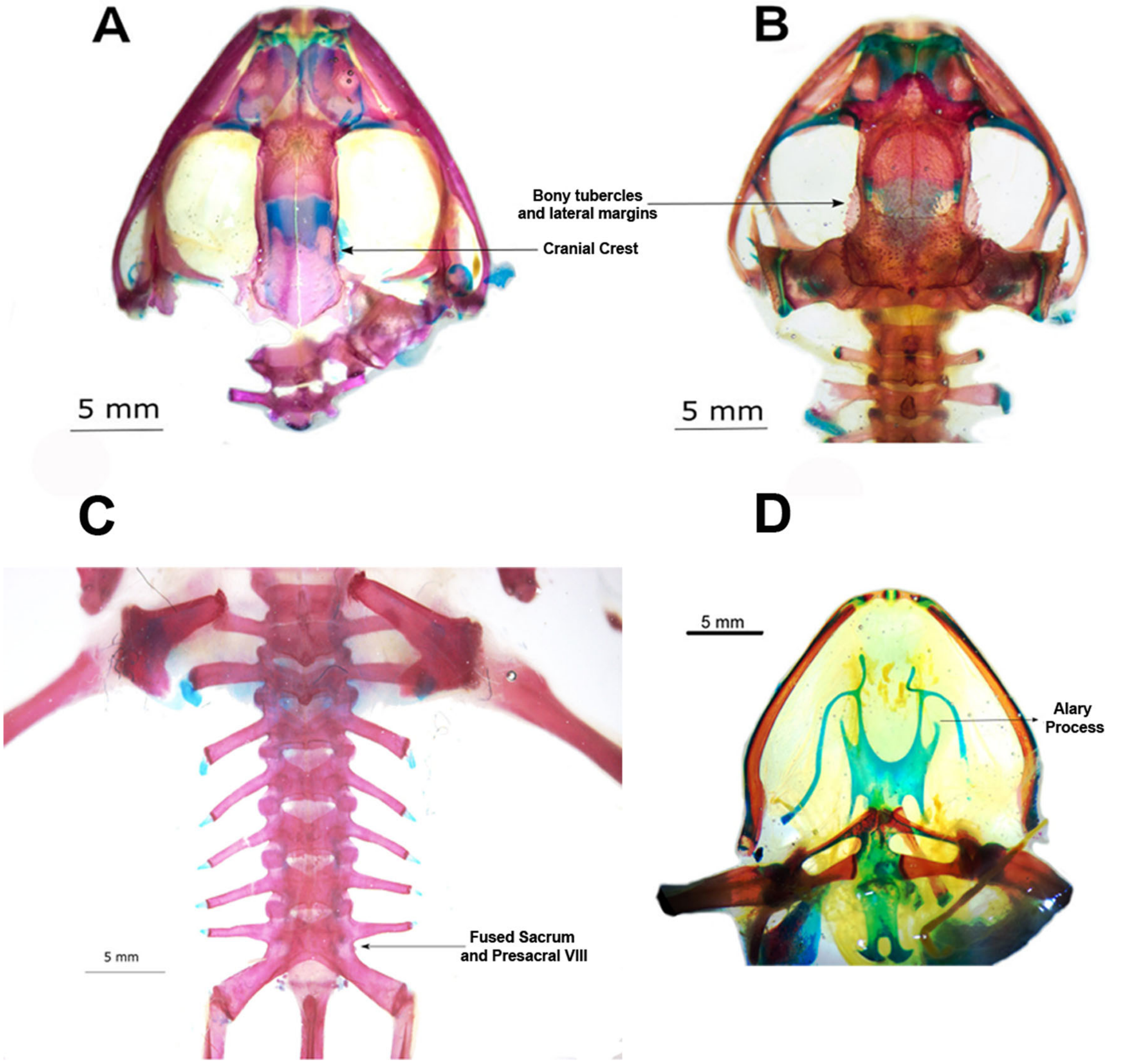

Fig. 7. Putative synapomorphies of *Serranobatrachus* gen. nov. Dorsal views of skulls. (A) *Serranobatrachus ruthveni* (ICN 23282), showing cranial crest on frontoparietals. (B) *Tachiramantis douglasi* (ICN 15526) frontoparietals bear small bony tubercles and lateral margins of these with cranial crests, ornamentation is also seen along the dorsal edge of the squamosal. (C) Note fusion of the sacrum and Presacral VIII in *Serranobatrachus sanctamartae* (ICN 13042). (D) Skull of *Tachiramantis douglasi* (ICN 15526), presence of alary processes of the hyoid plate.

has evolved at least twice in *Strabomantis* (*S. necerus* [Lynch, 1975] in the *S. biporcatus* species series and *S. sulcatus* in the *S. cornutus* species group), at least once in *Tachiramantis* (*T. douglasi*), and in the most recent common ancestor of *Serranobatrachus*. In the genus *Pristimantis* a cranial crest is present in a variety of species, including the *P. devillei* species group (present in *P. buckleyi* [Boulenger, 1882], *P. curtipes* [Boulenger, 1882], *P. devillei* [Boulenger, 1880], *P. duellmani* [Lynch, 1980b], *P. gentry* [Lynch & Duellman, 1997], *P. quinquagesimus* [Lynch & Trueb, 1980], *P. surdus* [Peters, 1863], *P. thymalopsoides* [Lynch, 1976], *P. truebae* [Lynch & Duellman, 1997], and *P. vertebralis* [Boulenger, 1886]). Cranial crests are also present in *P. thymelensis* (Lynch, 1972), placed in the *P. myersi* species group by Padial et al. (2014) but in our phylogeny placed outside of other species assigned to *P. myeri* species group by Padial et al. (2014), *P. galdi* (Jiménez de la Espada, 1870; see below), and in the following species that are not assignable to a particular *Pristimantis* species group according to Padial et al. (2014): *P. cryophilius*, *P. spinosus* (Lynch, 1979b), *P. supernatis* (Lynch, 1979c).

We observed a large sphenethmoid extending past the anterior edge of the nasals in *Serranobatrachus* gen. nov. We did not observe this condition in any of the other specimens examined (Appendix 1). Lynch (1989, 2003) proposed that a large sphenethmoid is a synapomorphy linking the species now assigned to the genus *Hypodactylus* (*H. adercus*, *H. latens*, and *H. nigrovittatus*) *sensu* Hedges et al. (2008).

Fusion of the sacrum and presacral vertebra VIII has been considered a possible diagnostic character of several groups of anurans (Báez & Pugener, 2003; Báez & Trueb, 1997; Cannatella & Trueb, 1988; Lynch, 1973; Noble, 1922; Tihen, 1960; Trueb, 1971). Joglar (1986) was the first to detect the fusion of the sacrum and presacral VIII in terraranas, reporting it in some species of the '*Eleutherodactylus* (*Euhyas*) *ricordii*' species group and two species of the '*E. gollmeri* species group' (now in *Craugastor*). Later, Lynch (2000) supported Joglar's (1986) results, reporting fusion of the sacrum and presacral VIII in the remaining five species allocated with the '*E. gollmeri*' species group and proposing this condition as a synapomorphy for the species group, composed of the following species: '*E. chac*' (Savage, 1987), '*E. daryi*' (Ford & Savage, 1984), '*E. gollmeri*' (Peters, 1863), '*E. greggi*' (Bumzahem, 1955), '*E. laticeps*' (Dumeril, 1853), '*E. lineatus*' (Brocchi, 1879), and '*E. loki*' (Shannon & Werler, 1955). Hedges et al. (2008) proposed the *Craugastor laticeps* species series and placed most of the '*Eleutherodactylus gollmeri*' species group *sensu* Savage (1987) in it, except '*E. daryi*', which was placed in their new subgenus *Campbellius* (*Craugastor*) on the basis of molecular evidence. Padial et al. (2014) recovered the subgenus *Campbellius* as the sister group of all other species of the genus *Craugastor*, and because sequence data were not available for *C. greggi* (Bumzahem, 1955), this species was considered unassigned to any particular group within *Craugastor*. Furthermore, Padial et al. (2014) recovered *Craugastor chac*, *C. gollmeri*, *C. laticeps*, *C. lineatus*, *C. mimus* (Taylor, 1955), and *C. noblei* (Barbour & Dunn, 1921) as a clade in their maximum likelihood analysis, but they left them unassigned to any *Craugastor* species group. None of the phylogenetic studies of *Craugastor* subsequent to Lynch (2000) included osteological characters, and there is no additional information on the axial skeleton of *Craugastor* species. Fusion of the sacrum and presacral VIII has evolved twice independently in *Craugastor*, at least once in *Tachiramantis* (*T. douglasi*), and in the most recent common ancestor of *Serranobatrachus* gen. nov.

Serranobatrachus gen. nov. and *Tachiramantis* share the presence of the alary processes of the hyoid (Fig. 7D). The alary process of the hyoid has also been reported for other brachycephaloids, including *Craugastor augusti*, *C. fleischmanni* (Boettger, 1892), *N. nigrovittata*, and *O. quixensis* by Heyer (1975), *Geobatrachus walker* by Ardila-Robayo (1979) and *Barycholos* by Motta et al. (2021). Kaiser et al. (1994), in their phylogenetic study of eastern Caribbean '*Eleutherodactylus*', found that this alary process is also present in *C. fitzingeri*, *Eleutherodactylus amplinympha* (Kaiser et al., 1994), *E. antillensis* (Reinhardt & Lütken, 1862), *E. barlagnei* (Lynch, 1965), *E. coqui* (Thomas, 1965), *E. johnstonei* (Barbour, 1914), *E. martinicensis* (Tschudi, 1838), and *E. pinchoni* (Schwartz, 1967*)*, whereas it is absent in *Prisitmantis euphronides* (Schwartz, 1967), *P. shrevei* (Schwartz, 1967), and *P. urichi* (Mole & Urich, 1894).

The absence of the alary process has also been reported for *P. huicundo* (Guayasamin, 2004), *P. obmutescens* (Lynch, 1980), *P. orcesi* (Lynch, 1972), *P. ortizi* (Guayasamin, 2004), *P. racemus* (Lynch, 1980), *P. simoteriscus* (Lynch et al., 1996), *P. simoterus* (Lynch, 1980), *P. thymelensis* (Lynch, 1972), and the *Prisitmantis leptolophus* species group (*P. acatallelus* [Lynch & Ruiz-Carranza, 1983], *P. leptolophus* [Lynch, 1980], *P. lasalleorum* [Lynch, 1995], *P. maculosus* [Lynch, 1991], *P. parectatus* [Lynch & Rueda-Almonacid, 1998], *P. scoloblepharus* [Lynch, 1991], and *P. uranobates* [Lynch, 1991], present and absent in *P. stictus* [González-Durán, 2016]; Gonzalez-Duran et al., 2017). We also scored this character for all available skeletons of *Pristimantis* deposited at the ICN collection (Appendix 1) and found that they also lack the alary process of the hyoid. Given the widespread absence of the alary process in this genus, we infer that this state is found in the most recent common ancestor of the clade; however, osteological data for related groups (especially *Yunganastes*, for which only the cranium has been described for two species, *Y. fraudator* and *Y. pluvicanorus* (De la Riva & Lynch, 1997)) are required to determine if this shared absence is apomorphic or plesiomorphic for *Pristimantis*. Nevertheless, additional evidence is required to test this hypothesis, as we did not study all recognized species groups within *Pristimantis*.

Content of the *Pristimantis galdi* and *P. lacrimosus* species groups

The former '*Eleutherodactylus galdi* species group' [= *Pristimantis galdi* species group, Hedges et al., 2008; Padial et al., 2014] was recognized by Lynch (1996) to accommodate those species that share bony tubercles along the lateral edges of the frontoparietals (Fig. 7B) and the dorsal edge of the zygomatic and otic rami of the squamosal: *Tachiramantis douglasi*, *Serrranobatrachus delicatus*, and *Pristimantis galdi* (Jiménez de la Espada, 1870). Lynch and Rueda-Almonacid (1997) subsequently assigned *P. tribulosus* to this group, suggesting that it was the sister species of

P. galdi. According to our results, the *P. galdi* species group should be restricted to *P. galdi* and *P. tribulosus. Pristimantis tayrona*, previously part of the *P. lacrimosus* species group, is now referred to *Tachiramantis*. No other species here transferred from *Pristimantis* to *Serranobatrachus* or *Tachiramantis* was previously assigned to any *Pristimantis* species group, so no further reformulation of the groups is needed.

Biogeography

Serranobatrachus gen. nov. and *Tachiramantis* are ecologically diverse within an apparent restricted geographic range. *Serranobatrachus* gen. nov. is endemic to the SNSM, while *Tachiramantis* is distributed along the northern part of the Cordillera Oriental, Serranía de Perijá, SNSM, and Serranía de Mérida. The number of SNSM endemic species varies across vertebrate groups, with 17 amphibians, 12 reptiles, 14 birds, and 1 mammal (UAESPNN, 2005); however, the number of SNSM endemics might be considerably underestimated due to insufficient knowledge of the systematics of these groups (Cadena et al., 2016).

Basic aspects of the origins of the SNSM flora and fauna remain poorly understood. Alexander Ruthven (1915, 1917, 1922) was the first to study the amphibians and reptiles of the SNSM. In the light of those studies, Rivero (1972) and Walker and Test (1955) proposed that SNSM anurans had similarities with the fauna of the Cordillera de la Costa of Venezuela. Lynch (1976) hypothesized affinities between the anuran faunas of the Antilles and the SNSM, but that was rejected by Lynch and Ruiz-Carranza (1985) who proposed a connection between the Colombian Andes and the SNSM. Later, Lynch (1996) provided the first cladistic evidence of a biogeographic connection between the SNSM and the Cordillera Oriental, proposing *T. douglasi* (Cordillera Oriental) and *S. delicatus* (SNSM) as sister species on the basis of the shared fusion of the sacrum and presacral VIII. Guayasamin et al. (2009) found the monotypic genus of glassfrogs, *Ikakogi* Guayasamin et al., 2009 endemic to the SNSM, to be the sister taxon of all other Centroleninae. Subsequently, Castroviejo-Fisher et al. (2014) suggest that the first split within Centrolenidae, isolating *Ikakogi tayrona* (Ruiz-Carranza & Lynch, 1991) from the clade containing all other glassfrogs, occurred during the Oligocene when the Cordillera Central and Cordillera Oriental experienced uplifts, probably facilitating the early colonization/vicariance of a proto-Sierra Nevada de Santa Marta. These authors also proposed that isolation of the SNSM from other mountain ranges was a plausible explanation for the monotypic genus in the SNSM, although they also deemed that extinctions and undiscovered species cannot be dismissed. Similarly, Grant et al. (2017) found that the SNSM endemic '*Colostethus*' *ruthveni* group, composed of '*C.*' *ruthveni* and an undescribed species, is sister to the widespread clade Dendrobatini, although they did not speculate about possible biogeographic causes.

Our phylogenetic analysis revealed a close relationship between the species occurring in the SNSM, Serranía de Perijá, and Cordillera Oriental of Colombia. Phylogenetic studies of other taxa have also found this biogeographic relationship. Benham et al. (2015) examined geographic and temporal patterns of diversification in *Metallura* Gould, 1848 hummingbirds and found a clade in which species of the Cordillera Oriental are sister to SNSM species, which together are the sister taxon of a clade composed of Serranía de Perijá species, all of which together are sister to a clade containing species from Cordillera de la Costa and Merida Andes. Recently, Sánchez-Pacheco et al. (2018) proposed another biogeographic relationship for the lizards of the genus *Oreosaurus* Boettger, 1891, finding that that *Oreosaurus* species from the SNSM are most closely related to a clade composed of species in the Venezuelan Coastal Range, Trinidad, and the tepuis.

In summary, two general biogeographic scenarios are currently supported for the SNSM vertebrate fauna: (1) biogeographic connections between the SNSM and the Andes of Colombia and the Serranía de Perijá and (2) a connection between the SNSM and the north-eastern portion of the Andes (Venezuelan Coastal Range). However, caution should be employed when generalizing these scenarios to other groups, given that the diversity and relationships of most of the SNSM vertebrate fauna remain poorly understood.

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Supplemental material

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