Treefrog diversity in the Neotropics: Phylogenetic relationships of Scinaxini (Anura: Hylidae: Hylinae)

Contents

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Abstract. *Scinax* is the most species-rich genus of Neotropical treefrogs, with 129 currently recognized species divided between two major clades, the *S. catharinae* and *S. ruber* clades. The *S. catharinae* clade includes 52 species currently placed in the *S. perpusillus* and *S. catharinae* groups, whereas the *S. ruber* clade is composed of 77 species, 13 of which are included in two species groups: the *S. rostratus* and *S. uruguayus* groups, with all 64 remaining species being unassigned to any group. Although some studies have addressed the phylogenetic relationships of the genus, its relationships remain poorly understood. To test the monophyly of the genus, its major clades, and the currently recognized species groups, and the relationships within and among them, we performed a total evidence phylogenetic analysis including sequences of five mitochondrial (portions of cytochrome b and cytochrome oxidase c subunit I, and 12S rRNA, 16S rRNA, NADH dehydrogenase subunit 1, plus three intervening tRNAs) and six nuclear genes (portions of chemokine receptor type 4, proopiomelanocortin, seven in absentia homolog 1, recombination activating gene 1, rhodopsin exon 1, and tyrosinase), and 159 phenotypic characters. The dataset included 121 of the 129 known species of *Scinax* and many unnamed species. Most species are represented by multiple specimens, including topotypic material for approximately 52% of the species. As a result of this analysis, we partition *Scinax* into three genera. We restrict *Scinax* to most species of the former *S. ruber* clade and divide its species among 13 species groups: the *S. auratus*, *S. boesemani*, *S. cruentomma*, *S. danae*, *S. elaeochroa*, *S. eurydice*, *S. funereus*, *S. fuscomarginatus*, *S. fuscovarius*, *S. granulatus*, *S. nasicus*, *S. rostratus*, and *S. squalirostris* groups; only one species (*S. pachycrus*) remains unassigned to any group. To eliminate the paraphyly of *Scinax*, we redefine *Julianus*—originally erected for the *S. uruguayus* group—to include the former *S. camposseabrai*. We recognize *Ololygon* for the species of the former *S. catharinae* clade and divide its species among seven species groups: the *O. agilis*, *O. argyreornata*, *O. belloni*, *O. cardosoi*, *O. catharinae*, *O. feioi*, and *O. perpusilla* groups. All species groups of the three recognized genera of Scinaxini are discussed, diagnosed, characterized—in many cases using phenotypic synapomorphies—and taxonomic comments are provided for many species. Our study further revealed 57 candidate species, an increase of 44.2% of the recognized species in the tribe, highlighting how far we are from fully understanding the diversity of this clade of Neotropical treefrogs.

Keywords. Amphibia; *Julianus*; *Ololygon*; *Scinax*; Taxonomy; Total Evidence.

INTRODUCTION

Hylidae is the most species-rich clade of arboreal anurans (1,045 recognized species; Frost, 2023). The diversity of this family is concentrated in Australopapua (Pelodryadinae, 231 species) and South America (595 species, most species of Phyllomedusinae and the hyline tribes Cophomantini, Dendropsophini, Lophyohylini, Pseudini, Scinaxini, and Sphaenorhynchini), with relatively smaller radiations in Central and North America and the West Indies (203 species, most species of Hylini and a few species from Cophomantini, Dendropsophini, Lophyohylini, and Scinaxini), and Eurasia (16 species, all in tribe Hylini). The phylogenetic knowledge of this family has steadily grown since the analyses of Faivovich et al. (2005) and Wiens et al. (2005), which were reflected in taxonomic proposals recognizing tribes and several new genera.

Subsequent studies focused on several smaller groups within the family (e.g., Aguiar et al., 2007; Garda and Cannatella, 2007; Hua at al., 2009; Moen and Wiens, 2009; Coloma et al., 2012; Salerno et al., 2012; Faivovich et al., 2013, 2021; Jungfer et al., 2013; Caminer and Ron, 2014, 2020; Guayasamin et al., 2015; Berneck et al., 2016; Caviedes-Solis and Oca, 2017; Peloso et al., 2018; Araujo-Vieira et al., 2019; Sturaro et al., 2020; Fouquet et al., 2021). Our understanding of the phylogenetic relationships of the major clades has increased as well (Faivovich et al., 2010a, 2018; Pinheiro et al., 2019; Blotto et al., 2021; Orrico et al., 2021), although major, densely sampled and evidence-heavy analyses are still lacking for Pelodryadinae (the results of Duellman et al. [2016] were based on GenBank sequences; relationships within this subfamily are in general poorly supported, the phylogenetic hypothesis was only marginally discussed, and 114 species have never been included in phylogenetic studies), and Scinaxini (Hylinae; Faivovich et al., 2005, 2018).

Scinaxini includes *Scinax* Wagler, 1830 (Faivovich et al., 2018), which is currently the most species-rich genus within Hylidae, with 129 species distributed from southern Mexico to central-eastern Argentina, extending to Trinidad and Tobago and St. Lucia (Frost, 2023). The species of *Scinax* occur in almost all major tropical and subtropical areas, with particularly high diversity in the Atlantic Forest of southeastern Brazil. They occupy diverse habitats, including both open and forested areas, and reproduce in temporary and permanent lentic water bodies (e.g., Duellman, 1970a; Cardoso and Sazima, 1980; Pombal et al., 1995a), streams and headwaters (e.g., Duellman and Wiens, 1992; Pombal and Bastos, 1996), or bromeliads (Peixoto, 1987).

Several species presently included in *Scinax* were described in or referred to the *Hyla rubra* group (Dunn, 1933). The group was subsequently redefined, and its content increased over the years to include the recognition of several internal groups (e.g., Cochran, 1952, 1955; Bokermann, 1964a; León, 1969; Savage and Heyer, 1969; Duellman, 1972a,b; Lutz, 1973a). Fouquette and Delahoussaye (1977) resurrected *Ololygon* Fitzinger, 1843 (type species: *Hyla strigilata* Spix, 1824) for all species then included in the *Hyla rubra* group. They further recognized five species groups (leaving some species unassigned), including the *O. rubra*, *O. catharinae*, *O. rostrata*, *O. staufferi*, and *O. x-signata* groups. Following Pombal and Gordo (1991), Duellman and Wiens (1992) resurrected *Scinax* Wagler, 1830 (type species: *Hyla aurata* Wied, 1821) for all the species previously included in *Ololygon*. Additionally, they grouped almost all known species in seven species groups (the *S. catharinae*, *S. perpusilla*, *S. rubra*, *S. rostrata*, *S. rizibilis*, *S. staufferi*, and *S. x-signata* groups). Subsequently, Pombal et al. (1995b) transferred all species of the *S. rizibilis* and *S. x-signata* groups to the *S. catharinae* and *S. rubra* groups, respectively.

Faivovich (2002) performed a phylogenetic analysis using multiple phenotypic character systems (external adult and larval morphology, osteology, myology, reproductive biology, behavior, and cytogenetics) scored for 36 species. *Scinax* was found to be monophyletic with two major internal clades, the *S. catharinae* and *S. ruber* clades, and many morphological synapomorphies were reported for *Scinax* and its major clades. *Scinax* was delimited by 10 synapomorphies, including an occluded frontoparietal

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fontanelle; a single origin of the m. extensor brevis superficialis digiti III from the ulnare; absence of the larval lingual papillae; and the ability to bend backwards finger II and toe I (Jungfer, 1986). The *S. catharinae* clade was delimited by five synapomorphies, mostly myological character-states, which included the m. depressor mandibulae lacking an origin from the dorsal fascia that covers the suprascapula. This clade comprised the *S. perpusillus* and *S. catharinae* groups, the latter composed of all species previously grouped in the *S. catharinae* group plus *S. agilis* and *S. berthae* (formerly in the then *S. staufferi* group) and delimited by three synapomorphies, among them the extensively elongated and curved posterior part of the cricoid ring. Faivovich (2002) did not test the monophyly of the *S. perpusillus* group, because the analysis included only one exemplar, but he recognized it based on two possible synapomorphies: the oviposition in bromeliads and the extreme reduction of webbing between toes II and III (Peixoto, 1987). The *S. ruber* clade included species previously grouped in the *S. rostratus*, *S. ruber*, and *S. staufferi* groups, and was delimited by three synapomorphies, among them, the vent tube positioned above the margin of the ventral fin in tadpoles. In the *S. ruber* clade, Faivovich (2002) recovered as monophyletic only the *S. rostratus* group, delimited by 10 synapomorphies, including the occurrence of a labial arm in the larval oral disc.

In a phylogenetic analysis of Hylidae based on DNA sequences of nuclear and mitochondrial genes and a dataset of foot musculature characters extracted from Burton (2004), Faivovich et al. (2005) corroborated the monophyly of the two major clades of *Scinax*. Their results recovered this genus as the sister taxon of *Scarthyla* and *Pseudis*, which, together with *Sphaenorhynchus*, *Xenohyla*, and *Dendropsophus* formed the tribe Dendropsophini, the one with the lowest support in Hylinae.

As the outgroup taxa analyzed by Faivovich (2002; e.g., *Aplastodiscus perviridis*, *Boana faber*) were found to be only distantly related to *Scinax*, Faivovich et al. (2005) reevaluated many of the character-states inferred as synapomorphies for *Scinax* and its major clades in the first study. On the basis of the available evidence (taxonomic distribution of the relevant characters among the closely related clades), *Scinax* was delimited by 4 of the 10 synapomorphies then known for the genus: webbing between toes I and II that does not extend beyond the subarticular tubercle of toe I; the ability to bend backwards finger II and toe I; the origin of the m. pectoralis abdominalis through well-defined tendons; and the m. pectoralis abdominalis overlapping m. obliquus externus (Silva, 1998; Faivovich, 2002). A single putative morphological synapomorphy delimited the *S. ruber* clade: the larval vent tube positioned above the margin of the ventral fin (Faivovich, 2002), whereas the synapomorphies of the *S. catharinae* clade were those of Faivovich (2002), except for the m. depressor mandibulae without an origin from the dorsal fascia at the level of the m. dorsalis scapulae, which optimized ambiguously in the hypothesis of Faivovich et al. (2005). The *S. catharinae*, *S. perpusillus*, and *S. rostratus* groups were recognized based on the morphological synapomorphies proposed by

Faivovich (2002), and a new group, the *S. uruguayus* group, was recognized in the *S. ruber* clade to avoid rendering *Scinax* paraphyletic. The *S. uruguayus* group included *S. pinimus* and *S. uruguayus* previously grouped in the former *Hyla uruguaya* group and two putative morphological synapomorphies supported its monophyly: bicolored iris and presence of two colored, keratinized plates on each side of the lower jaw-sheath in tadpoles (Kolenc et al., 2003).

Several subsequent molecular phylogenetic analyses corroborated the monophyly of *Scinax*, and the *S. catharinae* and *S. ruber* clades (Wiens et al., 2006, 2010; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018). In those analyses, the topological changes in the internal relationships of *Scinax* were minor and mostly associated with the inclusion of new taxa or related to weakly supported relationships. An example is the poorly supported position of *S. boesemani* as the sister taxon of *S. fuscovarius*, *S. nasicus*, and *S. ruber* in the analysis of Wiens et al. (2010), which is recovered as the sister taxon of *S. cruentomma* by Pyron and Wiens (2011), Pyron (2014), and Duellman et al. (2016). Other studies, focused on species delimitation and new species description, included phylogenetic analyses with several more species of *Scinax* (Ron et al., 2018; Vacher et al., 2020; Ferrão et al., 2018a, 2022), mostly using mitochondrial gene fragments, but provided no discussion of their results from a phylogenetic perspective.

In a reanalysis of GenBank sequences, Duellman et al. (2016) included 35 of the 129 currently known species of *Scinax*. These authors partitioned *Scinax*, as recognized by Faivovich et al. (2005), in three genera: *Julianus* (for the *S. uruguayus* group as defined by Faivovich et al., 2005), *Ololygon* (for the *S. catharinae* clade as defined by Faivovich, 2002 and Faivovich et al., 2005), and *Scinax* (for all remaining species of the *S. ruber* clade as defined by Faivovich et al., 2005). These taxonomic changes were not required to preserve the monophyly of *Scinax* sensu Faivovich et al. (2005). However, more problematic were the inadequate generic definitions and the disregard for phenotypic synapomorphies that would have improved the usefulness of their arrangement. Colaço and Silva (2016) did not recognize the taxonomic changes introduced by Duellman et al. (2016), stressing that these authors ignored most of the data presented by Faivovich (2002). Conte et al. (2016), Lourenço et al. (2016, 2019, 2020), Rodrigues et al. (2017), Faivovich et al. (2018), Ron et al. (2018), Baldo et al. (2019), Barreto et al. (2019), Dubois et al. (2021), Lacerda et al. (2021), Pezzuti et al. (2021), and Segalla et al. (2021) also considered *Julianus* and *Ololygon* junior synonyms of *Scinax*. In light of the shortcomings of the generic arrangement within Scinaxini proposed by Duellman et al. (2016) that hinder its application, as well as its limited adoption in subsequent taxonomic studies, we follow recent authors in employing *Scinax* sensu Faivovich et al. (2005) below and propose a revised taxonomy on the basis of our results (see "An evidence-based taxonomy of Scinaxini", below).

In terms of the position of *Scinax* in Hylinae, Wiens et al. (2006, 2010) obtained this genus as the poorly sup-

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ported sister taxon of *Sphaenorhynchus*. In turn, this clade is the sister taxon of a group composed of *Dendropsophus*, *Lysapsus*, *Pseudis*, *Scarthyla*, and *Xenohyla*, therefore recovering, with weak support, the monophyly of Dendropsophini as did Faivovich et al. (2005). Pyron and Wiens (2011), Pyron (2014), Duellman et al. (2016), and Jetz and Pyron (2018) also obtained *Scinax* (sensu Faivovich, 2002; Faivovich et al., 2005) as the sister taxon of *Sphaenorhynchus* with poor support (bootstrap with RAxML < 50%; Shimodaira–Hasegawa < 64%), but more distantly related to *Dendropsophus*, *Pseudis*, *Scarthyla*, and *Xenohyla*, implying the non-monophyly of Dendropsophini.

Duellman et al. (2016) arbitrarily raised the subfamilies of Hylidae (Hylinae, Pelodryadinae, and Phyllomedusinae) to family rank, and the tribes of Hylinae recognized by Faivovich et al. (2005) to subfamily-rank. Duellman et al. (2016) also restricted Dendropsophini (as Dendropsophinae) to *Dendropsophus* + *Xenohyla*, resurrected Pseudinae Fitzinger, 1843 for the clade including *Scarthyla*, *Lysapsus*, and *Pseudis*, and erected Scinaxinae for *Scinax* and *Sphaenorhynchus*, a poorly supported clade with 49% bootstrap support in their analysis. Faivovich et al. (2018) discussed the stability problem overlooked by Duellman et al. (2016) in recognizing a subfamily (Scinaxinae) for a poorly supported clade. Faivovich et al. (2018) continued to recognize hyline tribes as done by Faivovich et al. (2005), restricted Scinaxini to *Scinax*, erected the tribe Sphaenorhynchini for *Sphaenorhynchus*, and recognized Dendropsophini for *Dendropsophus* + *Xenohyla*, and Pseudini for *Scarthyla*, *Lysapsus*, and *Pseudis*. More recently, Araujo-Vieira et al. (2020a) erected a new monotypic genus in this tribe, *Gabohyla*, on the basis of the phylogenetic study of Sphaenorhynchini by Araujo-Vieira et al. (2019).

Forty-three species of Scinaxini have been named since the study of Faivovich (2002), representing an increase of roughly 33% in species diversity during the last 20 years (Frost, 2023). The *Scinax catharinae* clade currently includes 52 species, 12 species in the *S. perpusillus* group, and 40 in the *S. catharinae* group. The *S. ruber* clade is the most species-rich, including 77 species, 64 of which are not included in the two monophyletic groups currently recognized: the *S. rostratus* and *S. uruguayus* groups (Faivovich et al., 2005; Baldo et al., 2019). There is evidence suggesting that the species diversity of *Scinax* extends far beyond the known species since there are multiple unidentified specimens in biological collections, and many nominal species are likely composed of multiple species—cryptic or simply unrecognized—awaiting diagnosis (e.g., Fouquet et al., 2007a; Ferrão et al., 2016; Menezes et al., 2016).

In this paper, we perform a total evidence phylogenetic analysis of Scinaxini using molecular and phenotypic data with the goal of testing the monophyly of the genus, its major clades, and the currently recognized species groups. Furthermore, we reevaluate the polarity of the character-states inferred as synapomorphies at different levels by previous studies and propose a new monophyletic taxonomy consistent with the hypothesized relationships, establishing new species groups for several species previously unassigned to groups.

MATERIALS AND METHODS

Taxon sampling

Molecular dataset

We included DNA sequences for 121 of the 129 known species of *Scinax*, 72 from the *S. ruber* clade and 49 from the *S. catharinae* clade. Appendix S1 includes a list of species, voucher collection numbers, localities, and GenBank accession numbers of the sequences included in this study. We studied voucher specimens of all species of Scinaxini included in this study to corroborate species identity. Our efforts to correctly identify these vouchers were assisted by the inclusion of sequences of topotypes from 68 species (36 species from the *S. ruber* clade, and 32 from the *S. catharinae* clade), while for other 10 species we have samples collected less than 20 km away from the type locality (six species from the *S. ruber* clade, and four from the *S. catharinae* clade). For comparative purposes, we also examined the type material of several species of the tribe (see Appendix S2).

The phylogenetic analysis includes 93.8% of the recognized species of the genus. Tissue samples were unavailable for *Scinax baumgardneri*, *S. blairi*, *S. karenanneae*, *S. lindsayi*, and *S. wandae* (*S. ruber* clade), *S. atratus*, *S. jureia*, and *S. skuki* (*S. catharinae* clade). The available information suggests that *S. baumgardneri* has not been collected in the last 25 years (Barrio-Amorós, 1998), and *S. atratus*, *S. jureia*, and *S. lindsayi* are mostly known from their type series and have not been collected recently (Peixoto, 1989; Pombal and Gordo, 1991; Pyburn, 1993).

We complemented our new data with sequences for *Scinax* available on GenBank (Appendix S1) produced by Carnaval (2002), Salducci et al. (2002, 2005), Darst and Cannatella (2004), Faivovich et al. (2005, 2010a), Wiens et al. (2005, 2010), Fouquet et al. (2007a,b), Jansen et al. (2011), Bell et al. (2012), Brusquetti et al. (2014), Guarnizo et al. (2015), Klippel et al. (2015), Ferrão et al. (2016, 2017, 2018a, 2018b, 2022), Nogueira et al. (2016), Vences et al. (2016), Lyra et al. (2017), Lopes et al. (2017), Araujo-Vieira et al. (2020a), and Vacher et al. (2020). The final molecular dataset includes 1,279 terminals of *Scinax*; among which 775 were sequenced for this project and 504 were obtained from GenBank.

The outgroups were selected on the basis of the phylogenetic hypotheses of Faivovich et al. (2005), Wiens et al. (2010), Pyron and Wiens (2011), Pyron (2014), Duellman et al. (2016), and Jetz and Pyron (2018) to represent all major clades of Hylidae, with emphasis on the tribes of Hylinae. We included 56 outgroup taxa (see Appendix S1) and rooted the tree with *Phrynomedusa dryade* (Phyllomedusinae), an exemplar species of the genus that is the sister taxon of all other phyllomedusine genera (Faivovich et al., 2010a).

Phenotypic dataset

We included phenotypic data for 121 of the 129 known species of *Scinax* and 34 candidate species. Of

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these, 68 species plus 21 candidate species are from the *S. ruber* clade, including 3 species of the *S. uruguayus* group, 10 species and 3 candidate species of the *S. rostratus* group, and 57 species plus 17 candidate species unassigned to species groups, with two species represented respectively by two and three terminals because of taxonomic problems. The remaining 49 species belong to the *S. catharinae* clade, 12 species of which are from the *S. perpusillus* group and 35 species plus 13 candidate species are from the *S. catharinae* group (Appendix S2). The phenotypic dataset also included a subset of 33 of the 56 outgroup species included in the molecular dataset, representative of the major hylid clades (Appendix S2).

Molecular character sampling

The mitochondrial DNA sequences used for the phylogenetic analyses include portions of cytochrome *b* (385 bp), cytochrome oxidase c subunit I (COI, 646 bp), a fragment including the ribosomal 12S rRNA, the intervening tRNA^{Val} and the 16S rRNA (12S-tRNA^{Val}-16S; ≈2,450 bp), a fragment including the 3' section of 16S rRNA gene, and the intervening tRNA^{Leu} (16S-tRNA^{Leu}; ≈250 bp), NADH dehydrogenase subunit 1, and tRNA^{Ile} (ND1-tRNA^{Ile}; ≈1000 bp), giving a total of ≈4,731 bp of the mitochondrial genome. The nuclear protein-coding genes sequences include portions of chemokine receptor type 4 (CXCR4, 675 bp), proopiomelanocortin (POMC, 502 bp), seven in absentia homolog 1 (SIAH, 397 bp), recombination activating gene 1 (RAG1, 428 bp), rhodopsin exon 1 (RHOD, 316 bp), and tyrosinase (TYR, 532 bp), comprising 2,850 bp of the nuclear genome.

Laboratory protocols

Whole cellular DNA was extracted from frozen and ethanol-preserved tissues (liver or muscle) using either phenol-chloroform extraction, salt precipitation methods or the Qiagen DNeasy isolation kit. Primers used in PCR amplification and their citations are given in Appendix S3. PCR amplification was carried out in 25 µl reactions using 0.2 µl Taq (Thermo Fisher Scientific Inc.). The PCR protocol consisted of an initial denaturation step of 3 min at 94°C, 35 (for mitochondrial genes) or 45 (for nuclear genes) cycles of 30 s at 94°C, 40 s at 48–62°C, and 30–60 s at 60–72°C, and a final extension step of 10–15 min at 60–72°C. The PCR amplified products were cleaned with 0.5 µL of Exonuclease plus 1 µL of Alkaline Phosphatase per 20 µL of reaction and incubated for 30 min at 37°C. Sequencing was done on an automatic sequencer ABI 3730XL (Applied Biosystems) in both directions to check for potential errors and polymorphisms or by Microgen Sequencing Team (Macrogen Inc., Seoul, Korea). The chromatograms obtained from the automated sequencer were trimmed for quality and the contigs for each gene fragment were assembled using Sequencher v5.3 (Gene Codes Corporation, 2014) or Geneious 10.2.3 (Kearse et al., 2012).

Phenotypic character sampling

The terminology employed follows Duellman (1970a) for adult external morphology, Trueb (1973, 1993) for cranial and postcranial osteology, Fabrezi (1992, 1993) for carpal and tarsal osteology, Trewavas (1933) for laryngeal morphology, Jurgens (1971) for nasal cartilage morphology, Blotto et al. (2020) for hand and foot myology, Tyler (1971), Trewavas (1933), Horton (1982), and Elias-Costa et al. (2021) for submandibular myology, Diogo et al. (2008) for neck and head myology, Engelkes et al. (2021) for shoulder joint myology, Gaupp (1896) and Duellman and Trueb (1986) for abdominal myology, Luna et al. (2018) for nuptial pad morphology, Altig and McDiarmid (1999) for larval external morphology, and Wassersug (1976) for larval internal oral morphology. Throughout the text, hand digits were numbered II–V following Fabrezi and Alberch (1996); following Altig and McDiarmid (1999) the labial tooth rows are considered A (anterior) and P (posterior). For vocalizations, we employed the terminology of Köhler et al. (2017).

Osteological characters were mostly coded from cleared and double-stained specimens using alcian blue and alizarin red (Taylor and Van Dyke, 1985). Furthermore, for some species, osteological data were coded from µCT images of specimens available in MorphoSource (2023; see Appendix S2 for a list). Muscles were studied with the help of Lugol solution (Bock and Shear, 1972). The observations of pale nuptial pads, larval oral disc, and internal oral surfaces were facilitated with the topical application of methylene blue. Only males were examined to code characters of laryngeal morphology because females were unavailable for most species. The final phenotypic dataset included 159 characters, including 39 multistate characters, of which 27 were considered additive, following the generality criterion of Lipscomb (1992). These were coded according to Hawkins et al. (1997) and Strong and Lipscomb (1999). Species-level phenotypic polymorphisms were coded as ambiguities. See Appendix S4 for the sources of character-states that were scored based on information from the literature. Matrix edition was done with Mesquite v3.70 (Maddison and Maddison, 2021).

Phylogenetic analyses

We performed multiple alignments for each DNA fragment employing MAFFT version 7 (Katoh and Standley, 2013) using G-INS-i (global homology considered), with default parameters for gap opening and extension. The alignments were visualized in BioEdit (Hall, 1999) and concatenated using SequenceMatrix (Vaidya et al., 2011).

Numerous authors have discussed the rationale for using the parsimony optimality criterion for inferring phylogenetic hypothesis (Farris, 1983; Goloboff, 2003; Goloboff and Pol, 2005; Kluge and Grant, 2006; Grant and Kluge, 2009), and we favored it because the cladogram that minimizes transformations to explain the observed variation is the simplest one, maximizes evidential con-

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gruence, and has the greatest explanatory power. The preferred relation used to treat indels (insertions and deletions) and all substitutions was 1:1:1 (transition: transversion: unit indels), and the molecular and phenotypic characters were treated under equal weights.

For the total evidence analysis, we treated every specimen sequenced as a separate terminal for each ingroup species. Once the species limits were established based on molecular data, we duplicated the morphological entries for the species for each of its molecular terminals; that is, each conspecific terminal was given identical entries in the phenotypic matrix, following Grant et al.'s (2006) arguments. This procedure was not necessary for outgroups, as these included only one terminal per species.

We considered the results of the total evidence analysis to be the phylogenetic hypothesis that best explains the evidence because the analysis of all available evidence maximizes explanatory power (Kluge, 1989; Nixon and Carpenter, 1996; Grant and Kluge, 2003). The molecular dataset included DNA sequences for 1,335 terminals (56 outgroup and 1,279 ingroup terminals; Appendix S1). The phenotypic dataset included 191 terminals (158 Scinaxini, including several undescribed species, and 33 outgroup species; see Appendix S2). The total evidence analysis included 1,336 terminals, including all terminals from the molecular dataset combined with phenotypic data as described above.

For the maximum parsimony phylogenetic analyses, we employed TNT v1.5 and a Beta version of v1.6 (Goloboff et al., 2008; Goloboff and Catalano, 2016; Goloboff and Morales, 2023). Searches used the command "New Technology Search" under search level 50, which combines Ratchet, Tree Drifting, Sectorial Searches, and Tree Fusing (Goloboff, 1999; Nixon, 1999). For this driven search, we used the default options for these algorithms, hitting the most parsimonious length 500 times. The resulting trees were submitted to a round of TBR branch swapping. Searches employed the collapsing option "minimum length," which collapses every node whose minimum length is 0. Parsimony jackknife absolute frequencies (Farris et al., 1996) were calculated in TNT v1.5 using new technology requesting 10 hits with driven searches under search level 15, for a total of 1,000 replicates. Gaps were treated as fifth state, but to compare with the maximum likelihood analysis (see below), we also performed analyses with gaps treated as missing data.

Character-state transformations were considered synapomorphies if they were (i) unambiguous (without arbitrary selection of accelerated, ACCTRAN, or delayed optimization, DELTRAN) and (ii) shared by all dichotomized most parsimonious trees. For the graphic tree edition we used the TNT script forfai.run written by Pablo A. Goloboff (available at https://www.lillo.org.ar/phylogeny/tnt/scripts/forfai.run), which takes as input the most parsimonious trees and the trees resulting from the resample pseudoreplicates, and outputs a strict consensus with branch lengths and support values in Newick format. This file was read with FigTree v1.4.3 (Rambaut, 2014) for visualization and edition.

We performed a Maximum likelihood analysis with IQ-TREE v1.6.12 (Nguyen et al., 2015) using the same dataset (DNA sequences + phenotypic characters) as the total evidence analysis under parsimony. Models for each molecular partition were selected using ModelFinder (Kalyaanamoorthy et al., 2017). For morphological data, we used the two morphological ML models (Lewis, 2001) implemented in IQ-TREE (i.e., MK and ORDERED, for unordered and ordered characters, respectively) considering the ascertainment bias correction (ASC) method. We performed seven independent runs with different levels of perturbation strength (-pers 0.1–0.4) and setting the number of unsuccessful iterations to stop at 500 (-nstop 500). We employed the edge-linked-proportional partition model but separate substitution models and rate evolution between partitions (-spp option). The maximum likelihood analysis was conducted with 1,000 ultrafast bootstrap replicates (Minh et al., 2013; Hoang et al., 2018) using the option -bnni, which reduces the risk of overestimating branch supports caused by severe model violations. The resulting tree (from the best scoring run with the highest log-likelihood value) was visualized and edited in FigTree 1.4.3 (Rambaut, 2014). Partitions and models selected are detailed in Appendix S5.

Species identification, taxonomic evaluation, diagnoses, and definitions

Our dataset included terminals representing 121 recognized species of Scinaxini. While gathering tissues and producing sequences, we studied several voucher specimens. In many cases, our evaluation corroborated the original determinations; in others, they were corrected, and in several cases we concluded that the voucher specimen was an undescribed species. Further, for some species, some specimens were recovered as distantly related to the lineage that includes topotypic specimens or vouchers collected reasonably close to the type locality. For others, even when the monophyly of the species was corroborated, some internal clades showed unusually large sequence divergence. In most cases where we had these results, we did our best to re-study the vouchers to confirm or refute our initial taxonomic assessments.

To address the taxonomic status of each lineage, we considered (i) topological relationships (e.g., monophyly), (ii) uncorrected pairwise distances (UPDs) of a fragment of the 16S rRNA gene (≈570 bp; delimited by the primers AR and BR; see Vences et al., 2005a,b; Fouquet et al., 2007b; Appendix S3), and (iii) phenotypic characters (e.g., mostly external morphology of adults and larvae and vocalizations). Datasets containing exclusively sequences of the 16S rRNA gene fragment for each species group (as redefined in the Discussion section) were aligned in MAFFT under the strategy Q-INS-i, and UPDs were calculated in PAUP* (Swofford, 2002). In order to minimize missing data for the calculations of UPDs we excluded terminals lacking more than 50 bases in the extremes, unless they were the only sequence of a given species. In these cases, we per-

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formed different tests including and excluding terminals and/or trimming sequences to ensure that UPDs that were critical for our inferences were not artifacts of missing data.

We employed the concepts of Confirmed Candidate Species (CCS), Unconfirmed Candidate Species (UCS), and Deep Conspecific Lineages (DCL) as defined by Vieites et al. (2009) and Padial et al. (2010), but we added a phylogenetic component. CCS corresponds to lineages (individuals or groups of individuals) that differ genetically, not necessarily above a threshold value, and can either be differentiated by phenotypic characters (e.g., morphology, bioacoustics) from their closest relatives but are not formally recognized as a nominal species or are not the sister of the nominal species. UCS corresponds to lineages (individuals or groups of individuals) whose genetic distance from the sister species is above a threshold value, lack known phenotypic differences to diagnose them from their sister species, and have not been subjected to detailed studies of their phenotypic variation. Finally, DCLs are the sisters of nominal species that differ in genetic distances above threshold values, lack known phenotypic differences to diagnose them from their sister species, but have been subjected to detailed study of their phenotypic variation. That is, the difference between UCS and DCL is the amount of evidence that has been analyzed; for the former, the lack of diagnostic phenotypic characters is likely due to a lack of study, whereas in the latter, the lineages lack diagnostic phenotypic characters despite extensive study. Accordingly, DCL is only applicable when multiple sources of evidence have been studied in detail, and for this reason we only apply it in a single case. We employed as a heuristic tool the threshold value for interspecific UPDs of 3.0% for the 16S rRNA gene as suggested by Fouquet et al. (2007a) for identifying candidate species. We stress the heuristic nature of this tool and that each case is unique and amenable to be considered from different perspectives, with the assumption that further studies will test the status of all candidate species (see also Grant et al., 2006:60–62).

Our results showed that some recognized species include lineages that were not closely related. In these cases, we associated the name with the lineage including topotypes or specimens collected near the type locality and consider the other lineage(s) to be CCS. In similar topological situations, but when topotypes were not available, or when there is more than one lineage close to the type locality, the different lineages were labeled as species A, species B, etc. Each and every case was discussed individually.

Above species, the value of diagnoses that are not based on synapomorphies is limited. They are useful only to characterize species already inferred to be included in the diagnosed clades on the basis of molecular evidence, but have no predictive value for the inclusion of new species. As such, a species that has not been associated based on molecular data with a clade whose phenotypic diagnosis is simply a combination of characters cannot be assigned with confidence and remains dependent on a phylogenetic analysis testing the assignment.

For the accounts of the different clades that are recognized as a result of the phylogenetic analyses, we provide a diagnosis and a definition. The diagnoses refer to the nature of the evidence supporting the monophyly of each clade and include phenotypic synapomorphies, if any, followed by character combinations that allow the taxonomic differentiation of its species from those of other clades. Finally, the definition includes the characters associated with each clade, differentiating those that were included in the phylogenetic analyses as Ch. X.Y (character number.state number) from those that were not included. Within Scinaxini, all definitions employ the same numbering. Those for the tribe itself are not numbered, as they are mainly intended to characterize it in the context of Hylinae, and so are not comparable to those employed within the tribe.

List and description of characters

We understand characters as independent, self-sustained, proposals of transformation series between homologous character-states (Grant and Kluge, 2004). Characters modified from previous phylogenetic studies are indicated with an asterisk (*). Abbreviations in uppercase (Ch.) refer to characters employed in this study; those in lowercase (ch.) refer to characters from previous studies. The symbols (+) and (-) refer to multistate characters considered additive (ordered) or nonadditive (unordered), respectively. The phenotypic data matrix is in Appendix S6.

Adult osteology

0. Nasals, relation to sphenethmoid. (0) Nasals and sphenethmoid separated, (1) medial margins of nasals overlapping sphenethmoid.

Previous usage in phylogenetic studies: Liem (1970: ch. 20*); Cocroft (1994: ch. 4*); Faivovich (2002: ch. 0); Scott (2005: ch. 62*); Grant et al. (2006: ch. 135*); Araujo-Vieira et al. (2019: ch. 3); Orrico et al. (2021: ch. 3).

1. Nasals, relationship between medial margins (+). (0) Nasals widely separated medially, (1) nasals slightly separated medially, (2) nasals almost in medial contact. In state 1, the medial margins are at the level of the longitudinal axes that extend through the superior prenasal cartilages. In state 2, the medial margins juxtapose, but do not contact the septum nasi.

Previous usage in phylogenetic studies: Liem (1970: ch. 20*); Clarke (1981: ch. 1*); Silva (1998: ch. 3*); Mendelson et al. (2000: ch. 32*); Barg (2003: ch. 2*); Pugener et al. (2003: ch. 16* [adult morphological characters]); Nuin and do Val (2005: ch. 42*); Scott (2005: ch. 63*); Wiens et al. (2005: ch. 6*); Fabrezi (2006: ch. 1*); Pramuk (2006: ch. 3*); Araujo-Vieira et al. (2019: ch. 0).

2. Frontoparietal fontanelle, exposure (+). (0) Fontanelle almost completely exposed (Faivovich, 2002: fig. 4A), (1) fontanelle partially exposed longitudinally (Faivovich,

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2002: fig. 4B), (2) fontanelle partially exposed through a keyhole-shaped fenestra, (3) fontanelle partially occluded due to the medial proximity of the adjacent frontoparietals (Faivovich, 2002: fig. 4C), (4) fontanelle occluded due to the medial juxtaposition of the frontoparietals (Trueb, 1970: pl. 2). In most taxa that show state 0 (the exception being *Smilisca baudinii*), the frontoparietals at the level of the fontanelle are slender strips of bone that are variably divergent laterally. This determines that the posterior dorsolateral margins of the sphenethmoid are partially exposed. In state 2, the frontoparietals have a roughly uniform width, leaving a rectangular (*Scinax oreites* and *S. granulatus*) or subtly triangular (*S. trapicheiroi*) fenestra whose main width equals ⅓ of the interorbital width. Their inner margins may show various levels of irregular indentation.

We followed Faivovich (2002) in defining the degree of exposure of the fontanelle based on the morphology of the frontoparietal anterior to the tectum synoticum. The character-state "occluded frontoparietal fontanelle due to medial fusion of the frontoparietals" (ch. 2.4) was added to the original transformation series of Faivovich (2002: ch. 3). *Gabohyla pauloalvini* and *Sphaenorhynchus carneus* have the inner margins of the frontoparietals fused in a few points; however, as the fontanelle is partially occluded, we considered that these species share the partially exposed fontanelle due to the sagittal proximity of the adjacent frontoparietals (Ch. 2.3), as in *Nyctimantis siemersi*, *Itapotihyla langsdorffii*, *Scarthyla goinorum*, *Pseudis minuta*, *Xenohyla truncata*, some *Dendropsophus* (*D. minutus* and *D. sanborni*), *Sp. caramaschii*, and several species of Scinaxini (e.g., *Scinax agilis*, *S. garbei*, and *S. nasicus*).

Previous usage in phylogenetic studies: Duellman (1970a: ch. DD*); Heyer (1975: ch. 24*); Heyer and Liem (1976: ch. 4*); Lobo (1995: ch. 7*); Silva (1998: ch. 8*); Duellman (2001: ch. DD*); Faivovich (2002: ch. 3*, fig. 4); Mendelson et al. (2000: ch. 35*); Barg (2003: ch. 3*); Pugener et al. (2003: ch. 11* [adult morphological characters]); Nuin and do Val (2005: ch. 23*); Scott (2005: ch. 69*); Wiens et al. (2005: ch. 14*); Fabrezi (2006: ch. 5*); Grant et al. (2006: ch. 136*); Pramuk (2006: ch. 11*); Araujo-Vieira et al. (2019: ch. 4*); Orrico et al. (2021: ch. 4*).

3. Frontoparietals, medial margins of posterior portion (+). (0) Widely separated at the level of the tectum synoticum, with approximately regular margins (Faivovich, 2002: fig. 4B), (1) widely separated at the level of the tectum synoticum, with margins irregularly indented (Araujo-Vieira et al., 2019: fig. S3C), (2) medial margins excavated forming a small keyhole-like posteromedial fenestra (Faivovich, 2002: fig. 4D), (3) juxtaposed at the level of the tectum synoticum, leaving a narrow space between them (Araujo-Vieira et al., 2019: fig. S3D), (4) medially fused (Araujo-Vieira et al., 2019: fig. S3F). The morphology of the frontoparietals at the level of the tectum synoticum (approximately in the posterior third of the frontoparietals) is variable and independent of the morphology of

the frontoparietals anterior to the tectum synoticum (our Ch. 2). An example of this is that the frontoparietals are separated anteriorly and juxtaposed at the level of the tectum synoticum in *Scinax fuscovarius*, whereas they are juxtaposed anteriorly and separated posteriorly in *S. cuspidatus*.

Previous usage in phylogenetic studies: Silva (1998: ch. 10*); Grant et al. (2006: ch. 136*); Faivovich (2002: ch. 3*); Araujo-Vieira et al. (2019: ch. 5); Orrico et al. (2021: ch. 5*); Araujo-Vieira et al. (2019: ch. 5).

4. Exoccipitals, dorsal contact. (0) Fused, (1) dorsally separated by cartilaginous strip.

5. Squamosal, relation between otic ramus and ossified portion of crista parotica (-; Fig. 1A–F). (0) Slight or no overlap between otic plate and ossified portion of crista parotica, (1) broad overlap between otic plate and ossified portion of crista parotica, due mainly to greatly ossified crista parotica, (2) broad overlap between otic plate and ossified portion of crista parotica mainly due to an expanded otic plate and poorly ossified crista parotica, (3) broad separation between otic plate and ossified portion of crista parotica due to both small otic plate and poorly ossified portion of crista parotica, (4) broad separation between otic plate and ossified portion of crista parotica due to a small otic plate. We considered the separation due to a narrow gap and the slight overlap between otic plate and ossified portion of crista parotica as a single character-state (Fig. 1A–B), because this is interpreted as a minor difference in the extent of the dermal ossification of the otic plate. Further, a gap between the otic plate and the ossified portion of crista parotica can result from a large otic plate and/or the degree of ossification of the crista parotica. Therefore, we separated it into two discrete states: a broad gap between otic plate and crista parotica due to a small optic plate, in combination with a poorly ossified crista parotica (Ch. 5.3; Fig. 1E), and a broad gap between otic plate and crista parotica due mainly to a small otic plate (Ch. 5.4; Fig. 1F). In the latter state, the degree of ossification of the crista parotica is like that of the species that present a slight or no overlap between otic plate and ossified portion of crista parotica.

Previous usage in phylogenetic studies: Duellman (1970a: ch. EE*); Clarke (1981: ch. 5*); Duellman (2001: ch. EE*); Faivovich (2002: ch. 4*); Pugener et al. (2003: ch. 46* [adult morphological characters]); Wiens et al. (2005: ch. 23*); Scott (2005: ch. 65*); Fabrezi (2006: ch. 10*); Pramuk (2006: ch. 15*); Araujo-Vieira et al. (2019: ch. 28*); Orrico et al. (2021: chs. 10*, 11*).

6. Maxilla, posterior extension (+). (0) Posterior extreme of maxilla reaching approximately ½ of the X-Distance (see definition below), up to the middle of orbit, (1) posterior extreme of maxilla reaching approximately ⅔ of the X-Distance, surpassing the middle of orbit, (2) posterior extreme of maxilla reaching at least ≈⅚ of the X-Distance. The transformation series is defined with respect to (1) the total length of maxilla, and (2) the distance from

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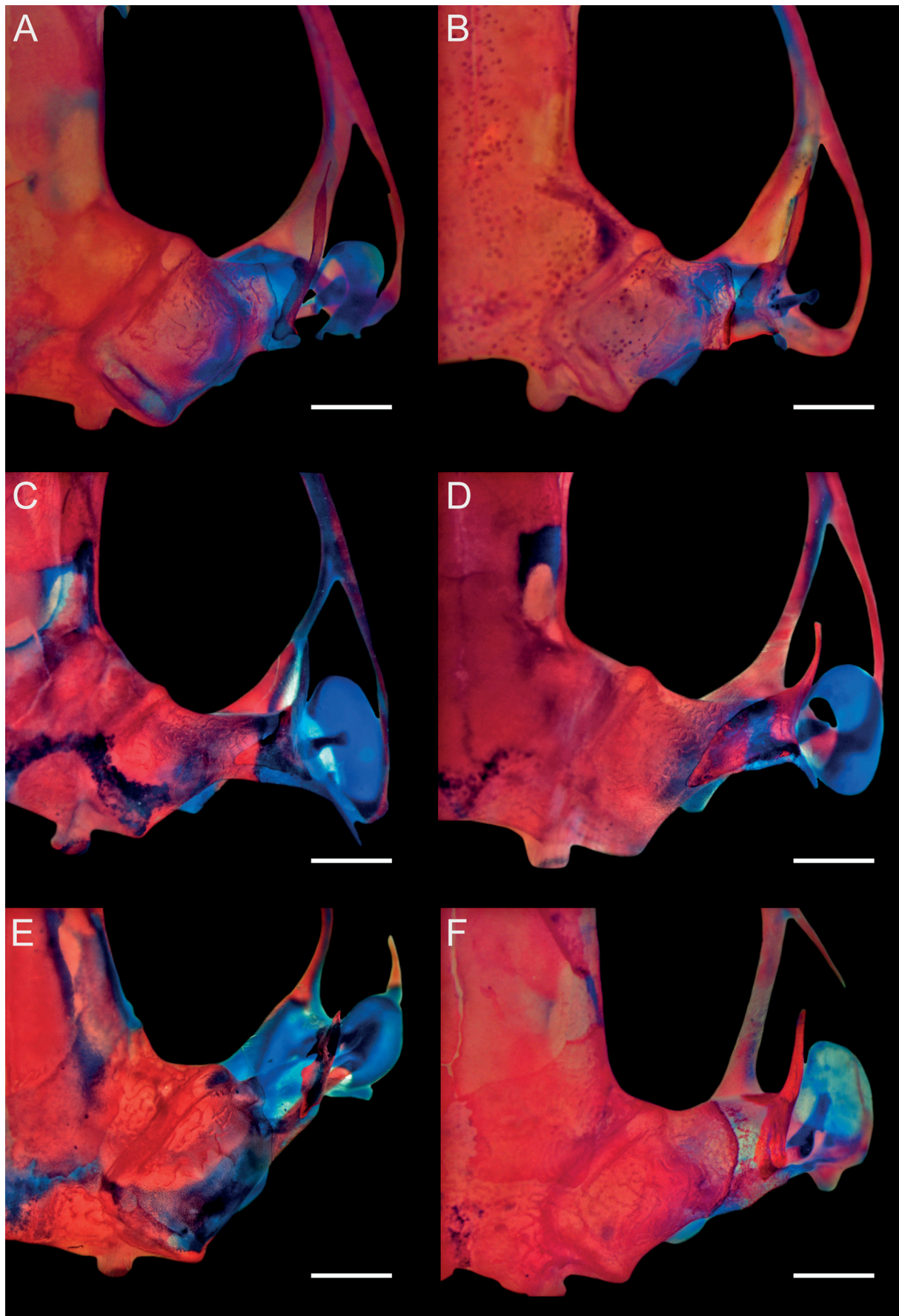
Figure 1. Dorsal view of the skull showing the relationship between the otic ramus of the squamosal and the ossified portion of crista parotica (Ch. 5). **(A)** *Scinax duartei* (CFBH 140, Ch. 5.0). **(B)** *S. tymbamirim* (CFBH 38953, Ch. 5.0). **(C)** *Boana albopunctata* (MACN 37015, Ch. 5.1). **(D)** *Scinax garbei* (CFBH 34283, Ch. 5.2). **(E)** *Sphaenorhynchus prasinus* (EI59, Ch. 5.3, same state that occurs in *S. caramaschii*, *S. carneus*, and *Gabohyla pauloalvini*). **(F)** *Xenohyla truncata* (MNRJ 333276, Ch. 5.4). Scale bars = 1.5 mm.

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the anterior extreme of the maxilla to the articulation between the ventral ramus of squamosal and quadratojugal, which we call X-Distance. We use the edges of the tympanum only to assist in the definition of the character-states.

Previous usage in phylogenetic studies: Duellman and Wiens (1992: ch. 7*); Pugener et al. (2003: ch. 26* [adult morphological characters]); Araujo-Vieira et al. (2019: ch. 13*).

7. Maxilla, toothed portion of the par dentalis (+). (0) Edentulous portion of pars dentalis 10–15% of the maxilla length, (1) edentulous portion of pars dentalis 35–40% of the maxilla length, (3) edentulous portion of pars dentalis 55–80% of the maxilla length. This character is inapplicable for *Sphaenorhynchus carneus* because maxillary teeth are absent.

Previous usage in phylogenetic studies: Silva (1998: ch. 23*); Barg (2003: ch. 9*); Araujo-Vieira et al. (2019: ch. 16*); Orrico et al. (2021: ch. 28*).

8. Palatoquadrate, tip of the basal process (Fig. 2A–D). (0) Simple, rounded, (1) bicapitate.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 5).

9. Exoccipitals, ventral contact. (0) Fused, (1) separated by a strip of cartilage.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 1); Grant et al. (2006: ch. 138); Orrico et al. (2021: ch. 50*).

10. Pterygoid, medial ramus, extension (+; Fig. 2A–D). (0) Short, medial ramus extending at most ⅓ distance between its origin and the basal process, (1) intermediate, medial ramus extending ½ distance between its origin and the basal process, (2) moderate, medial ramus covering basal process but not contacting prootic, (3) long, the medial ramus contacting prootic.

Previous usage in phylogenetic studies: Duellman (1970a: ch. GG*); Mendelson et al. (2000: ch. 8*); Duellman (2001: ch. GG*); Barg (2003: ch. 12*); Pugener et al. (2003: ch. 43* [adult morphological characters]); Pramuk (2006: ch. 12*).

11. Vomer, dentigerous process. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Duellman (1970a: ch. LL*); Barg (2003: ch. 13*); Pugener et al. (2003: ch. 35* [adult morphological characters]); Araujo-Vieira et al. (2019: ch. 31).

12. Vomer, relationship between medial margins of contralateral elements. (0) Slightly convex posteriorly and widely divergent anteriorly, (1) parallel, sometimes juxtaposed posteriorly; divergent anteriorly. The degree of anterior divergence is somewhat variable among species with state 0; the medial margins are laterally divergent from the septum nasi from ≈20° (directed to premaxilla; e.g., *Scinax auratus* and *S. fuscomarginatus*) to 45° (direct-

ed to articulation between premaxilla and maxilla; e.g., *Scinax berthae* and *Sphaenorhynchus caramaschii*). In species with state 1, the medial margins diverge laterally from the septum nasi ≈20° (directed to premaxilla). *Scinax constrictus* and *S. garbei* are polymorphic for this character.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 2).

13. Vomer, relationship between dentigerous process and main body (+). (0) Dentigerous process separated from the main body of the vomer, (1) dentigerous process connected to the main body by a constricted medial portion, (2) dentigerous process is continuous with main body of vomer.

Previous usage in phylogenetic studies: Scott (2005: ch. 43*); Araujo-Vieira et al. (2019: ch. 34, fig. S7); Orrico et al. (2021: ch. 27*).

14. Palatine, relative size (+). (0) Thin sliver, (1) ¾ of *planum antorbitale*, (2) palatine covering orbital margin of the *planum antorbitale*, (3) palatine medially reaching the lateral portion of sphenethmoid at the level of the orbitonasal foramen, (4) palatine medially reaching the neurocranial portion of sphenethmoid.

Previous usage in phylogenetic studies: Duellman (1970a: ch. Y*); Laurent (1973: ch. 9*); Duellman and Wiens (1992: ch. 8*); Lobo (1995: ch. 5*); Silva (1998: ch. 36*); Mendelson et al. (2000: ch. 9*); Duellman (2001: ch. Y*); Barg (2003: ch. 16*); Araujo-Vieira et al. (2019: ch. 40); Orrico et al. (2021: ch. 32*).

15. Oblique cartilage, fenestration of the cartilaginous plate. (0) Absent, (1) present. We observed a small piercing in a more posterior position, about ⅓ the size of the fenestra, generally in only one of the cartilaginous plates, in four species of Scinaxini (*Scinax canastrensis*, *S. constrictus*, *S. flavoguttatus*, and *S. longilineus*) that lack fenestration. We did not consider this piercing to be an instance of state 1.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 6).

16. Septum nasi, prenasal medial process. (0) Absent, (1) present. See characters 17 and 18 below.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 7); Orrico et al. (2021: ch. 54).

17. Septum nasi, prenasal medial process, shape (-). (0) Elongated, (1) slightly truncated or rounded, (2) triangular. In some species, the prenasal medial process is elongated anteroventrally, forming a cylindrical-shaped process (Ch. 17.0). In others, the base of the median prenasal process is wider, with a slightly truncated or rounded anterior margin in dorsal view (sometimes with a slight medial concavity); both shapes occur intraspecifically in Scinaxini (e.g., *Scinax berthae*). The triangular prenasal medial process has a wide base, narrowing approximately from the half of its length; the tip is pointed or slightly rounded (Ch. 17.2).

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18. Septum nasi, prenasal medial process, relative length. (0) Reaching the level of the alary process of the premaxilla, (1) surpassing the alary process of the premaxilla.

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 61).

19. Pars externa plectri, shape (+). (0) Distally expanded, (1) mediodistally expanded, (2) completely expanded.

Previous usage in phylogenetic studies: Duellman and Wiens (1992: ch. 10*); Silva (1998: ch. 54*); Barg
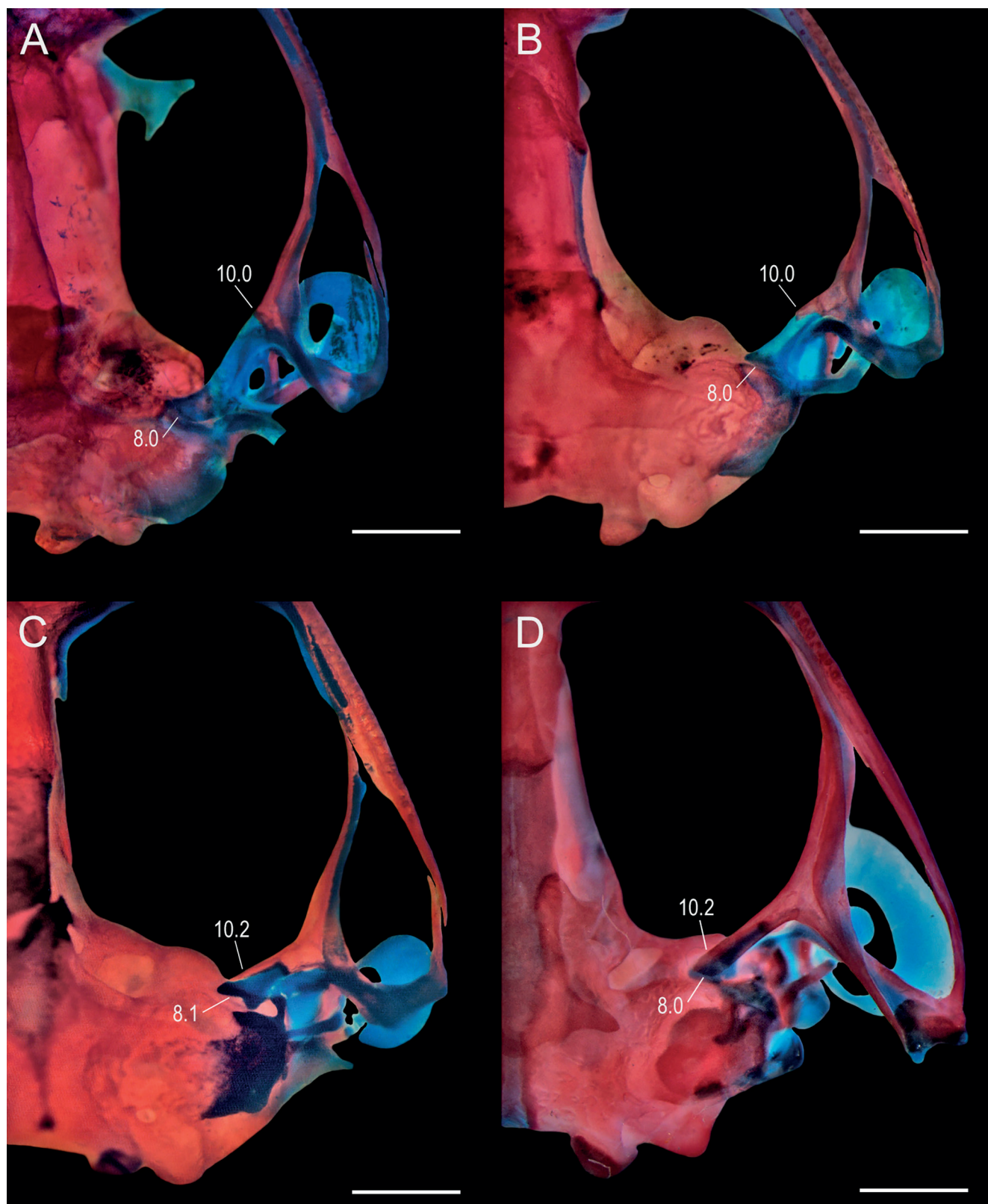
Figure 2. Ventral view of the skull showing the shape of the tip of the basal process of the palatoquadrate (Ch. 8) and the development of the medial ramus of the pterygoid (Ch. 10). **(A)** *Scinax camposseabrai* (UFMG 4673, Chs. 8.0 and 10.0). **(B)** *S. fontanarrosai* (LGE 2040, Chs. 8.0 and 10.0). **(C)** *S. berthae* (MACN 36986, Chs. 8.1 and 10.2). **(D)** *Pseudis minuta* (JF 1179, Chs. 8.0 and 10.2). Scale bars = 2 mm.

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(2003: ch. 34*); Scott (2005: ch. 77*); Araujo-Vieira et al. (2019: ch. 61*).

20. Suprascapula, anterior process. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Tyson (1987); Silva (1998: ch. 75); Faivovich, (2002: ch. 20, fig. 9); Barg (2003: ch. 53); Araujo-Vieira et al. (2019: ch. 85); Orrico et al. (2021: ch. 88).

21. Coracoid ridge. (0) Absent, (1) present.

This character was discussed by Chantell (1968) in some species of *Pseudacris* (Hylini).

Previous usage in phylogenetic studies: Silva (1998: ch. 79); Faivovich (2002: ch. 19, fig. 8); Barg (2003: ch. 56); Orrico et al. (2021: ch. 87).

22. Sacral diapophyses, shape (Fig. 3A–D). (0) Expanded diapophyses (index maximum/minimum length diapophysis > 4.5), (1) unexpanded diapophyses (index maximum/minimum length of diapophysis < 3.5). We coded the expansion of the sacral diapophyses according to Faivovich (2002) and Grant et al.'s (2006) definitions. They coded the expansion of the sacral diapophyses as the ratio of the width of the tip of the diapophyses, which is the width of associated cartilage, to the width of the base of the diapophyses. The irregular fringes of cartilage at the tip of the diapophyses are not included in the measurements.

All species of Scinaxini with unexpanded diapophyses have a ratio of maximum/minimum length of 2.1–3.1 as previously reported by Faivovich (2002); the ratio for expanded diapophysis is 4.5–8.0, with *Dendropsophus minutus* and *Boana albopunctata* exemplifying the extremes.

Previous usage in phylogenetic studies: Heyer (1975: ch. 34*); Heyer and Liem (1976: ch. 12*); Duellman and Wiens (1992: ch. 1*, fig. 5); Cocroft (1994: ch. 8*); Baez and Basso (1996: ch. 36*); Faivovich (2002: ch. 21, fig. 8); Barg (2003: ch. 67*); Pugener et al. (2003: ch. 57* [adult morphological characters]); Nuin and do Val (2005: ch. 33*); Scott (2005: ch. 14*); Fabrezi (2006: ch. 42*); Grant et al. (2006: ch. 143*); Pramuk (2006: ch. 51*); Araujo-Vieira et al. (2019: ch. 95*); Orrico et al. (2021: ch. 93*); Pereyra et al. (2021: ch. 29*).

23. Sacral diapophyses, lateral extension (Fig. 3A–D). (0) Short, (1) elongated. In *Scinax camposseabrai* and the *S. uruguayus* group the sacral diapophyses articulate with the anterior portion of the ilia through the medially expanded sesamoids (Chs. 24.2 and 24.3) instead of articulating directly with the ilia as observed in other species of *Scinax* that have rounded or trapezoidal sesamoids (Ch. 24.1). However, in *S. camposseabrai*, unlike the *S. uruguayus* group, the sacral diapophyses are extremely short (Fig. 3C); this shortening might be compensated by a medial expansion of the sesamoids. We recognize that these characters are part of a complex morphofunctional system, and a more thorough survey of morphology and ontogeny is necessary to determine the

degree of correlation between the lateral extension of the sacral diapophyses and sesamoids. We are probably underestimating the diversity of this complex system; however, as the degree of dependence between these characters is unclear, we coded both as independent characters in this analysis.

24. Medial sesamoid of the ilio-sacral articulation, shape (+; Fig. 3A–D). (0) Anteroposteriorly elongated, length at least twice width, (1) rounded or trapezoid, (2) slightly expanded medially, length half-width, (3) medially elongated, width at least three times length.

Previous usage in phylogenetic studies: Soliz and Ponssa (2016: ch. 63*, fig. 14).

25. Sesamoids of the ilio-sacral articulation, number (Fig. 3A–D). (0) One, medial, (1) two, one medial and one lateral. Two bilateral sesamoids are present in the ilio-sacral region in many species of Scinaxini; the medial is larger, rounded or trapezoidal, cartilaginous, and sometimes mineralized; the lateral is smaller, rounded and mineralized (Fig. 3B, D).

Previous usage in phylogenetic studies: Soliz and Ponssa (2016: ch. 53).

26. Intercalary elements between ultimate and penultimate phalanges, mineralization (+). (0) Not mineralized, (1) partially mineralized, (2) completely mineralized.

Previous usage in phylogenetic studies: Drewes (1984: ch. 24*); Silva (1998: ch. 73*); Faivovich (2002: ch. 22); Barg (2003: ch. 50*); Araujo-Vieira et al. (2019: ch. 101); Orrico et al. (2021: ch. 90).

27. Tip of the distal phalanx, shape. (0) Rounded, (1) expanded.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 23*, fig. 10).

28. Metacarpal IV, preaxial process. (0) Absent, (1) present. This process corresponds to the point of insertion of the slip to digit IV of the m. extensor digitorum.

The occurrence and taxonomic distribution of this character was discussed by Tyler and Davies (1978).

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 102).

29. Hyale, point of attachment in the skull (+). (0) Hyale attached to basal process, (1) hyale attached to limit between basal process and otic capsule, (2) hyale attached to otic capsule.

Previous usage in phylogenetic studies: Silva (1998: ch. 67*); Araujo-Vieira et al. (2019: ch. 71); Orrico et al. (2021: ch. 73*).

30. Hyale, anterior process. (0) Absent, (1) present.
Previous usage in phylogenetic studies: Liem (1970: ch. 13); Heyer (1975: ch. 30*); Heyer and Liem (1976: ch. 19); Drewes (1984: ch. 11*); Duellman and Wiens (1992: ch. 16, fig. 4); Silva (1998: ch. 60); Faivovich (2002:

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ch. 8); Barg (2003: ch. 38*); Nuin and do Val (2005: ch. 29); Scott (2005: ch. 83*); Wiens et al. (2005: ch. 42); Grant et al. (2006: ch. 117); Araujo-Vieira et al. (2019: ch. 64); Orrico et al. (2021: ch. 60).

31. Hyoid plate, contact with the posteromedial processes. (0) Posteromedial processes abut directly on hyoid plate, (1) posteromedial processes borne on short cartilaginous stalks.

Previous usage in phylogenetic studies: Liem (1970: ch. 10*); Drewes (1984: ch. 10); Faivovich (2002: ch. 9, fig. 5); Scott (2005: ch. 92*); Fabrezi (2006: ch. 29*).

32. Larynx, orientation relative to the posteromedial processes. (0) Slightly ventral, (1) strongly ventral.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 10).

33. Cricoid, esophageal process in males. (0) Absent, (1) present. The definition of the esophageal process is that of Faivovich (2002), who considered the esophageal process to be any projection oriented cardiacally that originates in the posterior part of the cricoid ring, at the point in which both sides of the cricoid ring meet or fuse.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 11, fig. 6); Scott (2005: ch. 99); Araujo-Vieira et al. (2019: ch. 72); Orrico et al. (2021: ch. 83).

34. Cricoid, cardiac process. (0) Adjacent to the anterior margin of the arytenoids, (1) curved ventrally.
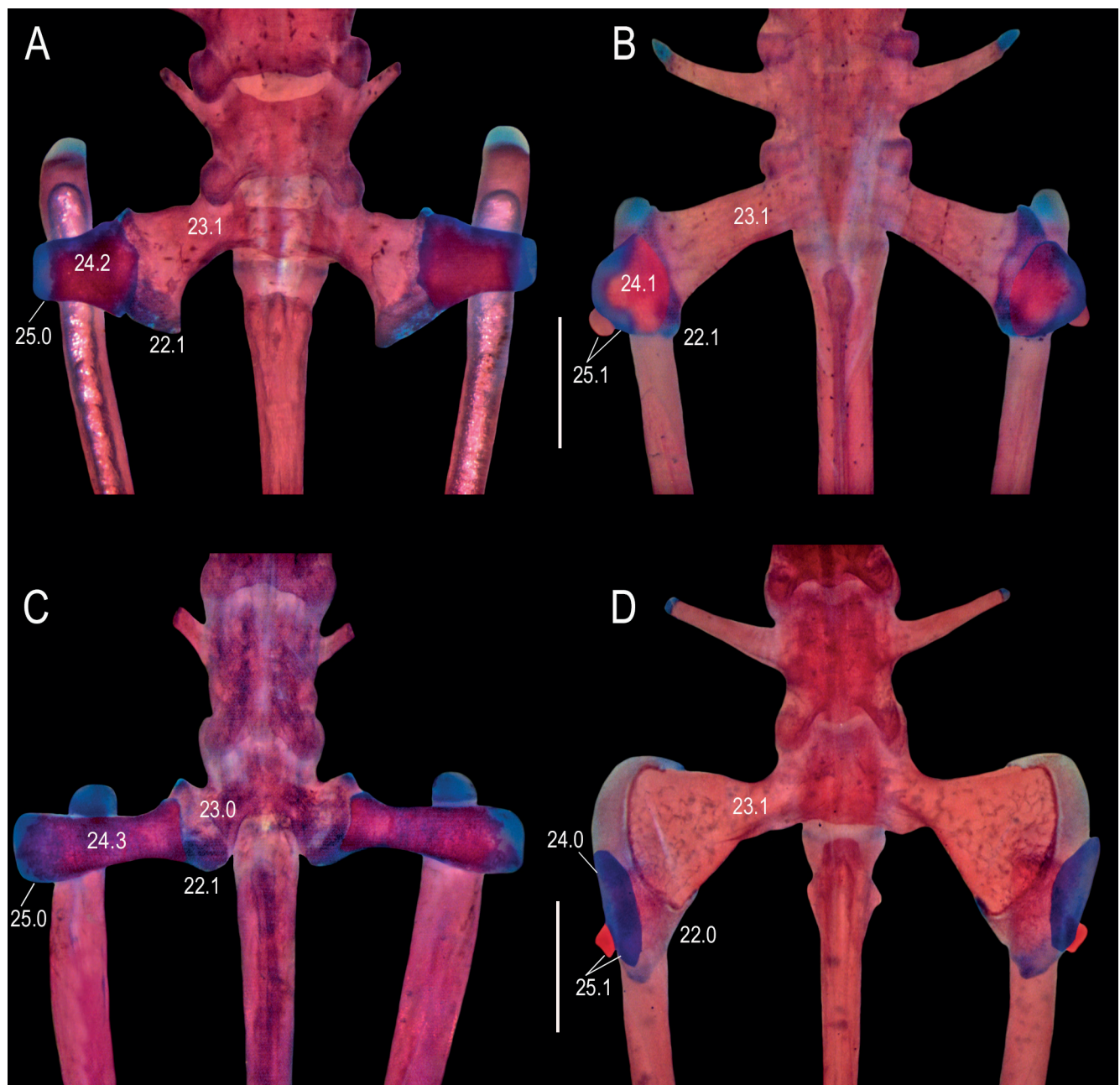
Figure 3. Dorsal view of sacral diapophyses showing states of Chs. 22–25. **(A)** *Scinax fontanarrosai* (LGE 2040, Chs. 22.1, 23.1, 24.2, and 25.0). **(B)** *S. crospedospilus* (CFBH 7224, Chs. 22.1, 23.1, 24.1, and 25.1). **(C)** *S. camposseabrai* (UFMG 4673, Chs. 22.1, 23.0, 24.3, and 25.0). **(D)** *Xenohyla truncata* (MNRJ 33276, Chs. 22.0, 23.1, 24.0, and 25.1). Scale bars = 2 mm.

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Previous usage in phylogenetic studies: Faivovich (2002: ch. 12).

35. Cricoid, cardiac process, shape (-; Fig. 4A–G). (0) Laminar, U-shaped, (1) laminar, W-shaped, (2) laminar, wider than adjacent parts of the ring, (3) subcylindrical, width similar to or slightly thinner than adjacent parts of the ring, (4) subcylindrical, slightly wider than adjacent parts of the ring, (5) laminar, width similar or slightly thinner than adjacent parts of the ring with a markedly medial concavity, (6) laminar, width similar or slightly thinner than adjacent parts of the ring. Two character-states (Chs. 35.5 and 35.6; Fig. 4E, F) were added to the original series of Faivovich (2002: ch. 13). From these, one (Char 35.6) was taken from Araujo-Vieira et al. (2019: ch. 74). We also observed a slight (e.g., *Scinax hayii* and *S. perereca*) or con-spicuous (e.g., *S. alter*, *S. tymbamirim*, and *S. imbegue*) medial depression in the anterior margin of the cardiac process in some species of Scinaxini that have a wider, laminar cardiac process (Ch. 35.2).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 13*, fig. 7); Araujo-Vieira et al. (2019: ch. 74*).

36. Cricoid ring, posterior portion (+). (0) Adjacent to the posterior margin of the arytenoids, (1) elongated and straight, (2) extensively elongated and curved. In *S. oreites* and most species of the *S. catharinae* group, the posterior part of the cricoid ring is extensively elongated cardiacally and curved, forming an esophagic process that lies far from the arytenoids. *Aplastodiscus perviridis*, *Hyla cinerea*, *Hyloscirtus palmeri*, *Itapotihyla langsdorffii*, *Phyllodytes luteolus*, and *Phyllomedusa sauvagii* show this
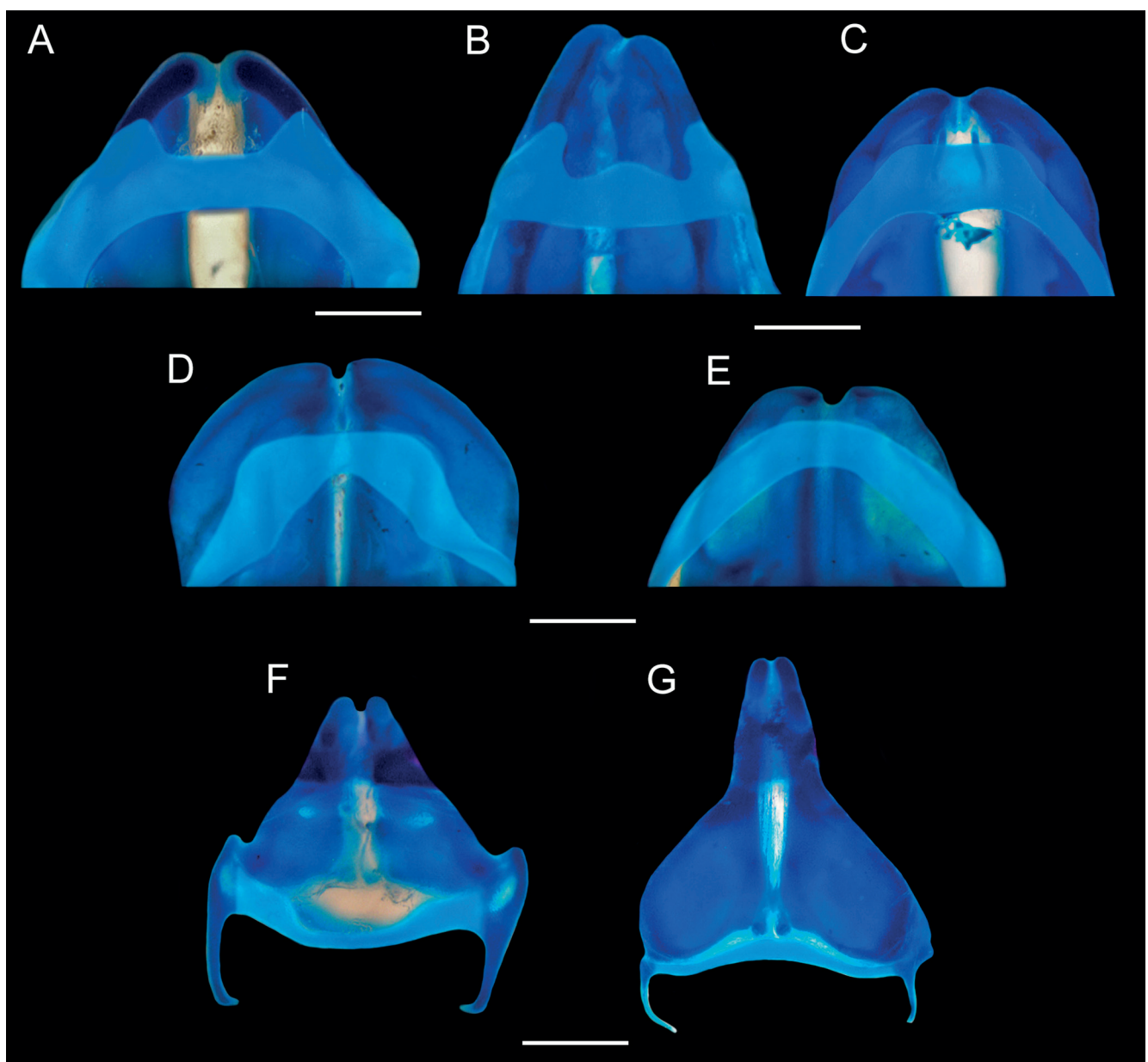
Figure 4. Some views of the cardiac process of the cricoid ring showing different states of Ch. 35. **(A)** *Aplastodiscus perviridis* (MACN 37040, Ch. 35.0). **(B)** *Boana albopunctata* (MACN 37015, Ch. 35.1). **(C)** *Scinax perereca* (MACN 36927, Ch. 35.2). **(D)** *S. camposseabrai* (UFMG 4673, Ch. 35.5). **(E)** *Sphaenorhynchus caramaschii* (CFBH 6937, Ch. 35.6). **(F)** *Scinax arduous* (CFBH 17997, Ch. 35.3). **(G)** *S. fuscomarginatus* (MACN 37012, Ch. 35.4). A–E are ventral views of the anterior part of the larynx. F and G are anterior views of the larynx. The cardiac processes are digitally highlighted. Scale bars = 1.5 mm.

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elongation, but it is somewhat shorter and not curved ventrally (Ch. 36.1). It is important to differentiate these states from the morphology of the esophagic process, which can be extensively elongated, cardiacally (*Boana albopunctata*), posteriorly (*Gabohyla pauloalvini*) or dorsally curved (*Sphaeonrhynchus carneus*).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 14, fig. 6).

37. Arytenoids, shape in dorsal view[1] (-). (0) Oval, (1) oval, with a slight medial constriction, (2) oval, with anterior and posterior constrictions, (3) subcircular, (4) quadrate, (5) rectangular.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 15).

38. Arytenoids, dorsomedial prominence (-; Fig. 5A–D). (0) Well developed, right triangle shaped, with major axis parallel to arytenoids, (1) well developed, right triangle shaped, with major axis perpendicular to arytenoids, (2) poorly developed, major axis parallel to arytenoids, (3) well developed, isosceles triangle shaped, with anterior margin slightly convex. The dorsomedial prominence of the arytenoid is a flat, cartilaginous extension of its pharyngeal portion (Faivovich, 2002). All species analyzed by Faivovich (2002) that have been scored previously as ch. 16.0 (our Ch. 38.0; Fig. 5A), in fact, share ch. 16.1 (our Ch. 38.1; Fig. 5B), and we corrected this typing error in our matrix. Faivovich (2002) suggested that ch. 16.2 (our Ch. 38.2; Fig. 5C) could be divided into more states, as there are different levels of reduction of the prominence. However, we were unable to objectively subdivide that character-state and, therefore, retain the original transformation series proposed by Faivovich (2002).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 16, fig. 6); Orrico et al. (2021: ch. 81).

39. Arytenoid, internal buttresses. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 17); Araujo-Vieira et al. (2019: ch. 75); Orrico et al. (2021: ch. 78).

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1 Arenas-Rodrígues and Hoyos (2022) described the laryngeal morphology of *Scinax kennedyi*, *S. ruber*, and *S. wandae* and attempted to summarize available data on this character system in hylids. The authors provided no locality data for their studied specimens, which, as is evident from our results, precludes the assignment of their observations to the lineages associated with these nominal taxa. Further, their study proposed some questionable homology relationships, such as the hypothesis that the dorsomedial prominence is homologous with apical cartilages (also known as santorini cartilages; Henle, 1839) and the internal buttresses. The apical cartilages are discrete elements that articulate with the arytenoids through connective tissue (Trewavas, 1933; Chacko, 1965) and the internal buttresses are cartilaginous structures that extend from the internal surfaces of the arytenoids (Martin, 1972), whereas the dorsomedial prominence is simply an extension of the pharyngeal surface of the arytenoid. Further, the internal buttresses and the dorsomedial prominence co-occur in some clades, including several Scinaxini (Faivovich, 2002).

40. Arytenoid, internal buttresses, number. (0) One, in medial position, (1) three, one in medial position and two on the distal thirds.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 18); Araujo-Vieira et al. (2019: ch. 76); Orrico et al. (2021: chs. 79*, 80*).

41. Rod of cartilage supporting each extreme of the vocal cords. (0) Absent, (1) present. This structure was first observed in *Scinax ruber* (as *Hyla rubra*) by Trewavas (1933) who called them "Cartilaginous support rods". Similar structures were also reported for South African bufonids (Lambiris, 1994).

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 77, fig. S11); Orrico et al. (2021: ch. 77*).

42. Arytenoids, fibrous masses. (0) Non-chondrified (alcian blue negative), (1) chondrified.

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 78*).

Adult external morphology

43. Hand and foot discs, shape (-). (0) Rounded, (1) elliptical, wider than long, (2) oval, longer than wide. Most species of Scinaxini have discs that are wider than long, and have been commonly called "truncate" in the literature of the group (e.g., Duellman, 1970a, 1973; Duellman and Wiens, 1992, 1993; Faivovich, 2002; Araujo-Vieira et al., 2019), but also described, perhaps more appropriately, as "elliptical" (e.g., Pombal et al., 1995a; Faivovich, 2005; Araujo-Vieira et al., 2016; Orrico et al., 2021). We agree with Faivovich et al. (2005) that the discs in *Scinax uruguayus* and *S. pinimus* cannot be considered truncate; although they are proportionally smaller than in most species with rounded discs, we consider that these species, including *S. fontanrrosai*, have rounded discs. We added oval discs (Ch. 43.2) to the original transformation series of Faivovich (2002) for those that are longer than wide, as they occur in *Acris crepitans*, *Lysapsus limellum*, *Phyllomedusa sauvagii*, *Pseudis minuta*, and *Pseudis platensis*.

Previous usage in phylogenetic studies: Duellman and Wiens (1992: ch. 22*); Faivovich (2002: ch. 24*); Araujo-Vieira et al. (2019: ch. 126); Orrico et al. (2021: ch. 156*).

44. Loreal region, shape. (0) Flat, (1) concave.

Previous usage in phylogenetic studies: Duellman and Wiens (1992: ch. 20*); Faivovich (2002: ch. 25).

45. Pectoral fold. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: char 26); Orrico et al. (2021: chs. 122–124*).

46. Pectoral fold in males, shape (+). (0) Compound fold, (1) preaxillar and shallow fold, (2) preaxillar and deep fold. The terminology of the different folds follows Tyler (1971), except for "compound fold," which follows

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Faivovich (2002). Character-state 46.2 is present in male *Scinax* with hypertrophied subgular vocal sacs (e.g., *S. cruentomma*, *S. fuscomarginatus*, and *S. wandae*); this co-occurrence should be explored in future studies.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 27*, fig. 11); Orrico et al. (2021: chs. 122–124*).

47. Pectoral glands in males. (0) Absent, (1) present. These pectoral glands are indicated externally by the presence of tightly packed, pale yellow acini. See Araujo-Vieira et al. (2020b) for comments on this character. Pectoral glands are also present in males of *Dendropsophus elegans*, *D. microps*, and *D. sanborni*. In males of some species of *Scinax* (e.g., *S. eurydice*, *S. granulatus*, *S. haddadorum*, and *S. pachycrus*) there is a white, slightly thickened area in the pectoral region that could be glandular, but we did not observe the presence of packed acini in

this region, and therefore scored these species as lacking pectoral glands. Glandular acini in the pectoral region were reported for *S. goya* (Andrade et al., 2018) and *S. feioi* (Lourenço et al., 2020), and we considered them to be homologous with those present in other species of *Scinax*. This assumption should be tested with histological studies.

48. Inguinal gland. (0) Absent, (1) present. Lourenço et al. (2016) noticed that when the inguinal glandular tissue is present in species of the *Scinax catharinae* clade, the variation in the development among species is possibly continuous, with *S. centralis* being extreme in hypertrophy, with the glandular acini very developed and concentrated, forming a bulge, visible even when the legs are folded, concealing the inguinal region (Brito et al., 2019). Lacerda et al. (2021) recognized three dif-
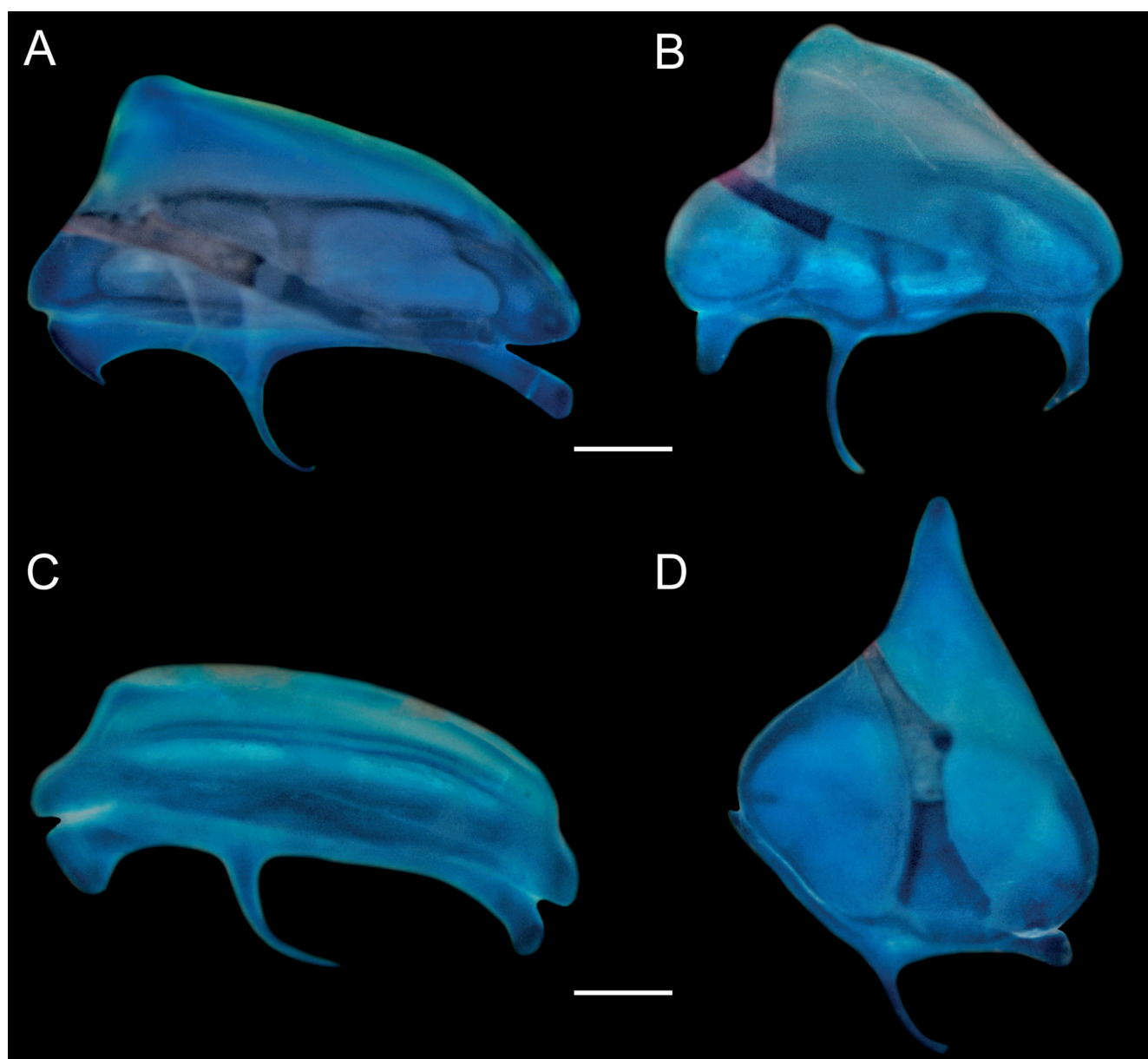
Figure 5. Lateral view of the larynges showing the different degrees of development of the dorsal prominence of the arytenoid (Ch. 38). **(A)** *Scinax hayii* (CFBH 35543, Ch. 38.0). **(B)** *S. berthae* (MACN 36987, Ch. 38.1). **(C)** *S. squalirostris* (CFBH 36971, Ch. 38.2). **(D)** *S. fuscomarginatus* (MCP 37006, Ch. 38.3). Scale bars = 1 mm.

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ferent states for taxonomic purposes: particularly hypertrophied glands (*S. centralis*); hypertrophied glands "often" delimiting a fold (*S. brieni*, *S. catharinae*, *S. hiemalis*, *S. jureia*, *S. obtriangulatus*, *S. pixinguinha*, and *S. ranki*), and glands present but not hypertrophied (*S. ariadne*, *S. caissara*, *S. canastrensis*, *S. flavoguttatus*, *S. garibaldiae*, *S. longilineus*, *S. luizotavioi*, *S. machadoi*, *S. skaios*, and *S. tripui*). We find that the variation shown by at least the last two states is difficult to partition into discrete character-states in the absence of histological study. The structure, variation, and taxonomic distribution of these glands deserve further studies, as do their role reproductive biology.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 28).

49. Glandular acini in the medial region of the forearm. (0) Absent, (1) present. Lourenço et al. (2016, 2019, 2020) reported the occurrence of glandular acini on the medial region of the forearm in some species of the *S. catharinae* clade. Araujo-Vieira et al. (2020b) noticed glandular acini on the medial margins of upper- and forearms of *S. fuscovarius* and *S. x-signatus*, and we observed it in some other species of *Scinax*. We tentatively consider the glands reported in both clades to be homologous but stress the need for additional studies on the histology and the variation in the extent of the distribution of the acini along the forelimbs, to better understand the structure and function of these glands.

50. Forearm, dermal ornamentation, elevated and conical tubercles arranged in a line. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Duellman and Wiens (1992); Faivovich (2002: ch. 29*).

51. Tarsus, dermal ornamentation, elevated and conical tubercles arranged in line. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Duellman and Wiens (1992); Faivovich (2002: ch. 30*).

52. Heel, dermal ornamentation, pointed tubercle. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Duellman (1970a: ch. P*); Duellman and Wiens (1992); Faivovich (2002: ch. 32*); Scott (2005: ch. 159*); Araujo-Vieira et al. (2019: ch. 124*); Orrico et al. (2021: chs. 154*, 155*).

53. Lower lip, labial tubercles (Fig. 6A–D). (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 31*).

54. Lower lip, labial tubercles, number (Fig. 6A–D). (0) One on each side at the level of the articulation between the mentomeckelian and dentary bones, (1) a series along the lower lip.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 31*).

55. Lower lip, labial tubercles, shape (-; Fig. 6A–D). (0) Small, rounded and flattened, (1) pointed, (2) crenulated dermal fold along the lower lip.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 31*).

56. Supracloacal region, pair of pointed tubercles (Fig. 7A–D). (0) Absent, (1) present. Lima et al. (2005) mentioned the presence of two tubercles above the cloaca in females of *Scinax constrictus*. Our observations showed that these pointed tubercles are present in both males and females of *S. acuminatus*, *S. boulengeri*, *S. constrictus* (Fig. 7C, D), *S. garbei*, *S. nebulosus*, *S. pedromedinae* (polymorphic), *S. proboscideus*, *S. rostratus*, and *S. sugillatus*.

57. Paracloacal region, pair of pointed dorsolateral tubercles (Fig. 7A–D). (0) Absent, (1) present.

58. Webbing, postaxial webbing of toe I (+). (0) Absent or basal webbing, (1) reaching subarticular tubercle, (2) reaching the midlength of penultimate phalanx, (3) reaching base of disc. In state 1, the webbing varies in extension between the proximal and distal margin of the subarticular tubercle. Peixoto (1987) reported the absence of webbing between toes I and II in species of the *Scinax perpusillus* group. However, our observations of several specimens of that group, added to observations of specimens of *S. agilis*, *S. argyreornatus*, *S. cardosoi*, and *S. melanodactylus* indicated that the webbing between toes I and II can be absent or present in those species. When present the webbing is basal, that is, the lateral fringes that meet between the toes are slightly broader at the base than along the sides of the digits. Therefore, we considered absence or presence of basal webbing between the toes I and II as the same character-state. Contrary to Faivovich's (2002) observations, we considered that *S. agilis* has basal webbing between toes I and II, as does *S. cardosoi* (ch. 58.0).

Previous usage in phylogenetic studies: Duellman and Wiens (1992: ch. 21*, fig. 3); Faivovich (2002: chs. 34*, 35*); Grant et al. (2006: ch. 37*); Araujo-Vieira et al. (2019: ch. 129*); Orrico et al. (2021: ch. 130*).

59. Webbing, postaxial webbing of toe II (+). (0) Absent, (1) reaching subarticular tubercle, (2) reaching proximal half of penultimate phalanx, (3) reaching base of disc. In state 1, the webbing varies in extension between the proximal and distal margin of the subarticular tubercle. Peixoto (1987) first noticed that species of the *S. perpusillus* group have reduced or absent webbing between toes II and III (our states 59.0 and 59.1). Following this report, Faivovich et al. (2005) considered the extreme reduction of webbing between toes II and III (our state 59.1) a putative synapomorphy of the *S. perpusillus* group. Our observations showed that all species of the *S. perpusillus* group have the postaxial webbing of toe II reaching the subarticular tubercle (59.1), a character-state shared with some species of the *S. catharinae* group.

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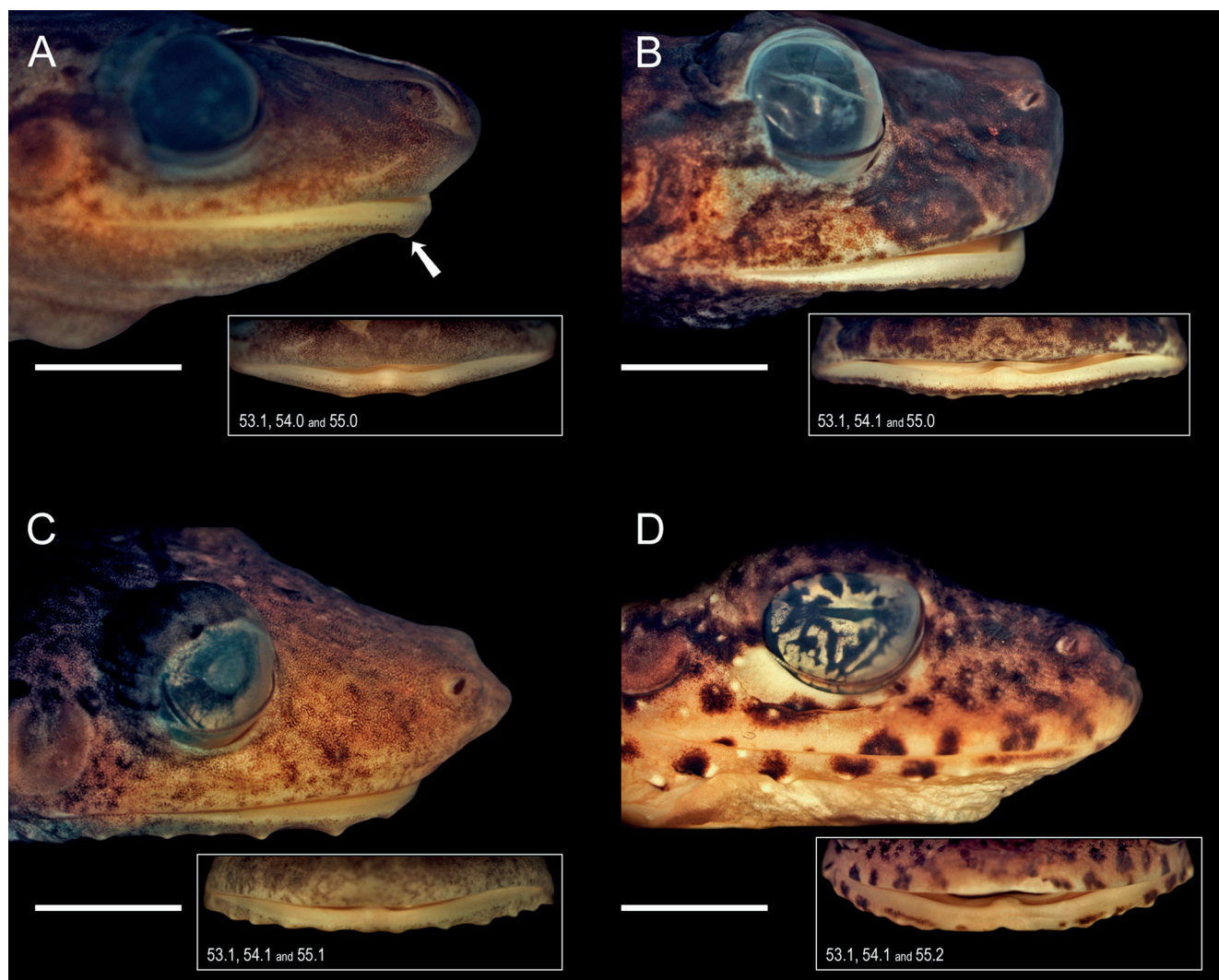
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Figure 6. Lateral and anterior (insets) views of the head showing the presence, number, and shape of labial tubercles (Chs. 53–55). **(A)** *Scinax cretatus* (CFBH 7348), a pair of small, rounded, and flattened tubercles at the level of mentomeckelian and dentary articulation (Chs. 53.1, 54.0, and 55.0; the arrow indicates the tubercle). **(B)** *S. brieni* (CFBH 29060), small, rounded, flattened tubercles along the lower lip (Chs. 53.1, 54.1, and 55.0). **(C)** *S. garbei* (CFBH 37081, Chs. 53.1, 54.1, and 55.1) pointed tubercles along the lower lip. **(D)** *Itapotihyla langsdorffii* (CFBH 12724), crenulated dermal fold (Chs. 53.1, 54.1, and 55.2). Scale bars = 2 mm.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 35); Grant et al. (2006: ch. 39*); Araujo-Vieira et al. (2019: ch. 124*); Orrico et al. (2021: ch. 132*).

60. Webbing, preaxial webbing of toe IV (+). (0) Reaching proximal half of antepenultimate phalanx, (1) reaching proximal half of penultimate phalanx, (2) reaching base of disc. We observed less webbing in species of the *S. uruguayus* group than in other species of the *S. ruber* clade. However, in the *S. ruber* clade the degree of interspecific variation in the webbing between toes III and V is continuous and difficult to partition into discrete states; the exceptions are the preaxial and postaxial webbing of toe IV.

Previous usage in phylogenetic studies: Grant et al. (2006: ch. 42*); Araujo-Vieira et al. (2019: ch. 130*); Orrico et al. (2021: ch. 135*).

61. Webbing, postaxial webbing of toe IV (+). (0) Reaching at most proximal half of antepenultimate phalanx, (1) reaching proximal half of penultimate phalanx, (2) reaching base of disc.

Previous usage in phylogenetic studies: Grant et al. (2006: ch. 43*); Araujo-Vieira et al. (2019: ch. 131*); Orrico et al. (2021: ch. 136*).

62. Vocal sac. (0) Absent, (1) present. The absence of the vocal sac is defined by the absence of vocal slits.

Previous usage in phylogenetic studies: Duellman (1970a: ch. G*); Liem (1970: ch. 36*); Drewes (1984: ch. 20*); Cannatella (1986: char 10*); Hillis and de Sá (1988: char 6); Mendelson et al. (2000: ch. 51); Grant et al. (2006: ch. 76*); Pramuk (2006: ch. 75*); Ohler and Dubois (2006: ch. 14*); Mendelson et al. (2011: ch. 31*); Moura et al. (2021: ch. 1).

63. Vocal sac, external differentiation (Fig. 8A, C, E, G, I, K). (0) Vocal sac not notably distended ("internal"), (1) vocal sac externally evident by loose, partially expanded skin ("external"). We follow Faivovich (2002) in defining the vocal sacs either as external (permanently expanded and thin walled) or internal (integument not differing from the surrounding throat or chest region) based on Bouleng-

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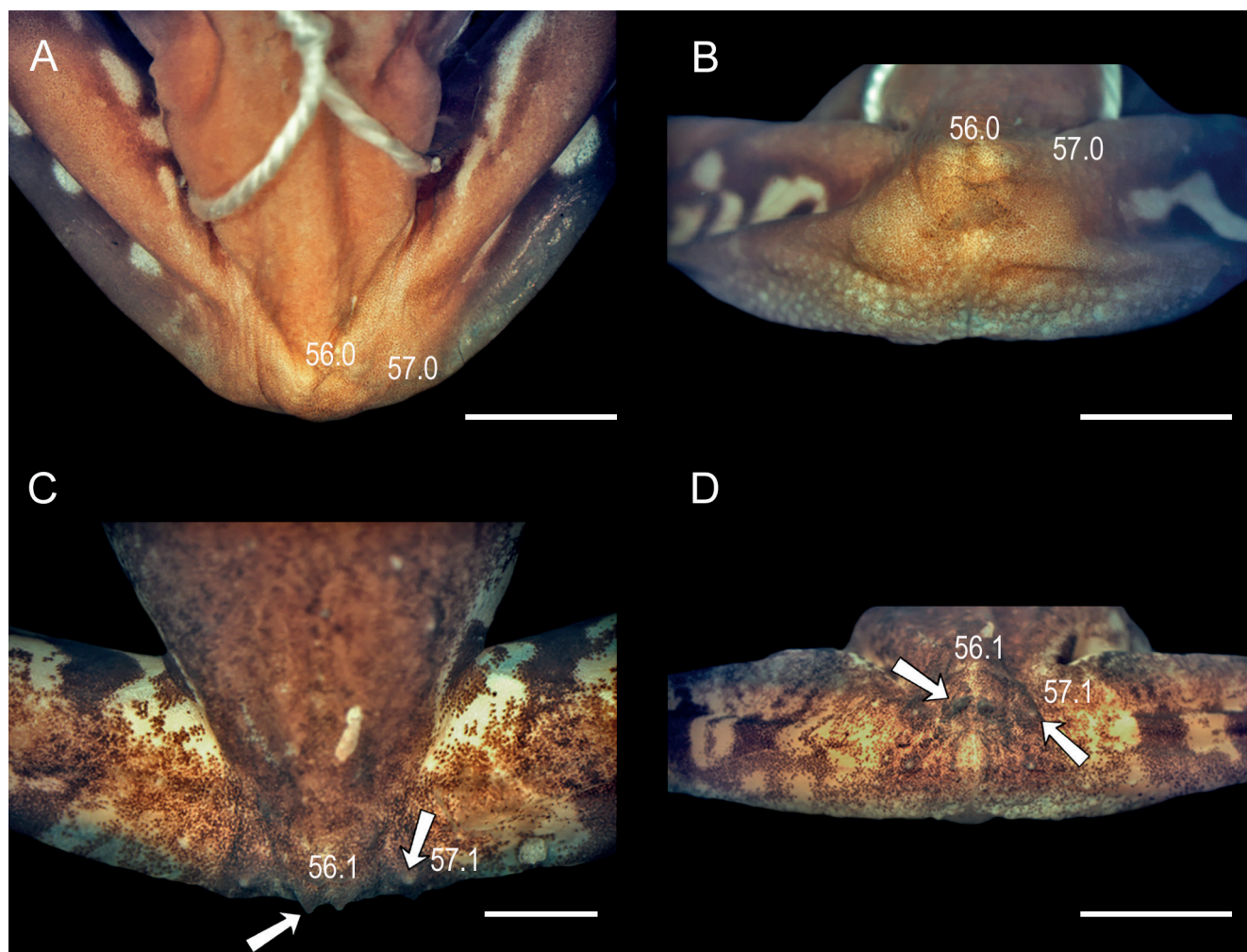
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Figure 7. Dorsal and posterior views of the cloacal region showing states of Chs. 56 and 57. **(A)** and **(B)** *Scinax hayii* (CFBH 53480, Chs. 56.0 and 57.0). **(C)** and **(D)** *S. nebulosus* (CFBH 16037, Chs. 56.1 and 57.1). The arrows in C and D indicate the presence of tubercles in the supracloacal and dorsolateral regions. Scale bars = 1.5 mm.

er's (1897) definitions; very likely, these could be refined with histological studies. Most species of the *Scinax catharinae* clade have an internal vocal sac (Fig. 8C); exceptions are *S. aromothyella*, *S. berthae*, *S. cardosoi*, *S. feioi*, *S. garibaldiae*, and *S. rizibilis* that have an externally expanded vocal sac (Fig. 8I).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 36).

64. Nuptial pad, occurrence of epidermal projections (EPs) on pad on finger II. (0) Absent (smooth pad), (1) present. There are some limitations to the study of epidermal projections of the nuptial pad employing low magnification (i.e., 5x–110x) when considering the known diversity in structure, size, and shape (Luna et al., 2018), particularly when the pad is pale (note that Luna et al., 2018 called these light-coloured pads). This character is only a first approximation to this diversity in Scinaxini, pending a study employing scanning electron microscopy.

65. Nuptial pad, occurrence on finger III. (0) Absent, (1) present. Lourenço et al. (2016, 2019, 2020) and Araujo-Vieira et al. (2020b) reported the occurrence of glandular acini present on the medial margin of finger III in males of

some species of the *Scinax catharinae* and *S. ruber* clades, respectively. Following Luna et al. (2018), we interpret these as a nuptial pad of finger III, stressing that its structure is different from that of finger II in that no epidermal projections seem to be present.

66. Nuptial pad on finger II, coloration. (0) Pale (cream or white), (1) dark (brown or black). This character refers to the coloration of the stratum corneum of the nuptial pad (Luna et al., 2018).

Previous usage in phylogenetic studies: Duellman (1970a: ch. N*); Ohler and Dubois (2006: ch. 24*); Pereyra et al. (2021: ch. 62).

Urogenital system

67. Visceral peritoneum covering the testes, coloration (-; Fig. 9A–F). (0) Iridescent white, (1) transparent, (2) small dark spots. The brown and black color (Fig. 9A–D) is a consequence of the concentration of melanin, whereas the iridescent white color results from the concentration of iridiphores (Fig. 9E). Faivovich (2002) treated the differences in melanin concentration leading to brown or black spots as different character-states. Our study of a much

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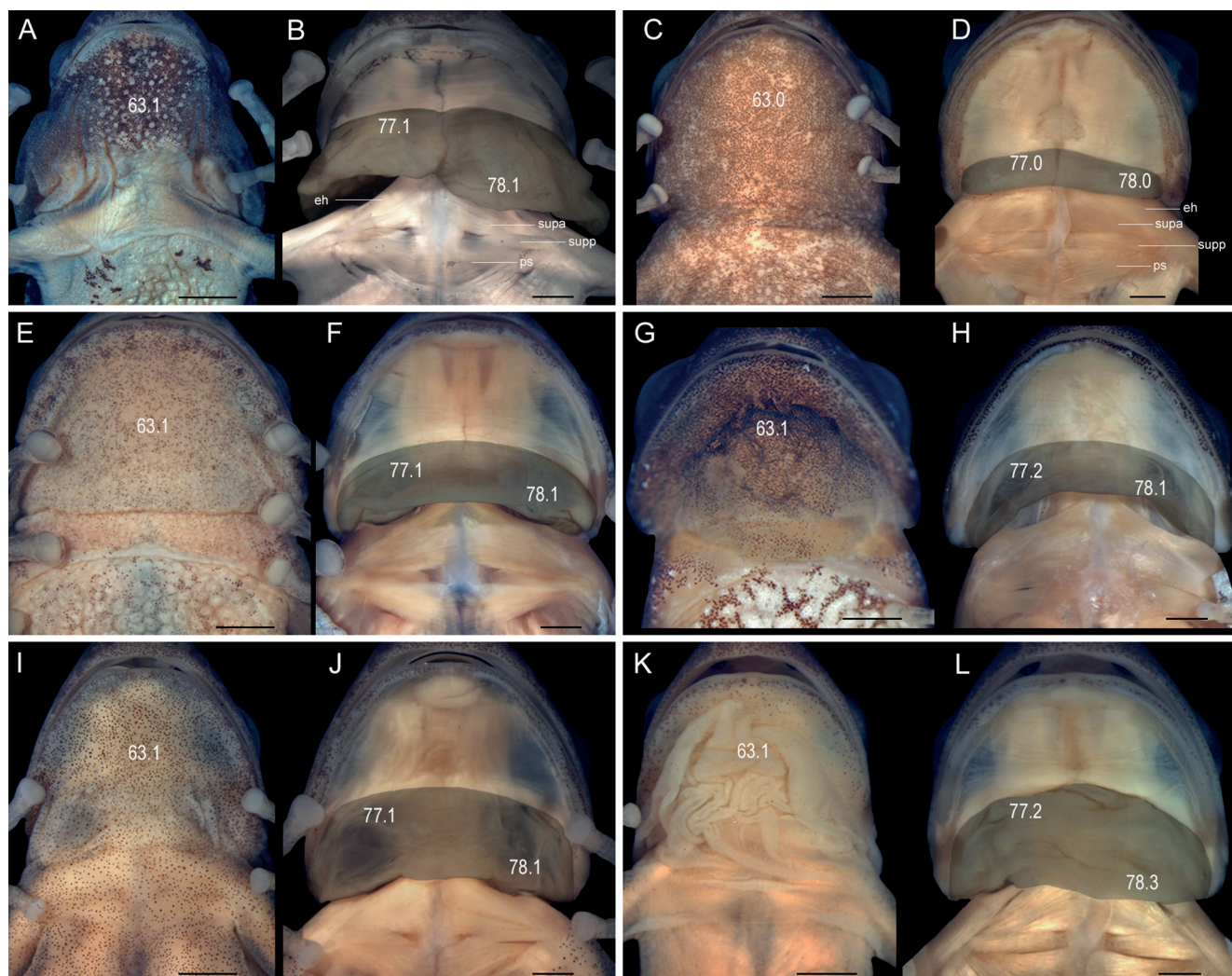
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Figure 8. On the left: external view of the vocal sac showing states of Ch. 63; on the right: the different degrees of development of the m. interhyoideus, Chs. 77 and 78. **(A)** and **(B)** *Scinax camposseabrai* (UFMG-A 4670, 4673, Chs. 63.1, 77.1, and 78.1). **(C)** and **(D)** *S. longilineus* (CFBH 17330, Chs. 63.0, 77.0, and 78.0). **(E)** and **(F)** *S. granulatus* (CFBH 3867, Chs. 63.1, 77.1, and 78.1). **(G)** and **(H)** *S. fontanarrosai* (LGE 2040, Chs. 63.1, 77.2, and 78.1). **(I)** and **(J)** *S. berthae* (MACN 37248, Chs. 63.1, 77.1, and 78.1). **(K)** and **(L)** *S. fuscomarginatus* (CFBH 24363, Chs. 63.1, 77.2, and 78.3). The m. interhyoideus is digitally highlighted. eh = m. episternohumeralis; supa = m. supracoracoideus portio anterior; supp = m. supracoracoideus portio posterior; ps = m. pectoralis portio sternalis. Scale bars = 5 mm.

larger number of species and specimens indicates that the two states describe a continuous gradient, and for that reason we consider it as a single character-state. The brown or black spots in the visceral peritoneum covering the testes can be densely (e.g., *Scinax argyreornatus, S. camposseabrai, S. fuscomarginatus,* and *Pseudis minuta;* Fig. 9B, D) or sparsely (e.g., *S. agilis, S. auratus, S. constrictus, S. nebulosus,* and *S. pinimus;* Fig. 9A, C) distributed. The study of these distribution patterns will likely result in more characters. Goldberg et al. (2019) described ontogenetic variation associated with sexual maturation in testes coloration. All specimens studied by us are sexually mature adult males.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 37*); Scott (2005: ch. 131*); Grant et al. (2006: ch. 67*); Orrico et al. (2021: ch. 196*).

Trunk musculature

68. Origin of m. pectoralis portio abdominalis, position (Fig. 10A–C). (0) Midbody, (1) pelvis. The m. rec-

tus abdominis, the m. pectoralis abdominalis, and two lateral muscles (mm. obliquus externus and transversus) form the abdominal musculature (Gaupp, 1896; Duellman and Trueb, 1986). The m. pectoralis abdominalis, lateral to the m. rectus abdominis, inserts on the humerus and originates either from the external lateral portion of the m. rectus abdominis or from the pelvis by a tendon.

In a study of larval abdominal muscle development of five species of Hylidae, Manzano and Perotti (1999) reported that the m. rectus abdominis is the first abdominal muscle to develop, but the subsequent development of the mm. pectoralis abdominalis and obliquus externus (muscles associated with the m. rectus abdominis) limits its anterolateral (m. pectoralis abdominalis) and lateral (m. obliquus externus) development. Our observations showed that the m. rectus abdominis in adults remains limited anterolaterally and laterally by the mm. pectoralis abdominalis and obliquus externus, respectively. This is observed throughout the juxtaposition or slight

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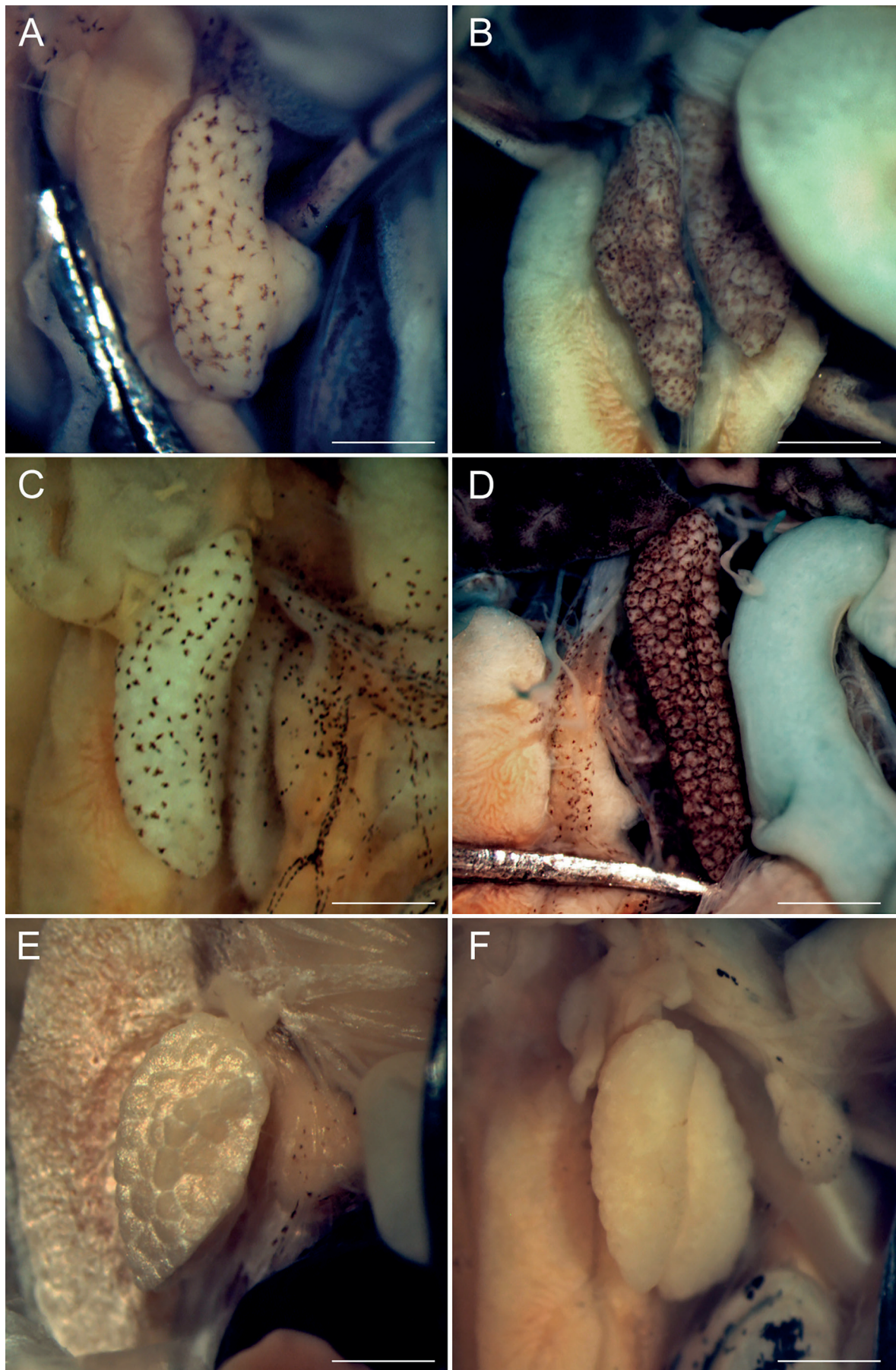
Figure 9. Ventral view of the testes showing the different degrees of coloration of the visceral peritoneum (Ch. 67). **(A)** *Scinax constrictus* (CFBH 12514, Ch. 67.2). **(B)** *S. argyreornatus* (CFBH 26236, Ch. 67.2). **(C)** *S. pinimus* (LGE 94, Ch. 67.2). **(D)** *S. camposseabrai* (UFMG 4673, Ch. 67.2). **(E)** *Sphaenorhynchus dorisae* (ZUEC 8427, Ch. 67.0, same state that occurs in *S. caramaschii* and *S. carneus*). **(F)** *S. squalirostris* (CFBH 35249, Ch. 67.1). Scale bars = 2 mm.

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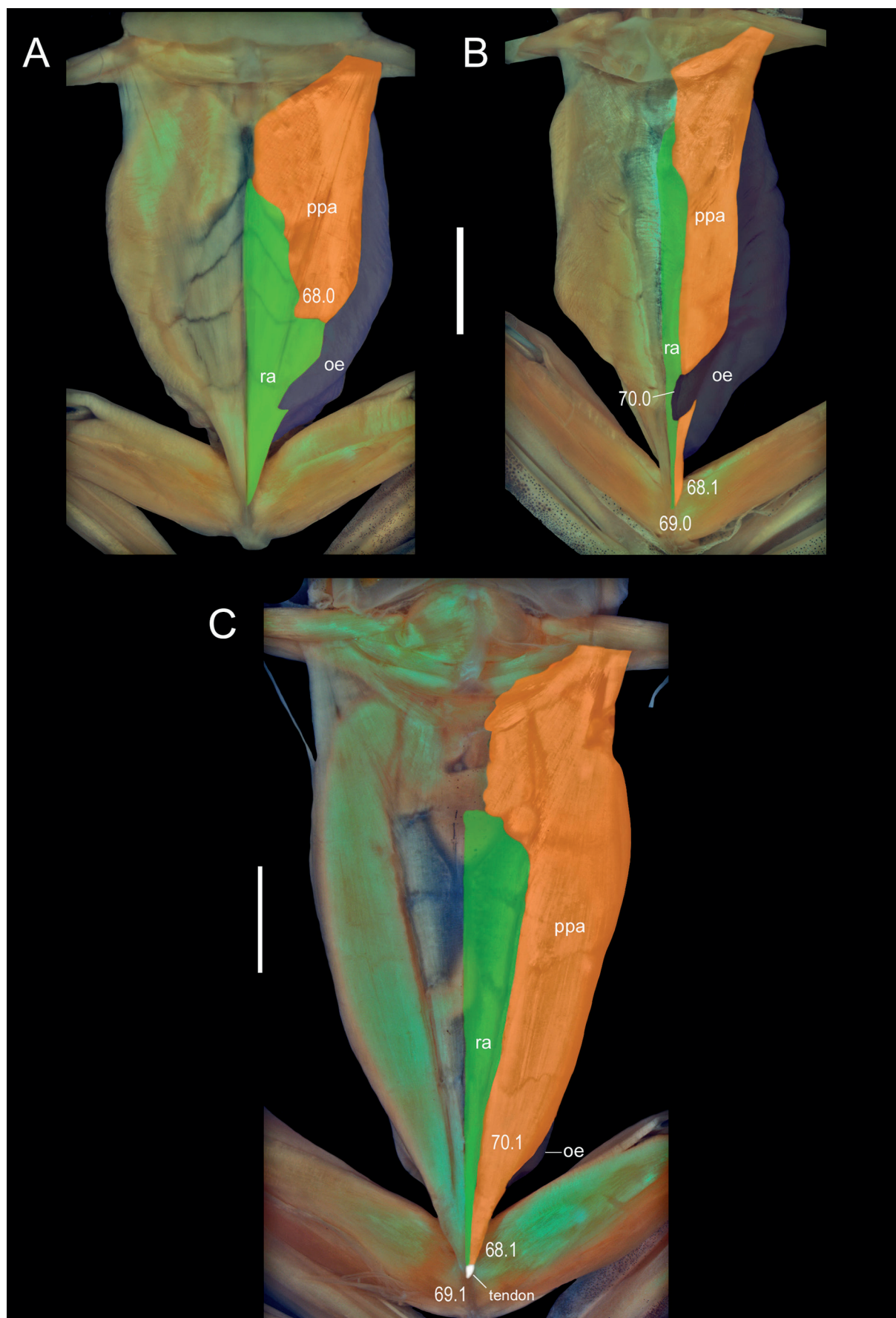**Figure 10.** Origin of the m. pectoralis portio abdominalis (Chs. 68 and 69) and the relationship between m. pectoralis abdominalis and m. obliquus externus (Ch. 70). **(A)** *Sphaenorhynchus botocudo* (MACN 46458, Ch. 68.0, same state that occurs in *S. caramaschii* and *S. carneus*). **(B)** *Dendropsophus minutus* (MCP 5387, Chs. 68.1, 69.0, and 70.0). **(C)** *Scinax perereca* (CFBH 2335, Chs. 68.1, 69.1, and 70.1). The m. obliquus externus (oe), m. pectoralis portio abdominalis (ppa), and m. rectus abdominis (ra) are digitally highlighted. Scale bars = 5 mm.

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overlapping of the m. rectus abdominis by the medial margins of the mm. pectoralis abdominalis and obliquus externus.

Faivovich (2002) took the coding of the outgroup taxa from Silva's (1998) analysis. However, we observed that many species scored as having the m. pectoralis abdominalis with origin at midbody (our Ch. 68.0; Fig. 10A) by Silva (1998) in fact have the origin on the pelvis via a well-defined tendon (our Ch. 68.2; Fig. 10C). One possible reason for Silva's (1998) incorrect observation is that the limits between the mm. rectus abdominis and pectoralis abdominalis are difficult to detect when the latter is overlapped by the m. obliquus externus. However, as the m. rectus abdominis is laterally limited and slightly overlapped by the m. obliquus externus, careful removal of the ventral fibers of the m. obliquus externus, where it overlaps the m. pectoralis abdominalis, enables observation of the fibers of the m. pectoralis abdominalis extending posteriorad to their origin on the pelvis (Fig. 10B, C).

Previous usage in phylogenetic studies: Silva (1998: ch. 103); Faivovich (2002: ch. 38); Araujo-Vieira et al. (2019: ch. 189); Orrico et al. (2021: ch. 103*).

69. Origin of m. pectoralis portio abdominalis from the pelvis, attachment (Fig. 10B–C).
(0) Tendon not evident, (2) tendon evident. This character is inapplicable for the species where the m. pectoralis portio abdominalis originates from the midbody.

Previous usage in phylogenetic studies: Silva (1998: ch. 103*); Faivovich (2002: ch. 38*); Araujo-Vieira et al. (2019: ch. 189*); Orrico et al. (2021: ch. 103*).

70. Relationship between m. pectoralis portio abdominalis and m. obliquus externus in ventral view (Fig. 10B–C).
(0) M. obliquus externus concealing ventrally the m. pectoralis portio abdominalis, (1) m. pectoralis portio abdominalis concealing m. obliquus externus. In state 0, the m. obliquus externus conceals the m. pectoralis abdominalis approximately from the middle of the first to the second myotome of the m. rectus abdominis (Fig. 10B). We considered this character to be inapplicable for species in which the m. pectoralis abdominalis originates at midbody (e.g., *Sphaenorhynchus caramaschii*), since this muscle originates approximately on the third myotome of the m. rectus abdominis, and therefore is unrelated to the m. obliquus externus (Fig. 10A).

Previous usage in phylogenetic studies: Silva (1998: ch. 104); Faivovich (2002: ch. 39).

Mandibular musculature

71. M. depressor mandibulae, origin from the dorsal fascia that covers the m. dorsalis scapulae (Fig. 11A–J).
(0) Absent, (1) present. In Scinaxini, this muscle can be formed by three portions: one originating from the dorsal fascia covering the mm. levator mandibulae and protractor pectoralis (in some cases), and extending to the m. dorsalis scapulae, another originating from the cartilaginous posterolateral process and adjacent areas of the crista parotica, and another originating from the posteroventral margin of the tympanic ring.

The fibers of the m. depressor mandibulae that originate from the dorsal fascia can have a broad origin covering the mm. levator mandibulae, protractor pectoralis, and dorsalis scapulae (Fig. 11C–F). When the origin is continuous, the fibers have either a slight depression between the m. dorsalis scapulae and the skull or form a thick, fan-shaped continuum from the skull to the scapula (Fig. 11C–F). On occasions, instead of a broad origin, there is a gap separating the fibers from the dorsal fascia at the level of the m. dorsalis scapulae from those that originate at the level of the mm. levator mandibulae and protractor pectoralis, forming two separate slips (Fig. 11A, B). The gap between the fibers from both origins is notable (⅔ of the height of the m. depressor mandibulae; Fig. 11A, B). Most species of Scinaxini have separated origins. Nevertheless, we also observed that there is a continuum between the continuous and separated conditions mentioned above and were unable to partition it into discrete states (see also Grant et al., 2006:90). Therefore, we only coded the presence and absence of the fibers m. depressor mandibulae originating on the m. dorsalis scapulae.

Previous usage in phylogenetic studies: Heyer (1975: ch. 12*); Heyer and Liem (1976: ch. 20*); Faivovich (2002: ch. 40); Nuin and do Val (2005: ch. 11*); Grant et al. (2006: ch. 72).

72. M. depressor mandibulae, origin from the tympanic ring.
(0) Absent, (1) present.

Previous usage in phylogenetic studies: Heyer (1975: ch. 12*); Faivovich (2002: ch. 41); Nuin and do Val (2005: ch. 11*); Grant et al. (2006: ch. 74).

Submandibular musculature and vocal sac anatomy

73. M. intermandibularis, relationship between contralateral elements.
(0) Aponeurosis, (1) raphe. The contralateral elements of the m. intermandibularis can meet in a median raphe or in an aponeurosis. If present, the aponeurosis of the m. intermandibularis varies in size, shape, and position (Tyler, 1971). It can be narrow (e.g., *Scinax alter* and *S. pinimus*), wide (e.g., *S. crospedospilus* and *S. cuspidatus*), rectangular (e.g., *S. auratus* and *S. imbegue*), diamond-shape (e.g., *S. acuminatus* and *S. crospedospilus*), apical (e.g., *Sphaenorhynchus caramaschii*), medial (e.g., *S. acuminatus* and *S. constrictus*), and posteromedial (e.g., *S. canastrensis* and *S. catharinae*). We were unable to apportion the observed variation among discrete character-states, as there is noticeable intraspecific variation. For example, the aponeurosis of *S. tymbamirim* can form either a narrow rectangular (CFBH 38953) or a diamond-shape (MNRJ 49209). As such, we scored only the occurrence of an aponeurosis or raphe in the medial region of the m. intermandibularis.

Previous usage in phylogenetic studies: Silva (1998: ch. 97*); Mendelson et al. (2000: ch. 50*); Araujo-Vieira et al. (2019: chs. 148*, 149*); Elias-Costa et al. (2021: ch. 5, figs. 1–2).

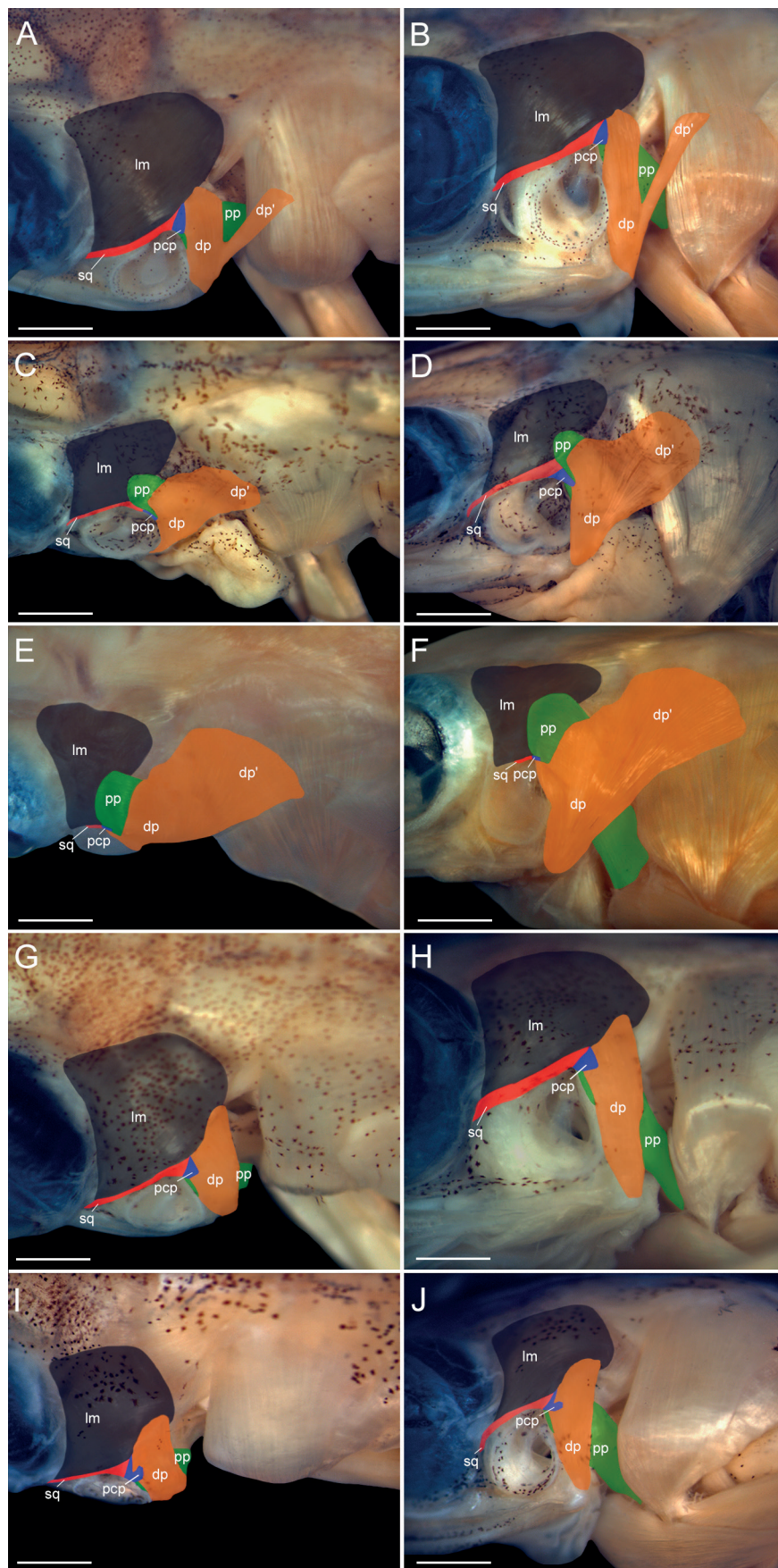Treefrog diversity in the Neotropics: Phylogenetic relationships of Scinaxini (Anura: Hylidae: Hylinae)
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Figure 11. Relationship between m. depressor mandibulae and scapula (Ch. 71). **(A)** and **(B)** *Scinax duartei* (CFBH 140, Ch. 71.1). **(C)** and **(D)** *S. campos-seabrai* (UFMG-A 4673, Ch. 71.1). **(E)** and **(F)** *Sphaenorhynchus lacteus* (ZUEC 5853, Ch. 71.1, same state that occurs in *S. caramaschii*). **(G)** and **(H)** *Scinax argeryonartus* (CFBH 26236, Ch. 71.0). **(I)** and **(J)** *S. fontanarrosai* (LGE 2040, state 71.0). A, C, E, G, and I dorsal view of skull; B, D, F, H, and J lateral view of skull. The m. depressor mandibulae (dp), m. depressor mandibulae on m. dorsalis scapulae (dp'), m. levator mandibulae (lm), m. protractor pectoralis (pp), posterolateral process of crista parotica (pcp), and squamosal (sq) are digitally highlighted. Scale bars = 2 mm.

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74. M. interhyoideus, relationship between contralateral elements (+). (0) Continuous, araphic, (1) interrupted by a median raphe, (2) interrupted by a median aponeurosis.

Previous usage in phylogenetic studies: Silva (1998: ch. 100*); Araujo-Vieira et al. (2019: ch. 150*); Elias-Costa et al. (2021: ch. 15).

75. M. intermandibularis, posterior fibers orientation. (0) Mediad, (1) anteromediad. In most species of Scinaxini, the posterior fibers of the m. intermandibularis extend anteromediad from the level of the mandible to the medial connective tissue giving a concave shape to the posterior edge of this muscle, in contrast to most other taxa included in this analysis in which the fibers extend mediad, giving a square shape to the posterior edge of the muscle.

76. M. interhyoideus in males, subgular shape (-). (0) Uniform, (1) weakly bilobate, (2) bilobate, (3) paired subgular. Faivovich (2002) defined this character in relation to the ventral development of the m. interhyoideus. However, we observed that at least three characters were being conflated in his character definition: shape, anterior extension, and posterior extension of the m. interhyoideus in the subgular region (see also Chs. 77–78).

Elias-Costa et al. (2021) described the diversity of the subgular morphology of the m. interhyoideus as five states in their ch. 19. Their ch. 19.0 and 19.1 correspond to the size and expansion of the m. interhyoideus and were considered in our Chs. 77–79, below; ch. 19.2 corresponds to bilobate vocal sacs whose variation was divided into Chs. 76.1 and 76.2, while their ch. 19.3 corresponds to Ch. 76.3. Their ch. 19.4, m. interhyoideus forming a tubular projection (present in *Lithobates*, *Pelophylax*, and *Rana*, not included in this analysis) was not observed in species examined in this study.

The most common subgular shape is the uniform m. interhyoideus (Ch. 76.0), in which the muscle does not have any medial constrictions in the posterior margin, forming a uniformly expanded subgular lobe. We refer to a weakly bilobate m. interhyoideus (Ch. 76.1) when the muscle has a shallow medial constriction in this posterior margin and forms small but continuous contralateral subgular lobes (e.g., *Scinax acuminatus*, *S. fuscovarius*, *S. rizibilis*, and *S. tsachila*), whereas the bilobate m. interhyoideus (Ch. 76.2) possesses a deep medial constriction in this posterior margin, forming one discrete lobe on each side of the subgular region (e.g., *Scinax camposseabrai* and *Smilisca baudini*). The paired subgular m. interhyoideus occurs in *Pseudis minuta*, in which the muscle forms paired ventrolateral lobes in the subgular region (Ch. 76.3).

There are cases (*Scinax hayii*, *S. montivagus*, *S. pachycrus*, and *S. perereca*) in which vocal sacs described as single subgular (Heyer et al., 1990; Pombal et al., 1995a; Juncá et al., 2015), upon dissection, are discovered to have a weakly bilobate m. interhyoideus. Consequently, all species described in the literature as having a single subgular vocal sac, but for which we had no specimens for direct observation, were scored as unknown for this character.

We could not study this character in *Scinax castroviejoi*, *S. ruberoculatus*, or *S. sateremawe*, for which the vocal sac was described as bilobate (De la Riva, 1993; Duellman and Wiens, 1993; Sturaro and Peloso, 2014; Ferrão et al., 2017, 2018b). However, based on our experience, vocal sacs of *Scinax* described as bilobate in the literature correspond to a weakly bilobate m. interhyoideus, leading us to tentatively score these species as having this character-state, pending corroboration through proper dissections.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 42*); Elias-Costa et al. (2021: ch. 19*, fig. 7).

77. M. interhyoideus in males, anterior extension (+; Fig. 8B, D, F, H, J, L). (0) Anterior margin extending ca. ⅕ mandible length, (1) anterior margin extending ca. ⅓ mandible length, (2) anterior margin extending ½ mandible length. The species of the *Scinax ruber* clade have external vocal sacs with more variation in shape (e.g., uniform, weakly bilobed, and bilobed) and degree of anterior and posterior development of the m. interhyoideus (Fig. 8A, B, E–H, K, L), whereas most species of the *S. catharinae* clade have an internal, single vocal sac, with a poorly developed m. interhyoideus (Fig. 8C, D, I, J). We consider the structure of the vocal sac skin (Ch. 63) as independent of the shape and development of the m. interhyoideus (Chs. 77–79).

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 151).

78. M. interhyoideus in males, posterior extension (+; Fig. 8B, D, F, H, J, L). (0) Posterior margin barely surpassing mandible, (1) posterior margin extending beyond mandible along m. episternohumeralis to ⅓–½ length of m. supracoracoideus portio anterior, (2) posterior margin extending to m. supracoracoideus portio posterior, (3) posterior margin extending to anterior edge of the m. pectoralis portio sternalis, (4) posterior margin extending to posterior edge of the m. pectoralis portio sternalis, (5) posterior margin surpasses the m. pectoralis portio sternalis. We coded this character based on specimens with distended and well-fixed vocal sacs. The taxonomic distribution of character-states for Chs. 77–79 suggests that they are independent.

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 152).

79. M. interhyoideus in males, posterolateral expansion (+). (0) Unexpanded, (1) expanded, restricted to post-tympanic region, (2) expanded, projected posteriorad. Although Faivovich (2002: ch. 43) considered the m. interhyoideus of in *Scinax cruentomma* to be posterolaterally expanded, occupying the space between head and body, we interpreted this lateral expansion as resulting from the subgular development of this muscle (see Ch. 76). Indeed, in species with a posterolaterally expanded m. interhyoideus, this expansion is independent of its development in

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the subgular region, and results from an increase in muscle mass on the post-tympanic region behind the angle of the jaws (Elias-Costa et al., 2021) or from a large lateral expansion of the muscle that forms a posterodorsally oriented lobe (see Elias-Costa et al., 2021: ch. 18, fig. 6).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 43*); Elias-Costa et al. (2021: ch. 18, fig. 6).

80. Vocal sac, internal mucosae (Fig. 12A–D). (0) Fused, forming single cavity, (1) separate, forming paired cavities. We considered the external morphology of vocal sacs, and internal relationship of the vocal sac mucosae to be independent characters, since some externally single, subgular sacs have the internal vocal sac mucosa disconnected (e.g., *Scinax catharinae*; for other examples
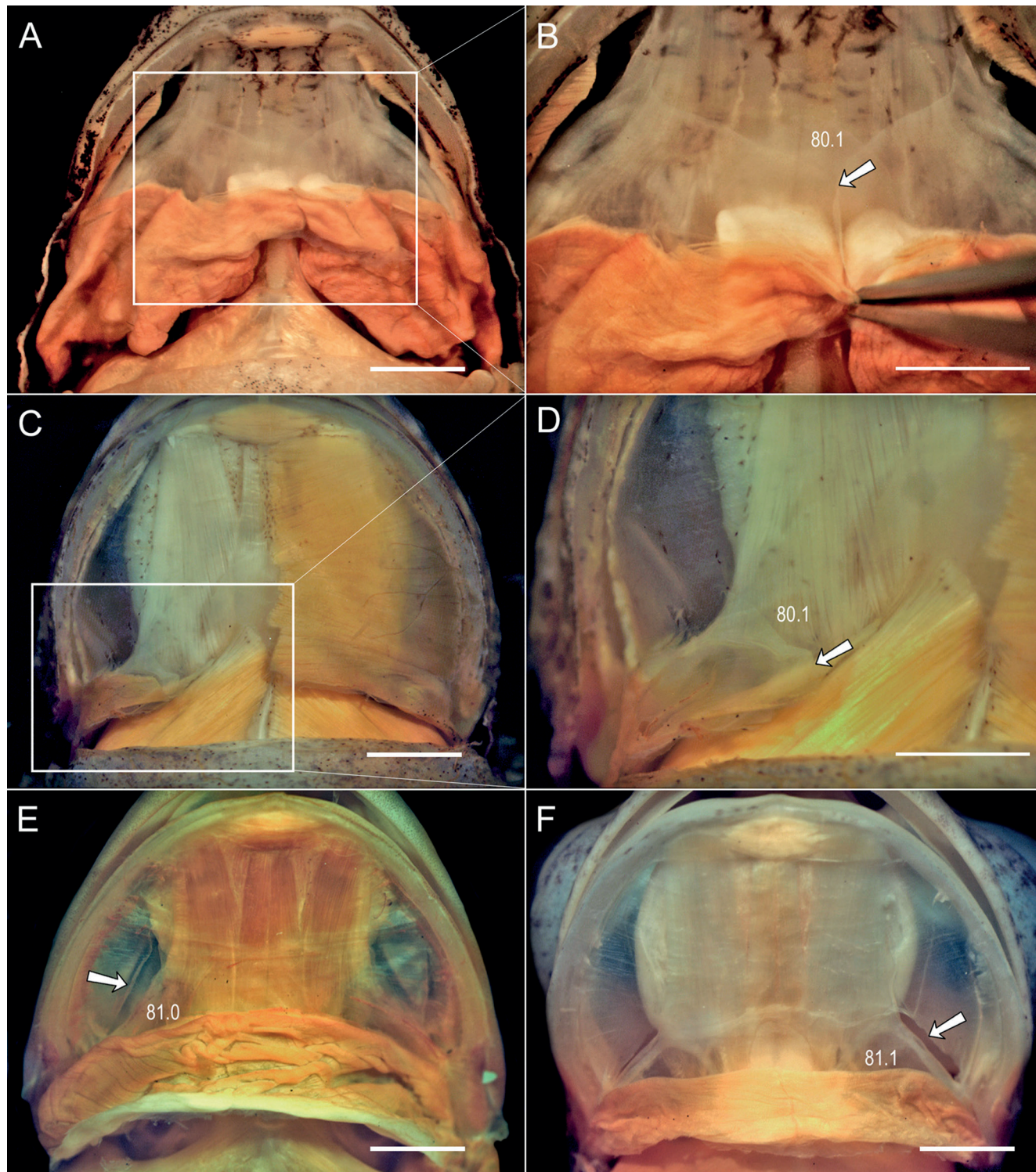

Figure 12. Ventral view of the submandibular region showing states of Chs. 80 and 81. **(A)** and **(B)** *Scinax camposseabrai* (MHNJCH 569, Ch. 80.1). **(C)** and **(D)** *S. catharinae* (CFBH 8499, Ch. 80.1). **(E)** *S. crospedospilus* (MNRJ 44658, Ch. 81.0); the shape and extension of the vocal slit are unclear in this species that has a loose fold delimiting laterally the vocal slit. **(F)** *S. albicans* (CFBH 35542, Ch. 81.1); the shape and extension of the vocal slit are clear in this species that has a well-marked fold delimiting laterally the vocal slit. The upper and middle arrows indicate the medial separation of the vocal sac mucosa. Lower arrows indicate the lateral limit of the vocal slits. Scale bars = 1.5 mm.

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of this independence in other groups see Elias-Costa et al., 2017:8). This character is inapplicable in the two species of *Scinax* in which the vocal is absent (*Scinax ariadne* and *S. skaios*; Lourenço et al., 2016).

Previous usage in phylogenetic studies: Moura et al. (2021: ch. 2).

81. Vocal slits, lateral edge (Fig. 12E, F). (0) Inconspicuous or slightly marked, (1) well defined. Tyler (1971) defined the vocal sac apertures (vocal slits) as an "unsupported" area between the lining of the mouth and the ventral superficial muscles that is traversed by the anterior cornu of the hyoid that invariably forms the medial margin of the aperture. In most species of Scinaxini, a loose fold of the lining of the mouth laterally delimits the vocal sac aperture, so that it is difficult to figure out the shape and extension of the vocal slit (Ch. 81.0; Fig. 12E). The size and shape of the vocal slits are clear in the species that have a well-marked fold that limits laterally the vocal slit (Ch. 81.1; Fig. 12F), the lining of the mouth that surrounds the vocal slit seems to be thicker in these species. Histological studies are necessary to better understand the nature of the three character-states that we define here. This character is inapplicable in the two species of *Scinax* where the vocal sac is absent.

Hand musculature

82. Lateral m. lumbricalis brevis digiti IV. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 166).

83. Lateral m. lumbricalis brevis digiti IV, length of tendon of insertion. (0) Short tendon, (1) long tendon. When the lateral m. lumbricalis brevis digiti IV is present, it inserts on the metacarpophalangeal joint and/or the proximal end of the basal phalanx IV via a short or long tendon. In the latter condition, the tendon adheres to the fascia of the m. flexor brevis profundus digiti IV before it reaches the metacarpophalangeal joint and/or the basal phalanx or inserts directly on the metacarpophalangeal joint and/or the proximal end of basal phalanx (see Ch. 84).

84. Lateral m. lumbricalis brevis digiti IV, relation of the tendon of insertion and the fascia of the m. flexor brevis profundus digiti IV. (0) Adhered to the fascia of m. flexor brevis profundus digiti IV, (1) free from the fascia of m. flexor brevis profundus digiti IV.

85. Lateral m. lumbricalis brevis digiti V: slip originating from the lateral corner of the flexor plate (Fig. 13A). (0) Absent, (1) present. The lateral m. lumbricalis brevis digiti V shows two levels of variation; the first refers to its presence or absence. The second level of variation refers to the origin the m. lumbricalis brevis digiti V, which may be from the flexor plate (this character); from the distal carpal 3-4-5 (on its anterodistal portion; Ch. 86), and from a connective tissue over the flexor

plate and m. flexor accessorius (Ch. 87). Independently of the point of origin, the lateral m. lumbricalis brevis digiti V originates via a long and slender tendon, runs adjacent to the tendo superficialis digiti V, and inserts via a short tendon on the metacarpophalangeal joint or the proximal end of the basal phalanx.

Note that Blotto et al. (2020: fig. 1B) described the slip from the connective tissue over the flexor plate and m. flexor accessorius in *Triprion petasatus* as a slip from the integument. However, it corresponds to the slip from the connective tissue over the flexor plate and m. flexor accessorius as defined here, which is particularly adhered to the integument.

We considered that the three slips of the lateral m. lumbricalis brevis digiti V (flexor plate, distal carpal 3-4-5, or connective tissue over the flexor plate and m. flexor accessorius) are independent characters since they coexist in *Phyllomedusa sauvagii* (from the flexor plate and distal carpal 3-4-5; Chs. 85 and 86), some Allophrynidae and Centrolenidae (*Allophryne relicta*, *A. ruthveni*, and *Espadarana prosoblepon*; from the flexor plate and the connective tissue over the flexor plate and m. flexor accessorius; BLB, personal obs.).

Previous usage in phylogenetic studies: Burton (1996: ch. 18*); Faivovich (2002: ch. 51); Araujo-Vieira et al. (2019: ch. 167*).

86. Lateral m. lumbricalis brevis digiti V, slip originating from distal carpal 3-4-5 (Fig. 13B). (0) Absent, (1) present.

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 167*).

87. Lateral m. lumbricalis brevis digiti V, slip originating on connective tissue over flexor plate and m. flexor accessorius. (0) Absent, (1) present.

88. Burton's ligament. (0) Absent, (1) present. This is a ligament that joins the anterior margin of the distal carpal 3-4-5 with the dorsum of the m. superficialis digiti V.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 52, fig. 13); Araujo-Vieira et al. (2019: ch. 169).

89. M. contrahentis digiti V, length of tendon of origin. (0) Short, (1) long.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 53).

90. M. flexor carpi radialis, development. (0) Origin of the m. flexor carpi radialis not contiguous with the distal portion of the insertion of the m. coracobrachialis, (1) origin of the m. flexor carpi radialis contiguous with the distal portion of the insertion of the m. coracobrachialis. The differences in the origin of the m. flexor carpi radialis are related to the development of this muscle. Like Faivovich (2002), we recognized only two states, but we note that in some species the m. flexor carpi radialis has a noticeably bulbous belly (viz., *Scinax ariadne*, *S. aromothyella*, *S. brieni*, *S. catharinae*, *S. garibaldiae*, *S. goya*, *S. jureia*, *S. lu-*

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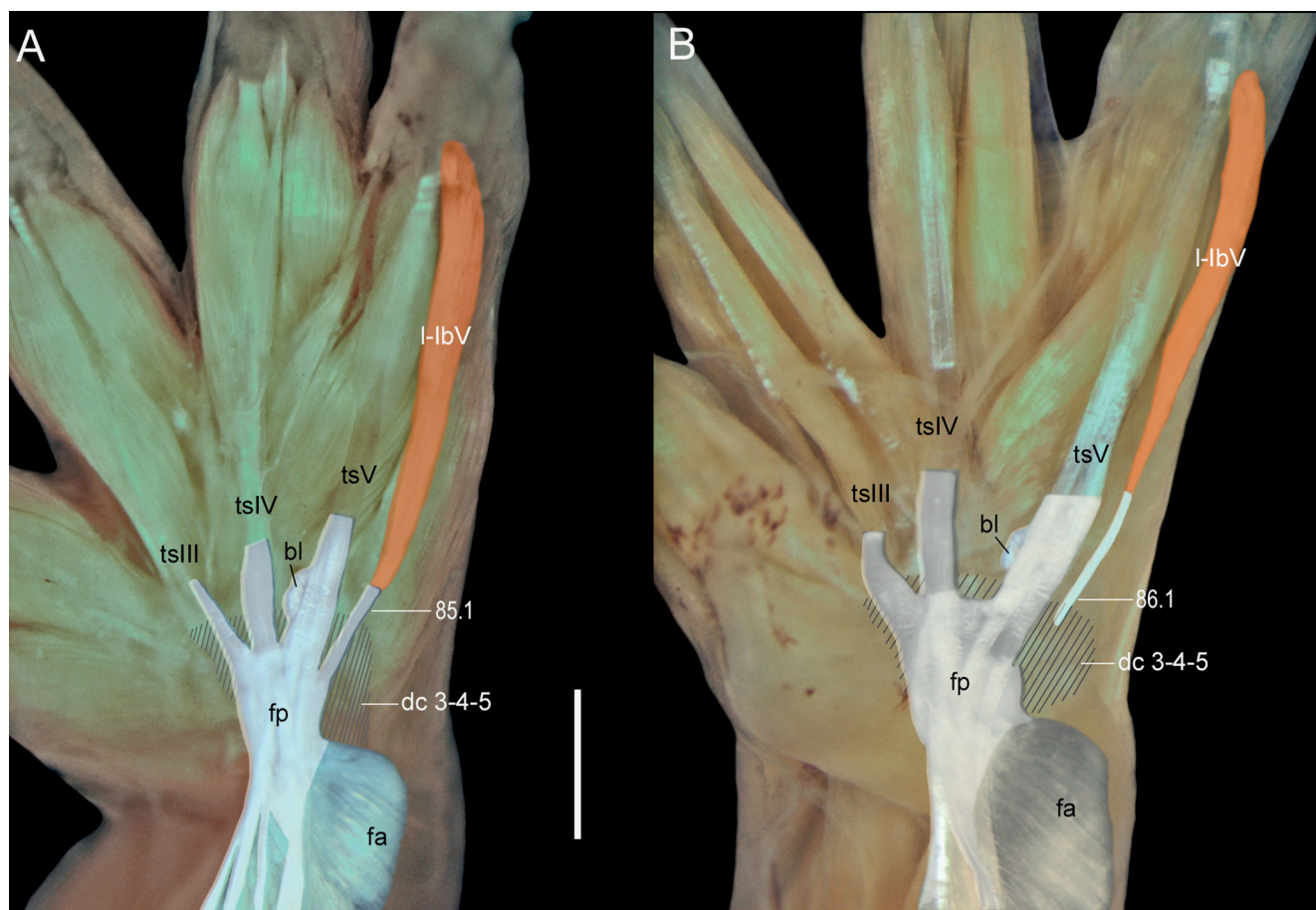
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Figure 13. Origin of lateral m. lumbricalis brevis digiti V (Chs. 85 and 86). **(A)** *Scinax similis* (CFBH 5018, Ch. 85.1). **(B)** *S. constrictus* (CFBH 12514, Ch. 86.1). The Burton's ligament (bl), m. flexor accessorius (fa), flexor plate (fp), m. lumbricalis brevis digiti V (I-lbV), and tendines superficiales digitorum III–V (ts III–V) are digitally highlighted. The dashed portion corresponds approximately to the distal carpal 3-4-5. Scale bars = 5 mm.

izotavioi, *S. longilineus*, *S. obtriangulatus*, and *S. skaios*) resulting in somewhat more robust forearms than those of other species scored with Ch. 90.0. Note that although Faivovich (2002) correctly referred to the origin of the m. flexor carpi radialis, he mistakenly employed the term insertion in the character-state definitions, a problem that is corrected here.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 50).

91. M. extensor digitorum, slip inserting on the metacarpophalangeal joint of digit IV (Fig. 14A–C). (0) Absent, (1) present. The m. extensor digitorum originates on the distal margin of the humerus and extends over the radioulna up to the dorsum of the hand, where it is divided into three slips that run towards the digits III, IV, and V (Burton, 1998; Faivovich, 2002; Blotto et al., 2020). Faivovich (2002) described a slip (as the main, medial slip, or midbranch) that inserts either on metacarpal IV or the tendon of the m. extensor brevis medius digiti IV (see our Chs. 92 and 93). Faivovich (2002: ch. 44, fig. 12) defined a character based on the number of insertions (a single or two insertion points) of the medial slip of the m. extensor digitorum (we consider his medial slip as a portion of our slip attaching to digit IV; see below). However, we redefined the character based on the insertion points and not on the number of insertions or subdivisions of the slip attaching to digit IV. Following this framework, we recognized three slips based on the point of insertion: (i) on the metacarpophalangeal joint of digit IV, approximately on its middle and dorsal surface and in common with the m. extensor brevis superficialis digiti IV (see Fig. 14A–B, labeled as 3); (ii) on the thin tendon of insertion of the m. extensor brevis medius digiti IV (see Fig. 14A–C, labeled as 1); and (iii) on metacarpal IV via a wide, very short tendon, or a fleshy insertion (see Blotto et al., 2020: fig. 1A, labeled as 2). Although we did not find the co-occurrence of the three slips simultaneously in any species (in which case their homology would be refuted by the conjunction test and supporting our hypothesis of three independent characters; Patterson, 1982), we observed the co-occurrence of all of its pairs: condition (i) + (ii) in the *Scinax catharinae* clade; (i) + (iii) in *Itapotihyla*, and (ii) + (iii) in some Pelodrydadinae (our pelodryadine sample is *Ranoidea eucnemis*, which has the m. extensor brevis medius digiti IV absent; however, this condition is present in other species of this group; BLB, personal obs.). Based on this fact and on the markedly different position, connectivity, and presumed function of each slip, we tentatively defined them as independent characters (Chs. 91–93).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 44*, fig. 12); Araujo-Vieira et al. (2019: ch. 170*).

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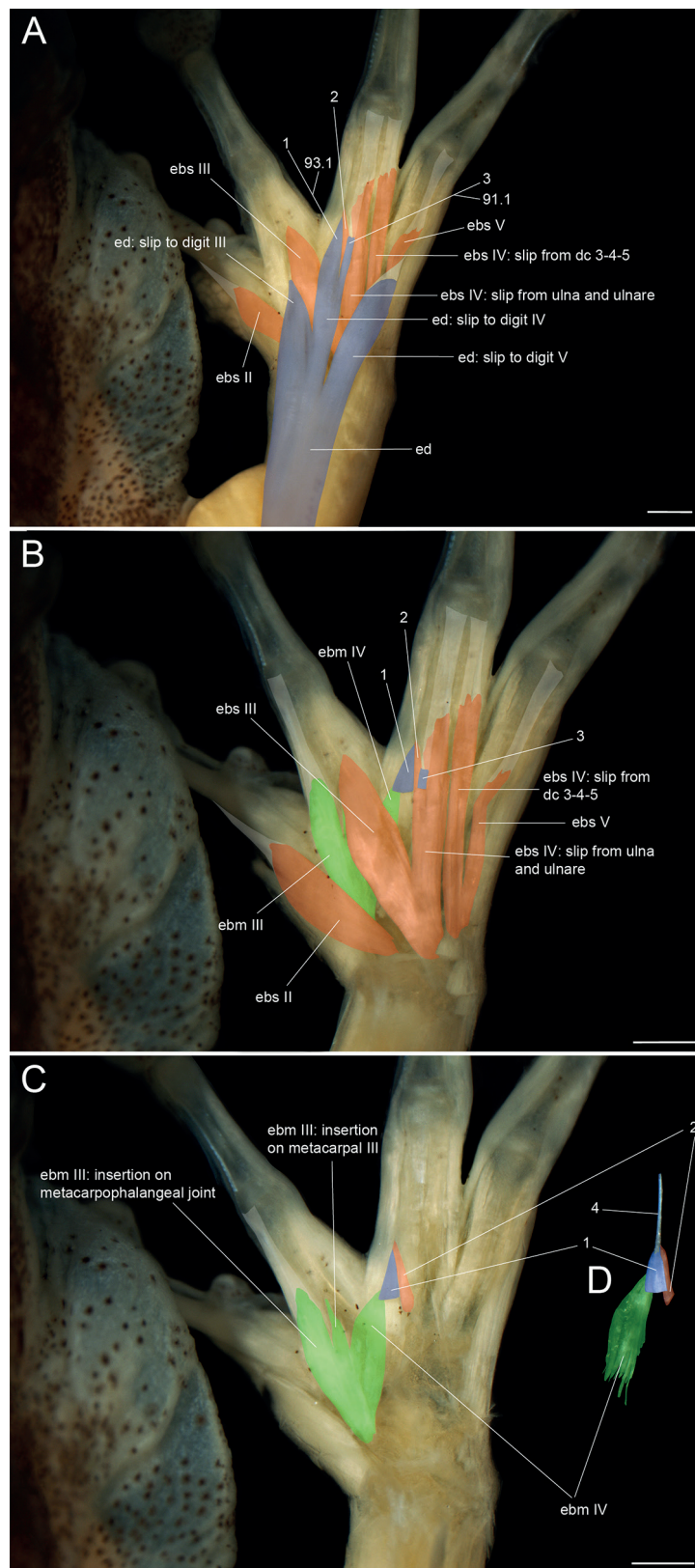
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Figure 14. Dorsal view of the hand of *Scinax rizibilis* (CFBH 35081, Chs. 91.1 and 93.1). **(A)** No muscles removed. Muscles removed in **(B)** m. extensor digitorum and distal end of m. extensor carpi ulnaris; **(C)** m. extensor digitorum, distal end of m. extensor carpi ulnaris, and mm. extensores breves superficiales digitorum II–V; and **(D)** dissected and isolated muscles corresponding to the dorsal view of the m. extensor brevis medius digiti IV, and distal portions of the m. extensor digitorum and the m. extensor brevis superficialis digiti IV. Labeled as "1": slip of the m. extensor digitorum inserting on the tendon of the m. extensor brevis medius digiti IV (Ch. 93.1). Labeled as "2": slip of the m. extensor brevis superficialis digiti IV (with origin from the ulna and ulnare) inserting on the tendon of the m. extensor brevis medius digiti IV. Labeled as "3": slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV on its middle and dorsal surface, in common with the m. extensor brevis superficialis digiti IV (slip with origin from the ulna and ulnare; Ch. 91.1). Labeled as "4": tendon of insertion of the m. extensor brevis medius digiti IV that inserts in common with slips of the m. extensor digitorum (labeled as 1) and m. extensor brevis superficialis digiti IV (labeled as 2); this tendon attaches to the medial region of the metacarpophalangeal joint. ed = extensor digitorum; ebm = extensor brevis medius; ebs = extensor brevis superficialis. Scale bars = 5 mm.

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92. M. extensor digitorum, slip inserting on metacarpal IV. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 45*).

93. M. extensor digitorum, slip inserting on m. extensor brevis medius digiti IV (Fig. 14A–D). (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 45*).

94. M. extensor digitorum, slip inserting on metacarpophalangeal joint of digit V. (0) Absent, (1) present. This slip may insert on the metacarpophalangeal joint via an independent tendon, or in common with other superficial muscles.

Previous usage in phylogenetic studies: Pereyra et al. (2021: ch. 45).

95. M. abductor indicis brevis dorsalis, slip inserting on prepollex. (0) Absent, (1) present. The m. abductor indicis brevis dorsalis originates from the element Y and has up to two slips, both with a fleshy insertion: one inserting on metacarpal II and the other on the prepollex.

96. M. abductor indicis brevis dorsalis, slip inserting on metacarpal II. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Pinheiro et al. (2022: ch. 15).

97. Lateral m. dorsometacarpalis indicis distalis. (0) Absent, (1) present. The mm. dorsometacarpales distales have a fleshy origin from the mediodistal and laterodistal ends of the metacarpals, pass along the fingers, and insert via a tendon on the dorsal sides of the terminal phalanges (Burton, 1996, 1998; Blotto et al., 2020). Faivovich (2002: chs. 55 and 57) reported that the lateral m. dorsometacarpalis indicis distalis and lateral m. dorsometacarpalis distalis digiti III can originate either from the distal margin or medial margin of the metacarpal; we observed that the fibers that originate from the medial margin belong, instead, to the lateral m. dorsometacarpalis indicis proximalis and lateral m. dorsometacarpalis proximalis digiti III, which have a fleshy origin from the proximal to the medial margins of the metacarpals II and III, respectively. For these reasons, we coded only the presence and absence of the mm. dorsometacarpales distales in the lateral or medial parts of digits II, III, and IV (see also Chs. 101 and 108). The absence of the lateral m. dorsometacarpalis indicis distalis was considered a synapomorphy of the *Scinax rostratus* group (sensu Faivovich, 2002; Faivovich et al., 2005).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 54).

98. M. extensor brevis superficialis digiti III, slip originating from the laterodistal end of radioulna (Fig. 15A–C). (0) Absent, (1) present. Contrary to Burton (1996) and Faivovich's (2002) observations, in Scinaxini we

observed that the m. extensor brevis superficialis digiti III has both a slip from the radioulna (with a long tendon of origin) and another from the ulnare (with a fleshy origin), instead of having a single slip originating on the ulnare (Fig. 15C). The m. extensor brevis superficialis digiti III has a single origin from the ulnare in *Gabohyla*, *Phyllomedusa sauvagii*, and *Sphaenorhynchus* (Fig. 15A).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 46*).

99. M. extensor brevis superficialis digiti III, slip originating from the laterodistal end of radioulna (Fig. 15B, C). (0) Fleshy or via a short tendon, resulting in muscle fibers arising at level of the radioulna, (1) via long tendon, resulting in muscle fibers arising distally to the radioulna, at the level of the ulnare. Among the species included in this analysis, the slip from the radioulna of the m. extensor brevis superficialis digiti III arises via a long tendon only in Scinaxini (Ch. 99.1). In this state, the fibers of the slip from the radioulna of the m. extensor brevis superficialis digiti III arise together (i.e., without a discrete gap) with those of the slip that originate from the ulnare (Fig. 15C).

100. M. extensor brevis medius digiti III, slip from element Y. (0) Absent, (1) present. See Blotto et al. (2020: ch. 11) for definition.

101. Lateral m. dorsometacarpalis distalis digiti III. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 56).

102. M. extensor brevis superficialis digiti IV, slip from laterodistal end of radioulna. (0) Absent, (1) present. Contrary to the interpretation of Faivovich (2002), the m. extensor brevis superficialis digiti IV has three slips, defined by their respective origins: laterodistal end of radioulna, ulnare, and lateral margin of distal carpal 3-4-5. In Scinaxini, the slip from the radioulna originates through a long common tendon with the slip from radioulna of the m. extensor brevis superficialis digiti III (see also Ch. 99).

103. M. extensor brevis superficialis digiti IV, slip from radioulna, insertion on m. extensor brevis medius digiti IV. (0) Absent, (1) present. Faivovich (2002: ch. 48) coded the degree of participation of the slip from the ulnare of the m. extensor brevis superficialis digiti IV in the insertion of the midbranch of the m. extensor digitorum. He determined that this participation might involve the whole ulnare slip or only some medial fibers, in which case the lateral portion inserts with a wide tendon on the proximal margin of the basal phalanx. However, our observations lead us to redefine the primary homology in relation to the point of insertion of the slips from radioulna and ulnare. When present, the slip from the radioulna can insert on the tendon of the m. extensor brevis medius digiti IV (Fig. 14B–D, labeled as 2) and/or on the dorsal surface of metacarpal IV at the level of the insertion of
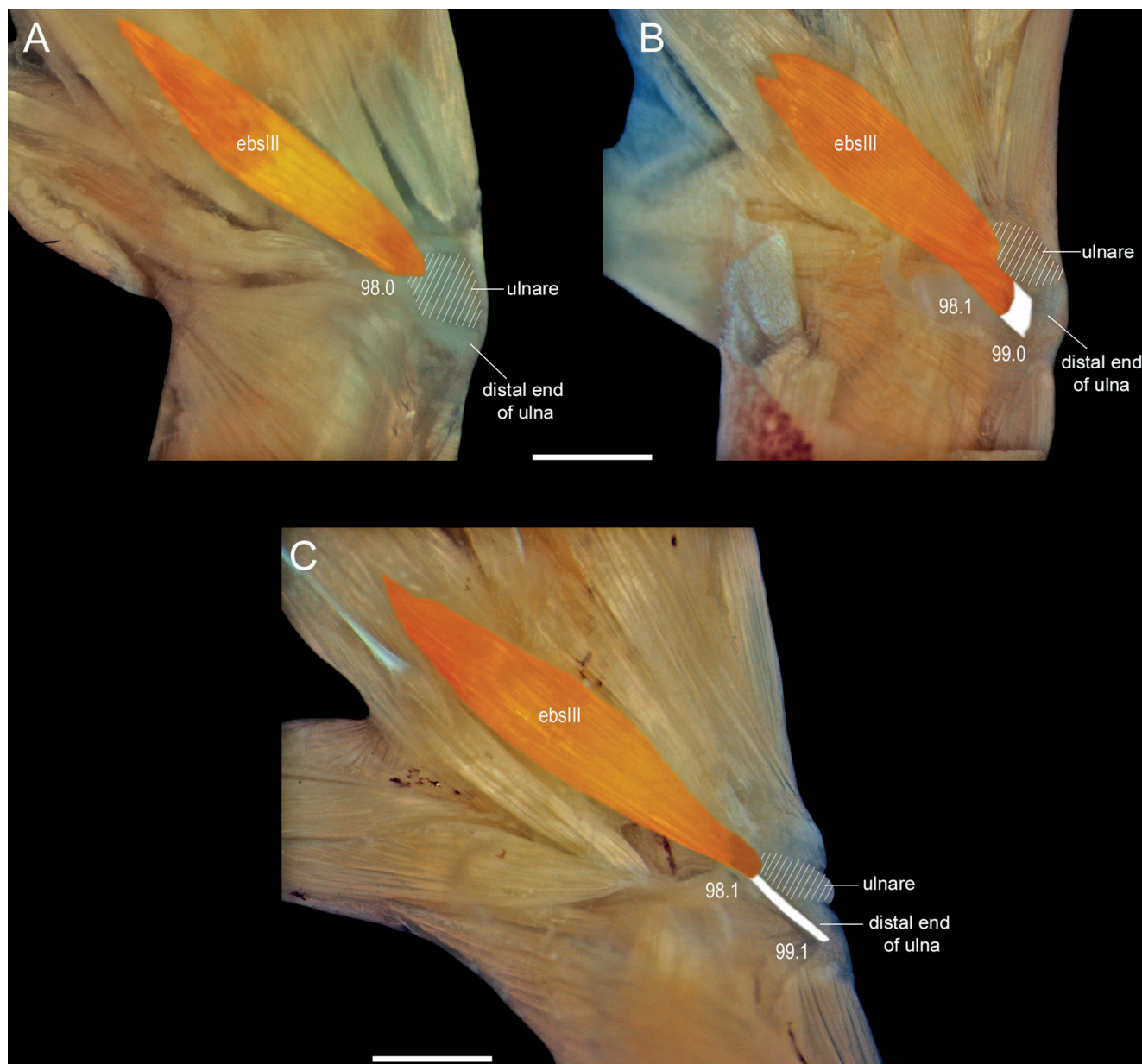
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Figure 15. Origin of the m. extensor brevis superficialis digiti III (Chs. 98 and 99). **(A)** *Sphaenorhynchus caramaschii* (CFBH 6934, Ch. 98.0). **(B)** *Dendropsophus elegans* (MNRJ 53265, Chs. 98.1 and 99.0). **(C)** *Scinax similis* (CFBH 5018, Chs. 98.1 and 99.1). The dashed portion corresponds approximately to the ulnare. The m. extensor brevis superficialis digiti III (ebs III) and its tendon of origin (white) are digitally highlighted. Scale bars = 5 mm.

the m. extensor digitorum on metacarpal IV. In the latter condition, a few fibers of the slip from radioulna can also be inserted on the tendon of the m. extensor digitorum (e.g., *Scinax caldarum* and *S. fuscovarius*). Otherwise, the slip that originates from the ulnare inserts on the tendon of the m. extensor brevis medius digiti IV, the dorsal surface of the metacarpal IV at the level of the insertion of the m. extensor digitorum on metacarpal IV, and/or the metacarpophalangeal joint of digit IV (see Chs. 104–106).

104. M. extensor brevis superficialis digiti IV, slip from ulnare, insertion on metacarpal IV. (0) Absent, (1) present. The insertion of the slip from the ulnare of the m. extensor brevis superficialis digiti IV on the dorsal surface of metacarpal IV and on the tendon of the m. extensor brevis medius digiti IV co-occurs in some species of *Scinax* (see Ch. 105). In this context, there are fewer

muscular fibers inserting on the tendon of the m. extensor brevis medius digiti IV than on the metacarpal IV.

105. M. extensor brevis superficialis digiti IV, slip from ulnare, insertion on tendon of m. extensor brevis medius digiti IV. (0) Absent, (1) present.

106. M. extensor brevis superficialis digiti IV, slip from ulnare, insertion on metacarpophalangeal joint of digit IV (can be partially shared with the intermediate m. dorsometacarpalis proximalis). (0) Absent, (1) present. The insertion on the metacarpophalangeal joint via a flat tendon is the most lateral insertion of the slip that originates on the ulnare. It inserts together with some lateral fibers of the slip from the radioulna (when present). This corresponds to ch. 48.0 from Faivovich (2002), in which the whole ulnare slip of the m. extensor brevis superficia-

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lis digiti IV inserts together with the medial branch of the m. extensor digitorum or, alternatively, on the tendon of the m. extensor brevis medius digiti IV (our Chs. 104 and 105) since the insertion of the slip from the ulnare on the metacarpophalangeal joint is absent in those species.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 48*).

107. Point of insertion of the tendon of the m. extensor brevis medius digiti IV (+). (0) Mediodistal margin of metacarpal IV, (1) metacarpophalangeal joint, (2) proximal interphalangeal joint. The m. extensor brevis medius digiti IV is absent in *Acris crepitans*, *Lysapsus limellum*, *Pseudacris regilla*, and *Ranoidea eucnemis* (Burton, 1996; present work), *Scinax nasicus* (polymorphic; Burton, 1996; Faivovich, 2002), and *S. staufferi* (Faivovich, 2002), therefore these were scored as inapplicable (except for *S. nasicus*). We coded the point of insertion of its tendon, which inserts on the distal margin of metacarpal IV, the metacarpophalangeal joint, or surpasses the basal phalanx to insert on the proximal interphalangeal joint. Contrary to Faivovich's (2002) observations, in all Scinaxini the m. extensor brevis medius digiti IV inserts on the metacarpophalangeal joint (Ch. 107.1). The m. extensor brevis medius digiti IV only inserts on the mediodistal margin of metacarpal IV in *Phyllomedusa sauvagii*.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 49*).

108. Medial m. dorsometacarpalis distalis digiti IV. (0) Absent, (1) present. Faivovich (2002: ch. 58) reported that the fibers of the medial m. dorsometacarpalis distalis digiti IV reach the distal margin of penultimate phalanx IV or the distal margin of basal phalanx IV. Our observations indicate that the medial m. dorsometacarpalis distalis digiti IV is absent in Scinaxini and present only in *Gabohyla*, *Sphaenorhynchus*, and *Xenohyla*, in which this muscle reaches the distal margin of the basal phalanx or the proximal half of the penultimate phalanx. We consider that Faivovich (2002) observed in Scinaxini the medial m. dorsometacarpalis proximalis digiti IV instead. However, in Scinaxini the fibers of this muscle only reach the basal phalanx, not the distal margin of the penultimate phalanx, leading us to conclude that Faivovich (2002) erroneously wrote "distal margin" instead "proximal margin" in the states for this character and reversed the state 58.0 for the state 58.1 in his data matrix. Therefore, we coded the occurrence of the medial m. dorsometacarpalis distalis digiti IV, and defined an additional character to accommodate the variation in the length of the fibers of the slip from metacarpal IV of the medial m. dorsometacarpalis proximalis digiti IV (see Ch. 109).

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 174).

109. Medial m. dorsometacarpalis proximalis digiti IV, slip from metacarpal IV, length of fibers. (0) At most reaching the distal margin of the metacarpal IV, (1) reaching at least the proximal margin of basal phalanx. When the fibers surpass the distal margin of metacarpal IV, they extend from the proximal margin (e.g., *Scinax crospedospilus* and *S. fuscomarginatus*) to the distal third of the basal phalanx of digit IV (*S. catharinae*). We were unable to objectively divide this variation with respect to the fraction of the phalanx that the fibers cover into discrete states, hence we coded the length of the fibers in two states, similar to Burton (1998).

110. Lateral m. dorsometacarpalis proximalis digiti IV, slip from metacarpal IV, length of fibers. (0) At most reaching distal margin of metacarpal IV, (1) reaching at least proximal margin of basal phalanx. The fibers that surpass the distal margin of metacarpal IV (Ch. 110.1) extend from the proximal margin (e.g., *Scinax alter* and *S. fuscomarginatus*) to the distal margin of the basal phalanx IV (e.g., *S. arduous*). This variation is continuous, so we coded the length of the fibers in two states.

111. Medial m. dorsometacarpalis proximalis digiti V, slip from metacarpal IV. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 175).

112. Medial m. dorsometacarpalis proximalis digiti V, slip from metacarpal IV, length of fibers. (0) At most reaching the distal margin of the metacarpal V, (1) reaching at least the proximal margin of the basal phalanx. Similar to Chs. 109.1 and 110.1, when the fibers surpass the distal margin of the metacarpal V, they continuously extend from the proximal margin (e.g., *Scinax nasicus* and *S. trapicheiroi*) to the distal margin of the basal phalanx V (e.g., *S. fuscomarginatus* and *S. perpusillus*).

113. Lateral m. dorsometacarpalis proximalis digiti V. (0) Absent, (1) present.

114. Lateral m. dorsometacarpalis proximalis digiti V, length of fibers. (0) At most reaching distal margin the metacarpal V, (1) reaching at least proximal margin of basal phalanx.

Foot musculature

115. Mm. flexores breves superficiales, structure. (0) Single muscle with a single tendon of insertion, (1) partially or totally divided into a medial and lateral slip, each with its own tendon of insertion. Burton (2004) defined his character 26 for the structure of the tendon of insertion of the mm. flexores breves superficiales as comprising three states: (0) undivided; (1) divided along its length into a medial tendon, from which arises tendo superficialis IV, and a lateral tendon from which arise tendines superficiales III and V, with cross-tendons between the divisions; and (2) divided along its length into a medial tendon, from which arise tendo superficialis IV and m. lumbricalis longus digiti V, and a lateral tendon from which arise tendo superficialis V and m. lumbricalis longus digiti IV.

From the comparison of the figures cited by Burton (2004: figs. 3c, 4a, b), in addition to our observations from

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many species studied by him, we concluded that: (1) the undivided condition of Burton (2004, his state 0) refers to a single tendon of insertion arising from a single muscle; this tendon splits distally into the tendines superficiales praehallucis and I–V, III–V, or IV–V, depending on the species; and (2) the divided condition of Burton (2004, his states 1 and 2) refers to two tendons of insertion that arise each from two partially or totally differentiated slips, a medial and a lateral one; these tendons of insertion of the mm. flexores breves superficiales are named, distally, as the tendines superficiales (III–V or IV–V depending on the species; see Blotto et al., 2020, 2022).

We observed a partial subdivision in some *Dendropsophus* (*D. elegans*, *D. kamagarini*, *D. microps*, *D. minutus*, and *D. sanborni*), which is similar to the divided condition. It differs in that the tendons of insertion of the medial and lateral slips are partially connected along their proximal length by an undefined, thin connective or tendinous tissue; we consider this condition as the divided one (Ch. 115.1) based on similarity. It is noteworthy that this morphology is probably the same reported by Burton (2004) for *Gastrotheca monticola*, *G. ovifera*, and *Hemiphractus johnsoni* (Hemiphractidae), species not studied by us; in any case, Burton (2004) scored these species as undivided. Further investigation is required, including the possibility of an additive transformation series in which the partial subdivision observed in the species of *Dendropsophus* mentioned above (and presumably *G. monticola*, *G. ovifera*, and *H. johnsoni*) is considered as an intermediate state between the undivided (0) and divided (1) conditions as defined here.

Furthermore, since we are scoring whether there is a division of the fleshy portion of the muscle into a medial and lateral slip, we consider as part of our state 1 the states 1 and 2 of Burton (2004). These two character-states from Burton differ in the specific elements to which the slips of the mm. flexores breves superficiales connect distally; however, we consider that this variation should be transferred to separate transformation series (characters) when it is better studied.

Previous usage in phylogenetic studies: Burton (2004: ch. 26*).

116. M. abductor brevis plantaris hallucis, additional insertion on the metatarsophalangeal joint. (0) Absent, (1) present. The m. abductor brevis plantaris hallucis originates from the medial margin of the aponeurosis plantaris and inserts as a single muscle through a thin, short tendon on the proximal third or half along the medioplantar surface of metatarsal I. In some species of *Scinax* (e.g., *S. belloni*, *S. canastrensis*, and *S. catharinae*), the fibers are divided at the tip into two slips; the medial one described above that attaches to metatarsal I and a lateral one that inserts via a thin, long tendon onto the medioplantar surface of the metatarsophalangeal joint of digit I.

117. M. flexor hallucis accessorius, point of insertion on metatarsal I. (0) At most extending along proximal half of metatarsal I, (1) along the whole length of the metatarsal I. The m. flexor hallucis accessorius originates via a short, flat tendon from distal tarsal 2–3, their fibers form a flat muscle with a broad, fleshy insertion along the whole length or on the proximal half of the medioplantar surface of metatarsal I.

118. Differentiated portion of the m. flexor accessorius distalis inserting on the proximal end of the tendo superficialis digiti II. (0) Absent, (1) present. The tendo superficialis digiti II arises from the distal edge of the aponeurosis plantaris (AP) and inserts on the distal phalanx II. In some species, the tendon has what seems to be a proximal muscular head, which is a differentiated portion of the m. flexor accessorius distalis (that inserts on the tendo superficialis digiti II). Consequently, the tendo superficialis digiti II appears to be the tendon of insertion of the m. flexor accessorius distalis, as described by Burton (2004: ch. 31, state 2), although it conserves the origin from the aponeurosis plantaris. The tendo superficialis digiti II observed in *Phyllomedusa sauvagii* is probably not homologous to those of other taxa since it arises only from a fusiform muscle that originates from the distal tarsal 2–3 (sensu Burton, 2004: fig. 3E), and not also from the aponeurosis plantaris, as does the tendo superficialis digiti II of other hylids. Therefore, we considered this character inapplicable for *Phyllomedusa sauvagii*, pending more studies.

Previous usage in phylogenetic studies: Burton (2004: ch. 31, part. fig. 3).

119. M. lumbricalis longus digiti III, accessory tendon of origin from tendo superficialis digiti III. (0) Absent, (1) present. A moderately long, thin tendon arises from the base of the tendo superficialis digiti III, next to the aponeurosis plantaris, and inserts on the medial half of the m. lumbricalis longus digiti III (see Blotto et al., 2020: fig. 3A, labeled as 7).

120. M. flexor brevis profundus digiti IV, slip inserting on metatarsal V (Fig. 16A, B). (0) Absent, (1) present. The m. flexor brevis profundus digiti IV arises via a long, flat tendon from the laterodistal end of the fibulare at the base of digit V, and usually inserts along the length of the lateroventral surface of the metatarsal IV. The presence of an additional slip inserting on metatarsal V was observed in all species of the *Scinax ruber* clade (Fig. 16A), except for *S. squalirostris* and those of the *S. uruguayus* group. All species of the *S. catharinae* clade and outgroups lack the slip inserting on the metatarsal V (Fig. 16B).

Previous usage in phylogenetic studies: Burton (2004: ch. F).

121. Medial m. lumbricalis brevis digiti V, insertion on metatarsal V. (0) Absent, (1) present. The medial m. lumbricalis brevis digiti V comprises a medial and a lateral slip in some species. Both slips originate via a common tendon with the lateral m. lumbricalis brevis digiti IV from the plantar cartilage. The lateral slip originates via a short tendon and inserts via a long, narrow tendon on

Figure 16. Slip of the m. flexor brevis profundus digiti IV inserting on metatarsal V (Ch. 120). **(A)** *Scinax similis* (CFBH 5018, Ch. 120.1). **(B)** *S. agilis* (CFBH 18054, Ch. 120.0). The m. flexor brevis profundus digiti IV (fbpIV), slip of the m. flexor brevis profundus digiti IV on metatarsal V (fbpIV') and its tendon of origin are digitally highlighted. mI–V = metatarsals I to V. Scale bars = 5 mm.

the lateroventral side of the metatarsophalangeal joint, whereas the medial slip originates through a long tendon and inserts via a short tendon on the medioventral surface of the metatarsophalangeal joint (see Blotto et al., 2020: fig. 3B). Burton (2004: ch. 38) suggested that when a single slip is present, it might be the product of the fusion of the medial and lateral tendons. If there is a single slip (possibly the product of the fusion), we also score the presence or absence of an insertion on metatarsal V within this transformation series, assuming that the insertion on metatarsal V of this single muscle is homologous with the insertion of the medial slip when it is differentiated into medial and lateral slips. The condition observed in *Phyllomedusa sauvagii* requires further comments. This species has medial and lateral slips differentiated; however, the lateral (and not the medial) inserts additionally on the metatarsal V. It is not clear at this point if it is homologous to the above-referred insertions on the metatarsal, and thus we coded it provisionally as missing data.

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 180).

122. M. abductor brevis plantaris digiti V, extension of insertion. (0) At most reaching the proximal two-thirds of metatarsal V, (1) reaching at least the distal quarter of metatarsal V. The m. abductor brevis plantaris digiti V arises via a broad tendon from the distal condyle of the

fibulare and has a fleshy insertion along the length of the lateral surface of metatarsal V. We coded the variation with respect to the fraction of the metatarsal V that the fibers cover.

Previous usage in phylogenetic studies: Blotto et al. (2022: ch. 38).

123. M. extensor digitorum longus, insertion on metatarsal II. (0) Absent, (1) present. The m. extensor digitorum longus arises from the distal surface of the tibiofibula via a long, narrow tendon and inserts on the dorsal surface of metatarsal III via a short tendon. In some species, there is an additional insertion via a narrow tendon in the dorsum of metatarsal II (e.g., *Scinax belloni*, *S. eurydice*, and *Xenohyla truncata*).

Previous usage in phylogenetic studies: Burton (2004: ch. 48*); Araujo-Vieira et al. (2019: ch. 183*).

124. M. extensor brevis superficialis hallucis, lateral insertion via a tendon on digit II. (0) Absent, (1) present. The m. extensor brevis superficialis hallucis inserts on the prehallux, metatarsal I, and metatarsophalangeal joint of the hallux. In some outgroups (e.g., *Dendropsophus*, *Phyllodytes luteolus*, and *Xenohyla truncata*) and all species of Scinaxini (unknown for the *S. uruguayus* group), there is an additional insertion via a narrow tendon that passes along the medial margin of digit II, inserting on the metatarso-

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phalangeal joint of digit II (in common with the medial m. dorsometatarsalis proximalis digiti II or m. lumbricalis brevis digiti II) or its distal phalanx (in common with the tendo superficialis digiti II). These insertions on digit II were considered as part of the m. extensor brevis medius hallucis by Burton (2004: ch. G part., fig. 6), but we reidentified it as a portion of the m. extensor brevis superficialis hallucis (BLB and KA-V, personal obs.). These three points of insertion (i.e., m. dorsometatarsalis proximalis digiti II, m. lumbricalis brevis digiti II, and tendo superficialis digiti II) occur in the same region on the digit II (despite the different elements to which they are associated), and they do not co-occur. Based on this, we consider here the occurrence of the insertion on digit II, while the variation related to the different points of insertion on this digit should be eventually considered in a separate multistate character.

Previous usage in phylogenetic studies: Burton (2004: ch. G*, fig. 6); Araujo-Vieira et al. (2019: ch. 184).

125. *Lateral m. dorsometatarsalis hallucis proximalis, length of fibers*. (0) Reaching distal margin of metatarsal I, (1) reaching at least proximal margin of basal phalanx.

126. *Lateral m. dorsometatarsalis hallucis distalis*. (0) Absent, (1) present. This muscle is present in *Scinax acuminatus*; note that Faivovich (2002) scored it as absent.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 59); Burton (2004: char 56*).

127. *Lateral m. dorsometatarsalis distalis digiti II*. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 60); Burton (2004: ch. 56*); Araujo-Vieira et al. (2019: ch. 186).

128. *Lateral m. dorsometatarsalis distalis digiti III*. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 61); Burton (2004: ch. 56*).

129. *Lateral m. dorsometatarsalis distalis digiti III, length of fibers*. (0) Reaching the distal margin of basal phalanx, (1) reaching distal margin of the penultimate phalanx.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 62).

130. *Lateral m. dorsometatarsalis distalis digiti IV*. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Burton (2004: ch. 56*).

131. *Medial m. dorsometatarsalis distalis digiti V*. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 63); Burton (2004: ch. 56*).

132. *Lateral m. dorsometatarsalis distalis digiti V*. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 64); Burton (2004: ch. 56*); Araujo-Vieira et al. (2019: ch. 187).

133. *Lateral m. dorsometatarsalis distalis digiti V, length of fibers*. (0) Reaching distal margin of basal phalanx, (1) reaching distal margin of penultimate phalanx.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 65); Araujo-Vieira et al. (2019: ch. 188).

Larval morphology

134. *Oral disc, posterior gap in the row of marginal papillae*. (0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 66); Grant et al. (2006: ch. 92); Araujo-Vieira et al. (2019: ch. 137); Orrico et al. (2021: ch. 170*).

135. *Oral disc, continuity between the lateral margins and the posterior part*. (0) Continuous, (1) discontinuous. In most species of the *Scinax rostratus* group, *S. auratus*, *S. cuspidatus*, *S. crospedospilus*, *S. juncae*, and *Scarthyla goinorum*, the lateral margins of the oral disc are completely separated from the posterior part, which in these taxa correspond to the labial arm supporting P-3 (see Ch. 137).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 67).

136. *Oral disc, shape of posterior margin when folded*. (0) Straight, (1) concave. In larvae of many species of the *S. catharinae* clade, the posterior margin of the oral disc has a characteristic concave shape when folded, in contrast to the straight posterior margin in tadpoles of *S. cardosoi*, the *S. perpusillus* groups, and the *S. ruber* clade.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 68).

137. *Oral disc, P-3 labial tooth row position (+)*. (0) Inside oral disc, (1) directly on margin of the oral disc, (2) forming labial arm. The P-3 labial tooth row shows three different topological situations in the larvae of the taxa included in this analysis. The first condition is the most common within Type IV anuran larvae (Orton, 1953), in which P-3 is contained within the margins of the oral disc. In the second condition, present in larvae of *Scinax acuminatus* and *S. quinquefasciatus* (also present in *Sphaenorhynchus dorisae*, not included in this analysis; see Araujo-Vieira et al., 2019:485), P-3 is shorter than P-1 and P-2 and develops on the margin of the oral disc. In the last condition, P-3 develops on a projection present in larvae of the species of the *S. rostratus* group, *S. auratus*, *S. cuspidatus*, *S. crospedospilus*, *S. juncae*, and *Scarthyla goinorum*, which was first termed the labial arm by McDiarmid and Altig (1990).

Previous usage in phylogenetic studies: Duellman and Wiens (1992: ch. 18*); Faivovich (2002: ch. 69).

138. *Oral disc, P-3 labial tooth row length (+)*. (0) Equal to P-2, (1) ca. ½ of P-2, (2) ca. ¼ of P-2.

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Previous usage in phylogenetic studies: Faivovich (2002: ch. 70).

139. Oral disc, anterior gap in row of marginal papillae. (0) Absent, (1) present. We are aware that there is variation in the width of the anterior gap, particularly in larvae of the *Scinax catharinae* clade (e.g., compare the gap in *S. melanodactylus* and *S. longilineus*; Pezzuti et al., 2021). We did not quantify this variation but expect that its study will result in additional states for this character.

Previous usage in phylogenetic studies: Silva (1998: ch. 110*); Faivovich (2002: ch. 71).

140. Oral disc, marginal papillae on the posterior margin of the oral disc, size. (0) Same size as marginal papillae on angular and anterior margins of oral disc, (1) at least twice the size of the marginal papillae on angular and anterior margins of oral disc (Kolenc et al., 2003: fig. 1C; Barreto et al., 2019: fig. 1D). The marginal papillae are small in the angular and anterior portions, and more scarce and larger, at least approximately twice the size of the smaller ones, in the posterior portion of the oral disc in species of the *Scinax uruguayus* group, *S. camposseabrai*, and *S. quinquefasciatus* (Kolenc et al., 2003; Baldo et al., 2019; Barreto et al., 2019). Larvae of *Dendropsophus minutus*, *Sphaenorhynchus caramaschii*, and *Sp. carneus* also have a few large marginal papillae, at least approximately twice the size of the smaller ones, located mainly in the posterior portion of the oral disc and arranged together or alternating with the small ones (Kenny, 1969; Suárez-Mayorga and Lynch, 2001a; Araujo-Vieira et al., 2015a). This character was considered inapplicable for the species that have the labial arm projection (see Ch. 130).

Previous usage in phylogenetic studies: Araujo-Vieira et al. (2019: ch. 136).

141. Oral cavity, lingual papillae. (0) Absent, (1) present (pair).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 72).

142. Oral cavity, keratinized spurs behind the lower jaw-sheath, dorsal to the infralabial papillae. (0) Absent, (1) present. These spurs were reported as absent for *S. longilineus* and *S. trapicheiroi* (Faivovich, 2002); however, we observed non-colored, weakly developed keratinized spurs in these species, like those described for *S. berthae* by Alcalde et al. (2011: fig. 3H).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 73).

143. Oral disc, position (+). (0) Ventral, (1) subterminal, (2) terminal. The terms ventral, subterminal, and terminal used to describe the position of the oral disc are those employed by Faivovich (2002). These terms define the position of the oral disc in reference to an imaginary line that separates the oral disc from the body. If this line is perpendicular to the main body axis, the oral disc is terminal; if the line forms an acute angle with the main body axis, the oral disc is subterminal; if the line is nearly parallel to the main body axis, the oral disc is ventral.

Previous usage in phylogenetic studies: Duellman (1970: ch. VV*); Duellman and Trueb (1983: ch. F*); Duellman (2001a: ch. VV*); Faivovich (2002: ch. 74); Araujo-Vieira et al. (2019: ch. 134); Orrico et al. (2021: ch. 168*).

144. Vent tube, position. (0) Dextral, (1) medial. Faivovich et al. (2005) reported that *Gabohyla pauloalvini* (as *Sphaenorhynchus pauloalvini*) and *Sphaenorhynchus* (*Sp. bromelicola*, *Sp. platycephalus*, and *Sp. prasinus*) have a dextral vent tube attached to the free margin of the ventral fin like that of most species of the *Scinax catharinae* clade (Faivovich, 2002). However, our observations on larvae of *Sphaenorhynchus* indicated that they present a medial vent tube (sensu Altig and McDiarmid, 1999: fig. 3.5 H and L), as reported by Araujo-Vieira et al. (2019: ch. 145).

Previous usage in phylogenetic studies: Inger (1967: ch. "Vent (larvae)," 375, Table 1); Kluge and Farris (1969: ch. "Vent (larvae)," 30, 31); Grant et al. (2006: ch. 96); Barrionuevo (2017: ch. 93); Araujo-Vieira et al. (2019: ch. 145); Pereyra et al. (2021: ch. 75).

145. Dextral vent tube, position relative to lower caudal fin. (0) Above the margin of the lower fin, (1) at the margin of the lower fin.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 75*, fig. 14); Araujo-Vieira et al. (2019: ch. 134*); Orrico et al. (2021: ch. 185*).

146. Eyes, position. (0) Eyes not visible ventrally, (1) eyes visible ventrally. We follow Faivovich (2002) in expressing the degree of lateralization of the eyes in relation to their visibility in ventral view.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 76).

147. Spiracle, medio-distal portion of internal wall. (0) Fused to the body wall, (1) free from the body wall.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 77).

148. Intestinal mass, coiling axis. (0) Orthogonal or suborthogonal to the longitudinal body axis, (1) subparallel to the longitudinal body axis. Faivovich (2002) defined the orientation of the intestinal mass in relation to the longitudinal body axis drawing an imaginary line through its coiling axis. This line can be orthogonal to the longitudinal axis of the body or subparallel to the longitudinal body axis. Subsequent study of tadpoles from multiple species indicated that the original definition implied rigidity in terms of the angle between the coiling axis and longitudinal body axis that was exceeded even by the intraspecific variation in larvae scored as having an orthogonal coiling axis. For this reason, we modified state 0 to orthogonal or suborthogonal, with the understanding that the coiling axis varies 90°–110° with respect to the longitudinal body axis. The subparallel configuration varies 140°–170°.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 78*, fig. 15).

149. Nostril, fleshy projection of medial margin.
(0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 79); Araujo-Vieira et al. (2019: ch. 133); Orrico et al. (2021: ch. 184*).

150. Golden spots or stripes between eyes and nostrils.
(0) Absent, (1) present.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 80).

151. Oral disc, keratinized dark plates on sides of lower jaw-sheath.
(0) Absent, (1) present. Among the species included in this analysis, the keratinized, dark plates on the sides of the lower jaw-sheath are present only in larvae of *S. camposseabrai* and the *S. uruguayus* group (Kolenc et al., 2003; Faivovich et al., 2005; Alcalde et al., 2011; Barreto et al., 2019). Keratinized plates have been described in larvae of other hylids, the pelodryadines *Litoria peronii* and *L. verreauxi*, and distant groups of anurans, such as several species of *Hylambates*, *Kassina*, *Paracassina*, *Phlyctimantis*, and *Semnodactylus* (Hyperoliidae), *Astylosternus robustus* (Arthroleptidae), and the *Lithobates pipiens* group (Ranidae; Altig and McDiarmid, 1999; Anstis, 2002, 2013; Altig, 2006; Channing et al., 2013).

Chromosome morphology

152. Morphology of chromosome pair 1.
(0) Metacentric, (1) submetacentric. Cardozo et al. (2011) suggested that the submetacentric morphology of pair 1 is most likely a synapomorphy of the *Scinax catharinae* clade. Pair 1 is also submetacentric in the karyotypes of *Dendropsophus* (2n = 30; e.g., Medeiros et al., 2003; Suárez et al., 2013) as in the *Scinax catharinae* clade, but probably not homologous with it; it is significantly smaller, and its size is equivalent to pairs 3 and 4 of the hylines with 2n = 24 (Gruber et al., 2005; Cardozo et al., 2011). This character was treated as inapplicable for the species included in this analysis having a 2n different from 24. Peixoto et al. (2015) reported a metacentric morphology of pair 1 in *S. belloni*, but in their figs. 1–3 the pair 1 seems to be submetacentric like the other species of the *Scinax catharinae* clade.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 81).

153. NOR-bearing chromosomes (-).
(0) Pair 1, (1) pair 2, (2) pair 3, (3) pair 4, (4) pair 5, (5) pair 6, proximal position, (6) pair 6, distal position, (7) pair 7, proximal position, (8) pair 7, distal position, (9) pair 8, (10) pair 9, proximal position, (11) pair 9, distal position, (12) pair 11, proximal position, (13) pair 11, distal position, (14) pair 12. Data regarding the location of the NOR (Nucleolar Organizer Region) are available for some species of Scinaxini (see Barrio and Pistol de Rubel, 1970; Bogart, 1973; Anderson, 1991; Cardozo et al., 2011; Nogueira et al., 2015a,b;

Lourenço et al., 2016; Baldo et al., 2019). Faivovich (2002: ch. 82) scored the NORs on pair 10 in *Scinax elaeochroa* (Anderson, 1991) and on pair 12 in *S. fuscovarius*, *S. hayii* (Baldissera et al., 1993), *S. perereca* (Pombal et al., 1995a), and *S. staufferi* (Anderson, 1991). However, Cardozo et al. (2011) reported the NORs on pair 11 in *S. fuscovarius*, *S. hayii*, and *S. perereca*. Considering the new information provided by Cardozo et al. (2011) and given the morphological similarity of the small-sized chromosomes pairs 10, 11 and 12, we reevaluated the states employed by Faivovich (2002) and considered the NORs to be located on pair 11 for all those species. This reasoning was not extended to other groups such as *Boana*, in which other chromosome markers allowed chromosomes 11 and 12 to be distinguished (Ferro et al., 2018). We considered the NOR-bearing chromosomes in *Dendropsophus* as inapplicable considering the difficulties in establishing homology with the small chromosomes of other hylids (Suárez et al., 2013).

Previous usage in phylogenetic studies: Cocroft (1994: ch. 47*); Faivovich (2002: ch. 82*); Pereyra et al. (2021: ch. 89*).

154. Number of chromosomes (+).
(0) 22, (1) 24, (2) 26, (3) 30.

Previous usage in phylogenetic studies: Heyer, 1975 (ch. 37*); Duellman and Trueb (1983: ch. A*); Grant et al. (2006: ch. 173*); Araujo-Vieira et al. (2019: ch. 192); Orrico et al. (2021: ch. 164*).

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155. Oviposition site (-).
(0) Aquatic, permanent or temporary ponds, (1) aquatic, streams, (2) aquatic, axils of bromeliads, (3) aquatic, subterranean nests near ponds or streams, (4) terrestrial, leaves overhanging water. We follow Faivovich (2002) in defining the states of this character in terms of the location of oviposition and not the reproductive environment (i.e., open or closed areas). For states (0) and (1) we assumed that the oviposition site was the same as the location males used for calling in species for which there is no explicit mention of oviposition (Faivovich, 2002).

Previous usage in phylogenetic studies: Heyer and Liem (1976: ch. 42*); Silva (1998: ch. 116*); Faivovich (2002: ch. 83*); Mendelson et al. (2000: ch. 47*); Grant et al. (2006: ch. 107*); Araujo-Vieira et al. (2019: ch. 191*); Orrico et al. (2020: ch. 200*); Pereyra et al. (2021: ch. 85*).

156. Calling position.
(0) Not head down, (1) head down. This character was first discussed by Duellman and Wiens (1992). The definition of state 0 stems only from descriptive economy, to avoid listing all the other variable positions in which treefrogs engage while calling, including horizontal, vertical head-up, slightly inclined downwards and upwards, in most cases being these positions commonly adopted by the same individual during vocal activity.

Previous usage in phylogenetic studies: Faivovich (2002: ch. 84).

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157. Toe I and finger II backward-bending behavior.
(0) Absent, (1) present. The ability to bend finger I and toe I backward on the same plane was first reported by Jungfer (1986), who observed this behavior in *Scinax boulengeri*, *S. elaeochroa*, and *S. garbei*. Faivovich (2002) observed this behavior in *S. berthae*, *S. acuminatus*, *S. nasicus*, *S. fuscovarius*, *S. granulatus*, *S. perereca*, and *S. squalirostris*. Subsequently, there were no literature reports of this behavior for other species of *Scinax*, but we have observed it for many other species, including *S. aromothyella*, *S. caissara*, *S. fontanarrosai*, *S. pinimus*, *S. littoralis*, *S. similis*, and *S. uruguayus*. See Jungfer (1986: fig. 8) for photographs of this behavior. We follow Faivovich (2002) in assuming that species whose webbing reaches the base of the disc of toe I are unable to perform this behavior (see Ch. 58).

Previous usage in phylogenetic studies: Faivovich (2002: ch. 85).

158. Physiological chlorosis. (0) Absent, (1) present. The high concentration of biliverdin associated with a carrier protein of the serpin family (biliverdin-binding serpin, BBS) confers a blue-green hue to bones and soft tissues known as physiological chlorosis; it is evident in living specimens and contributes in different degrees to their coloration (Barrio, 1965; Taboada et al., 2020). The biochemical basis of chlorosis, its evolution, and its ecological role in frogs was extensively discussed by Taboada et al. (2020). Barrio (1965) reported chlorosis in low concentrations in *Scinax nasicus* as measured spectroscopically; in this study, we considered physiological chlorosis as present only when it was visually evident in living specimens (scored from direct observations or photographs). DB and JF have extensive field experience with this species in Argentina and never found specimens with green tissues; CB, FK, and JAL have similar experience in Uruguay, and twice they collected juveniles of this species with green bones in Paysandú and Artigas. Considering the extremely low occurrence, we are not sure if this represents natural variation or a pathologic condition, and for that reason, we coded it as polymorphic in this species. Polymorphic occurrence of chlorosis has also been reported for *S. quinquefasciatus* (Ron et al., 2018) and is evident in photographs of specimens from some populations in Ecuador that are considered here as *Scinax* sp. 37. The physiology of chlorosis still requires extensive studies. This phenomenon has been mentioned in the taxonomic literature in several families (for review, see Taboada et al., 2020), but it has never been included in phylogenetic analyses.

RESULTS

The total evidence parsimony analyses considering gaps as fifth state resulted in 2,386 most parsimonious trees of 92,744 steps. The strict consensus tree condensed to species level is shown in Figs. 17–19 (also in Appendix S7). The analysis recovered *Scinax* (sensu Faivovich et al., 2005) as monophyletic (100% jackknife).

Its sister taxon is a poorly supported clade (< 50% jackknife) composed of Dendropsophini, Hylini, Lophyohylini, Pseudini, and Sphaenorhynchini (Fig. 17). Within *Scinax* (Figs. 18, 19), the *S. catharinae* clade is recovered monophyletic (100% jackknife). The *S. catharinae* group is not monophyletic, as the *S. perpusillus* group is nested within it (Fig. 18). The clade including *S. agilis* and *S. melanodactylus* is the sister of all remaining species of the *S. catharinae* clade, followed by *S. argyreornatus* and two major clades. One of these includes *S. feioi*, *S. cardosoi*, and the monophyletic *S. perpusillus* group. The other major clade includes all remaining species of the *S. catharinae* group. The *S. ruber* clade (sensu Faivovich et al., 2005) as well as its *S. rostratus* and *S. uruguayus* groups (Fig. 19) are well supported (jackknife ≥ 90%). The interspecific relationships are generally well supported (≥ 90% jackknife) within the *Scinax catharinae* and *S. ruber* clades; exceptions are the poorly supported (65% jackknife) monophyly of the *S. perpusillus* group as the sister taxon of *S. cardosoi* and related lineages, and some poorly supported (< 50% jackknife) monophyletic groups within each clade that are discussed in the following sections. The results of the maximum likelihood analyses using IQ-TREE (Appendix S8) and the total evidence parsimony analysis treating gaps as missing data are highly congruent with the total evidence results treating gaps as fifth state in terms of the well-supported clades, with all incongruence involving poorly supported nodes in the parsimony analyses. For the purposes of our discussion, we consider the strict consensus of the optimal phylogenetic hypotheses resulting from the total evidence analysis treating gaps as fifth state.

Furthermore, the resulting phylogenetic hypothesis combined with additional molecular (pairwise distances for 16S rRNA gene), morphological and bioacoustic evidence allowed the delimitation of 57 candidate species of *Scinax*. Our results revealed nine confirmed candidate species (CCSs) and 10 unconfirmed candidate species (UCSs) in the *S. catharinae* clade, and 10 CCSs and 28 UCSs in the *S. ruber* clade.

DISCUSSION

The position of Scinaxini in Hylinae: a reassessment of the phenotypic evidence

Our results rejected the monophyly of both the tribe Dendropsophini as defined by Faivovich et al. (2005) and the *Scinax* + *Sphaenorhynchus* clade of Duellman et al. (2016), corroborating Faivovich et al.'s (2018) recognition of Sphaenorhynchini and the restriction of Scinaxini to *Scinax*. The monophyly of Hylini is corroborated, as is the monophyly of Pseudini and Dendropsophini sensu Duellman et al. (2016). The latter two whether newly defined (Pseudini) or redefined (Dendropsophini), are applied to clades that have consistently been recovered since Faivovich et al. (2005). Scinaxini is the poorly supported (jackknife < 50%) sister taxon of a clade composed of the exemplars of Dendropsophini, Pseudini, Hylini, Lophyo-

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hylini, and Sphaenorhynchini. The relationships among these tribes are poorly supported (Fig. 17) and have been highly variable in recent analyses, with Scinaxini obtained as the sister taxon of Pseudini, closely related to Sphaenorhynchini and Dendropsophini (Faivovich et al., 2005), or the sister taxon of Sphaenorhynchini (always poorly supported), closely or distantly related to Dendropsophini and Pseudini (Wiens et al., 2006, 2010; Pyron and Wiens,

2011; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018).

Relatively recent phylogenetic analyses using high-throughput DNA sequencing with a low (Feng et al., 2017; Hime et al., 2021) or very low (Streicher et al., 2018; Hutter and Duellman, 2023) sampling density of hylids recovered–when the sampling included exemplars of all hyline tribes–the exemplars of Scinaxini as sister taxon of
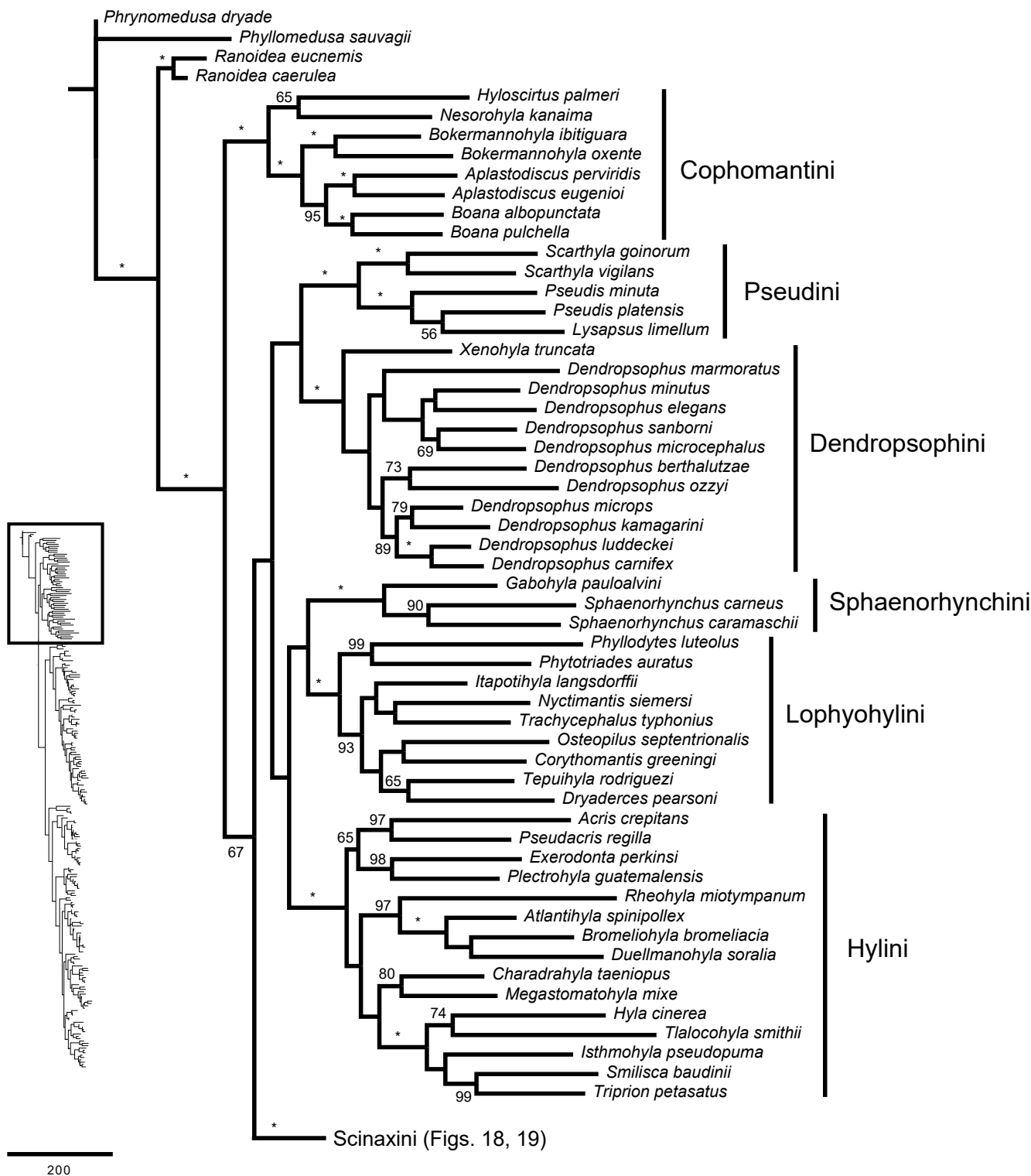

Figure 17. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 1 of 3: Outgroups. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.
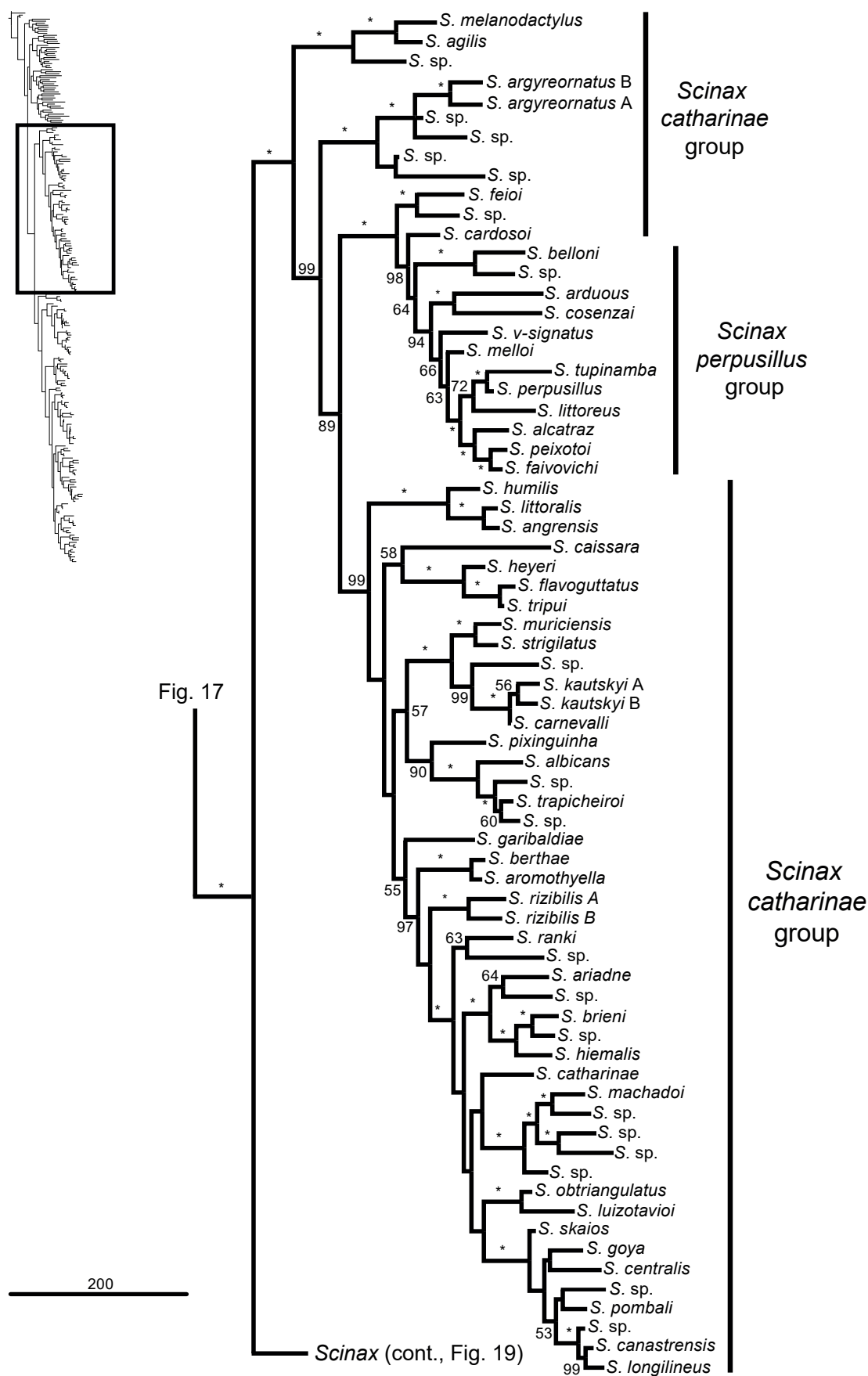
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Figure 18. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 2 of 3: The *Scinax catharinae* clade. The topology is condensed to species level and shows the current taxonomy of Scinaxini. All species labeled "sp." are candidate species discussed in the text and shown in detail in the figures corresponding to the species groups. Note that *S. insperatus* is nested within *S. perpusillus*. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.
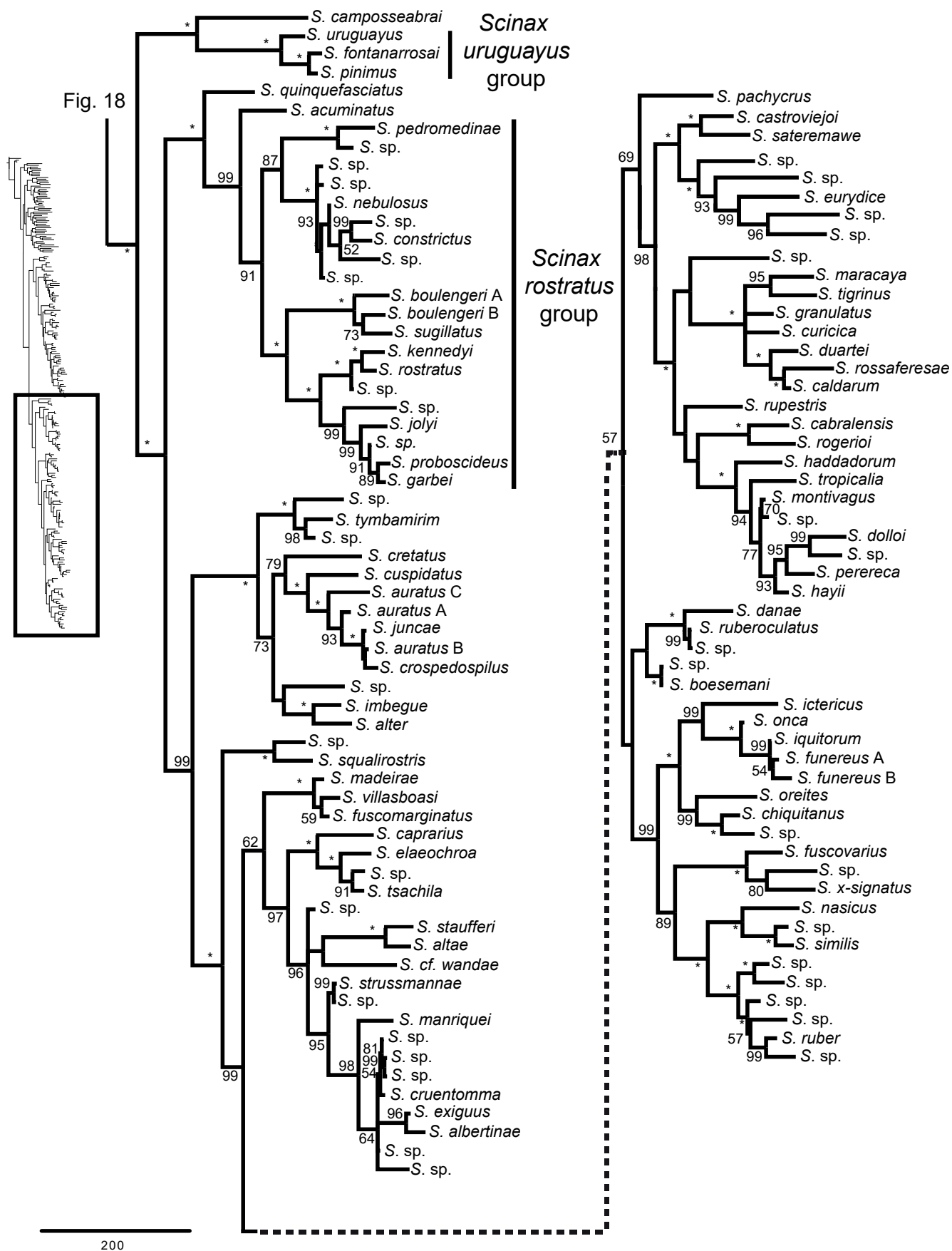
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Figure 19. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 3 of 3: The *Scinax ruber* clade. The topology is condensed to species level and shows the current taxonomy of Scinaxini. All species labeled "sp." are candidate species discussed in the text and shown in detail in the figures corresponding to the species groups. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency. Dashed lines connecting parts of the tree are not proportional to branch-lengths.

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Sphaenorhynchini, or of a clade including Dendropsophini, Hylini, Lophyohylini, Pseudini, and Sphaenorhynchini.

The main goal of our analysis was to provide a rigorous test of the monophyly of Scinaxini and its internal relationships, and not the relationships between Scinaxini and other hylids nor the relationships within each of the other hyline tribes, given that previous studies have performed stronger tests of those relationships (Faivovich et al., 2005, 2018; Wiens et al., 2006, 2010; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018; Araujo-Vieira et al., 2019; Pinheiro et al., 2019; Blotto et al., 2021; Orrico et al., 2021). Nevertheless, some putative morphological synapomorphies proposed for Scinaxini and outgroups merit discussion.

Duellman and Wiens (1992) suggested (i) reduced webbing on the hand and (ii) presence of an anterior process of the hyale as possible morphological synapomorphies of *Scarthyla + Scinax*. The monophyly of this clade is rejected in our analyses, corroborating other studies that included DNA sequences (Faivovich et al., 2005; Wiens et al., 2005; Wiens et al., 2006, 2010; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018). First, *Scarthyla* and *Scinax* share the absence of webbing between fingers II and III, and basal webbing between fingers III, IV, and V. We did not include characters describing the amount of hand webbing in our analysis, but if we consider that the extension along the edge of each digit varies independently (as argued by Grant et al., 2006), multiple characters could be conflated here. Therefore, further examination is required to delimit character-states that describe the levels of hand webbing reduction in Hylidae. Then, the presence of an anterior process on the hyale is plesiomorphic at the level of the common ancestor of all hylid tribes (Ch. 30.1); otherwise, the absence of an anterior process of the hyale is a synapomorphy of *Sphaenorhynchus* (Ch. 30.0; see also Araujo-Vieira et al., 2019: ch. 64.0), with many instances of homoplasy within Hylidae (also absent at least in *Dendropsophus*, *Boana albopunctata*, *Hyla cinerea*, *Itapotihyla langsdorffii*, *Phyllomedusa sauvagii*, and *Smilisca baudinii*, just considering the outgroups included in our study).

The monophyly of *Scarthyla*, *Scinax*, and *Sphaenorhynchus*, as proposed by Duellman and Wiens (1992), is also rejected by our analyses and previous studies (Faivovich et al., 2005; Wiens et al., 2005, 2006; Duellman et al., 2016). Duellman and Wiens (1992) proposed three putative morphological synapomorphies for this group: (i) narrow sacral diapophyses; (ii) anteriorly inclined alary processes of the premaxillae; and (iii) tadpoles with large, laterally positioned eyes.

The shape of the sacral diapophyses sensu Duellman and Wiens (1992) was redefined by Faivovich (2002: ch. 21), who suggested that unexpanded sacral diapophyses are a synapomorphy of *Scinax*. Subsequently, Faivovich et al. (2005) suggested that this character-state might be a synapomorphy of a more inclusive clade of Hylinae. In our analyses, unexpanded sacral diapophyses (our Ch. 22.1) are a synapomorphy of at least the common ancestor of Hylinae (Appendix S9), while the expanded sacral di-

apophysis (our Ch. 22.0) is a synapomorphy of the *S. uruguayus* group (sensu Faivovich et al., 2005; Baldo et al., 2019), with many instances of homoplasy within Hylidae (in our outgroups at least[2] in Dendropsophini, *Aplastodiscus + Boana*, *Gabohyla pauloalvini*, *Hyla cinerea*, *Osteopilus septentrionalis*, *Phyllomedusa sauvagii*, *Smilisca baudinii*, *Sphaenorhynchus carneus*, *Trachycephalus typhonius*, and *Triprion petasatus*).

Araujo-Vieira et al. (2019: ch. 19) and Orrico et al. (2021: ch. 15) included the orientation of the alary processes of the premaxilla with different character definitions in their phylogenetic studies. Our phenotypic dataset did not include this character because in *Scinax* there is an extensive amount of interspecific variation in the position of the alary process, with a continuum from the anteriorly inclined to the vertical process, impeding a discrete definition of the character-states. This situation is different from that reported for *Gabohyla*, *Scarthyla*, *Sphaenorhynchus*, *Xenohyla*, and some species of *Dendropsophus* (Duellman and de Sá, 1988; Duellman and Wiens, 1992; Araujo-Vieira et al., 2019; Orrico et al., 2021); the ancestral character reconstruction of the position of the alary process in Hylinae will require a clarification of the diversity of this character in *Scinax*, for a reasonable definition of the character-states.

We were unable to objectively delimit states to describe proportional eye size in larvae. However, regarding eye position, the character-state eyes not ventrally visible as defined by Faivovich (2002: ch. 76.0; our Ch. 146.0) optimizes ambiguously on our topology (Appendix S9). It could be a synapomorphy of the *S. catharinae* clade (Ch. 146.0, with instances of homoplasy at least in a few species of the *S. ruber* clade, *Gabohyla*, and species of the tribes Cophomantini, Hylini, and Lophyohylini), or plesiomorphic at the level of the common ancestor of Hylinae.

Faivovich et al. (2005) proposed that the undivided tendon of the mm. flexor breves superficiales (Burton, 2004: ch. 26.0; see our Ch. 115.0) could be a synapomorphy of the clade composed of *Lysapsus*, *Pseudis*, *Scarthyla* (Pseudini), and *Scinax* (Scinaxini). Our results rejected the monophyly of these tribes (see also Wiens et al., 2006, 2010; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016) and indicate that the single mm. flexores breves superficiales with a single tendon of insertion optimizes ambiguously on our topology. It could be a synapomorphy of Scinaxini (Ch. 115.0, with at least some instances of homoplasy in the tribes Hylini, Lophyohylini, and Pseudini), or plesiomorphic at the level of the common ancestor of the sister taxon of Cophomantini (Appendix S9).

Izecksohn (1959, 1998) suggested a possible sister group relationship between *Xenohyla* and *Scinax* on the basis of (i) the presence of a coracoid ridge (our Ch. 21.1) and (ii) a subgular, internal vocal sac (our Ch. 63.0). The coracoid ridge is present in all species of *Scinax*, *Dendropsophus*, *Gabohyla*, *Scarthyla*, *Xenohyla*, almost all *Sphaenorhynchus* observed in this study, and several other hylids, suggesting that this might be a synapomor-

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2   Phenotypic characters are not scored for all outgroup terminals.

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phy of a more inclusive clade (Appendix S9). The subgular, internal vocal sac is a synapomorphy of the *S. catharinae* clade, with a reversal in one of its internal clades and an independent origin in *X. truncata* (Appendix S9).

Two morphological synapomorphies have been proposed for Dendropsophini as defined by Faivovich et al. (2005): (i) the absence of "nuptial excrescences" (referring to the absence of a dark stratum corneum in the nuptial pad, our Ch. 66.0) and (ii) the absence of lingual papillae in the larvae (our Ch. 141.0). In our results, the pale nuptial pad is a synapomorphy of Hylinae (Appendix S9); however, this inference is contingent on our outgroup sample, which lacks exemplars of some clades that have dark nuptial pads (e.g., *Myersiohyla*; Faivovich et al., 2013), and in the context of a more thoroughly sampled phylogenetic hypothesis for Hylinae the ancestral character reconstruction state would likely be different. The absence of lingual papillae in larvae optimizes ambiguously; it could be a synapomorphy of *Scinax* (with instances of homoplasy in all species of *Dendropsophus*, *Phyllodytes*, and *Scarthyla*, whose larvae have been studied; Wassersug, 1980; Duellman and de Sá, 1988; Echeverria, 1997a; Faivovich, 2002; Vera Candioti et al., 2004; Dias et al., 2019), or plesiomorphic at the level of the sister taxon of Cophomantini (Appendix S9).

Subsequent to Faivovich et al. (2005), molecular phylogenetic analyses of Hylidae have corroborated (Wiens et al., 2006, 2010) or rejected (Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018) the monophyly of Dendropsophini, but *Scinax* has consistently been recovered as sister to *Sphaenorhynchus*, albeit with poor support (bootstrap with RAxML < 50%; Shimodaira–Hasegawa < 64%). The phylogenetic position of Scinaxini within Hylinae remains unstable; we are not aware of any putative phenotypic synapomorphy shared by Scinaxini and Sphaenorhynchini.

Phenotypic synapomorphies of *Scinax*

The monophyly of *Scinax* is well supported (100% jackknife) and delimited by molecular evidence and 13 phenotypic transformations. For a complete list of the phenotypic synapomorphies see the Section "An evidence-based taxonomy of Scinaxini," below, and Appendix S9. Our results corroborate that (i) elliptical discs of fingers and toes (our Ch. 43.1, with a reversal in the *S. uruguayus* group), (ii) the m. pectoralis portio abdominalis concealing the m. obliquus externus (our Ch. 70.1) and (iii) the ability to bend finger II and toe I backwards (our Ch. 157.1) as synapomorphies of *Scinax* as suggested by Duellman and Wiens (1992), Faivovich (2002), and Faivovich et al. (2005).

Nevertheless, contrary to Faivovich's (2002) observations, the m. extensor brevis superficialis digiti III with a single origin from the ulnare is not a synapomorphy of *Scinax*, because it originates from both radioulna and ulnare (see our Ch. 98) in all species of *Scinax*. Rather, the synapomorphy of *Scinax* is (iv) the m. extensor brevis superficialis digiti III originating from the laterodistal end of

the radioulna via a long tendon (Ch. 99.1). This character optimizes ambiguously for this node in the phylogenetic hypotheses in which *Scinax* is sister to Sphaenorhynchini (Wiens et al., 2006, 2010; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016) because this muscle has a single origin from the ulnare in species of this tribe, rendering Ch. 99 inapplicable.

In addition to the four character-states mentioned above, Faivovich (2002) also inferred the following synapomorphies of *Scinax*: (v) occluded frontoparietal fontanelle (equivalent to what we considered here a partially occluded fontanelle, our Ch. 2.3); (vi) unexpanded diapophysis (our Ch. 22.1); (vii) postaxial toe webbing of toe I that does not extend beyond the subarticular tubercle (our Ch. 58.1)—also suggested by Duellman and Wiens (1992) as synapomorphy of *Scinax*—; (viii) origin of the m. pectoralis abdominalis via well-defined tendons (our Ch. 69.1); (ix) presence of the slip of the lateral m. lumbricalis brevis digiti V originating from the lateral corner of the flexor plate (our Ch. 85.1); and (x) the absence of lingual papillae (our Ch. 141.0).

In our analysis, the partially occluded frontoparietal fontanelle (Ch. 2.3) is not a synapomorphy of *Scinax*; it optimizes as a synapomorphy of a more inclusive clade, the sister taxon of Cophomantini (Appendix S9). As reported previously by Faivovich et al. (2005), the unexpanded sacral diapophyses (Ch. 22.1) optimize ambiguously; they could be a synapomorphy of Hylinae or even a more inclusive clade of Hylidae (Appendix S9). Alternatively, in the phylogenetic context of Pyron and Wiens (2011) and Pyron (2014), in which *Scinax* is the sister taxon of Sphaenorhynchini, but distantly related to Dendropsophini and Pseudini, the unexpanded sacral diapophyses optimize as a synapomorphy of *Scinax*, with several instances of homoplasy in Hylinae (also present in *Acris crepitans*, *Bokermannohyla ibitiguara*, *Hyloscirtus palmeri*, *Itapotihyla langsdorffii*, *Nyctimantis siemersi*, *Phyllodytes*, *Pseudis*, *Scarthyla*, some species of *Sphaenorhynchus*, and *Tepuihyla rodriguezi*, from the outgroups included in this study).

The postaxial toe webbing of toe I that does not extend beyond the subarticular tubercle (Ch. 58.1) optimizes ambiguously in the common ancestor of *Scinax*, due to missing data and homoplasy in Cophomantini (Appendix S9). A denser sampling of this tribe could contribute to clarify the issue.

Our observations indicate that the m. pectoralis abdominalis originating via well-defined tendons (our Ch. 69.1) is present in all species of *Scinax*, as suggested by Silva (1998), but also occurs in several outgroup taxa, including our exemplar species of Pelodryadinae (*Ranoidea eucnemis*). In the context of a denser sampled phylogenetic hypothesis for Hylidae, it could be a synapomorphy either of Hylinae (see also Faivovich et al., 2005; Wiens et al., 2006, 2011; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018) or a more inclusive clade of Hylidae.

The lateral m. lumbricalis brevis digiti V originating from the lateral corner of the flexor plate (our Ch. 85.1) optimizes ambiguously in our analysis; it could be plesio-

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morphic for Hylinae or it could be a synapomorphy of *Scinax* (Appendix S9). Nevertheless, it is a synapomorphy of *Scinax* in the context of the phylogenetic hypotheses of Faivovich et al. (2005), Wiens et al. (2006, 2011), Pyron and Wiens (2011), Pyron (2014), Duellman et al. (2016), and Jetz and Pyron (2018), with instances of homoplasy in *Dendropsophus kamagarini*, *D. microps*, *D. minutus*, *Rheohyla miotympanum*, and *Xenohyla truncata*.

Finally, the last character-state proposed as a synapomorphy of *Scinax* by Faivovich (2002), the absence of larval lingual papillae (our Ch. 141.0), was also hypothesized to be a synapomorphy of Dendropsophini (as formerly defined, including, besides *Dendropsophus* and *Xenohyla*, *Scinax*, *Sphaenorhynchus*, and the clades now recognized as Pseudini) by Faivovich et al. (2005). This was based on the absence of these papillae in *Dendropsophus*, *Scarthyla*, and *Scinax* (Wassersug, 1980; Duellman and de Sá, 1988; Echeverria, 1997a; Faivovich, 2002; Vera Candioti et al., 2004; Dias et al., 2019), with an inferred reversal in *Lysapsus* and *Pseudis* (de Sá and Lavilla, 1997; Vera Candioti, 2004), and noticing that it was unknown at that time in *Sphaenorhynchus* and *Xenohyla*. The lingual papillae are now known to be absent in *Xenohyla* (Dias et al., 2023), and present in *Gabohyla* and *Sphaenorhynchus* (Araujo-Vieira et al., 2019; P.H. Dias, personal comm.) and the remaining outgroup taxa whose larvae have been studied (Faivovich, 2002; Vera Candioti, 2007; TLP, personal obs.). In our results, the absence of lingual papillae in larvae optimizes ambiguously at the level of the sister taxon of Cophomantini and the sister taxon of *Scinax* (Appendix S9). In other phylogenetic hypotheses in which *Scinax* is likewise not closely related to *Dendropsophus* and *Scarthyla* (Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016), this character-state is a synapomorphy of *Scinax*, with known instances of homoplasy at least in Dendropsophini, *Phyllodytes*, and *Scarthyla* (Wassersug, 1980; Duellman and de Sá, 1988; Echeverria, 1997a; Faivovich, 2002; Vera Candioti et al., 2004; Dias et al., 2019, 2023).

Duellman and Wiens (1992) suggested that the concave loreal region (our Ch. 44.1) could be a synapomorphy of *Scinax*. This character optimizes ambiguously in our analysis (Appendix S9); it could be a synapomorphy of *Scinax*, with instances of homoplasy in some outgroup taxa or a synapomorphy of a more inclusive clade (also present at least in *Itapotihyla langsdorffii*, *Osteopilus septentrionalis*, *Phyllodytes luteolus*, *Pseudacris regilla*, *Ranoidea eucnemis*, *Smilisca baudini*, *Tepuihyla rodriguezi*, and *Triprion petasatus* among outgroups that we studied). It optimizes as a synapomorphy of *Scinax* in three different phylogenetic scenarios: *Scinax* as sister taxon of *Pseudis* + *Scarthyla* (Faivovich et al., 2005); *Scinax* as sister taxon of *Gabohyla* + *Sphaenorhynchus* and closely related to *Dendropsophus*, *Pseudis*, *Scarthyla*, and *Xenohyla* (Wiens et al., 2006, 2010); and *Scinax* as sister taxon of *Gabohyla* + *Sphaenorhynchus*, but distantly related to *Dendropsophus*, *Pseudis*, *Scarthyla*, and *Xenohyla* (Pyron and Wiens, 2011; Pyron, 2014).

Finally, Burton (2004: ch. F) also suggested that the m. flexor brevis profundus digiti IV (as m. flexor ossis

metatarsus IV) with an additional insertion on the metatarsal V (our Ch. 120.1) could be a synapomorphy of *Scinax*. Our observations indicate that it is a synapomorphy of the clade that includes all exemplars of *S. ruber* clade but *S. camposseabrai* + the *S. uruguayus* group, with a reversal to single insertion on metatarsal IV in *S. squalirostris* (Ch. 120.0).

Julianus, *Ololygon*, and *Scinax* sensu Duellman et al. (2016)

Since the early 1980s, some authors (Almeida and Cardoso, 1985; Pombal et al., 1995b; Langone and Cardoso, 1997) have referred to the recognition of the former "*rubra*" and "*catharinae*" groups (as defined by León, 1969; Duellman, 1970a; and Lutz, 1973a) into at least two genera on the basis of morphological and behavioral characters, and reproductive biology. The results of the cladistic analyses of Faivovich (2002) and Faivovich et al. (2005) were congruent with the recognition of two major clades, the *Scinax ruber* and *S. catharinae* clades. Subsequent molecular analyses corroborated the monophyly of *Scinax* and its major clades (e.g., Wiens et al., 2010; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018).

Our results corroborated the monophyly of *Scinax* (sensu Faivovich et al., 2005), as well as its two major clades, the *S. catharinae* and *S. ruber* clades with 100% jackknife support (Figs. 18–19). Duellman et al. (2016) resurrected *Ololygon* for the *S. catharinae* clade and restricted *Scinax* to the species of the *S. ruber* clade sensu Faivovich (2002) and Faivovich et al. (2005) minus the *S. uruguayus* group sensu Faivovich et al. (2005), for which they described the new genus *Julianus*. The genera were poorly defined by Duellman et al. (2016) based on a few characteristics shared by most of the species included in the three genera, without any regard to synapomorphies proposed either by earlier authors or themselves.

Ololygon was defined as "Small to medium-sized frogs with slightly truncate discs on fingers and toes, webbing reduced between fingers and absent between fingers I and II; venter immaculate, eggs deposited in streams or terrestrial bromeliads" (Duellman et al., 2016:26; fingers numbered I–IV). *Scinax* was defined as "Small to medium-sized frogs with slightly truncate discs on fingers and toes, webbing reduced between fingers and absent between fingers I and II; venter immaculate; eggs deposited in ponds" (Duellman et al., 2016:28). *Julianus* was defined as "Small frogs with slightly truncate discs on fingers and toes, webbing reduced between fingers and absent between fingers I and II; venter immaculate; eggs deposited in ponds" (Duellman et al., 2016:28). The fact that the characters used to define *Julianus* are identical to those of *Scinax* and differ from those used to diagnose *Ololygon* only in oviposition site, besides not allowing the confident assignment of any of the recognized species to any of the genera, begs the question of what taxonomic problems were solved by recognizing the three genera.

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We recognize *Ololygon* in the same sense as Duellman et al. (2016) and provide in the section below a complete diagnosis. Furthermore, based on our results, we redefine the *O. catharinae* group (Faivovich, 2002) and the *O. perpusilla* group (Faivovich et al., 2005), and erect five new species groups in this genus.

Duellman et al. (2016) erected *Julianus* for the *Scinax uruguayus* group and recognized *Scinax* for all remaining species of the *S. ruber* clade as defined by Faivovich et al. (2005). In our results, *S. camposseabrai* is recovered as the well-supported (100% jackknife) sister of the *S. uruguayus* group, which together form the sister of the remaining species of the *S. ruber* clade (Fig. 19). This position of *S. camposseabrai* renders *Scinax* sensu Duellman et al. (2016) paraphyletic. Considering our phylogenetic hypothesis, there are two alternative taxonomic changes to preserve the monophyly of *Scinax*: (1) recognize the entire clade as *Scinax*, with *Julianus* as a junior synonym of *Scinax*, or (2) redefine *Julianus* to include *S. camposseabrai* and restrict *Scinax* to the remaining species of that clade. As such, the decision to retain *Julianus* and *Scinax* or treat them as a single taxonomic unit (for which *Scinax* has priority) is subjective (as is every decision involving the partitioning of a monophyletic taxonomic unit). However, given that phenotypic synapomorphies support the monophyly of both clades, we prefer the second option (see the Section "An evidence-based taxonomy of Scinaxini" for synapomorphies of these genera).

Therefore, we redefine *Scinax* (excluding *S. camposseabrai*) as a well-supported taxon (100% jackknife) delimited by molecular data and three phenotypic synapomorphies. Also, we redefine *Julianus* to include *S. camposseabrai*, forming a well-supported (100% jackknife) clade delimited by molecular data and seven phenotypic synapomorphies (see "An evidence-based taxonomy of Scinaxini," below). The external morphological differences between adult *S. camposseabrai* and *Julianus* are notable (see Bokermann, 1968; Baldo et al., 2019); however, larvae of these species share colored keratinized plates on the sides of the lower jaw-sheath and the marginal papillae on the posterior margin of the oral disc at least twice the size of the marginal papillae in the angular and anterior margins (see Alcalde et al., 2011; Baldo et al., 2019; Barreto et al., 2019).

Julianus + *Scinax* is well supported (100% jackknife; Fig. 19) and delimited by molecular evidence. The single phenotypic synapomorphy proposed previously (as the *Scinax ruber* clade sensu Faivovich et al., 2005) was the position of the vent tube above the margin of the ventral fin in larvae (Faivovich, 2002; Faivovich et al., 2005). However, this character-state (our Ch. 145.0) optimizes ambiguously on our topology, being either plesiomorphic for Scinaxini or a synapomorphy of *Julianus* + *Scinax* (Appendix S9). In a phylogenetic context in which Scinaxini is closely related to Dendropsophini and Pseudini (Faivovich et al., 2005; Wiens et al., 2006, 2010), this character-state is plesiomorphic for *Scinax* because it is also present in at least some larvae of *Dendropsophus* (e.g., *D. elegans*, *D. microps*, *D. minutus*, *D. sanborni*, *D. kamagarini*; this

work; TLP, personal obs.; P.H. Dias, personal comm.), *Xenohyla truncata*, and *Scarthyla goinorum* (the vent tube is medial in *Scarthyla vigilans*; Suárez-Mayorga and Lynch, 2001b). However, in alternative hypotheses in which Scinaxini is distantly related to these taxa (Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016), it could be a synapomorphy of *Julianus* + *Scinax*.

Within *Scinax*, we redefine the *S. rostratus* group (Faivovich, 2002) and recognize 12 new species groups. Only one species remains unassigned to any group. The species groups were delimited to facilitate the taxonomic research in *Scinax*, considering clades as phenotypically homogeneous and as well supported as feasible. We employed the earliest described species to name the new species groups; in the cases of several redefined groups, we refrained from using names previously reported in the literature to avoid confusion regarding their contents.

In the diagnoses below, we provide lists of phenotypic synapomorphies and comment on ambiguous optimizations of other potential synapomorphies when relevant; homoplasies with outgroup taxa are referred only for the tribe and genera, not for species groups (see Appendix S9 for a complete list of synapomorphies and optimization of all phenotypic characters). In the case of the genera and species groups of Scinaxini, we include comparisons based on synapomorphies and commonly employed diagnostic characters (both are differentiated), and a characterization. These are followed by comments on phylogenetic relationships, phenotypic evidence, and taxonomy.

An evidence-based taxonomy of Scinaxini Duellman et al., 2016

Scinaxinae Duellman et al., 2016. Type genus *Scinax* Wagler, 1830.

Scinaxini—Faivovich et al. (2018). First treatment as a tribe of Hylinae Rafinesque, 1815.

Sister taxon. Scinaxini is the sister taxon of a poorly supported clade including Dendropsophini, Hylini, Lophyohylini, and Sphaenorhynchini.

Diagnosis. The tribe Scinaxini is well supported (100% jackknife) and delimited by molecular evidence and 13 phenotypic synapomorphies. These include (1) round or trapezoid-shaped medial sesamoid of the ilio-sacral articulation (Ch. 24.1); (2) elliptical discs on fingers and toes (Ch. 43.1, homoplastic with *Pseudacris regilla*, and with one reversal to round discs in an internal clade of *Julianus*); (3) compound pectoral fold, with pre-and postaxillar elements (Ch. 46.0, with reversals to single preaxillar pectoral fold in an internal clade of *Julianus* and some species of *Scinax*, Ch. 46.1, and other instance of homoplasy in *Smilisca baudinii*); (4) m. pectoralis portio abdominalis concealing the m. obliquus externus (Ch. 70.1); (5) inconspicuous or slightly marked lateral margin of vocal slits (Ch. 81.0, with one instance of homoplasy in *Ololygon humilis* and *Xenohyla truncata*); (6) Burton's ligament pres-

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ent (Ch. 88.1, with reversals in *O. humilis* and the *S. squalirostris* group); (7) absence of the slip of the m. abductor indicis brevis dorsalis inserting on the prepollex (Ch. 95.0, with reversals to the presence of this slip in a few species of *Scinax*, Ch. 95.1); (8) m. extensor brevis superficialis digiti III originating from the laterodistal end of radioulna via a long tendon (Ch. 99.1, with one instance of homoplasy in *Pseudacris regilla*); (9) presence of the slip of the m. extensor brevis superficialis digiti IV originating from the laterodistal end of radioulna (Ch. 102.1, absent in *O. luizotavioi*, Ch. 102.0); (10) presence of medial m. lumbricalis brevis digiti V inserting on metatarsal V (Ch. 121.1, with instances of homoplasy in internal clades of the *Ololygon catharinae* group and Hylini); (11) presence of lateral insertion of the m. extensor brevis superficialis hallucis via a tendon on digit II (Ch. 124.1, with instances of homoplasy in Dendropsophini and Lophyohylini); (12) presence of keratinized spurs behind the lower jaw-sheath, dorsal to the infralabial papillae (Ch. 142.1, with reversals in internal clades of the *O. catharinae* and the *S. rostratus* groups, and other instances of homoplasy in *Itapotihyla langsdorffii*, *Phyllodytes luteolus*, and *Pseudis platensis*); and (13) ability to bend finger II and toe I backwards (Ch. 157.1).

From a taxonomic perspective, the elliptical discs on fingers and toes differentiate most Scinaxini (except for an internal clade of *Julianus*) from all other tribes of Hylinae. The postaxial webbing of toe I reaching the subarticular tubercle, or basal/absent (traditionally expressed as reduced webbing between toes I and II; e.g., Duellman and Wiens, 1992) differentiates Scinaxini from Pseudini, Sphaenorhynchini, and most Cophomantini, Dendropsophini, Hylini, and Lophyohylini. Scinaxini can be further differentiated from Cophomantini, Lophyohylini, and, at least, some Hylini, by the prepollex comprising 2–3 cylindrical distal elements (an enlarged prepollex comprising a blade- or protruded spine-shaped distal element; Pinheiro et al., 2022), and from some Cophomantini, and most Hylini and Lophyohylini by the pale nuptial pad (dark in most species of these latter two tribes; Duellman, 2001; Blotto et al., 2021; Pinheiro et al., 2022). The m. pectoralis portio abdominalis concealing the m. obliquus externus is unique to Scinaxini, at least among hylids. In terms of larval morphology, the dextral vent tube differentiates larvae of Scinaxini from Sphaenorhynchini and most Pseudini (median vent tube; Suárez-Mayorga and Lynch, 2001b; Santana et al., 2013, 2016; Araujo-Vieira et al., 2019), and the absence of a fleshy projection on the medial margin of the nostril differentiate larvae of Scinaxini from Sphaenorhynchini and most larvae of Cophomantini (this paper; Kolenc et al., 2008; Sánchez, 2010; Faivovich et al., 2013; Pezzuti et al., 2015, 2021; Araujo-Vieira et al., 2019). The 2/3 LTRF differentiates larvae of Scinaxini from Dendropsophini (except for *Xenohyla* that has 2/3, *Dendropsophus* have at most one A- and two P- tooth rows; Orrico et al., 2021; Dias et al., 2023), and most Cophomantini and Lophyohylini (at least four P- tooth rows; except for several species in the *Boana albopunctata*, *B. pulchella*, and *B. punctata* groups, a few species of *Bokermannohyla*,

and many highly modified phytotelm- dwelling larvae of Lophyohylini; Kolenc et al., 2008; Faivovich et al., 2013; Pezzuti et al., 2015, 2021; Pinheiro et al., 2019; Blotto et al., 2021).

Characterization. These small to medium-sized treefrogs (12–53 mm) are characterized by elliptical discs on fingers and toes (round only in a an internal clade of *Julianus*), webbing absent between fingers II and III and reduced between other fingers; postaxial webbing of toe I reaching the subarticular tubercle; concave loreal region (flat only in one species of *Julianus*); presence or absence of pectoral fold (absent in *Scinax squalirostris* and most species of *Ololygon*); external or internal, single, weakly bilobate, or bilobate subgular vocal sac[3]; presence or absence of inguinal and pectoral glands; nuptial pad pale (dark only in one species, *O. melanodactyla*); absence of dermal ornamentation in cranial bones; prepollex composed of 2–3 cylindrical distal elements; tadpoles with terminal, subterminal, or ventral oral disc; posterior margin of the oral disc straight or concave when folded; presence or absence of a labial arm in the oral disc; uniform or irregular sized marginal papillae (presence of larger papillae on the posterior margin of the oral disc in *Julianus* and *S. quinquefasciatus*); labial tooth row formula 2(2)/3 or 2(2)/3(1); presence or absence of keratinized spurs behind the lower jaw-sheath; presence or absence of keratinized, dark plates on the sides of the lower jaw-sheath (present in *Julianus*); absence of a fleshy projection on medial margin of the nostril; eyes visible or not visible ventrally; dextral

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3 Our phylogenetic analysis included four characters (Chs. 76–79) related to the morphology of the m. interhyoideus. The combination of different character-states involving this muscle with the occurrence of vocal slits (and therefore the interior mucosae) corresponds to the terms commonly employed to describe the external morphology of the vocal sac. As such, it would have been redundant to also include the external morphology of the vocal sac in our analysis. For purely taxonomic purposes, however, the combination of a uniform m. interhyoideus (Ch. 76.0) that ventrally surpasses the mandible posteriorly, reaching or not the anterior half of the m. supracoracoideus portio anterior (Chs. 78.0 and 78.1), corresponds to a **single vocal sac that does not reach the pectoral fold or region** (if the pectoral fold is absent, as in the *Scinax squalirostris* group). The combination of a weakly bilobate m. interhyoideus (Ch. 76.1) that ventrally surpasses the mandible, reaching or not the anterior half of the m. deltoideus (Chs. 78.0 and 78.1), corresponds to a **weakly bilobate vocal sac that does not reach the pectoral fold or region.** This definition, as employed here, corresponds to the externally lateralized (Andrade and Cardoso, 1987; Haddad and Pombal, 1987) or normal and lateralized (Faivovich, 2002) vocal sacs reported for *Ololygon brieni*, *O. hiemalis*, *O. obtriangulata*, *O. ranki*, and *O. rizibilis*. The combination of a uniform or weakly bilobate m. interhyoideus (Ch. 76.0 or 76.1) that ventrally surpasses the mandible and reaching the anterior margin of the m. pectoralis esternalis (Ch. 78.3), corresponds to a **single or weakly bilobate vocal sac that reaches the pectoral fold or region.** The latter usually corresponds to an enlarged vocal sac. The combination of a bilobate m. interhyoideus (Ch. 76.2) with the posterior margin surpassing the mandible and reaching from one third to half of the length of the m. supracoracoideus portio anterior (Ch. 78.1), with a posterolateral expansion restricted to the post-tympanic region (Ch. 79.1) corresponds to a **bilobate vocal sac.** The case of the paired subgular vocal sac is simpler, corresponding to the occurrence of a paired subgular m. interhyoideus. A vocal sac is absent when the slits (and therefore internal mucosae) are absent (Moura et al., 2021).

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vent tube positioned above or at the margin of the ventral fin; 24 chromosomes; acoustic repertoire composed of calls with one multipulsed note or different types of calls with two or three note-types. These treefrogs occupy diverse habitats, including both open and forested areas, and reproduce in temporary and permanent lentic water bodies (e.g., Duellman, 1970a; Cardoso and Sazima, 1980; Pombal et al., 1995a), streams, and headwaters (e.g., Duellman and Wiens, 1992; Pombal and Bastos, 1996; Faivovich, 2002), or bromeliads (Peixoto, 1987).

Content. Three genera. *Julianus* Duellman et al., 2016; *Ololygon* Fitzinger, 1843; and *Scinax* Wagler, 1830.

Distribution. Southern Mexico to central-eastern Argentina, Trinidad and Tobago, and St. Lucia (Frost, 2023; see also Appendix S1).

Comments. This taxon was considered a subfamily by Duellman et al. (2016), a proposal rejected by Faivovich et al. (2018) who first considered Scinaxini as a tribe of Hylinae to include only the genus *Scinax* (sensu Faivovich et al., 2005). For this reason, five synapomorphies (Chs. 43.1, 70.1, 99.1, 141.0, and 157.1) mentioned above for the tribe are redundant with those proposed for *Scinax* as discussed earlier (see the section "Phenotypic synapomorphies of *Scinax*"); the other eight synapomorphies are proposed in this study. Previous analyses (Wiens et al., 2006, 2010; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018) recovered Scinaxini (as *Scinax*) as the poorly supported sister taxon of Sphaenorhynchini (as *Sphaenorhynchus*). However, our results recovered Scinaxini as the poorly supported sister taxon of a large clade including most other hyline tribes, except Cophomantini. Based on the poor evidence supporting the outgroup relationships of Scinaxini, we consider the sister taxon of this tribe to be unresolved.

Most of the synapomorphies listed above for the tribe are unaffected by the unstable position of Scinaxini. Nevertheless, the optimizations of Chs. 46.0 and 99.1 are affected if Scinaxini is recovered as the sister taxon of Sphaenorhynchini (Wiens et al., 2006, 2010; Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018). These characters optimize ambiguously in the hypothetical ancestor of Scinaxini + Sphaenorhynchini because they are inapplicable for the latter (absence of pectoral folds and slip of the m. extensor brevis superficialis digiti III originating from the radioulna).

Rodrigues et al. (2017) presented a short characterization of Scinaxini (considering them as *Scinax*) based on the few described larval chondrocrania and hyobranchial skeletons. This includes (1) suprarostral with the corpora fused medially, forming a continuous V-open shape in frontal view; (2) corpus and alae fused to various degrees or (rarely) separated (joined by syndesmosis); (3) cornua trabeculae diverging distally forming a V in dorsal view; (4) processus quadrato ethmoidalis absent; (5) processus pseudopterigoideus absent; (6) commissura quadratoorbitalis absent; and (7) presence of a larval processus

oticus. Chondrocrania are still known for few species of Scinaxini, and this characterization requires further elaboration, both from the perspective of character polarity—which was not discussed by Rodrigues et al. (2017)—and because many character-states are known to occur also at least in Dendropsophini (e.g., 4, 5, 6; Dias et al., 2019) and Pseudini (e.g., 3, 6, 7; Alcalde and Barg, 2006).

Ololygon Fitzinger, 1843

Type species: *Hyla strigilata* Spix, 1824, by original designation.

Ologigon—Miranda-Ribeiro, 1923. Incorrect subsequent spelling.

Ololigon—Miranda-Ribeiro, 1923. Incorrect subsequent spelling.

Ololygon—Fouquette and Delahoussaye, 1977. Resurrected name from the synonymy of *Hyla* to be employed for the former *Hyla catharinae* and *Hyla rubra* groups.

Scinax Wagler, 1830. Resurrection by Duellman and Wiens, 1992. Senior synonym of *Ololygon* following Pombal and Gordo, 1991.

Ololygon—Duellman et al., 2016:26. Part. Removed from the synonymy of *Scinax* Wagler, 1830.

Scinax—Colaço and Silva (2016:195). Senior synonym of *Ololygon*.

Sister taxon. *Julianus* + *Scinax*.

Diagnosis. This genus is well supported (100% jackknife) and delimited by molecular evidence and 19 phenotypic synapomorphies. These include (1) exoccipital bones dorsally and (2) ventrally fused (Chs. 4.0 and 9.0, respectively, both with reversals to elements not fused in *Ololygon angrensis* and an internal clade of *Ololygon*, also homoplastic in some outgroups); (3) anterior process of the suprascapula absent (Ch. 20.0, with instances of homoplasy at least in *Gabohyla pauloalvini* and *Sphaenorhynchus carneus*); (4) posterior part of the cricoid ring extensively elongated and curved (Ch. 36.2, with a reversal optimizing ambiguously in the *O. belloni* + *O. perpusilla* groups, also homoplastic instances of homoplasy in *S. oreites* and and at least in *Bokermannohyla ibitiguara*); (5) postaxial toe webbing of toe I absent or basal (Ch. 58.0, with a reversal to webbing reaching the distal margin of the subarticular tubercle in the *O. catharinae* group, Ch. 58.1); (6) vocal sac internal (Ch. 63.0, with reversals to vocal sac externally evident in an internal clade of the *O. catharinae* group, the *O. cardosoi* group, and *O. feioi*, although optimizing ambiguously in the latter two taxa); (7) m. depressor mandibulae without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0, with a single reversal to a muscle with an origin from the dorsal fascia in the *O. feioi* group); (8) presence of the slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV (Ch. 91.1, with instances of homoplasy in *S. crospedospilus*, *S. quinquefasciatus*, and at least *Itapotihyla*

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langsdorffii among the outgroups); (9) absence of the slip of the m. extensor digitorum inserting on metacarpal IV (Ch. 92.0); (10) presence of the slip of the m. extensor digitorum inserting on the m. extensor brevis medius digiti IV (Ch. 93.1, with one instance of homoplasy in *Phyllomedusa sauvagii*); (11) slip from radioulna of the m. extensor brevis superficialis digiti IV inserted on the m. extensor brevis medius digiti IV (Ch. 103.1, with reversals in some internal clades of the *O. catharinae* group); (12) slip from the ulnare of the m. extensor brevis superficialis digiti IV inserted on the m. extensor brevis medius digiti IV (Ch. 104.0, with instances of homoplasy in some outgroups); (13) lateral m. dorsometacarpalis proximalis digiti V absent (Ch. 113.0, with instances of homoplasy in *Julianus* and two internal clades of *Scinax*); (14) m. abductor brevis plantaris hallucis with an additional insertion on the metatarsophalangeal joint (Ch. 116.1, with one instance of homoplasy in *S. quinquefasciatus*); (15) lateral m. dorsometatarsalis distalis digiti III present (Ch. 128.1, with instances of homoplasy in *Julianus camposseabrai*, Sphaenorhynchini and some other outgroups); (16) lateral m. dorsometatarsalis distalis digiti V present (Ch. 132.1, with reversals in *O. cardosoi* and an internal clade of the *O. perpusilla* group, also homoplastic with Sphaenorhynchini and a clade of Hylini); (17) tadpoles with posterior margin of the folded oral disc concave (Ch. 136.1, with at least one reversal to straight margin in the clade including the *O. belloni*, *O. cardosoi*, and *O. perpusilla* groups, or in a more inclusive clade including also the *O. feioi* group); (18) P-3 length equal to that of P-2 (Ch. 138.0, with several instances of homoplasy in species of *Scinax* and in outgroups); and (19) oral disc ventral (Ch. 143.0, with instances of homoplasy in some species of *Scinax* and several outgroups).

The species of *Ololygon* differ from other Scinaxini by the combination of the absence of the pectoral fold and internal vocal sac; papillae on the posterior labium of the oral disc of the same size as those on the lateral margins; lack of keratinized, dark plates on the sides of the lower jaw-sheath; vent tube positioned at the margin of the ventral fin in most known tadpoles; absence of the anterior process of the suprascapula (synapomorphy of this genus, Ch. 20.0); m. depressor mandibulae without an origin from the dorsal fascia that covers the suprascapula (synapomorphy of this genus, Ch. 71.0); presence of the slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV (synapomorphy of the genus, Ch. 91.1); and presence of the slip of the m. extensor digitorum inserting on the m. extensor brevis medius digiti IV (synapomorphy of the genus, Ch. 93.1). When the pectoral fold is present in *Ololygon* (the *O. agilis* group), these species can be differentiated from *Julianus* and *Scinax* by the small adult snout–vent length (SVL; males 12.0–16.0 mm, females 13.2–17.3 mm) and internal vocal sac. In the species of *Ololygon* in which the vocal sac is externally evident (*O. aromothyella*, *O. berthae*, *O. cardosoi*, *O. feioi*, *O. garibaldiae*, and *O. rizibilis*), the pectoral fold is absent. Furthermore, in the only cases in which the vent tube is positioned above the margin of the ventral

fin (*O. flavoguttata* and *O. machadoi*), the pectoral fold is absent, and the vocal sac is internal.

Characterization. (1) SVL in males 12.0–42.8 mm, females 13.2–48.2 mm; (2) pectoral fold absent or present (Ch. 45.0 or 45.1); (3) vocal sac internal or externally evident (Ch. 63.0 or 63.1); (4) vocal sac subgular, single or bilobate, does not reach the level of the pectoral fold or region; (5) snout in dorsal view pointed, mucronate, subovoid, rounded with or without mucronate tip, or subelliptical with or without acute tip; (6) tubercles in the lower lip absent or present, rounded or pointed[4]; (7) dorsal skin smooth, with scattered tubercles, densely covered with tubercles or rugose; (8) postaxial webbing of toe I absent or basal, or reaching the subarticular tubercle (Ch. 58.0 or 58.1); (9) postaxial webbing of toe II reaching the subarticular tubercle, midlength of the penultimate phalanx, or the base of the disc (Ch. 59.1, 59.2, or 59.3); (10) epidermal projections in the nuptial pad absent or present (Ch. 64.0 or 64.1); (11) spicules absent in the nuptial pad, inner margin of arm, and pectoral region; (12) pectoral glands absent in males (Ch. 47.0); (13) inguinal glands absent or present (Ch. 48.0 or 48.1); (14) iris bronze, brown, copper, golden, gray, light brown, or silver, with a median horizontal black streak; (15) dorsal pattern uniform, with dorsolateral stripes, or marbled with irregular blotches, and interocular and sacral markings; (16) hidden surfaces of thighs uniform, reticulated, or with other markings; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole visible or not visible ventrally (Ch. 146.0 or 146.1); (19) oral disc ventral (Ch. 143.0); (20) posterior margin of the folded oral disc straight or concave (Ch. 136.0 or 136.1); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis subparallel or orthogonal/suborthogonal to the main body axis (Ch. 148.0 or 148.1); (25) vent tube medial or dextral, above or at the margin of the ventral fin (Ch. 145.0 or 145.1); (26) spots or large frontal band golden/yellow between the eyes and the nostrils of larvae absent or present (Ch. 150.0 or 150.1); (27) oviposition in bromeliads, ponds, or streams (Ch. 155.0, 155.1, or 155.2); (28) complex acoustic repertoire with different types of pulsed notes (long and short notes) combined in multi-note calls emitted in variable combinations of spectral and temporal parameters[5]; (29) anterior process of the

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4   This characteristic is a combination of different states of our Chs. 53, 54, and 55 (in this case 53.0 or 53.1 and 55.0 or 55.1). It is employed solely for taxonomic purposes.

5   The vocalizations in most species of *Ololygon* have a high pulse rate and complex structure that is further complicated by the biological context of emission (e.g., Peixoto et al., 2016; Hepp et al., 2017). For all characterizations of vocalizations in Scinaxini, we took into account the parameters of the vocalizations identified as advertisement or type A calls (e.g., Hepp et al., 2017; Bang and Giaretta, 2018), excluding those considered aggressive, territorial encounter, or type B or C calls. The homology of different components such as the notes of a call is not always straightforward (Robillard et al., 2006). In our experience, type A calls are simply the first to be pro-

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suprascapula absent (Ch. 20.0); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV present (Ch. 91.1); (31) m. depressor mandibulae with or without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0 or 71.1); (32) m. depressor mandibulae with or without an origin from the tympanic annulus (Ch. 72.0 or 72.1); (33) chromosome pair 1 submetacentric (Ch. 152.1); and (34) NOR in chromosome pair 6, pairs 2 and 6, or pairs 6 and 11, proximal or distal (Ch. 153.1, 153.5, 153.6, 153.12, or 153.13).

Contents. Fifty-two recognized species assigned to seven species groups. Nine CCSs; 10 UCSs.

Distribution. Northeastern, southeastern, and central-eastern Brazil, extending southward to eastern Argentina, Uruguay, and eastern Paraguay (Frost, 2023).

Comments. We corroborated all phenotypic transformations proposed by Faivovich (2002), as synapomorphies of *Ololygon* (as the *Scinax catharinae* clade; our Chs. 20.0, 63.0, 71.0, 91.1, and 93.1), and we inferred other 14 phenotypic synapomorphies. The absence of webbing between toes I and II was considered a singular characteristic of the *O. perpusilla* group by Peixoto (1987). However, our observations of several specimens of this group, added to observations on many specimens of *O. agilis*, *O. argyreornata*, *O. cardosoi*, and *O. melanodactyla* indicate that the webbing between toes I and II—here referred to as postaxial webbing of toe I—can be absent or present as a basal webbing in these species as well. Therefore, we considered the absence and presence of a basal postaxial webbing of toe I as the same character-state (Ch. 58.0). Our results support this transformation as a synapomorphy of *Ololygon*, with one reversal to postaxial webbing reaching the distal margin of the subarticular tubercle in an internal clade of *Ololygon* (Ch. 58.1).

An externally non-distended vocal sac (internal, Ch. 63.0) has been considered a synapomorphy of the *Scinax catharinae* clade sensu Faivovich (2002) and Faivovich et al. (2005). Our results show that in Scinaxini an internal vocal sac evolved in *Ololygon*, with a subsequent reversal to external vocal sac (Ch. 63.1) in an internal clade of the *O. catharinae* group, and in the *O. cardosoi* and *O. feioi* groups where there is an ambiguous optimization (Appendix S9).

Many authors have observed that the vocal sac is poorly developed or differentiated externally in the species of the *Ololygon catharinae* group (e.g., Liu, 1935; Cardoso and Haddad, 1982; Heyer et al., 1990; Pombal

and Bastos, 1996). The poorly developed or differentiated vocal sac in various species of *Ololygon* results from a combination of the occurrence of vocal slits, internal mucosae, undifferentiated gular skin (internal vocal sac), and a poorly developed m. interhyoideus (our Chs. 77.0 and 78.0). The vocal sac in *Julianus* and *Scinax* is characterized by loose, expanded gular skin, which is folded in species of the *S. squalirostris*, *S. cruentomma*, and *S. fuscomarginatus* groups (as described below in the Diagnosis section of these groups), and a more developed m. interhyoideus than that of *Ololygon*.

Faivovich (2002) reported that *Ololygon agilis* showed a mosaic of character-states occurring in *Ololygon* (e.g., internal vocal sac, our Ch. 63.0) and *Scinax* (e.g., the presence of a pectoral fold, our Ch. 45.1). The tadpole of *O. melanodactyla* (Abreu et al., 2015), a species in the *O. agilis* group, represents a typical tadpole of *Ololygon* and, therefore, shares many character-states with the remaining species of *Ololygon*. The species of the *O. agilis* group share some adult morphological character-states with the remaining species of *Ololygon*. Furthermore, contrary to Faivovich's (2002: chs. 61 and 64) observations, the lateral mm. dorsometatarsales distales digitorum III and V (our Chs. 128.1 and 132.1) are present in the *O. agilis* group and in several other species of *Ololygon* (absent in many species of *Scinax*). These are synapomorphies of *Ololygon*, with some reversals in its internal clades, and other instances of homoplasy in a few species of *Julianus* and *Scinax*, and some species of Dendropsophini and Sphaenorhynchini (see Diagnosis for *Ololygon* above).

Three character-states present in species of the *Ololygon agilis* group are also typical in *Scinax*. These include the presence of pectoral fold (our Ch. 45.1), and the absence of the lateral mm. dorsometatarsales hallucis distalis and distalis digiti II (our Chs. 126.0 and 127.0). The presence of a pectoral fold (Ch. 45.1) is the only state that optimizes ambiguously due to the shared occurrence in species of the *O. agilis* group and *Scinax* (Appendix S9). It is not possible to determine if the presence of the pectoral fold is a synapomorphy of Scinaxini (with one reversal in the sister taxon of the *O. agilis* group) or evolved independently in the *O. agilis* group and *Julianus* + *Scinax*. The optimization of this character will likely become clear as the position of Scinaxini within Hylinae becomes better understood. Character-states 126.0 and 127.0 are plesiomorphic for Scinaxini; and the presence of the lateral mm. dorsometatarsales hallucis distalis and distalis digiti II (Chs. 126.1 and 127.1) are synapomorphies of the sister taxon of the *O. agilis* group (Appendix S9).

Dias and Pie (2021) identified the occurrence of narial vacuities in the oral roof of larvae (*Ololygon belloni*, *O. littorea*, *O. perpusilla* and *O. v-signata*), the two cell types in the vacuities (known only in *O. littorea*), and the presence of a single rounded, large postulation in the prenarial arena of the oral roof as putative synapomorphies of the *O. perpusilla* group or a potentially more inclusive clade, as these occur in some other species of *Ololygon* (Conte et al., 2007; Alcalde et al., 2011; Kirchmeyer et al., 2019). The taxonomic distribution of these character-states is still

duced, which by no means suggest that they have necessarily a role for female attraction instead of male repulsion (although we are unaware of explicit tests). We understand that different authors may assign the same call type to different calls on the basis of their personal experience, but within *Ololygon* species that produce complex calls the first note is usually a long-trilled call similar to those of *Julianus* and *Scinax*. Therefore, although we recognize the problems of our approach, we also assume that we are minimizing the risk of comparing non-comparable behavioral units (i.e., incomparable calls).

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too poorly known in Scinaxini, and for this reason, we did not include them in our dataset, pending studies on larvae of more species.

The keratinized spurs behind the lower jaw-sheaths were considered absent in many species of the former *Scinax catharinae* clade (Faivovich, 2002; Conte et al., 2007). However, our observations on larvae of Scinaxini showed that most species of *Ololygon* have weak spurs like those observed in *O. aromothyella* and *O. berthae* (Alcalde et al., 2011: fig. 3H). The presence of keratinized spurs (Ch. 142.1) is a synapomorphy of Scinaxini, where it has been lost in some species of *Ololygon* and *Scinax* (including an internal clade of the *S. rostratus* group).

Cardozo et al. (2011) proposed as putative synapomorphies of *Ololygon* (as the *Scinax catharinae* clade) the submetacentric morphology of chromosome pair 1 (Ch. 152.0) and the NORs placed proximally in chromosome pair 6 (Ch. 153.5). However, because these character-states are still unknown in the species of the *O. agilis* group, they optimize ambiguously in our analysis; it is unclear if they are synapomorphies of *Ololygon* or the sister taxon of the *O. agilis* group (Appendix S9).

Previous phylogenetic analyses included a few species of *Ololygon* (e.g., Faivovich et al., 2005; Pyron, 2014; Duellman et al., 2016; Jetz and Pyron, 2018). In a recent reanalysis, Duellman et al. (2016) included DNA sequences available on GenBank only for six of the 46 species of *Ololygon* known species at that time; three belonging to the *O. perpusilla* group (actually, *O. faivovichi* and *O. peixotoi*, as the species identified as *O. perpusilla* has the same sequences of *O. faivovichi*) and other three from the *O. catharinae* group (*O. berthae*, *O. catharinae*, and *O. obtriangulata*). Based on our results, in this genus we refine the *O. perpusilla* group as characterized by Peixoto (1987) and defined by Faivovich et al. (2005) by excluding *O. belloni* and a closely related candidate species for which we define the *O. belloni* group; redefine the *O. catharinae* group of Faivovich (2002) by excluding *O. agilis*, *O. melanodactyla*, and one closely related candidate species for which we recognize the *O. agilis* group; excluding *O. argyreornata*, *O. skuki*, and five closely related candidate species, for which we recognize the *O. argyreornata* group; recognize the *O. cardosoi* group for the nominal species; and the *O. feioi* group for the nominal species and one closely related candidate species (Figs. 20 and 21).

The *Ololygon agilis* group is the sister taxon of the remaining species of *Ololygon*, followed by the *O. argyreornata* group and a clade that includes two major clades. One of these major clades includes the *O. belloni*, *O. cardosoi*, *O. feioi*, and *O. perpusilla* groups; the other includes all the other species of *Ololygon*, which we placed in a redefined *O. catharinae* group (Figs. 22–25). The internal relationships of the *O. agilis*, *O. argyreornata*, *O. belloni*, *O. cardosoi*, *O. feioi*, and *O. perpusilla* groups are well supported in general (≥ 80% jackknife). In the *O. catharinae* group multiple clades are recovered with high support values, but relationships among most of them are poorly supported (50% jackknife).

The *Ololygon agilis* group

Sister taxon. The clade including the *Ololygon argyreornata*, *O. belloni*, *O. catharinae*, *O. cardosoi*, *O. feioi*, and *O. perpusillus* groups.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular evidence and a single phenotypic synapomorphy: fibers of lateral m. dorsometatarsalis distalis digiti V reaching the distal margin of the penultimate phalanx of toe V (Ch. 133.1, with one instance of homoplasy in *Sphaenorhynchus*).

This group further differs from the other groups of *Ololygon* by the combination of SVL in males 12.0–16.0 mm, females 13.2–18.9 mm (SVL males > 26.0 mm, females > 41.0 mm in the *O. feioi* group; males > 17.0 mm, females > 23.0 mm in the *O. cardosoi* group; females > 19.8 in the *O. catharinae* group); presence of pectoral fold (absent in all other groups of *Ololygon*); internal vocal sac (externally evident in the *O. cardosoi* and *O. feioi* groups, and in some species of the *O. catharinae* group); dorsal skin smooth (with scattered tubercles or rugose in the *O. argyreornata*, *O. feioi*, and *O. perpusilla* groups; densely covered with tubercles in the *O. belloni* group); absent or basal postaxial webbing of toe I (reaching the subarticular tubercle in the *O. catharinae* group); postaxial webbing of toes II reaching midlength of the penultimate phalanx, or base of the disc (reaching the subarticular tubercle in the *O. belloni*, *O. cardosoi*, *O. feioi*, and *O. perpusilla* groups); dorsal pattern with distinctive white dorsolateral band, dorsally bordered by dark brown stripe, and black longitudinal line on the interocular region, variable in some specimens that do not have interocular line (distinctive white dorsolateral band absent in the other species groups of *Ololygon*); concave posterior margin of the folded oral disc (straight in the *O. belloni*, *O. cardosoi*, and *O. perpusilla* groups); oviposition in ponds or streams (in bromeliads in the *O. perpusilla* group); m. depressor mandibulae without origin from the dorsal fascia that covers the suprascapula (with origin in the dorsal fascia in the *O. feioi* group); and m. depressor mandibulae with origin from the tympanic annulus (without origin from the tympanic annulus in the *O. argyreornata* group, and most species of the *O. catharinae* group).

Characterization. (1) SVL males 12.0–16.0 mm, females 13.2–18.9 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac internal (Ch. 63.0); (4) vocal sac subgular, single, does not reach the level of the pectoral fold; (5) snout subovoid in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth; (8) postaxial webbing of toe I absent or basal (Ch. 58.0); (9) postaxial webbing of toe II reaching midlength of the penultimate phalanx of toe II, or base of the disc of toe II (Ch. 59.2 or 59.3); (10) epidermal projections in the nuptial pad absent or present (Ch. 64.0 or 64.1); (11) spicules in the nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris gray or bronze, with median

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horizontal black streak; (15) dorsal pattern with white dorsolateral band, dorsally bordered by dark brown stripe, and black longitudinal line on the interocular region (variable in some specimens that do not have interocular line); (16) hidden surfaces of thighs uniform; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole not visible ventrally (Ch. 146.0); (19) oral disc ventral (Ch. 143.0); (20) posterior margin of the folded oral disc concave (Ch. 136.1); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates absent on the sides of the lower jawsheath (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent

tube at the margin of the ventral fin (Ch. 145.1); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds or streams (Ch. 155.0 or 155.1); (28) complex vocal repertoire with two pulsed note-types (long and short notes) combined in multi-note calls, note duration of both note-types combined 10.6–400 ms, 14–30 notes per call; (29) anterior process of the suprascapula absent (Ch. 20.0); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV present (Ch. 91.1); (31) m. depressor mandibulae without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33)–(34) unknown.
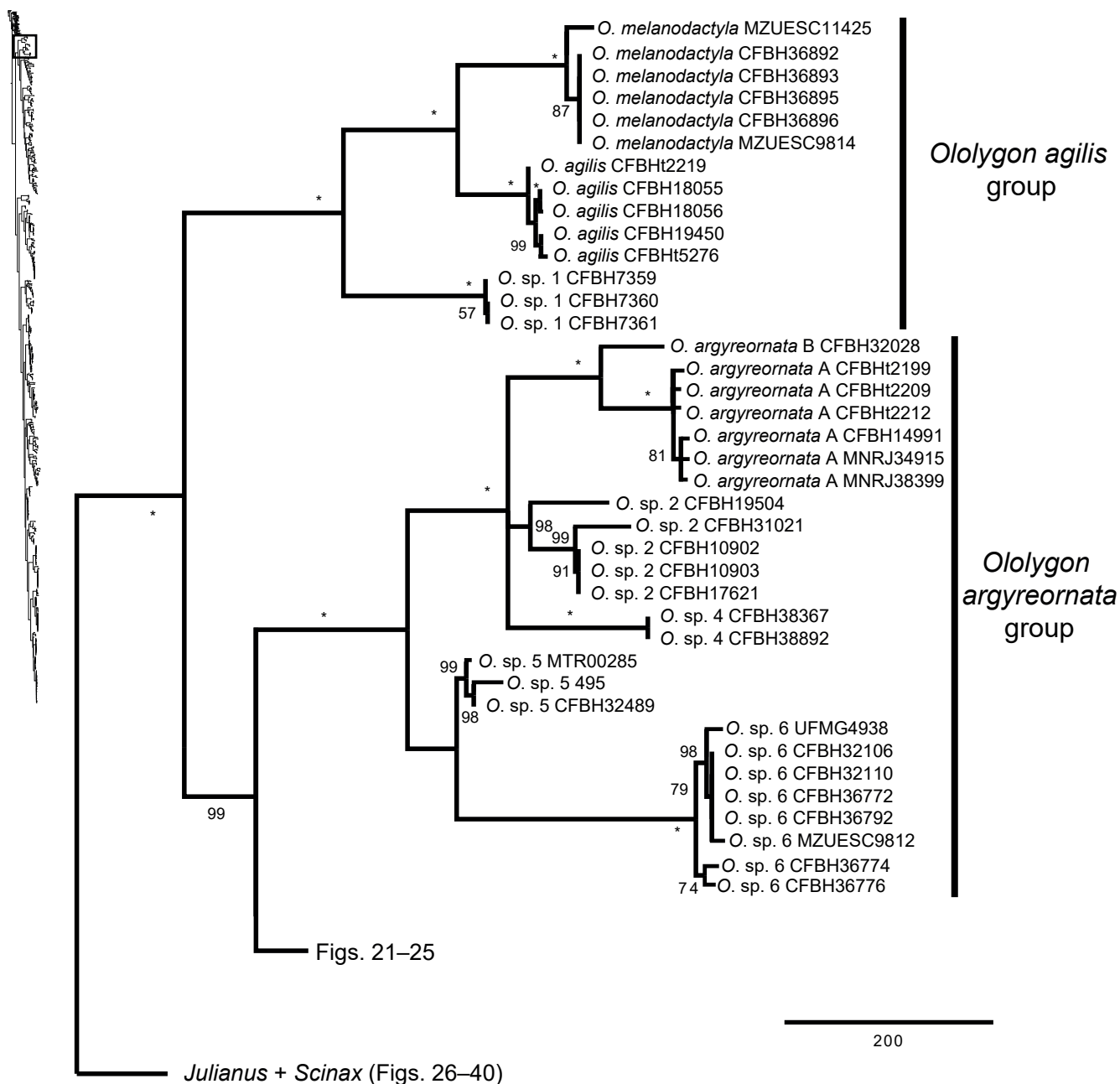
Figure 20. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 1 of 21: The *Ololygon agilis* and *O. argyreornata* groups. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.
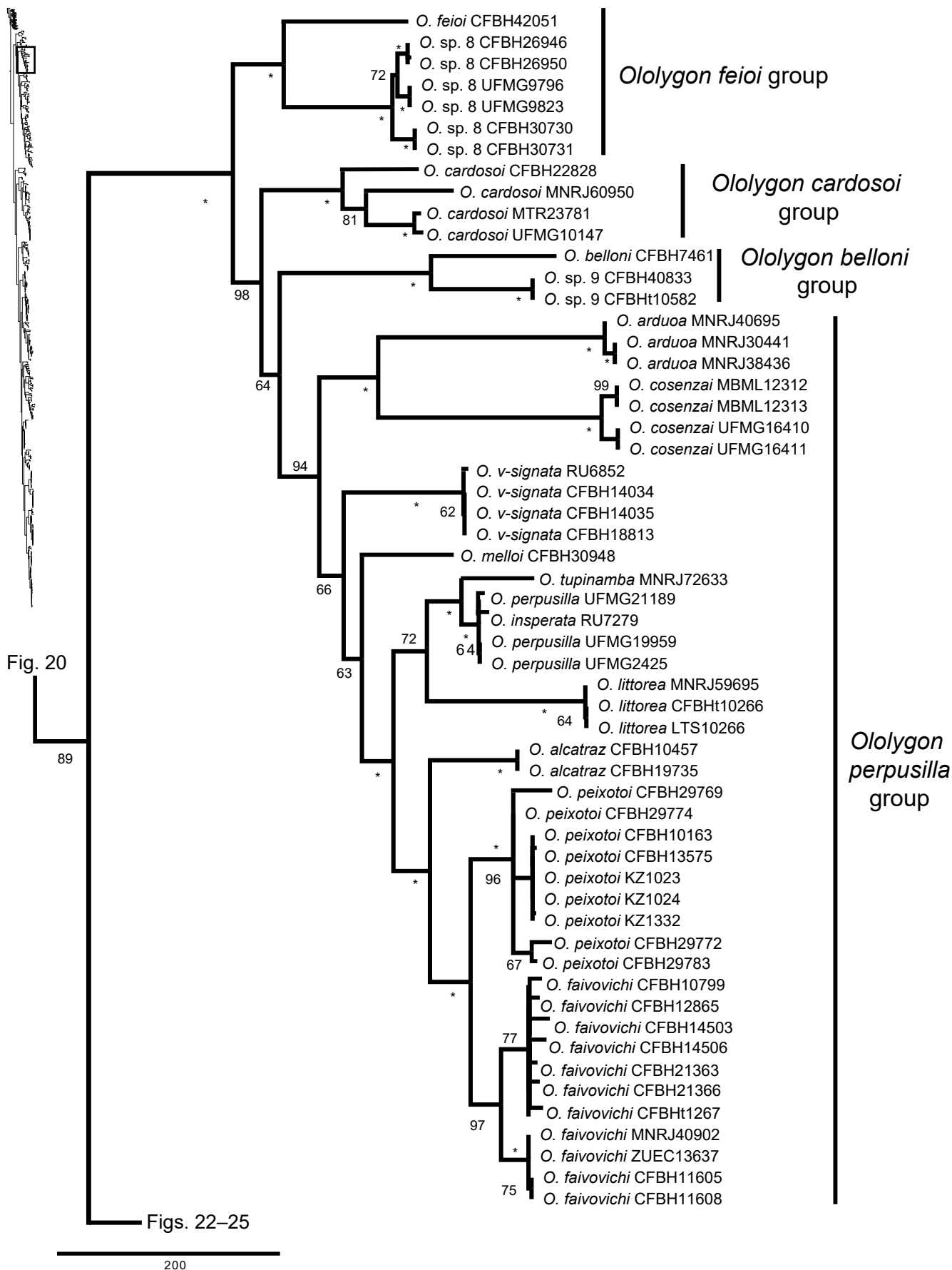
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Figure 21. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 2 of 21: The *Ololygon feioi, O. cardosoi, O. belloni,* and *O. perpusilla* groups. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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Contents. Two recognized species: *Ololygon agilis* (Cruz and Peixoto, 1983) and *Ololygon melanodactyla* (Lourenço et al., 2014). One CCS, *Ololygon* sp. 1.

Distribution. Northeastern and southeastern Brazil, from Alagoas to Espírito Santo (Peixoto et al., 2003; Toledo, 2005; Passos et al., 2012; Cardoso et al., 2014; Lourenço et al., 2014).

Comments. In the original description, *Ololygon agilis* was related to *O. berthae* based on overall similarities in the dorsal pattern coloration (Cruz and Peixoto, 1983) and Duellman and Wiens (1992) allocated both in the *Scinax staufferi* group (sensu Fouquette and Delahoussaye, 1977). Later, Faivovich (2002) transferred both species to the *S. catharinae* group within the *S. catharinae* clade. In the results of Faivovich (2002), *O. agilis* (as *S. agilis*) was recovered as sister taxon of all other included species of the former *S. catharinae* group.

Ololygon agilis* and *O. melanodactyla* are sister species (Fig. 20), morphologically similar, and have been confused in the past. The two species differ in that the latter has a dark nuptial pad and hypertrophied forearms in adult males, whereas in the former the nuptial pad is pale and the forearms of adult males are slender (Lourenço et al., 2014). *Ololygon* sp. 1, from Passo de Camaragibe, Alagoas, Brazil is recognized as a CCS for being the sister taxon of *O. agilis* + *O. melanodactyla* (Fig. 20). This candidate species was first reported by Toledo (2005) as *S. agilis*. Subsequently, Lourenço et al. (2014) identified male specimens of *O. melanodactyla* occurring in the same locality of *Ololygon* sp. 1. However, because all voucher specimens of *Ololygon* sp. 1 (CFBH 7359–7361) included in our analyses are females, we could not compare them to specimens of *O. melanodactyla*. Further, we could not identify any diagnostic phenotypic character distinguishing females of *Ololygon* sp. 1 from those of *O. agilis* or *O. melanodactyla*. Future studies will be required to determine if *O. melanodactyla* is sympatric with the candidate species or if only *Ololygon* sp. 1 occurs in Passo de Camaragibe. In the last case, *O. melanodactyla* would be restricted to the coastal sandbanks and forested areas near these environments from northern Espírito Santo to Sergipe, Brazil. The UPDs between the samples of *Ololygon* sp. 1, and *O. agilis* and *O. melanodactyla* are 4.2–12.0% (Appendix S10: Table 1). See Appendix S11 for the names applied in previous studies to voucher specimens of species of this group.

The sister taxon of the *Ololygon agilis* group, which includes all remaining species of *Ololygon* placed in six groups described in subsequent sections, is well supported (99% jackknife) and delimited by molecular evidence and four morphological synapomorphies. These include the dorsal prominence of the arytenoids well developed, right triangle shaped, with major axis perpendicular to arytenoids (Ch. 38.1, with reversals in *O. cardosoi*, an internal clade of the *O. perpusilla* group, some internal clades of the *Scinax catharinae* group, and other instances of homoplasy in an internal clade of the *S. rostratus* group, and in Sphaenorhynchini); preaxial webbing of toe IV reach-ing the proximal half of antepenultimate phalanx In toe IV (Ch. 60.0, with some instances of homoplasy in *O. melanodactyla*, *Scinax*, *Julianus*, and several outgroup taxa); lateral m. dorsometatarsalis hallucis distalis present (Ch. 126.1, with instances of homoplasy in the sister taxon of *S. quinquefasciatus* in the *S. rostratus* group, and one species of *Julianus*); and lateral m. dorsometatarsalis distalis digiti II present (Ch. 127.1, with instances of homoplasy in one species of *Julianus*).

Other relevant literature. Bastazini et al. (2007: community ecology); Nunes et al. (2007: vocalization); Cardoso et al. (2014: natural history); Hepp et al. (2017: vocalization). It is unclear to which species these contributions refer. All specimens are from sites at the northern shores of Bahia (between Salvador and Alagoas) and may refer to *Ololygon melanodactyla*.

The *Ololygon argyreornata* group

Sister taxon. The clade including the *Ololygon belloni*, *O. cardosoi*, *O. catharinae*, *O. feioi*, and *O. perpusilla* groups.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular evidence and two phenotypic synapomorphies: (1) differentiated portion of the m. flexor accessorius distalis inserting on the proximal end of the tendo superficialis digiti II present (Ch. 118.1, with instances of homoplasy in an internal clade of the *Scinax rostratus* group, and one internal clade of the *Ololygon catharinae* group), and (2) fibers of the m. abductor brevis plantaris digiti V reaching at most the proximal two-thirds of metatarsal V (Ch. 122.0, with instances of homoplasy in *Scinax*, and internal clades of the *O. perpusilla* and *O. catharinae* groups).

The species of this group are further distinguished from other species groups of *Ololygon* by the combination of SVL in males 13.8–20.8 mm, females 18.1–25.1 mm (SVL in males > 26.0 mm, females > 41.0 mm in the *O. feioi* group); lack of pectoral fold (present in the *O. agilis* group); internal vocal sac (externally evident in the *O. cardosoi* and *O. feioi* groups, and some species in the *O. catharinae* group); dorsal skin with scattered tubercles (smooth in the *O. agilis* and *O. cardosoi* groups, densely covered with tubercles in the *O. belloni* group); absent or basal postaxial webbing of toe I (reaching the subarticular tubercle in the *O. catharinae* group); postaxial webbing of toe II reaching midlength of the penultimate phalanx (reaching subarticular tubercle in the *O. belloni*, *O. cardosoi*, *O. feioi*, and *O. perpusilla* groups); dorsal pattern with two dorsolateral stripes, or a single vertebral stripe, with or without transversal band or blotch on the interocular and region (distinctive white dorsolateral band, dorsally bordered by dark brown stripe in the *O. agilis* group; dorsal pattern with two stripes, one lateral and one dorsolateral, and one vertebral line, continuous or interrupted in the *O. cardosoi* group); concave posterior margin of the folded oral disc (straight in the *O. belloni*, *O. cardosoi*, and *O. perpusilla* groups); oviposition in ponds (in bromeliads

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in the *O. belloni* and *O. perpusilla* groups); m. depressor mandibulae without origin from the dorsal fascia that covers the suprascapula (with origin from the dorsal fascia in the *O. feioi* group); and m. depressor mandibulae without origin from the tympanic annulus (with origin from the tympanic annulus in the *O. agilis*, *O. belloni*, *O. cardosoi*, *O. feioi*, and *O. perpusilla* groups, and in *O. canastrensis* of the *O. catharinae* group).

Characterization. (1) SVL males 13.8–20.8 mm, SVL females 18.1–25.1 mm; (2) pectoral fold absent (Ch. 45.0); (3) vocal sac internal (Ch. 63.0); (4) vocal sac, subgular, single, that does not reach the level of the pectoral region; (5) snout mucronate or subelliptical in dorsal view; (6) rounded tubercles in the lower lip absent or present; (7) dorsal skin with scattered tubercles; (8) postaxial webbing of toe I absent or basal (Ch. 58.0); (9) postaxial webbing of toe II reaching the midlength of the penultimate phalanx of toe II (Ch. 59.2); (10) epidermal projections in the nuptial pad absent or present (Ch. 640 or 64.1); (11) spicules in the nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands absent in males (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris gray to dull bronze with a median horizontal black streak; (15) dorsal pattern with dorsolateral stripes, sometimes delimiting a vertebral stripe, with or without transversal lines on the interocular and sacral regions; (16) hidden surfaces of thighs uniform or with blotches; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole not visible ventrally (Ch. 146.0); (19) oral disc ventral (Ch. 143.0); (20) posterior margin of the folded oral disc concave (Ch. 136.1); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube at the margin of the ventral fin (Ch. 145.1); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) complex vocal repertoire with pulsed notes combined in long multi-note calls, note duration 20–90 ms, 130–280 notes per call; (29) anterior process of the suprascapula absent (Ch. 20.0); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV present (Ch. 91.1); (31) m. depressor mandibulae without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0); (32) m. depressor mandibulae without an origin from the tympanic annulus (Ch. 72.0); (33) chromosome pair 1 submetacentric (Ch. 152.1); and (34) NOR in chromosome pair 6, proximal (Ch. 153.5).

Contents. Two recognized species: *Ololygon argyreornata* (Miranda-Ribeiro, 1926); *Ololygon skuki* (Lima et al., 2011). Four UCSs, *Ololygon* spp. 2, 4–6.

Distribution. Northeastern and southeastern Brazil, from Alagoas to Santa Catarina, and westwards to southern Minas Gerais (e.g., Izecksohn and Carvalho-e-Silva, 2001; Lima et al., 2011).

Comments. According to Lima et al. (2011) and Rodrigues et al. (2017), adults and tadpoles of *Ololygon skuki* are morphologically similar to those of *O. argyreornata* (Miranda-Ribeiro, 1926; Carvalho-e-Silva and Carvalho-e-Silva, 1998), and this is considered evidence to place it in the present group. Lima et al. (2011) distinguished between these two species on the basis of the shape of the snout in dorsal view, the shape of the external metacarpal tubercle of adults, and different colorations on hidden areas of the inguinal region, thigh, tibia, and foot. Rodrigues et al. (2017) differentiated them on the basis of larval morphology (LTRF 2/3 in *O. skuki*; 2(2)/3 in *O. argyreornata*), but Dubeux et al. (2020) reported LTRF 2/3 or 2(2)/3 for *O. skuki*. Also, our observations on adult specimens from both species indicate that the morphological characters employed by Lima et al. (2011) are insufficient to differentiate adults of *O. skuki* and *O. argyreornata*. Tissue samples from topotypic specimens of *O. skuki* were unavailable for this study; in the meantime, we consider *O. skuki* a valid species pending a taxonomic revision (see below).

Our results showed that *Ololygon argyreornata* as currently known corresponds to at least six distinct lineages throughout its distribution in Brazil (Fig. 20). Two of these lineages include the available populations from Espírito Santo located ≈30 and ≈80 km (the lineage with specimens from Santa Tereza and Vitoria) and ≈60 km (the lineage represented by a specimen from Linhares) from the type locality of *O. argyreornata* ("Rio Mutum," Miranda-Ribeiro, 1926, corrected to "Rio Mutum, Colatina" by Bokermann, 1966a). Considering this proximity, the fact that UPDs between both lineages are 2.9–3.4% (Appendix S10: Table 2), and that we are not aware of phenotypic differences between them, we treat them as *O. argyreornata* A and B, respectively, until DNA sequences from topotypic material and a full taxonomic study of this group determine which of these lineages corresponds to the nominal taxon. We are not aware of any evident diagnostic phenotypic character distinguishing *O. argyreornata* and *O. skuki* from the other four lineages that we identified. However, their UPDs from *O. argyreornata* A and B are 2.7–11.6%, and UPDs among them are 3.3–9.0%; for these reasons we consider them as UCSs. The lineage with smaller UPDs with *O. argyreornata* A and B, *O.* sp. 2 (2.7–4.1%) and its relationships with that species and *O.* sp. 4 are unresolved (Fig. 20). *Ololygon* sp. 2 is the southernmost lineage and is represented by populations from Rio de Janeiro (Niterói), São Paulo (Ubatuba), and Paraná (Morretes). *Ololygon* sp. 4 is from Minas Gerais (Rio Preto), and the two other lineages are from the southern coast of Bahia, *Ololygon* sp. 5 (Ilhéus) and *Ololygon* sp. 6 (Porto Seguro and Prado). We also note that one of these two latter UCSs could correspond to *O. skuki*.

Other relevant literature. Miranda-Ribeiro (1955: taxonomy of *O. argyreornata*); Bokermann (1966b: vocalization of *O. argyreornata*); Pombal et al. (1995b: vocalization,

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likely of *Ololygon* sp. 3); Carvalho-e-Silva and Carvalho-e-Silva (1998: natural history and tadpole, likely of *Ololygon* sp. 2); Teixeira and Vrcibradic (2004: ecology and natural history likely of *O. argyreornata* B); Teixeira and Rödder (2007: ecology and natural history likely of *O. argyreornata* A); Nunes and Fagundes (2008: karyotype likely of *O. argyreornata* A); Cardozo et al. (2011: karyotype likely of *Ololygon* sp. 3); Hepp et al. (2017: vocalization likely of *Ololygon* sp. 3); Pederassi et al. (2012: ecology and natural history likely of *Ololygon* sp. 2); Muscat et al. (2017; natural history likely of *Ololygon* sp. 3).

The *Ololygon feioi* group

Sister taxon. The clade including the *Ololygon belloni*, *O. cardosoi*, and *O. perpusilla* groups.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data and one phenotypic synapomorphy, the m. depressor mandibulae with origin from the dorsal fascia at the level of the m. dorsalis scapulae (Ch. 71.1).

Species of this group can be distinguished from other species of *Ololygon* by the combination of SVL in males 26.6–36.3 mm, females 41.5–45.5 mm (SVL males < 21.0 mm, females < 26.0 mm in the *O. agilis* and *O. argyreornata* groups; SVL males ≤ 26.0 mm, females < 32.0 mm in the *O. belloni*, *O. cardosoi*, and *O. perpusilla* groups); lack of pectoral fold (present in the *O. agilis* group); external vocal sac (internal in the *O. agilis*, *O. argyreornata*, *O. belloni*, and *O. perpusilla* groups, and most species of the *O. catharinae* group); dorsal skin with scattered tubercles (smooth in the *O. agilis* and *O. cardosoi* groups, densely covered with tubercles in the *O. belloni* group); absent or basal postaxial webbing of toe I (reaching the distal margin of the subarticular tubercle in the *O. catharinae* group); postaxial webbing of toe II reaching the distal margin of the subarticular tubercle (reaching midlength of the penultimate phalanx or base of the disc in the *O. agilis* and *O. argyreornata* groups); dorsal pattern with irregular blotches, and interocular and sacral markings (dorsal pattern with distinctive white dorsolateral band, dorsally bordered by dark brown stripe in the *O. agilis* group; uniform in the *O. belloni* group; two stripes and one vertebral line in the *O. cardosoi* group; dorsolateral stripes and an inverted V-shaped sacral blotch in the *O. perpusilla* group); oviposition in ponds or streams (in bromeliads in the *O. perpusilla* group); m. depressor mandibulae with origin from the dorsal fascia that covers the suprascapula (without origin from the dorsal fascia in all other groups of *Ololygon*); and m. depressor mandibulae with origin from the tympanic annulus (without origin from the tympanic annulus in the *O. argyreornata* group, and most species of the *O. catharinae* group).

Characterization. (1) SVL males 26.6–36.3 mm, females 41.5–45.5 mm; (2) pectoral fold absent (Ch. 45.0); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single that does not reach the level of the pectoral region;

(5) snout mucronate in dorsal view; (6) rounded or pointed tubercles in the lower lip present; (7) dorsal skin with scattered tubercles; (8) postaxial webbing of toe I absent or basal (Ch. 58.0); (9) postaxial webbing of toe II reaching the subarticular tubercle (Ch. 59.1); (10) epidermal projections present in the nuptial pad (Ch. 64.1); (11) spicules in the nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze with a median horizontal black streak; (15) dorsal pattern with irregular blotches, and interocular and sacral markings; (16) hidden surfaces of thighs with irregular markings; (17) physiological chlorosis absent (Ch. 158.0); (18)–(26) unknown; (27) oviposition in ponds or streams (Ch. 155.0 or 155.1); (28)–(30) unknown; (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33)–(34) unknown.

Contents. *Ololygon feioi* (Lourenço et al., 2020) **new comb.** One CCS, *Ololygon* sp. 8.

Distribution. Southeastern Brazil, in Espírito Santo and Minas Gerais (Lourenço et al., 2020).

Comments. *Ololygon feioi* is recovered as the sister taxon of a candidate species, *Ololygon* sp. 8 (Fig. 21). Adults of *O. feioi* and *Ololygon* sp. 8 have been confused in collections with *O. flavoguttata*. *Ololygon feioi* is from Santa Maria do Salto, northeast Minas Gerais, Brazil (Lourenço et al., 2020); it is separated by ≈450 km SSW from *Ololygon* sp. 8, which occurs in Piedade de Caratinga, east of Minas Gerais and two localities in Vargem Alta and Santa Teresa, central and southeast Espírito Santo, Brazil. They differ in UPDs of 8.7–8.8% (Appendix S10: Table 3) and some phenotypic characters (F. Brusquetti, personal comm.), and for this reason, it is considered a CCS.

The clade including the *Ololygon belloni*, *O. cardosoi*, *O. feioi*, and *O. perpusilla* groups is delimited only by molecular evidence (100% jackknife). Putative morphological synapomorphies of this clade include nasals non-overlapping with sphenethmoid (Ch. 0.0, with one reversal to internal margins of nasals overlapping the sphenethmoid in *O. littorea*, Ch. 0.1) and tadpoles with a straight posterior margin of folded oral disc (Ch. 136.0). These character-states optimize ambiguously in the hypothetical ancestor of this clade, because they are still unknown in the species of the *O. feioi* group.

The *Ololygon cardosoi* group

Sister taxon. The *Ololygon belloni* + *O. perpusilla* groups.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular evidence and 10 phenotypic apomorphies. These include (1) fontanelle partially exposed through a keyhole-shaped fenestra (Ch. 2.2, with instances of homoplasy in *Ololygon heyeri* and some spe-

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cies of *Scinax*); (2) medial prenasal process of the septum nasi surpassing the alary process of the premaxilla (Ch. 18.1, with instances of homoplasy in *O. arduoa*, some species of the *O. catharinae* group, *Julianus*, and *Scinax*); (3) dorsomedial prominence of the arytenoids poorly developed (Ch. 38.2, with instances of homoplasy in *O. centralis*, *O. littorea*, *O. perpusilla*, *O. strigilata*, and *O.* sp. 24); (4) lateral m. dorsometacarpalis distalis digiti III absent (Ch. 101.0, with instances of homoplasy in *O. v-signata*); (5) m. flexor hallucis accessorius with proximal point of insertion on metatarsal I (Ch. 117.0, with instances of homoplasy in *Scinax maracaya*, *S. rogerioi*, *Julianus fontanarrosai*, *J. pinimus*, and *Ololygon aromothyella* + *O. berthae*); (6), (7), (8) lateral mm. dorsometatarsales hallucis distalis and distales digitorum II and III absent (Chs. 126.0, 127.0, and 128.0, respectively; 126.0 and 127.0 with instances of homoplasy in an internal clade of the *O. perpusilla* group, Ch. 128.0 with one instance of homoplasy in *O. littorea*; Chs. 127.0 and 128.0 with instances of homoplasy in internal clades of the *O. catharinae* group); and (8) and (9) medial and lateral m. dorsometatarsalis distalis digiti V absent (Chs. 131.0 and 132.0, both with instances of homoplasy in species of the *O. perpusilla* group, and internal clades of the *O. catharinae* group).

The species in this group are differentiable from other groups of *Ololygon* by the combination of SVL in females 24.3–29.1 mm (females > 41.0 mm in the *O. feioi* group, < 20.0 mm in the *O. agilis* group); lack of pectoral fold (present in the *O. agilis* group); vocal sac externally evident (internal in the *O. agilis*, *O. argyreornata*, *O. belloni*, and *O. perpusilla* groups, and most species of the *O. catharinae* group); absent or basal postaxial webbing of toe I (reaching the subarticular tubercle in the *O. catharinae* group); dorsal skin smooth (with scattered tubercles or rugose in the *O. argyreornata*, *O. feioi*, and *O. perpusilla* groups; densely covered with tubercles in the *O. belloni* group); postaxial webbing of toe II reaching the subarticular tubercle (reaching midlength of the penultimate phalanx or base of the disc in the *O. agilis* and *O. argyreornata* groups); dorsal pattern with two stripes, one lateral extending from the posterior corner of the eye to the inguinal region, and one dorsolateral extending from the eyelid throughout the dorsum to the inguinal region, and one vertebral line, continuous or interrupted, extending from the tip of the snout to the tip of the urostyle (distinctive white dorsolateral band, dorsally bordered by dark brown stripe in the *O. agilis* group; irregular blotches, and interocular and sacral markings in the *O. feioi* group; uniform in the *O. belloni* group; uniform, with dorsolateral stripes delimiting or not a central region, or with marbling of irregular blotches, and interocular and sacral markings in the *O. catharinae* group); straight posterior margin of folded oral disc (concave in the *O. agilis*, *O. argyreornata*, and *O. catharinae* groups); oviposition in ponds or streams (in bromeliads in the *O. belloni* and *O. perpusilla* group); m. depressor mandibulae without origin from the dorsal fascia that covers the suprascapula (with origin from the dorsal fascia in the *O. feioi* group); and m. depressor mandibulae with origin from the tympanic annulus (without

origin from the tympanic annulus in the *O. argyreornata* group, and most species of the *O. catharinae* group).

Characterization. (1) SVL males 17.5–26.0 mm, females 24.3–29.1 mm; (2) pectoral fold absent (Ch. 45.0); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac, subgular, single, does not reach the level of the pectoral region; (5) snout mucronate in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth; (8) postaxial webbing of toe I absent or basal (Ch. 58.0); (9) postaxial webbing of toe II reaching subarticular tubercle (Ch. 59.1); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in the nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands present (Ch. 48.0); (14) iris golden with a median horizontal black streak; (15) dorsal pattern with two stripes, one lateral extending from the posterior corner of the eye to the inguinal region, and one dorsolateral extending from the eyelid throughout the dorsum to the inguinal region, and one vertebral line, continuous or interrupted, extending from the tip of the snout to the tip of the urostyle; (16) hidden surfaces of thighs with irregular blotches; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole not visible ventrally (Ch. 146.0); (19) oral disc ventral (Ch. 143.0); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.1); (25) vent tube at the margin of the ventral fin (Ch. 145.1); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds or streams (Ch. 155.0 or 155.1); (28) complex vocal repertoire with different types of long and short pulsed notes emitted singly or combined in multi-note calls, 1–25 notes per call; (29) anterior process of the suprascapula absent (Ch. 20.0); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV present (Ch. 91.1); (31) m. depressor mandibulae without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.0); (33)–(34) unknown.

Contents. One species. *Ololygon cardosoi* Carvalho-e-Silva and Peixoto, 1991.

Distribution. Southeastern Brazil, from Espírito Santo to São Paulo, and Minas Gerais (Carvalho-e-Silva and Peixoto, 1991; Pinto et al., 2009; Linares et al., 2011; Carvalho et al., 2015a; Moroti et al., 2017a).

Comments. Carvalho-e-Silva and Peixoto (1991) included *Ololygon cardosoi* in the former *O. staufferi* group (sensu Fouquette and Delahoussaye, 1977) based on similarities of adult size and dorsal color pattern. Subsequently, Faivovich

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et al. (2005) tentatively assigned this species to the former *Scinax ruber* clade but considered it unassigned to any group. Carvalho et al. (2015a) reported that the vocalization repertoire of *O. cardosoi* (as *S. cardosoi*) resembles the complex vocal repertoires (i.e., multiple call types emitted in variable combinations) of species of the former *S. catharinae* clade more than species of the *S. ruber* clade (sensu Faivovich, 2002; Faivovich et al., 2005), which tend to have simpler call structures (i.e., a single type of multipulsed note).

Kirchmeyer et al. (2019) described the external morphology and internal oral morphology of the tadpole of *Scinax cardosoi* and transferred this species to *Ololygon* (sensu Duellman et al., 2016 and the former *Scinax catharinae* clade sensu Faivovich et al., 2005) on the basis of adult and larval external morphology and call parameters similarities shared between *O. cardosoi* and other *Ololygon* species. Our observations on the type series of *O. cardosoi* corroborated that this species is part of *Ololygon* as redefined here mainly on the basis of the absence of pectoral folds, a characteristic shared by species of this genus. However, unlike Lourenço et al. (2014) and Kirchmeyer et al. (2019), we agree with Lourenço et al. (2020) that the vocal sac is external in *O. cardosoi*. Our analysis corroborated the placement of the *O. cardosoi* group within *Ololygon* (Fig. 21) as sister taxon forming a well-supported clade (98% jackknife) delimited by molecular evidence, with the poorly supported *O. belloni* + *O. perpusilla* groups (65% jackknife).

The type locality of *Ololygon cardosoi* is Vale da Revolta, Teresópolis, Rio de Janeiro, Brazil. Tissue samples were unavailable from topotypic specimens. Nevertheless, our results show that there are at least three lineages from Minas Gerais, Brazil, under the name *O. cardosoi* (Fig. 21), which are morphologically similar to the type series of *O. cardosoi*, and we were unable to identify any diagnostic phenotypic characters distinguishing them. The UPDs among them are 2.4–4.4% (Appendix S10: Table 4). One lineage is from a locality in Arantina, Minas Gerais, distant ≈140 km NW from the type locality of *O. cardosoi*. The other two lineages are from southern Minas Gerais (Eugenópolis), and the central part of the Serra da Espinhaço in central Minas Gerais (Santana do Riacho and Itambé do Mato Dentro), respectively. The lack of sequences from topotypic specimens and detailed morphological studies do not allow us to identify which of these lineages should be considered UCSs and which, if any, corresponds to *O. cardosoi*. The fact that we recover three lineages is the only reason why we are recognizing a monotypic species group.

Other relevant literature. Moroti et al. (2017b: behavior).

The *Ololygon belloni* group

Sister taxon. The *Ololygon perpusilla* group.

Diagnosis. No phenotypic synapomorphies are known for this well-supported group (100% jackknife) that is delimited by molecular evidence. The species in this group differ from other groups of *Ololygon* by the combination of SVL in males 19.8–23.0 mm, females 26.3–29.2 mm (SVL males > 26.0 mm, females > 41.0 mm in the *O. feioi* group); lack of pectoral fold (present in the *O. agilis* group); internal vocal sac (externally evident in the *O. cardosoi* and *O. feioi* groups, and in some species of the *O. catharinae* group); dorsal skin densely covered with tubercles (dorsal skin smooth, with scattered tubercles, or rugose in all other species of *Ololygon*); absent or basal postaxial webbing of toe I (reaching the distal margin of the subarticular tubercle in the *O. catharinae* group); postaxial webbing of toe II reaching subarticular tubercle II (reaching midlength of the penultimate phalanx or base of the disc in *O. agilis* and *O. argyreornata* groups); dorsal pattern uniform (dorsal pattern with distinctive white dorsolateral band, dorsally bordered by dark brown stripe in the *O. agilis* group; dorsal pattern with two stripes, one lateral and one dorsolateral, and one vertebral line, continuous or interrupted in the *O. cardosoi* group; with dorsolateral stripes, sometimes delimiting a central area on the body and an inverted V-shaped sacral blotch in the *O. perpusilla* group); straight posterior margin of folded oral disc (concave in the *O. agilis*, *O. argyreornata*, and *O. catharinae* groups); oviposition in bromeliads (Ch. 149.2; in ponds or/and streams in the *O. agilis*, *O. argyreornata*, *O. catharinae*, and *O. feioi* groups); m. depressor mandibulae without origin from the dorsal fascia that covers the suprascapula (with origin from the dorsal fascia in the *O. feioi* group); and m. depressor mandibulae with origin from the tympanic annulus (without origin from the tympanic annulus in the *O. argyreornata* group, and most species of the *O. catharinae* group).

Characterization. (1) SVL males 19.8–23.0 mm, females 26.3–29.2 mm; (2) pectoral fold absent (Ch. 45.0); (3) vocal sac internal (Ch. 63.0); (4) vocal sac subgular, single, does not reach the level of the pectoral region; (5) snout mucronate in dorsal view; (6) rounded tubercles in the lower lip absent; (7) dorsal skin densely covered with tubercles; (8) postaxial webbing of toe I absent or basal (Ch. 58.0); (9) postaxial webbing of toe II reaching the subarticular tubercle (Ch. 59.1); (10) epidermal projections in the nuptial pad absent (Ch. 64.0 or 64.1); (11) spicules in the nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris golden with a median horizontal black streak; (15) dorsal pattern uniform; (16) hidden surfaces of thighs uniform; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole not visible ventrally (Ch. 146.0); (19) oral disc ventral (Ch. 143.0); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube in the margin of the ventral fin (Ch. 145.1); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposi-

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tion in bromeliads (Ch. 155.2); (28) vocal repertoire with pulsed notes, combined call duration 59–69 ms, notes per call 2–3; (29) anterior process of the suprascapula absent (Ch. 20.0); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV present (Ch. 91.1); (31) m. depressor mandibulae without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 submetacentric (Ch. 152.1); and (34) NOR in chromosome pair 6, proximal (Ch. 153.5).

Content. *Ololygon belloni* (Faivovich et al., 2010b). One UCS, *Ololygon* sp. 9.

Comments. Our results corroborate the monophyly of the *Ololygon perpusilla* group as conventionally defined, although with low support (65% jackknife). This weak support involves the monophyly of *O. belloni* + *Ololygon* sp. 9 with all other species of the group, whose monophyly is better supported (94% jackknife; Fig. 21). In the ML analysis, *O. belloni* + *Ololygon* sp. 9 is recovered with low support (57% bootstrap) as the sister taxon of the *O. cardosoi* group (Appendix S8).

    Ololygon belloni was included in the *O. perpusilla* group (then as *Scinax*) by Faivovich et al. (2010b) because of the reduction of webbing between toes II-III and the supposition—subsequently corroborated by Silva-Soares et al. (2010)—of oviposition in bromeliads. The low support for the monophyly of the *O. perpusilla* group as currently recognized is remarkable considering that the phenotypic synapomorphy that supports its monophyly, oviposition in bromeliads, is a unique character-state among Scinaxini, and in general quite infrequent among hylids, although with some exceptions (e.g., Lophyohylini; Blotto et al., 2021). It is because of this low support that we prefer to recognize a separate *O. belloni* group. Its relationships with the *O. perpusilla* group require additional study; it has an important impact on our understanding of the evolution oviposition in bromeliads.

    Ololygon sp. 9 is morphologically similar to *S. belloni* and was collected in Muniz Freire, Espírito Santo, Brazil only 40 km W from the type locality of this species (Castelo, Espírito Santo). Both lineages, however, differ in UPDs of 3.9% (Appendix S8: Table 5), and for this reason *Ololygon* sp. 9 is considered a UCS.

    Observations on *Ololygon littorea*, *O. perpusilla*, *O. v-signata* (Alves-Silva and Silva, 2009), *O. arduoa*, *O. belloni*, and *O. cosenzai* (JVAL, personal obs.) indicated that the ability to lay eggs in small clutches and to split the clutch among several oviposital events could be a synapomorphy of the *O. belloni* + *O. perpusilla* groups (Alves-Silva and Silva, 2009; JVAL, personal obs.). However, this behavior is still unknown in the *O. cardosoi* and *O. feioi* groups, and therefore its optimization is still unclear.

Other relevant literature. Silva-Soares et al. (2010: tadpole of *Ololygon belloni*); Peres and Simon (2011: vocalizations of *O. belloni*); Peixoto et al. (2015: karyotype of *O. belloni*); Peixoto et al. (2016a: discussion on calls of the *O. perpusilla* group, including *O. belloni*); Bang et al. (2022: vocalizations of *O. belloni*).

The *Ololygon perpusilla* group

Sister taxon. The *Ololygon belloni* group.

Diagnosis. No phenotypic synapomorphies are known for this well-supported group (94% jackknife) that is delimited by molecular evidence. The species in this group differ from other groups of *Ololygon* by the combination of SVL in males 14.5–25.2 mm, females 18.6–31.6 mm (SVL males > 26.0 mm, females > 41.0 mm in the *O. feioi* group); lack of pectoral fold (present in the *O. agilis* group); internal vocal sac (externally evident in the *O. cardosoi* and *O. feioi* groups, and in some species of the *O. catharinae* group); dorsal skin with scattered tubercles or rugose (smooth in the *O. agilis* and *O. cardosoi* groups; densely covered with tubercles in the *O. belloni* group); absent or basal postaxial webbing of toe I (reaching the distal margin of the subarticular tubercle in the *O. catharinae* group); postaxial webbing of toe II reaching subarticular tubercle (reaching midlength of the penultimate phalanx or base of the disc in *O. agilis* and *O. argyreornata* groups); dorsal pattern with dorsolateral stripes, sometimes delimiting a central area on the body and an inverted, and V-shaped sacral blotch (dorsal pattern with distinctive white dorsolateral band, dorsally bordered by dark brown stripe in the *O. agilis* group; with two stripes, one lateral and one dorsolateral, and one vertebral line, continuous or interrupted in the *O. cardosoi* group; uniform in the *O. belloni* group); straight posterior margin of folded oral disc (concave in the *O. agilis*, *O. argyreornata*, and *O. catharinae* groups); oviposition in bromeliads (in ponds or/and streams in the *O. agilis*, *O. cardosoi*, and *O. catharinae* groups); m. depressor mandibulae without origin from the dorsal fascia that covers the suprascapula (with origin from the dorsal fascia in the *O. feioi* group); and m. depressor mandibulae with origin from the tympanic annulus (without origin from the tympanic annulus in the *O. argyreornata* group, and most species of the *O. catharinae* group).

Characterization. (1) SVL males 14.5–25.2 mm, females 18.6–31.6 mm; (2) pectoral fold absent (Ch. 45.0); (3) vocal sac internal (Ch. 63.0); (4) vocal sac subgular, single, does not reach the level of the pectoral region; (5) snout mucronate in dorsal view; (6) rounded tubercles in the lower lip absent or present; (7) dorsal skin with scattered tubercles or rugose; (8) postaxial webbing of toe I absent or basal (Ch. 58.0); (9) postaxial webbing of toe II reaching the subarticular tubercle (Ch. 59.1); (10) epidermal projections in the nuptial pad present or absent (Ch. 64.0 or 64.1); (11) spicules in the nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris gray, copper, golden, or light brown, with a median horizontal black streak; (15) dorsal pattern with dorsolateral stripes or lines, sometimes delimiting a central area; presence of

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interocular and inverted V-shaped sacral blotch, continuous or interrupted; (16) hidden surfaces of thighs with blotches; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole not visible ventrally (Ch. 146.0); (19) oral disc ventral (Ch. 143.0); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube in the margin of the ventral fin (Ch. 145.1); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent or present in larvae (Ch. 150.0 or 150.1); (27) oviposition in bromeliads (Ch. 155.2); (28) complex vocal repertoire with pulsed notes of different temporal and spectral parameters emitted in multi-note calls, combined call duration 18–2127 ms, combined notes per call 1–23; (29) anterior process of the suprascapula absent (Ch. 20.0); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV present (Ch. 91.1); (31) m. depressor mandibulae without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 submetacentric (Ch. 152.1); and (34) NOR in chromosome pair 6, proximal (Ch. 153.5).

Content. Twelve recognized species: *Ololygon alcatraz* (Lutz, 1973b); *Ololygon arduoa* (Peixoto, 2002); *Ololygon atrata* Peixoto, 1989; *Ololygon cosenzai* (Lacerda et al., 2012); *Ololygon faivovichi* (Brasileiro et al., 2007a); *Ololygon insperata* (Silva and Alves-Silva, 2011); *Ololygon littorea* Peixoto, 1988; *Ololygon melloi* Peixoto, 1989; *Ololygon peixotoi* (Brasileiro et al., 2007b); *Ololygon perpusilla* (Lutz and Lutz, 1939); *Ololygon tupinamba* (Silva and Alves-Silva, 2008); and *Ololygon v-signata* (Lutz, 1968a).

Distribution. Southeastern Brazil, from Espírito Santo and Minas Gerais to Santa Catarina, including several offshore islands in Rio de Janeiro and São Paulo (Izecksohn and Carvalho-e-Silva, 2001; Brasileiro et al., 2007a,b; Bell et al., 2012; Bittencourt-Silva and Silva, 2013; Silva and Alves-Silva, 2013; Lacerda et al., 2015).

Comments. The reduced webbing between toes II and III has been considered a synapomorphy of this group (Peixoto, 1987; Faivovich, 2002; Faivovich et al., 2005). However, the reduced postaxial webbing of toe II reaching the subarticular tubercle (Ch. 59.1) is, in fact, present in all species of the *Ololygon belloni*, *O. cardosoi*, *O. feioi*, and *O. perpusilla* groups, and some species of the *O. catharinae* group. This character-state optimizes as a synapomorphy of the clade including all these groups with a reversal to postaxial webbing of toe II reaching the proximal half of penultimate phalanx (Ch. 59.2) in an internal clade of the *O. catharinae* group.

The complex vocalizations of the *Ololygon perpusilla* and *O. belloni* groups are quite characteristic. Pombal and Bastos (2003) suggested that advertisement calls composed of 3–6 pulses, separated by 23–59 ms were a putative synapomorphy of the group. This was questioned by Peixoto et al. (2016a) based on overlapping values of these parameters in some species of the *O. catharinae* group. An integration of knowledge on vocalizations and an analysis of the homology of its components in the *O. perpusilla* group with those of other species of *Ololygon* is still pending.

Alves-Silva and Silva (2009) noticed differences in the place of oviposition in the bromeliad among species of the *Ololygon perpusilla* group. They reported that in *O. perpusilla*, *O. v-signata*, and *O. littorea* eggs are placed in the water, while some unnamed species placed their eggs just outside the water, adhered to the leaf. The significance of these differences in egg deposition site, its dependence on the water level of the bromeliad tank, and its taxonomic distribution in species of the *O. belloni* and *O. perpusilla* groups require additional studies before it could be considered as informative variation for these species groups.

Eleven species belonging to the *Ololygon perpusilla* group as redefined here were included in our analysis, significantly increasing previous taxonomic sampling that included at most three species (populations from litoral areas of São Paulo to which the name *O. perpusilla* was applied at the time, *O. faivovichi*, and *O. peixotoi*; Bell et al., 2012; Pyron, 2014; Duellman et al., 2016). Tissue samples were unavailable only for *O. atrata*. Although this species is morphologically similar to *O. melloi* (Peixoto, 1989), its position within the *O. perpusilla* group remains uncertain.

The monophyly of *Ololygon arduoa* and *O. cosenzai* is well supported (100% jackknife), and this clade is the sister taxon of a poorly supported clade (66%) including *O. v-signata* and *O. melloi* as successive sister taxa of a well-supported clade (100% jackknife) including the remaining species of the group, *O. alcatraz*, *O. faivovichi*, *O. littorea*, *O. peixotoi*, *O. perpusilla*, and *O. tupinamba* (Fig. 21).

Ololygon littorea is recovered as the sister taxon of a clade including *O. tupinamba* and a lineage where *O. insperata* (topotypic specimen) is nested within *O. perpusilla*. These two species have similar sequences (UPDs 0.2%; Appendix S10: Table 5) and only differ by having different colorations on the inguinal region and hidden surfaces of limbs (yellow markings absent in *O. insperata* and yellow markings evident in *O. perpusilla*; Silva and Alves-Silva, 2011). In the ML analysis, *O. insperata* is recovered as the sister taxon of the samples of *O. perpusilla* (100% bootstrap; Appendix S8). A study in progress will elucidate the taxonomic status of these species.

A major clade includes three species from coastal regions and offshore islands in São Paulo. *Ololygon alcatraz*, an island endemic (Ilha dos Alcatrazes), is well supported (100% jackknife) as the sister taxon of a clade including continental and island populations of *O. faivovichi* and *O. peixotoi*.

Bell et al. (2012) found that the continental populations identified as *Ololygon perpusilla* from northern São Paulo (Boracéia, Ubatuba, Santa Virginia, and the offshore Ilha do Mar Virado) were poorly supported as the sister taxon of *O. faivovichi*. Our results recover the monophyly

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of these lineages (98% jackknife), which differ in UPDs of 1.5–1.7% (Appendix S10: Table 5). Considering these small distances, the fact that they are sister clades, and that specimens of *O. perpusilla* (Morro da Urca, Rio de Janeiro, Rio de Janeiro, Brazil) from 30 km E from its type locality (Recreio dos Bandeirantes, Rio de Janeiro, Rio de Janeiro) have UPDs of 4.9–5.2% with the populations of northern São Paulo (Appendix S10: Table 5), we recognize the latter tentatively as *O. faivovichi*. Although Brasileiro et al. (2007a) reported phenotypic differences between the latter and *O. perpusilla*, they only studied topotypes of this species. See comments below for *O. peixotoi*.

Bell et al. (2012) also found that the continental populations from southern São Paulo identified as *Ololygon perpusilla* (Juréia and Curucutú) were similar to *O. peixotoi* from Ilha da Queimada Grande. These authors considered that the minimal genetic structure was the result of the recent isolation of the Ilha da Queimada Grande caused by sea level changes in the late Pleistocene, and the phenotypic differentiation may be attributed to differences in ecological pressures on islands versus the mainland. Our study of the voucher specimens of Juréia and Curucutú that Bell et al. (2012) identified as *O. perpusilla* indicates that they should be considered *O. peixotoi*. UPDs between *O. peixotoi* and *O. faivovichi* are 0.8–2.7% (considering both coastal and island populations; Appendix S10: Table 5); these low UPDs and the association of the island and coastal populations with these two names indicate the need for a reevaluation of the diagnostic characters and taxonomic status of both species.

Other relevant literature. Leão (1950a,b: natural history of *Ololygon peixotoi*); Peixoto (1988: tadpole of *O. littorea*); Peixoto (1989: tadpole of *O. melloi*); Peixoto, 1995 (habitat); Peixoto (2002: tadpole of *O. arduoa*); Lopez et al. (2002: natural history of *O. perpusilla*); Oliveira and Navas (2004; natural history of *O. faivovichi* and *O. peixotoi*, as *Scinax perpusillus*); Teixeira et al. (2006: natural history of *O. arduoa*, as *S. perpusillus*); Brasileiro et al. (2007b; calls of *O. peixotoi*); Duryea et al. (2008: microsatellite markers); Sabagh et al. (2011, 2012, 2020: natural history of *O. littorea* and *O. perpusilla*); Silva and Alves-Silva (2011: vocalizations of *O. insperata*); Lacerda et al. (2012: vocalizations of *O. cosenzai*); Guimarães et al. (2014: larva of *O. cosenzai*); Pontes et al. (2013: vocalizations of *O. littorea*); Silva and Alves-Silva (2013: distribution of *O. v-signata*); Sabagh and Rocha (2014: natural history of *O. littorea* and *O. perpusilla*); Lacerda et al. (2015: calls and tadpole of *O. arduoa*); Peixoto et al. (2015: karyotype of *O. arduoa*, *O. cosenzai*, *O. v-signata*, and *Ololygon* sp.); Peixoto et al. (2016a: calls of *O. v-signata* and discussion on calls from the group); Silva et al. (2017: skin histology of *O. perpusilla* and *O. v-signata*); Dias and Pie (2021: tadpole of *Ololygon v-signata*).

The *Ololygon catharinae* group

Sister taxon. The clade including the *Ololygon belloni*, *O. cardosoi*, *O. feioi*, and *O. perpusilla* groups.

Diagnosis. This group is well supported (99% jackknife) and delimited by molecular evidence and two phenotypic synapomorphies: (1) subcircular arytenoids in dorsal view (Ch. 37.3, with one instance of homoplasy in *Scinax boulengeri* + *S. sugillatus*), and (2) postaxial webbing of toe I reaching the distal margin of the subarticular tubercle (Ch. 58.1, with instances of homoplasy in *Julianus* + *Scinax* and some outgroups).

The species in this group differ from other groups of *Ololygon* by the combination of lack of pectoral fold (present in the *O. agilis* group); postaxial webbing of toe I reaching the distal margin of the subarticular tubercle (synapomorphy of this group, Ch. 58.1; absent or basal postaxial webbing of toe I in all other groups of *Ololygon*); dorsal pattern uniform, with dorsolateral stripes delimiting or not a central region, or with marbling of irregular blotches, and interocular and sacral markings (dorsal pattern with distinctive white dorsolateral band, dorsally bordered by dark brown stripe in the *O. agilis* group); concave posterior margin of folded oral disc (straight in the *O. belloni*, *O. cardosoi*, and *O. perpusilla* groups); oviposition in ponds and/or streams (in bromeliads in the *O. belloni* and *O. perpusilla* groups); m. depressor mandibulae without origin from the dorsal fascia that covers the suprascapula (with origin from the dorsal fascia in the *O. feioi* group); and m. depressor mandibulae without origin from the tympanic annulus in most species of the group (single exception *O. canastrensis*; with origin from the tympanic annulus in the *O. agilis*, *O. belloni*, *O. cardosoi*, *O. feioi*, and *O. perpusilla* groups).

Characterization. (1) SVL males 14.6–42.8 mm, SVL females 19.9–48.2 mm; (2) pectoral fold absent (Ch. 45.0); (3) vocal sac internal or externally evident (Ch. 63.0 or 63.1); (4) vocal sac single or bilobate, does not reach the level of the pectoral region; (5) snout in dorsal view pointed, mucronate, subovoid, rounded with or without mucronate tip, or subelliptical with or without acute tip; (6) rounded tubercles in the lower lip absent or present; (7) dorsal skin smooth, with scattered tubercles, or rugose; (8) postaxial webbing of toe I reaching subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the subarticular tubercle, midlength of the penultimate phalanx, or base of the disc (Chs. 59.1, 59.2, and 59.3); (10) epidermal projections in the nuptial pad absent or present (Ch. 64.0 or 64.1); (11) spicules in the nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent or present (Ch. 48.0 or 48.1); (14) iris bronze, brown, golden, gray, or silver, with median horizontal black streak; (15) dorsal pattern uniform or with dorsolateral stripes delimiting or not a central region on the body with marbling of irregular blotches, and interocular and sacral markings[6]; (16) hidden surfaces of thighs reticulated or with blotches or bars; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes

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6   The dorsal color pattern in the *Ololygon catharinae* group is complex and our synthetic description might not capture all known variation, particularly of the intricacy of the marbled patterns (e.g., compare *O. ariadne* and *O. flavoguttata*).

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of the tadpole visible or not visible ventrally (Ch. 146.0 or 146.1); (19) oral disc ventral (Ch. 143.0); (20) posterior margin of the folded oral disc concave (Ch. 136.0); (20) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube medial or dextral, above or at the margin of the ventral fin (Ch. 145.0 or 145.1); (26) spots or large frontal golden/yellow band between the eyes and the nostrils absent or present (Ch. 150.0 or 150.1); (27) oviposition in ponds and/or streams (Ch. 155.0 or 155.1); (28) complex vocal repertoire with short and long pulsed notes with spectral and temporal variation, emitted singly or combined in multi-note calls[7] (combined notes per call 1–620); (29) anterior process of the suprascapula absent (Ch. 20.0); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV present (Ch. 91.1); (31) m. depressor mandibulae without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0); (32) m. depressor mandibulae with or without an origin from the tympanic annulus (Ch. 72.0 or 72.1); (33) chromosome pair 1 submetacentric (Ch. 152.1); and (34) NOR in chromosome pair 6, proximal and interstitial (Chs. 153.5 and 153.6), pairs 2 and 6, proximal in 6 (Chs. 153.1 and 153.5), or pairs 6 and 11, proximal and distal, respectively (Chs. 153.1 and 153.13).

Contents. Thirty-three recognized species: *Ololygon albicans* (Bokermann, 1967a); *Ololygon angrensis* (Lutz, 1973b); *Ololygon ariadne* (Bokermann, 1967a); *Ololygon aromothyella* (Faivovich, 2005); *Ololygon berthae* (Barrio, 1962); *Ololygon brieni* (De Witte, 1930); *Ololygon caissara* (Lourenço et al., 2016) **new comb.**; *Ololygon canastrensis* (Cardoso and Haddad, 1982); *Ololygon carnevallii* Caramaschi and Kisteumacher, 1989; *Ololygon catharinae* (Boulenger, 1888a); *Ololygon centralis* (Pombal and Bastos, 1996); *Ololygon flavoguttata* (Lutz and Lutz, 1939); *Ololygon garibaldiae* (Lourenço et al., 2019) **new comb.**; *Ololygon goya* Andrade et al., 2018; *Ololygon heyeri* Peixoto and Weygoldt, 1987; *Ololygon hiemalis* (Haddad and Pombal, 1987); *Ololygon humilis* (Lutz, 1954); *Ololygon jureia* (Pombal and Gordo, 1991); *Ololygon kautskyi* Carvalho-e-Silva and Peixoto, 1991; *Ololygon littoralis* (Pombal and Gordo, 1991); *Ololygon longilinea* (Lutz, 1968b); *Ololygon luizotavioi* Caramaschi and Kisteumacher, 1989; *Ololygon machadoi* (Bokermann and Sazima, 1973); *Ololygon muriciensis* (Cruz et al., 2011); *Ololygon obtriangulata* (Lutz, 1973b); *Ololygon pixinguinha* (Lacerda et al., 2021) **new comb.**; *Ololygon pombali* (Lourenço et al., 2013); *Ololygon ranki* (Andrade and Cardoso, 1987); *Ololygon rizibilis* (Bokermann, 1964a); *Ololygon skaios* (Pombal et al., 2010); *Ololygon strigilata* (Spix, 1824); *Ololygon trapicheiroi* (Lutz, 1954); and *Ololygon tripui* (Lourenço et al.,

2010). Four UCSs, *Ololygon* spp. 3, 10, and 12–13; eight CCSs, *Ololygon* spp. 7, 11, 14–19.

Distribution. Northeastern, southeastern, and central-eastern Brazil. *Ololygon aromothyella* and *O. berthae* also occur in eastern Argentina, eastern Paraguay, and Uruguay.

Comments. The monophyly of the *Scinax catharinae* group as previously defined by Faivovich (2002) and Faivovich et al. (2005) is rejected in our analysis, as commented earlier. Nevertheless, some putative morphological synapomorphies proposed for the former *S. catharinae* group deserve comments.

Duellman and Wiens (1992) suggested that the absent or very reduced anterior gap in the marginal papillae of the oral disc in larvae and oviposition in streams were synapomorphies of the *Scinax catharinae* group as defined by them (including *S. albicans*, *S. argyreornatus*, *S. ariadne*, *S. brieni*, *S. catharinae*, *S. flavoguttatus*, *S. heyeri*, *S. humilis*, *S. littoralis*, *S. machadoi*, and *S. obtriangulatus*). Subsequently, Faivovich (2002) suggested that oviposition in streams was a synapomorphy of a clade that was more exclusive than the former *S. catharinae* group of Duellman and Wiens (1992)—excluding *S. berthae*, *S. rizibilis*, and *S. aromothyella* (as *Scinax* sp. 1). The anterior gap in the marginal papillae of the oral disc is absent (our 139.0) at least in *Ololygon albicans*, *O. ariadne*, *O. flavoguttata*, *O. heyeri*, *O. pombali*, *O. rizibilis*, *O. strigilata*, *O. trapicheiroi*, *O. tripui*, and *O.* sp. 7. While there is no doubt about the independent origins of the complete papillae along the anterior labium in *O. ariadne*, *O. pombali*, and *O.* sp. 7, it remains ambiguous if it is homologous in the other species (being a fourth independent origin) or if it evolved independently in the different clades. This ambiguity stems from the unknown larvae for some species, such as *O. caissara* and *O. garibaldiae* (see Appendix S9: optimization of individual phenotypic characters, Ch. 139).

Our results indicate that the oviposition site in lentic water bodies is the ancestral state in Scinaxini (Ch. 155.0), while the oviposition in streams (Ch. 155.1) optimizes as a synapomorphy of the clade including the *Ololygon belloni*, *O. cardosoi*, *O. catharinae*, *O. feioi*, and *O. perpusilla* groups, with at least two subsequent reversals to oviposition in lentic water bodies in *O. caissara*, and in the internal clade of *Ololygon* (*O. garibaldiae*, *O. berthae*, *O. aromothyella*, *O. rizibilis*, and *O. ranki* reproduce in lentic water bodies) that is in a pectinate series leading to a clade where there is a new transformation into oviposition in streams. Some species of *Ololygon* usually reproduce in streams or temporary and permanent ponds (Chs. 155.0 and 155.1); these include *O. cardosoi* (the *O. cardosoi* group), *O. melanodactyla* (the *O. agilis* group), *O. brieni*, *O. carnevallii*, *O. hiemalis*, *O. humilis*, *O. littoralis*, *O. luizotavioi*, *O. strigilata*, and *O. trapicheiroi* (the *O. catharinae* group). Oviposition in streams (Ch. 155.1) further evolved at least two times in *Scinax* (*S. haddadorum* and *S. rupestris*) and is polymorphic in *S. cabralensis*, *S. danae*, and *S. exiguus* (Chs. 155.0 and 155.1 in these species).

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[7]   Some very long multi-note calls described for species in the *O. catharinae* group (duration up to 52 s; Pereyra et al., 2012) could be described as call series comprising multiple calls (see Köhler et al., 2017).

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Faivovich (2002) proposed that the partial mineralization of intercalary elements between ultimate and penultimate phalanges (our Ch. 26.1), the posterior part of the cricoid ring extensively elongated and curved (our Ch. 36.2), and the laterodistal origin of the lateral m. dorsometacarpalis distalis digiti III (Faivovich 2002: ch. 57; not included in our study; see discussion for Ch. 97) were synapomorphies of the *S. catharinae* group as formerly defined. In our analysis, Ch. 26.1 is plesiomorphic for Scinaxini, with some reversals in *Scinax*, *Ololygon*, and several outgroups, whereas the posterior part of the cricoid ring extensively elongated and curved (Ch. 36.2) is a synapomorphy of *Ololygon*, with some reversals in internal clades of this genus, and other instance of homoplasy in *S. oreites*.

Faivovich (2002) and Faivovich et al. (2005) also considered the posterior margin of the larval oral disc concave when folded as a diagnostic character of the *Scinax catharinae* group. In our results, this character-state (136.1) optimizes as a synapomorphy of *Ololygon*, with at least one reversal to straight posterior margin (Ch. 136.0) in the clade including the *O. belloni*, *O. cardosoi*, and *O. perpusilla* groups, or in a more inclusive clade also including the *O. feioi* group.

The former *Scinax catharinae* group of Faivovich (2002) included *S. agilis* as the sister taxon of all other studied species. Faivovich (2002) proposed five synapomorphies for this group, exclusive of *S. agilis*. These are (i) strong inclination of the larynx in relation to the posteromedial process (our Ch. 32.1), (ii) arytenoids oval with anterior and posterior constrictions in dorsal view (our Ch. 37.2), (iii) dorsal prominence of the arytenoids developed medially (our Ch. 38.1), (iv) no fiber of the m. depressor mandibulae originating at the tympanic annuli (our Ch. 72.1), and (v) presence of the lateral m. dorsometatarsalis hallucis distalis (our Ch. 126.1). In our results, character-states (iii) and (v) are synapomorphies of the sister taxon of the *Ololygon agilis* group. Character-states (i), (ii), and (iv) optimize ambiguously. While (i) and (iv) could be synapomorphies of the sister taxon of the *O. agilis* group or arise independently in the *O. argyreornata* and *O. catharinae* groups, (ii) could be a synapomorphy of the sister taxon of the *O. agilis* group or arise in the *O. argyreornata*, and *O. belloni* + *O. perpusilla* groups; in this case, the ambiguous optimization is a result of unknown character-states in species of the *O. feioi* group.

In a study of the cranial anatomy of tadpoles of five species of Scinaxini, Alcalde et al. (2011) noticed that chondrocrania and hyobranchial skeleton of the two species of the former *Scinax catharinae* group available to them, *Ololygon aromothyella* and *O. berthae* (here recovered as sister species), share the long and slightly divergent free portion of the cornua trabeculae, the long and thin processus articularis, the wide and rounded processus muscularis, the tripartite cartilago suprarostralis, slender lower jaw cartilages, a medially directed processus anterolateralis and ceratobranchialia III and IV joined by commissurae proximales. These observations partially apply to the description of chondrocranium and hyobranchial skeleton of *O. skuki* by Rodrigues et al. (2017), although in that species ceratobranchialia III and IV are not joined by a commisura proximalis. The generality of all these observations for other species of *Ololygon* requires corroboration.

The interspecific relationships are generally well resolved in the *Ololygon catharinae* group (Figs. 22–25), although not particularly well supported (several clades with < 50% jackknife). The topological conflicts are restricted to conspecific terminals (Figs. 23–25). Overall, the consensus recovers several well-supported clades that are related through a poorly supported pectinate structure (Figs. 22, 24–25). These results are discussed in detail below.

The sister taxon of most species of the *Ololygon catharinae* group is a clade that includes *O. angrensis*, *O. humilis*, and *O. littoralis* (100% jackknife; Fig. 22). *Ololygon humilis* has been differentiated from *O. littoralis* (Pombal and Gordo, 1991) based on female SVL and call structure (Hepp et al., 2017). UPDs between *O. humilis*, and *O. angrensis* and *O. littoralis* are 1.9–4.8 (Appendix S10: Table 6). The last two species are morphologically similar (Lutz, 1954, 1973b; Pombal and Gordo, 1991), as are their calls (Garey et al., 2012; Hepp et al., 2017), and in need of a clear diagnosis[8]. Our results indicate UPDs of 1.9–3.4% between both species (Appendix S10: Table 6). They occupy adjacent coastal areas in Brazil, *O. angrensis* in southern Rio de Janeiro and northern São Paulo, and *O. littoralis* in southern São Paulo southwards to Paraná and Santa Catarina (Carvalho-e-Silva et al., 2008; Conte et al., 2009; Lucas and Garcia, 2011).

The clade including *Ololygon angrensis*, *O. humilis*, and *O. littoralis* is followed by a poorly supported clade (58% jackknife) where *O. caissara* is the sister taxon of a well-supported clade (100% jackknife) composed of *O. flavoguttata*, *O. heyeri*, and *O. tripui* (Fig. 22). These three species share yellow/orange or light green flash coloration in the inguinal region and hidden surfaces of flanks and thighs (yellow/orange occurs as well in *O. aromothyella* and *O. berthae*). *Ololygon caissara*, a species from the coastal forest in southern São Paulo, Brazil is distinguishable from all species of *Ololygon* by having glandular acini in the mental region and differs by its size, snout shape in dorsal view, toe webbing extension, and others (see Lourenço et al., 2016).

Our results recovered the terminals of *Ololygon tripui* monophyletic, with two lineages (Fig. 22). One of these (90% jackknife) corresponds to topotypes from Ouro Preto, Minas Gerais, Brazil and a population from Caparaó, Minas Gerais (≈170 km ESE from Ouro Preto). The other lineage includes samples (UFMG 7791, 10598–10599) from Nova Lima and Rio Acima, Minas Gerais. The intraspecific UPDs are 0.0–2.2% (Appendix S10: Table 7). The

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8   The anterior gap in the marginal papillae of the oral disc of *Ololygon littoralis* (Pombal and Gordo, 1991) is absent in the described larvae of *O. angrensis* (Carvalho-e-Silva et al., 1995). However, Lourenço (2013) questioned the identification of the tadpole of *O. angrensis*, and, for that reason, we treated it as unknown for the purposes of scoring this species in the phenotypic dataset.
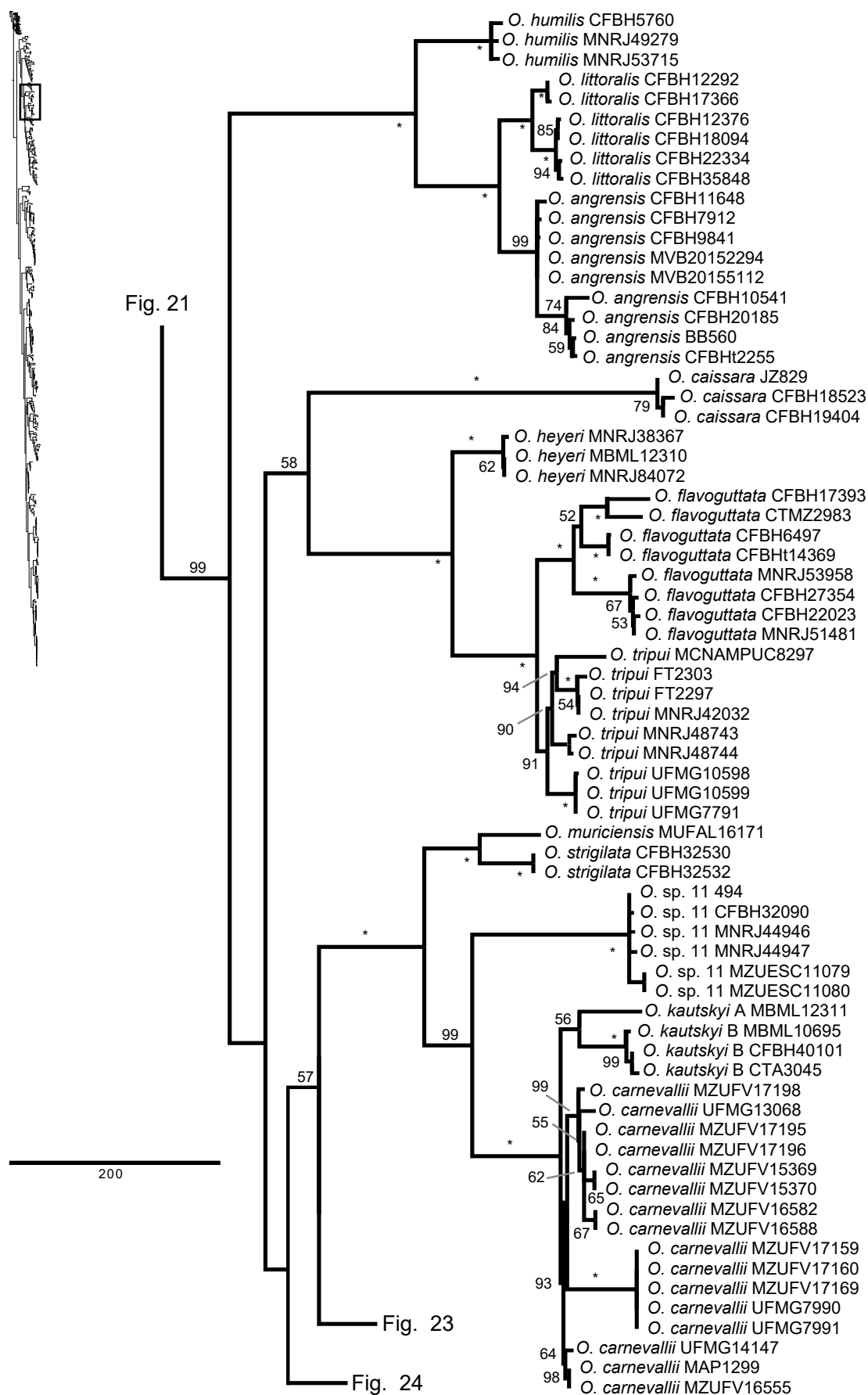
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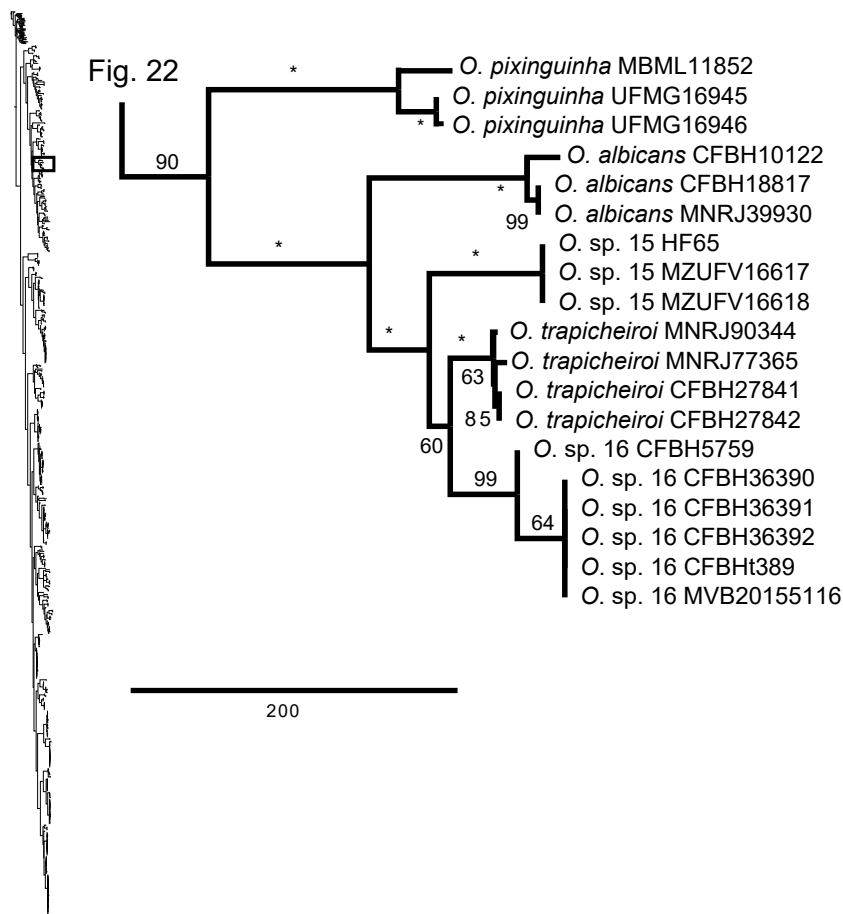
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Figure 22. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 3 of 21: The *Ololygon catharinae* group, part 1 of 4. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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populations of *O. flavoguttata* are monophyletic (100% jackknife), including specimens from Rio de Janeiro (Itatiaia, Nova Friburgo, and Teresópolis) and São Paulo (São Luis do Paraitinga and topotypes from São José do Barreiro) in Brazil, and have intraspecific UPDs of 0.0–2.2%. UPDs between *O. tripui* and *O. flavoguttata* are 1.4–2.9% (Appendix S10: Table 7). Despite the UPDs, *O. tripui* differs from *O. flavoguttata* mainly by having smaller SVL in males and females, subovoid snout, more developed nuptial pad, and light green coloration on inguinal regions and hidden portions of flanks and thighs (Lourenço et al., 2010).

The clade that follows is poorly supported (57% jackknife) and includes two clades, both well supported (90% and 100% jackknife). One of these comprises *Ololygon albicans*, *O. pixinguinha*, *O. trapicheiroi*, and two candidate species *Ololygon* spp. 15–16 (Fig. 23). *Ololygon pixinguinha* was recently described from Santa Teresa (Espírito Santo, Brazil; Lacerda et al., 2021) and in this paper we add specimens from Santa Bárbara do Leste (Minas Gerais, Brazil). This species is recovered as the sister taxon of the other species in the clade. *Ololygon albicans* is known from Rio de Janeiro and is represented in our analysis by topotypes (Parque Nacional Serra dos Órgãos, Teresópolis; Bokermann, 1967a) and one specimen from Petrópolis, on the western side of the mountain chain. UPDs between

these specimens are 0.5% (Appendix S10: Table 8). *Ololygon* sp. 15 is a CCS from Cataguases, Minas Gerais that differs from *O. trapicheiroi* by its dorsal pattern (interocular mark that extends backwards into the dorsum in *O. trapicheiroi*; reduced and not extending in *Ololygon* sp. 15) and a longer snout than *Ololygon* sp. 16. UPDs between *O.* sp. 15, and *O. trapicheiroi* and *O.* sp. 16 are 2.2–2.7% (Appendix S10: Table 8).

Ololygon trapicheiroi is known from Rio de Janeiro including the island of Ilha Grande, and eastern Minas Gerais (Lutz, 1954; Izecksohn and Carvalho-e-Silva, 2001; Luna-Dias et al., 2009; Silveira, 2011; Folly et al., 2020). This species, represented in our analyses by topotypes, is recovered as the poorly supported (62% jackknife) sister taxon of *Ololygon* sp. 16 (Fig. 23). The latter is considered a CCS due to phenotypic differences (e.g., interocular mark that extends backwards into the dorsum in *O. trapicheiroi*; reduced and not extending in *Ololygon* sp. 16). For this CCS we have samples from the western coastal areas of Rio de Janeiro (Angra dos Reis, Ilha de Trinidade) and eastern São Paulo (Ubatuba). These two species have UPDs of 2.0–3.0% (Appendix S10: Table 8).

The other clade includes *Ololygon carnevallii*, *O. kautskyi* A, *O. kautskyi* B, *O. muriciensis*, *O. strigilata*, and one CCS (*Ololygon* sp. 11; Fig. 22). *Ololygon muriciensis* and *O. strigilata* are sister species, and the sister taxon

Figure 23. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 4 of 21: The *Ololygon catharinae* group, part 2 of 4. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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of the other species (99% jackknife). *Ololygon* sp. 11 has been confused with *O. strigilata* (see below) and is the sister taxon of a clade including the two lineages associated with *O. kautskyi* (*O. kautskyi* A and *O. kautskyi* B) and *O. carnevallii* (Fig. 22).

One problem regarding the recognition of *Ololygon* during the 1980s was the identity of its type species *O. strigilata* (see Cardoso and Sazima, 1980; Cardoso and Haddad, 1982; Faivovich, 2002). *Ololygon strigilata* was not associated with any known population until Pimenta et al. (2007) reviewed the nomenclatural history of *O. strigilata* and designated a neotype from Fazenda "Pedra Formosa," Ibirapitanga, southern Bahia, Brazil. They also reported specimens from other localities in the Atlantic Forest of southern Bahia, as did Mira-Mendes et al. (2013) and Nogueira et al. (2016, 2022). Our analyses show that specimens originally identified as *O. strigilata* from some localities in southern Bahia (Amargosa, Camacán, Ilhéus, Jussari), ca. 150 km S from the type locality of *O. strigilata*, show notable sequence divergence (7.2–7.8%; Appendix S10: Table 9) from topotypic specimens (CFBH 32530 and 32532). Furthermore, those specimens are more closely related (99% jackknife) to the two lineages associated with *O. kautskyi* and *O. carnevallii* than to *O. strigilata* (Fig. 22). These results suggest that at least two different species are being conflated under the name *O. strigilata*, and as they are not monophyletic, we recognize *Ololygon* sp. 11 as a CCS. Our study of the voucher specimens and the material from Jussari that Pimenta et al. (2007) referred to *O. strigilata* (*Ololygon* sp. 11 in this study) and specimens from Camacán (UESC 8625, 9080, 9082) does not reveal any consistent morphological diagnostic character.

Ololygon muriciensis is a species morphologically similar to *O. strigilata*. The species is only known for its type locality in Murici, Alagoas, Brazil (Cruz et al., 2011), and a topotype was included in this project. Our results recover it as the sister taxon of *O. strigilata* (100% jackknife). The study of the holotype and two paratypes of *O. muriciensis* did not corroborate the characters differentiating this species from *O. strigilata* listed by Cruz et al. (2011), nor resulted in any other morphological difference. Our results, however, indicate that both species differ in UPDs of 3.2–3.5% (Appendix S10: Table 9), and for this reason, we consider *O. muriciensis* as a valid species. We stress, however, the need for a taxonomic reassessment of all populations under the names *O. strigilata* and *O. muriciensis* (Pimenta et al., 2007; Camurugi et al., 2013; Nogueira et al., 2016; Freitas et al., 2018).

Ololygon kautskyi was described from Domingos Martins, Espírito Santo, Brazil (Carvalho-e-Silva and Peixoto, 1991); S.P. Carvalho-e-Silva (personal comm.) kindly informed us that it was collected in Clube de Campo Eldorado, Domingos Martins. We included four samples identified as this species from Cariacica, Domingos Martins (≈10 km E from the type locality), and Santa Teresa, Espírito Santo. Our results indicate that there are two lineages associated with *O. kautskyi*. One of these (identified as *O. kautskyi* A) is represented by a single sample from Domingos Martins, and it is poorly supported (56% jackknife) as the sister taxon of the other lineage (*O. kautskyi* B). *Ololygon kautskyi* B is represented by samples from Cariacica, Domingos Martins, and Santa Teresa. Both lineages are syntopic in Domingos Martins (Biriricas), where UPDs between the samples are 2.8%. We are not aware of any diagnostic phenotypic character that distinguishes both lineages. UPDs between *O. kautskyi* A and *O. kautskyi* B, and *O. carnevallii* are 2.4–3.7% (Appendix S10: Table 9).

Ololygon carnevallii is represented by specimens from Marliéria (type locality; Caramaschi and Kisteumacher, 1989) and several localities in Minas Gerais, Brazil. Our results recover a clade with samples from Mesquita and Conceição de Mato Dentro, a clade from Caratinga, Cataguases and Marliéria, and a clade from Braúnas, Leme do Prado, and Sapucaia de Guanhães. These results are congruent with the results of Myers et al. (2021) and this topology is mostly delimited by COI sequences produced by these authors. Available 16S sequences for the estimation of UPDs are limited to only two of these clades, being 0.0–2.5%, with the largest UPDs (2.4–2.5%) between specimens of Conceição de Mato Dentro (and presumably those most closely related from Caratinga) and those from the other localities (for which 16S is available; Appendix S10: Table 9). Tadpoles of *O. carnevallii* were described based on specimens from Conceição de Mato Dentro (Pezzuti et al., 2016). Subsequent comparisons with tadpoles from adjacent areas to the type locality indicated no significant differences, and none were found in adults and vocalizations between these populations (TLP and FSFL, personal obs.).

The recently described *Ololygon garibaldiae* is poorly supported (< 50% jackknife) as the sister taxon of a major clade with all the remaining species of the *O. catharinae* group, including 16 described species and nine candidate species (*Ololygon* spp. 3, 7, 10, 12–14, 17–19; Fig. 24). It is well supported (97% jackknife) and delimited by molecular data. We are not aware of any morphological synapomorphy for this clade.

Some species in this clade were previously included in the former *Scinax rizibilis* group (sensu Andrade and Cardoso, 1987) because they have bilobate vocal sacs (*S. brieni*, *S. berthae*, *S. hiemalis*, *S. jureia*, *S. luizotavioi*, *S. obtriangulatus*, *S. ranki*, and *S. rizibilis*; Andrade and Cardoso, 1987; Haddad and Pombal, 1987; Caramaschi and Kisteumacher, 1989). Subsequently, Pombal et al. (1995b) placed the *S. rizibilis* group into the former *S. catharinae* group (sensu Duellman and Wiens, 1992), suggesting that those species did not form a distinct group because the laterally expanded vocal sacs were considered an intraspecific variable characteristic. As in a previous analysis (Faivovich, 2002), the former *S. rizibilis* group (sensu Andrade and Cardoso, 1987) is not monophyletic in our results (Figs. 24–25).

Our results reject the monophyly of *Ololygon aromothyella*, *O. berthae*, and *O. rizibilis* (Faivovich, 2002; Fig. 24), as they form two clades that are successive sister taxa of the other clades. These three species are characterized by having a moderately developed m. interhy-
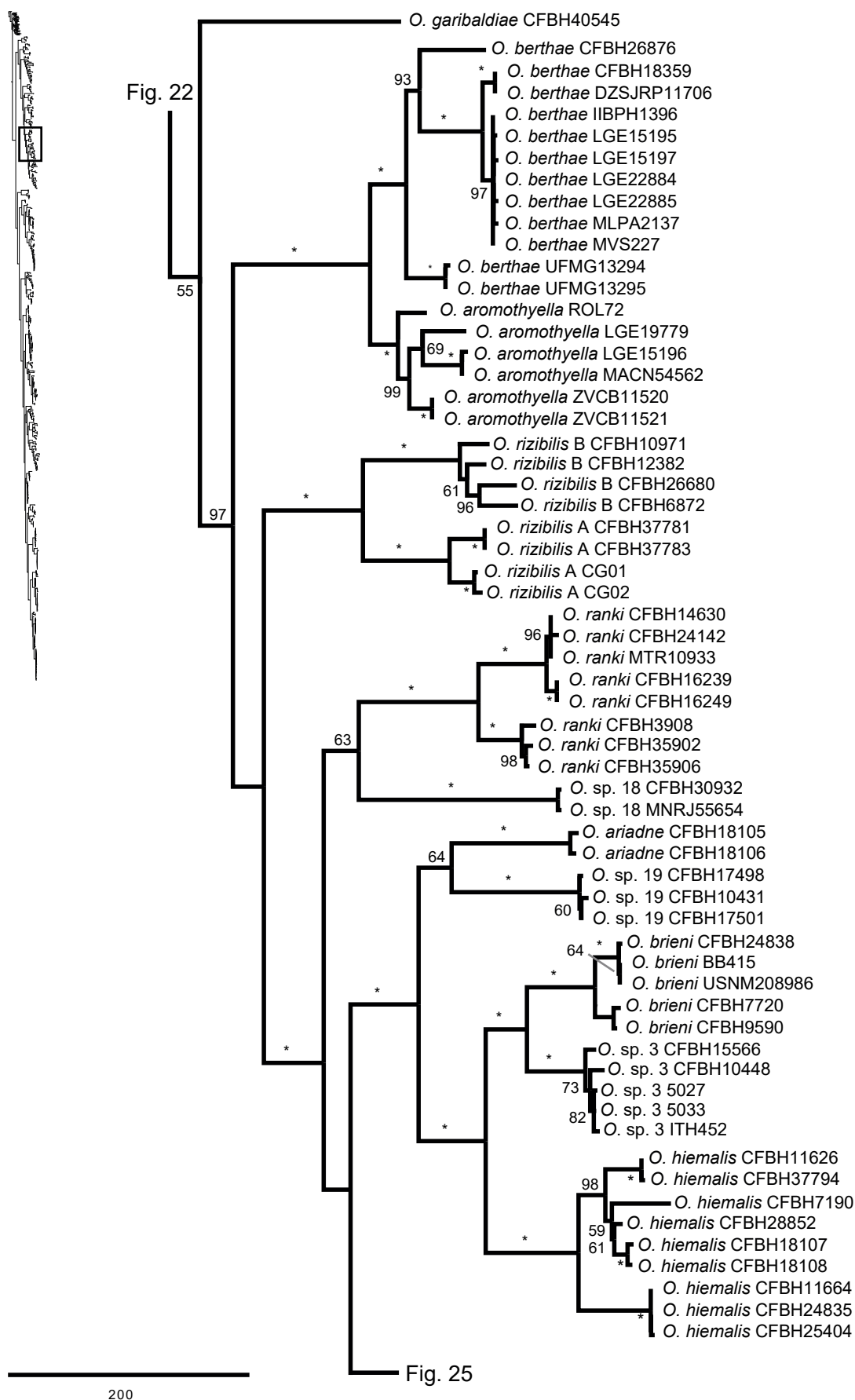
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Figure 24. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 5 of 21: The *Ololygon catharinae* group, part 3 of 4. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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oideus, and oviposition site in permanent or temporary ponds. Furthermore, they are so far the only species in the *O. catharinae* group known to share a long-call pattern (Hepp et al., 2017; Bang and Giaretta, 2018), being a long series of short, squawk-like notes with gradually ascending amplitude and long duration (also occurring in the *O. argyreornata* group).

It should be mentioned that the relationships of *Ololygon garibaldiae*, *O. aromothyella*, *O. berthae*, and *O. rizibilis* involve one of the few relevant areas of incongruence between the parsimony and the ML results. In the ML results (Appendix S8), all these species are monophyletic (90% bootstrap); *O. garibaldiae* is weakly supported (58% boostrap) as the sister taxon of *O. rizibilis* A + *O. rizibilis* B, and this clade as sister to *O. aromothyella* + *O. berthae*. The reasons for this incongruence could stem from a number of factors (e.g., Edwards, 2009; Lemmon et al., 2009; Simmons, 2012, 2014; Padial et al., 2014; Xi et al., 2016; Mendes and Hahn, 2018).

Ololygon aromothyella was considered most similar to *O. berthae* (Faivovich, 2005), with which it has been confused in the past (Langone and Prigioni, 1988). Our study included samples from distant localities (up to 750 km airline) in Argentina, Brazil, and Uruguay. All these were recovered monophyletic (Fig. 24), with UPDs of 1.0–1.7% (Appendix S10: Table 10). UPDs between this species and its sister taxon, *O. berthae*, are 2.2–3.2%.

Ololygon berthae is the most broadly distributed species of *Ololygon* (see Nascimento et al., 2016 for a recent review), with ≈2000 km (airline) separating the two most distant localities from which we included sequences (Magdalena, Buenos Aires, Argentina and Itatiaiçu, Minas Gerais, Brazil). This broad distribution has been known since the original description of this species (Barrio 1962, 1964). Although Punta Lara, Buenos Aires, Argentina is the type locality, the type series included two paratypes from São Bernardo do Campo, São Paulo, Brazil (LIH 1088–1089). Possibly, the considerable distance separating the localities, or the fact that São Bernardo do Campo is the type locality of *O. rizibilis* (Bokermann, 1964a) led to doubts by Lutz (1973a) regarding the identity of the paratypes, suggesting that these paratypes could be *O. rizibilis*. These concerns were also expressed by Andrade and Cardoso (1987). Faivovich (2005) studied the available Brazilian paratype (LIH 1088, housed in MACN), the holotype, and other specimens, and concluded that the paratype is indistinguishable from *O. berthae*.

Our results recover all samples of *Ololygon berthae* monophyletic (Fig. 24), with internal UPDs of 0.3–3.2% (Appendix S10: Table 10). The two specimens from Itatiaiçu, Minas Gerais, are the sister clade of all other samples and show a substantial sequence divergence (2.5–3.2%) from the specimens in its sister clade, which includes samples from Ribeirão Grande, São Paulo, Brazil to Magdalena, Buenos Aires, Argentina. There is an evident gap in sequence divergence between the specimens of Minas Gerais and those of São Paulo (2.5–3.0%), which considerably exceeds the internal sequence divergence of the clade including the samples from São Paulo to Buenos

Aires (0.4–1.9%; Appendix S10: Table 10). Furthermore, Pezzuti et al. (2021) noticed some differences in the tadpoles from Itatiaiçu, Minas Gerais compared to the description available for Punta Lara, Buenos Aires, Argentina (de Sá et al., 1997). These include the presence of many submarginal papillae and the absence of flagelliform tail tip, as well other distinct coloration aspects. As more material from the Minas Gerais and São Paulo becomes available, a taxonomic study will be required to determine if these lineages correspond to more than one species.

The following clade is well supported (100% jackknife) and includes two lineages associated with *Ololygon rizibilis* (Fig. 24). This species is known in the Brazilian states of Paraná, Rio Grande do Sul, Santa Catarina, São Paulo, and Minas Gerais (Figueiredo et al., 2016; Lourenço et al., 2016). Our analyses show two lineages that differ in UPDs of 2.7–4.0% (Appendix S10: Table 11). One of the lineages includes specimens from Serra do Brigadeiro, southwest Minas Gerais and Bertioga, coastal region of São Paulo. The latter is ≈20 km E from the type locality of *O. rizibilis* in Campo Grande, Santo André, São Paulo (Bokermann, 1964a). The other lineage includes specimens from Ribeirão Branco, SW São Paulo and highland localities in Paraná and Santa Catarina, with one specimen (CFBH 26680) from Parque Ecológico da Guarapiranga (São Paulo) ≈37 km NW from the type locality of *O. rizibilis*. Considering that we are not aware of morphological differences between both lineages, the relative proximity of both to the type locality, and that there are some preliminary observations indicating differences in the call (PCAG, personal obs.), we consider them as *O. rizibilis* A and *O. rizibilis* B, respectively. The inclusion of topotypes of *O. rizibilis* will clarify which of these lineages corresponds to the species. In case it is associated with *O. rizibilis* A, the name *Hyla mirim* Lutz, 1973b (type locality: Rio Vermelho, outside São Bento do Sul, Santa Catarina), considered a junior synonym of *Hyla rizibilis* by Andrade and Cardoso (1987), would be available for the lineage *O. rizibilis* B.

Haddad et al. (1990) and Bastos et al. (2010) reported the occurrence of bubble nests in a population of *Ololygon rizibilis* B (Ribeirão Branco, São Paulo) built by the female during the amplexus, and a similar nest was observed in populations from Santa Catarina (PCAG, personal obs.). When describing the spawning of topotypic *S. rizibilis*, Bokermann (1964a) stated that a clutch laid by a recently collected couple was typical of the "*Hyla* of the *rubra* and *catharinae* groups" and did not report bubble nests (an observation also corroborated by personal communication in Haddad et al., 1990). Unpublished information on the lineage *O. rizibilis* A indicates that it also has bubble nests (PCAG, personal obs.). Field observations on the reproductive mode of topotypic *O. rizibilis* are necessary to corroborate the observations of Bokermann (1964a).

The following clade is well supported (100% jackknife) and delimited only by molecular evidence. Although several internal clades with 2–7 species are individually well supported, relationships among them are generally poorly supported (≤ 50% jackknife; Figs. 24–25).

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Ololygon ranki is recovered as a single lineage represented by two clades (Fig. 24); one including specimens from Cristina, Minas Gerais, and Campos do Jordão, São Paulo, and another of topotypic specimens from Morro do Ferro, Minas Gerais. UPDs between specimens of these clades are 1.5–2.0% (Appendix S10: Table 12). Bang and Giaretta (2017) reported that *O. hiemalis* and *O. ranki* were phenotypically indistinguishable, differing only in some quantitative acoustic parameters (pulse rate, call, and note duration). Our results recover both species as only distantly related (see below for comments on the position of *O. hiemalis*), supporting them as different species. *Ololygon* sp. 18 (Teresópolis, Rio de Janeiro, Brazil) is a CCS that differs from most species of *Ololygon* by its large male SVL, snout shape, toe webbing, and size of the nuptial pad. It is poorly supported (63% jackknife) as the sister taxon of *O. ranki* (Fig. 24), from which it differs in UPDs of 6.3–7.0% (Appendix S10: Tab. 12).

Ololygon ariadne, *O. hiemalis*, *O. brieni*, and two candidate species (*Ololygon* spp. 3 and 19; Fig. 24) are monophyletic and well supported (99% jackknife). The monophyly of *O. ariadne* and *Ololygon* sp. 19 is poorly supported (64% jackknife), and this clade is the sister taxon of the clade including *O. brieni*, *O. hiemalis*, and *Ololygon* sp. 3. *Ololygon* sp. 19 (Ilha Bela, São Paulo, Brazil) has UPDs of 4.2–5.7% with the other species in this clade (Appendix S10: Table 13). Although at this point we cannot distinguish *Ololygon* sp. 19 from *O. brieni*, we consider it a CCS because it is not closely related to this species. Furthermore, it differs from *O. hiemalis* by the lack of an enlarged inguinal gland, and from *O. ariadne* by the presence of a vocal sac.

Ololygon hiemalis is recovered as a lineage represented by two well-supported clades (98% and 100% jackknife; Fig. 24): one from central São Paulo (Jundiaí and Cotia), and the other from the coastal region of São Paulo (Bertioga and Santo André) and from northeast São Paulo (São José do Pinhal and São José do Barreiro). Tissue samples of topotypic specimens were unavailable for this species, but we have sequences from Jundiaí, ≈42 km SSE from its type locality in Campinas, São Paulo (Haddad and Pombal, 1987). UPDs between all samples of *O. hiemalis* are 0.2–1.7% (Appendix S10: Table 13). These and the absence of diagnostic phenotypic characters distinguishing these clades suggest that they belong to a single species. We could not include samples of the specimens that were cited as *O. hiemalis* from Teresópolis, Rio de Janeiro by Caram et al. (2011) and Carvalho-e-Silva et al. (2020).

Our results show two lineages associated with *Ololygon brieni* (Fig. 24). One of these, with specimens from northeastern São Paulo (Bertioga, São Luiz de Paraitinga) including its type locality (Paranapiacaba, São Paulo, Brazil; De Witte, 1930; Bokermann, 1966b), for which we apply the name *O. brieni*. This lineage differs in UPDs of 2.3–2.8% from the other lineage from southern São Paulo (Tapiraí, Parrelheiros, and Estação Ecológica da Juréia-Itatins; Appendix S10: Table 13). Our observations on this material and the type series of *O. brieni* so far failed to find characters differentiating them. However, it is noticeable

that an UPD of 2.5% is observed along ≈50 km, separating the closest localities for both lineages (Appendix S10: Table 13); for this reason, we consider *Ololygon* sp. 3 to be a UCS. It also includes specimens from Estação Ecológica da Juréia-Itatins, the type locality of *O. jureia* (Pombal and Gordo, 1991); however, our observations indicate that this UCS differs from *O. jureia* by the much-reduced toe webbing between toes II–V.

Ololygon catharinae is poorly supported (< 50% jackknife) as the sister taxon of *O. machadoi* and four candidate species (Fig. 25). We included specimens of *O. catharinae* from Santa Catarina and Rio Grande do Sul, Brazil. The samples from Santa Catarina comprise two specimens from different localities on the offshore island of Florianópolis, and specimens from Siderópolis and Treviso, ≈120 km SW on the continent. The sample from Rio Grande do Sul is from Cambará do Sul, ≈80 km farther SW. Our results (Fig. 25) recover the sample from the central area of Florianópolis (Córrego Grande) as the sister of all other samples, while that of the southern tip of that island (Praia dos Naufragados) is well supported (100% jackknife) as sister taxon of the specimens from the continent. Interestingly, UPDs between the specimen from Córrego Grande and all other samples are 1.8–1.9%, while that between the specimen of Praia dos Naufragados and specimens from the continent is 0.8–0.9%; the samples from the continent have identical sequences (Appendix S10: Table 14). Remarkably, the UPD between the two samples of Florianópolis, separated by only 25 km, is 1.5%. This genetic diversity points to the need for a taxonomic reassessment of *O. catharinae* to understand how many species are included under this name[9], and with which, if any, of the populations that we included should the name be applied. Overall, regardless of how many species are included under the name *O. catharinae*, the lack of support for the relationships of this clade with the others is curious considering its remarkable similarity with *O. brieni*.

Ololygon machadoi is recovered in a well-supported clade (100% jackknife) with one CCS (*Ololygon* sp. 7) and three UCSs (*Ololygon* spp. 10, 12–13; Fig. 25), all from different areas in the Espinhaço Mountain range of Bahia and Minas Gerais, Brazil. UPDs between these candidate species and *O. machadoi* are 3.2–5.4% (Appendix S10: Table 15). *Ololygon* sp. 7 is a CCS from Catas Altas, Minas Gerais; it differs from topotypic *O. machadoi* in having an enlarged forearm and larger SVL. Pezzuti et al. (2021) described the tadpole of this species (as *Ololygon* aff. *machadoi*) and noticed some differences (including an interruption of P-1 and a higher tail fin) with the tadpoles of

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9   Boulenger (1888a) reported the type locality as "Sierra de Catharina," an imprecise toponym. Bokermann (1966a) considered that it is probably a local name employed in the area of Palhoça (currently Águas Mornas, Santa Catarina), which was explored by the collector Julius Michaelis (Kwet, 2016). Lutz (1973a) believed the type locality to correspond to mountains in northern Santa Catarina. Boulenger (1888a, b, 1894, 1907) and Mertens (1952) reported "Sierra de Catharina," Lages, and Teresópolis (subsequently Queçaba, and currently Águas Mornas) as the localities explored in Santa Catarina by Michaelis. *Ololygon catharinae* is known to occur in Águas Mornas, Santa Catarina (PCAG, personal obs.).
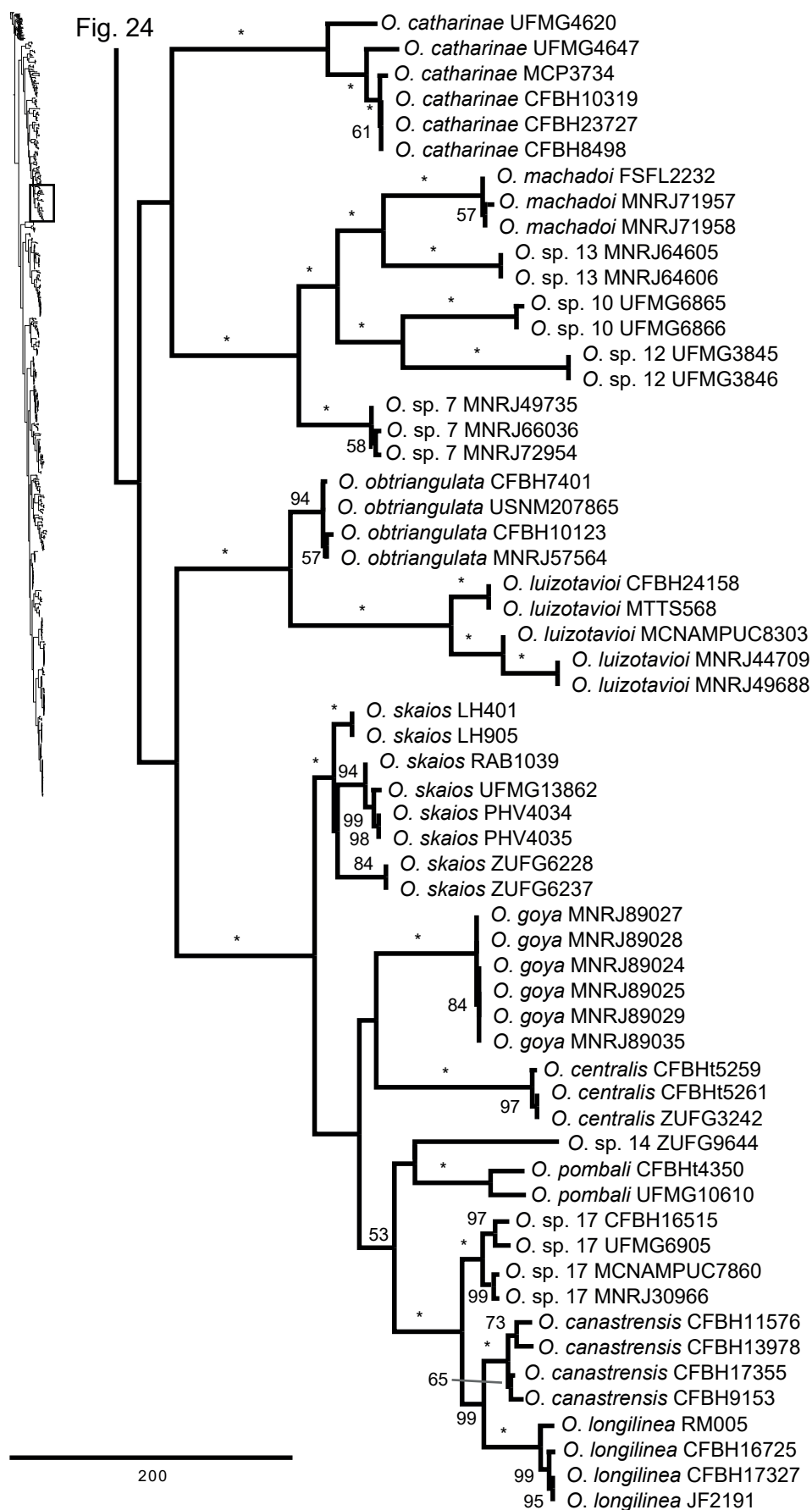
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Figure 25. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 6 of 21: The *Ololygon catharinae* group, part 4 of 4. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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O. machadoi from the type locality (Bokermann and Sazima, 1973) that require corroboration with a larger sample of larvae of both species.

Ololygon sp. 10 is from Conceição do Mato Dentro, Minas Gerais, not far away from the type locality of *O. machadoi* (≈25 km; Minas Gerais, Jaboticatubas [currently Santana do Riacho], Serra do Cipó), but UPDs are 4.8–5.4% (Appendix S10: Table 15). *Ololygon* sp. 12 is known from Mucugê, Central Bahia, ≈700 km NW from the type locality of *S. machadoi*. *Ololygon* sp. 13 is known from Gouveia, Minas Gerais, ≈100 km N from the type locality of *O. machadoi*. We are not aware of any phenotypic character differentiating *O. machadoi* from *Ololygon* sp. 10, 12, and 13, and for that reason, these are considered UCSs.

The following clade (Fig. 25) is composed of *Ololygon obtriangulata* and *O. luizotavioi* (100% jackknife). Samples of *O. obtriangulata* are available from Brejo da Lapa, Parque Nacional Itatiaia (topotype) and Petrópolis, Rio de Janeiro, and São Luiz do Paraitinga, São Paulo (Fig. 25). UPDs between the samples from Rio de Janeiro are 0.0%, and between these and the one from São Paulo are 0.6% (Appendix S10: Table 16). *Ololygon obtriangulata* was poorly diagnosed originally (Lutz, 1968a, 1973a), and the distribution and variation of this species remain poorly known. The identification of adults and larvae from Boracéia, in the Serra do Mar, São Paulo, considered as *O. obtriangulata* by Heyer et al. (1990), needs to be reassessed. *Ololygon obtriangulata* differs from *O. luizotavioi* by its color pattern, and UPDs are 4.2–5.2% (Appendix S10: Table 16).

Ololygon luizotavioi is represented by specimens from Ouro Branco and Catas Altas (topotypes), both in Minas Gerais, ≈60 km from each other, a specimen (CFBH 24158) from Estrada da Cachoeira da Maromba, Parque Nacional de Itatiaia, Rio de Janeiro, and another specimen (CFBH 46028) from Castelo, Espírito Santo, ≈200 km W and SW, respectively from the core area of distribution of *O. luizotavioi* (Fig. 25). Interestingly, UPDs between the samples of Ouro Branco and Catas Altas are 1.8%; we find these to be relatively large considering the short distances involved, and the situation is worthy of additional study (Appendix S10: Table 16). UPDs between the populations of Minas Gerais and those from Rio de Janeiro and Espírito Santo are 2.4–3.0%, while the two latter differ by 1.2% (Appendix S10: Table 16). We could not find morphological differences between the voucher specimens.

Several species from gallery forests in the Cerrado and transitional areas with Atlantic Forest, *Ololygon canastrensis*, *O. centralis*, *O. goya*, *O. longilinea*, *O. pombali*, *O. skaios*, and two CCSs are recovered in a well-supported clade (100% jackknife; Fig. 25). These species are characterized by the externally evident inguinal glands (particularly hypertrophied in *O. centralis*; Lourenço et al., 2013, 2014); the exceptions being *O. goya* and *O. pombali*, which lack them (Lourenço et al., 2013; Andrade et al., 2018). Within this clade, interspecific relationships are poorly supported but fully resolved (Fig. 25), with *O. skaios* as the sister taxon of one clade including *O. centralis* and

O. goya, and a clade with *O. canastrensis*, *O. longilinea*, *O. pombali*, and two candidate species.

Our samples of *Ololygon skaios* include one topotype (Santa Rita do Novo Destino, Goiás, Brazil; Pombal et al., 2010), specimens from Niquelândia, Alto Paraíso de Goiás, and Caiapônia, all in Goiás, Brazil. UPDs among these are 1.1–1.5% (Appendix S10: Table 17). We further included the two sequences (LH 401 and 905) from Chapada dos Guimarães, Mato Grosso produced by Nogueira et al. (2016). These authors proposed that these specimens (referred to as *Scinax* sp.) could be a new species, without advancing any compelling evidence other than sequence divergence in mitochondrial (12S and 16S) and nuclear (rhodopsin) genes with *O. berthae*, *O. catharinae*, *O. strigilata*, and other species of *Julianus* and *Scinax*. In our results (Fig. 25), these specimens differ from *O. skaios* in UPDs of 2.3–2.8% (Appendix S10: Table 17), with the caveat that these UPDs could be underestimated[10]. These sequences are tentatively considered to belong to *O. skaios*, expanding its known distribution ≈500 km W, and making this species the westernmost species of *Ololygon*.

Ololygon skaios, like *O. ariadne*, lacks vocal slits (Lourenço et al., 2016), and therefore, a vocal sac. Although *O. ariadne* was explicitly considered to lack a vocalization (Bokermann and Sazima, 1972) and none has been described nor heard in the field (ACCL, D. Baêta, CFBH, and JF, personal obs.), this is not the case with *O. skaios*. The vocalization of the latter was described by Pombal et al. (2010) and further compared with other calls of *Ololygon* by Hepp et al. (2017), providing an interesting example of a frog that lacks a vocal sac emitting calls that are very similar to those of closely related species that possess a vocal sac, as known for a few other anurans (e.g., *Phasmahyla*; Faivovich et al., 2010a; Dias et al., 2011; *Atelopus*; Boistel et al., 2011).

Ololygon sp. 14 is from Paracatu, Minas Gerais, Brazil; it differs in UPDs of 5.1–9.2% from the other taxa in this clade (Appendix S10: Table 17); however, we are not aware of any phenotypic character that diagnoses this species, and it is considered a CCS based on its phylogenetic position. *Ololygon longilinea* is represented by two well-supported (100% jackknife) distinct lineages (Fig. 25): one represented by topotype samples from Poços de Caldas, Minas Gerais, and the other with samples from Carrancas, Nova Lima, and Cristina, Minas Gerais. *Ololygon canastrensis* is represented by a single lineage that includes topotypes and specimens from nearby localities, nested with high support (100% jackknife) within the lineages of *O. longilinea* (Fig. 25). The lineages of *O. longilinea* and *O. canastrensis* have UPDs of 1.3–2.3% (Appendix S10: Ta-

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10 There are problems in all sequences produced by Nogueira et al. (2016), presumably because "poorly aligned positions and divergent region portions of 16S" (Nogueia et al., 2016:51) excluded for analyses were also excluded from the sequences deposited on GenBank. This is evidenced by a 41-bp gap between positions 247–287 of the 16S fragment delimited by the primers AR–BR (or Wilk2) in the sequences of these specimens (LH 401 and 905) and those of *Ololygon* sp. 11 and *O. agilis*, also produced by the same authors. This gap is absent in all sequences produced for the current project, including those of *Ololygon* sp. 11, *O. agilis*, and *O. skaios*.

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ble 17). Despite these low genetic divergences, *O. canastrensis* differs from *O. longilinea* mainly by having smooth dorsal skin and brown stripes on the hidden portions of thigh (granular dorsal skin and irregular blotches on the hidden portions of thigh in *O. longilinea*), and therefore are tentatively considered as distinct species. However, we could not identify any diagnostic character distinguishing the two lineages of *O. longilinea*; for the time being, we consider the lineage with samples from Carrancas, Nova Lima, and Cristina, as the CCS *Ololygon* sp. 17. UPDs with *O. longilinea* are 2.3% (Appendix S10: Table 17).

Faivovich (2002) provided phenotypic evidence for the monophyly of *Ololygon canastrensis* and *O. longilinea*. Larvae of these two species share with that of *O. pombali* shorter bodies in relation to tail length, a higher tail, more anterior origin of dorsal fin, shorter rostrum, and more robust tail musculature than other larvae of *Ololygon* (Pezzuti et al., 2016). The larva of *O. pombali* furthermore has an enlarged oral disc with multiserial rows of marginal papillae (Lourenço et al., 2013; Pezzuti et al., 2016) that our results reveal to be homoplastic with *O. ariadne* (Bokermann, 1967a), indicating the independent evolution in *Ololygon* of characters associated with life in fast flowing waters.

Tissue samples were unavailable for *Ololygon jureia*, which is known only from the type series from Juréia-Itatins, in coastal São Paulo, and to our knowledge has not been collected since the original description. It is tentatively placed in the *O. catharinae* group on the basis of the character combination mentioned in its diagnosis (Pombal and Gordo, 1991).

Other relevant literature. Barrio (1962: vocalization of *O. berthae*); Bokermann (1964a: tadpole and vocalization of *O. rizibilis*); Bokermann (1967b: tadpole of *O. ariadne*); Bokermann and Sazima (1973: tadpole and vocalization of *O. machadoi*); Heyer (1980: vocalizations of *O. albicans*); Haddad and Pombal (1987: tadpole and vocalization of *O. hiemalis*); Andrade and Cardoso (1987: tadpole and vocalization of *O. ranki*); Peixoto and Weygoldt (1987: tadpole and vocalization of *O. heyeri*); Heyer et al. (1990: tadpoles of *O. flavoguttata* and a species identified as *O. obtriangulata*; see text regarding the latter); Andrade and Cardoso (1991: vocalizations of *O. longilinea* and *O. ranki*; tadpole of *O. longilinea*); Pombal and Gordo (1991: tadpole of *O. littoralis*); Taboga and Dolder (1993, 1994: spermatozoid morphology in *O. ranki*); Carvalho-e-Silva and Carvalho-e-Silva (1994: tadpoles of *O. albicans* and *O. trapicheiroi*); Carvalho-e-Silva et al. (1995: tadpole of *O. kautskyi*); Pombal and Bastos (1996: vocalization of *O. centralis*); Carvalho-e-Silva and Carnaval (1997: natural history and tadpole of *O. flavoguttata*); de Sá et al. (1997: tadpole of *O. berthae*); Carvalho-e-Silva and Carvalho-e-Silva (1998: natural history and tadpole of *O. humilis*); Bastos and Haddad (1999, 2001, 2002: vocalizations, behavior, and reproductive biology of *O. rizibilis*); Gomes et al. (2002: antipredator behavior and physiology of *O. hiemalis*); Rico et al. (2004: reproductive biology of *O. trapicheiroi*); Nascimento and Fernandez (2006: reproductive

biology of *O. albicans*); Van Sluys et al. (2006: reproductive biology of *O. trapicheiroi*); Alcantara et al. (2007: reproductive biology of *O. centralis*); Bertoluci et al. (2007: tadpole of *O. luizotavioi*); Conte et al. (2007: tadpole of *O. catharinae*); Kolenc et al. (2007: tadpole of *O. aromothyella*); Lourenço et al. (2009: vocalizations of *O. luizotavioi*); Pombal et al. (2010: vocalizations of *O. skaios*); Alcalde et al. (2011: tadpoles of *O. aromothyella* and *O. berthae*); Bastos et al. (2011: vocalizations of *O. centralis*); Pereyra et al. (2012: vocalizations of *O. aromothyella* and *O. berthae*); Toledo et al. (2012: reproductive biology of *O. littoralis*); Lourenço et al. (2013: tadpole of *O. pombali*); Camurugi et al. (2013: tadpole of *O. strigilata*, see text above for taxonomic problems with this species); Mira-Mendes et al. (2013: vocalizations of *O. strigilata*); Moura et al. (2015: reproductive biology of *O. luizotavioi*); Peixoto et al. (2016b: cytogenetics of *O. tripui*); Pezzuti et al. (2016: tadpoles of *O. canastrensis* and *O. carnevallii*); Bang and Giaretta (2017, 2018: vocalizations of *O. canastrensis, O. hiemalis, O. pombali,* and *O. ranki*); Hepp et al. (2017: vocalizations of *O. heyeri, O. humilis, O. longilinea,* and *O. trapicheiroi*); Silva et al. (2017: skin histology of *O. angrensis, O. flavoguttata, O. humilis,* and *O. trapicheiroi*); Andrade et al. (2018: vocalizations of *O. goya*); Targueta et al. (2018: karyotype of *O. centralis*); Brito et al. (2019: skin histology of *O. centralis*); Castro et al. (2020: microsatellites of *O. centralis*); Folly et al. (2020: distribution of *O. trapicheiroi*); Mendonça et al. (2020; natural history of *O. catharinae*); Pereira-Ribeiro et al. (2020: natural history of *O. kautskyi*); Reis et al. (2020: karyotypes likely of *Ololygon* sp. 7, as *O. machadoi*, from Mariana, Minas Gerais); Bang et al. (2021: vocalizations and distribution of *O. centralis*); Lacerda et al. (2021: vocalizations of *O. pixinguinha*); Pezzuti et al. (2021: tadpoles of *O. berthae, O. longilinea, O. luizotavioi, O. tripui,* and *Ololygon* sp. 7); Caramaschi et al. (2022: status of the type series of *O. heyeri*); Pederassi et al. (2022: vocalizations of *O. hiemalis*).

Julianus Duellman et al., 2016

Type species. *Hyla uruguaya* Schmidt, 1944.

Juliana—Duellman et al. (2016:28). Incorrect subsequent spelling.

Sister taxon. *Scinax.*

Diagnosis. This genus is well supported (100% jackknife) and delimited by molecular evidence and seven phenotypic synapomorphies. These include (1) broad separation between otic plate of the otic ramus of squamosal and ossified portion of crista parotica due to a small otic plate (Ch. 5.4, with one reversal to slight or no overlap between otic plate and ossified portion of crista parotica in *Julianus fontanarrosai*; other instances of homoplasy at least in *Dendropsophus microps, Phyllodytes luteolus,* and *Xenohyla truncata*); (2) medial ramus of pterygoid short (Ch. 10.0); (3) medial ilio-sacral sesamoid slightly expand-

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ed medially, length half-width (Ch. 24.2; *J. camposseabrai* has a medially elongated ilio-sacral sesamoid, width at least three times length, Ch. 24.3); (4) esophageal process of cricoid ring in males absent (Ch. 33.0, with some instances of homoplasy in internal clades of *Scinax*, and several outgroups); (5) visceral peritoneum of testes with dark spots (Ch. 67.2, with instances of homoplasy in some species of *Ololygon* and *Scinax*, and *Lysapsus* + *Pseudis*); (6) marginal papillae on the posterior margin of the oral disc larger than those on the lateral margins in tadpoles (Ch. 140.1, with instances of homoplasy in *Scinax quinquefasciatus*, *Dendropsophus minutus*, and *Sphaenorhynchus*); and (7) colored keratinized plates on the sides of the lower jaw-sheath (Ch. 151.1).

The species included in this genus can also be differentiated from other genera of Scinaxini by the combination of presence of pectoral fold (absent in most species of *Ololygon*); single or bilobate, dark, externally evident vocal sac; papillae on the posterior labium larger than those on the lateral margins in tadpoles (synapomorphy of this group, Ch. 140.1; same size in all species of *Ololygon* and *Scinax*); and presence of keratinized dark plates on the sides of the lower jaw-sheath of tadpoles (synapomorphy of this genus, Ch. 151.1; absent in all species of *Ololygon* and *Scinax*).

Characterization. (1) SVL in males 19.1.0–34.0 mm, females 23.8–35.9 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single or paired, does not reach the level of the pectoral fold; (5) snout rounded; (6) tubercles in the lower lip absent; (7) dorsal skin with scattered tubercles; (8) postaxial webbing of toe I reaching margin of subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the subarticular tubercle (Ch. 59.1); (10) epidermal projections in the nuptial pad absent (Ch. 64.1); (11) spicules in nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands absent or present in males (Ch. 47.0 or 47.1); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze or bicolor golden/brown; (15) dorsal pattern with mottling and irregular blotches, a large cephalic V-shaped marking present or absent; (16) hidden surfaces of thighs uniform or with irregular light blotches; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole visible ventrally (Ch. 146.0); (19) oral disc subterminal (Ch. 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) marginal papillae on the posterior labium larger than those in the lateral margins (Ch. 140.1); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath present (Ch. 151.1); (24) intestinal coiling axis subparallel to the main body axis (Ch. 148.1); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds (Ch. 150.0); (28) advertisement call with 1 note/call, note duration 17–200 ms, and 2–31 pulses per note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent (Ch. 91.0); (31) m. depressor mandibulae with or without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0 or 71.1); (32) m. depressor mandibulae with or without an origin from the tympanic annulus origin (Ch. 72.0 or 72.1); (33) chromosome pair 1 metacentric (Ch. 152.0); and (34) NOR in chromosome pair 11, proximal (Ch. 153.12).

Contents. Four recognized species: *Julianus camposseabrai* (Bokermann, 1968) **new comb.**; *Julianus fontanarrosai* (Baldo et al., 2019) **new comb.**; *Julianus pinimus* (Bokermann and Sazima, 1973); and *Julianus uruguayus* (Schmidt, 1944).

Distribution. Northeastern and southeastern Brazil, northeastern Argentina, and Uruguay (Cândido et al., 2012; Baldo et al., 2019).

Comments. *Julianus pinimus* and *J. uruguayus* (as *Scinax pinimus* and *S. uruguayus*) were placed in the former *S. uruguayus* group of the *S. ruber* clade by Faivovich et al. (2005) based on two putative synapomorphies: (i) bicolored iris in adults and (ii) the presence of keratinized and colored plates on the sides of the lower jaw-sheath of larvae (Kolenc et al., 2003; Faivovich et al., 2005). Faivovich et al. (2005) also suggested that (iii) the presence of marginal papillae on the posterior margin of the oral disc being larger than those of the lateral margins and (iv) the reduction in toe webbing could be putative synapomorphies of this group. Duellman et al. (2016) erected the new genus *Julianus* for these two species. More recently, Baldo et al. (2019) described *J. fontanarrosai* (as *S. fontanarrosai*) and placed it in the *S. uruguayus* group based on the putative synapomorphies (i) and (ii) proposed by Faivovich et al. (2005). Baldo et al. (2019) further suggested two additional synapomorphies for this group: (v) the short medial ramus of the pterygoid and (vi) the medially expanded ilio-sacral sesamoid.

The position of *Julianus camposseabrai* as the sister taxon of *J. uruguayus* (*J. fontanarrosai* + *J. pinimus*) is well supported in our analyses (100% jackknife; Fig. 26). Described by Bokermann (1968) on the basis of specimens from Maracás, Bahia, Brazil, Lutz (1973a) considered *Hyla camposseabrai* as a subspecies of *Hyla x-signata* Spix, 1824 because of overall similarities in the dorsal color pattern. Duellman and Wiens (1992) considered it a synonym of *Scinax x-signatus* (Spix, 1824) until Caramaschi and Cardoso (2006) resurrected *S. camposseabrai* as a valid species of the former *S. ruber* clade (sensu Faivovich et al., 2005). Although Caramaschi and Cardoso (2006) mentioned similarities with the former *S. ruber* group sensu Pombal et al. (1995a), such as the posterior surface of thighs with flash colors, advertisement call, and breeding in open areas (Bokermann, 1968), they did not associate *J. camposseabrai* with any of the then recognized species groups (the former *S. rostratus* and *S. uruguayus* groups). Subsequently, Barreto et al. (2019) suggested that *J. camposseabrai* was closely related to *J. fontanarrosai* (as *S.* aff.
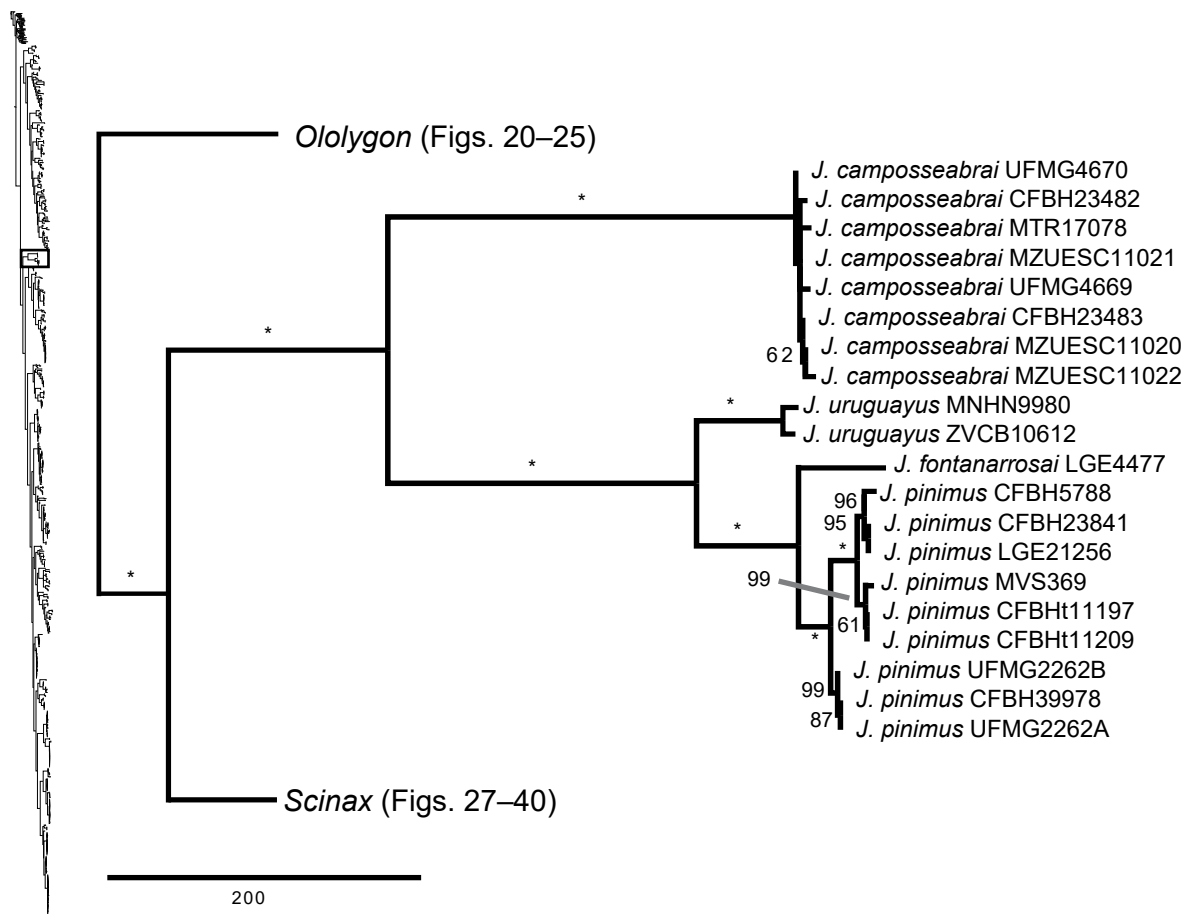
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Figure 26. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 7 of 21: *Julianus*. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

pinimus), *J. pinimus*, and *J. uruguayus* based on morphological similarities in the oral disc of tadpoles (see Kolenc et al., 2003; Faivovich et al., 2005; Alcalde et al., 2011).

Tadpoles of *Julianus camposseabrai* share with those of *J. fontanarrosai*, *J. pinimus*, and *J. uruguayus* (i) the presence of keratinized and colored plates on the sides of the lower jaw-sheath (our Ch. 151.1) and (ii) large marginal papillae on the posterior margin of the oral disc (our Ch. 140.1)—Kolenc et al. (2003); Barreto et al. (2019); Baldo et al. (2019). These two character-states, previously considered synapomorphies of the former *S. uruguayus* group by Faivovich et al. (2005), are therefore synapomorphies of *Julianus* as listed in the diagnosis. Further, the presence of well-developed, higher than wide, concave, and conspicuously keratinized jaw sheaths seems to be unique to larvae of *Julianus* and could be a synapomorphy of this genus.

Furthermore, tadpoles of *Julianus fontanarrosai* (as *Scinax* aff. *pinimus*; Alcalde et al., 2011), *J. pinimus* (Baldo et al., 2019), and *J. uruguayus* (as *S. uruguayus*; Alcalde et al., 2011) have distinctive traits in the oral cavity that distinguish them from other larvae of Scinaxini that have been studied (see Alcalde et al., 2011: Appendix I and Baldo et al., 2019). They have large, wide, multifid, and overlapping infralabial papillae; large lateral ridge papillae; and well-defined buccal floor arena and ventral velum. The large, wide, multifid, and overlapping infralabial pa-

pillae are also present in *J. camposseabrai* (Barreto et al., 2019). Alcalde et al. (2011) reported several musculoskeletal characters in larvae of *J. fontanarrosai* (as *Scinax* aff. *pinimus*) and *J. uruguayus* that were absent in the other three species of Scinaxini that they studied (*Ololygon aromothyella*, *O. berthae*, *S. acuminatus*): cornua trabeculae with short and wide free portions, processus articularis short and wide, processus muscularis narrow and directed anteriorly, cartilago suprarostralis forming a single structure, lower jaw cartilages massive, ceratobranchialia II–IV continuous with the planum hypobranchiale, and m. subarcualis rectus I formed by two slips. The taxonomic distribution of these character-states requires study in larvae of *J. camposseabrai* and of the other genera of Scinaxini to assess their polarity.

Of the remaining character-states inferred as synapomorphies of the former *Scinax uruguayus* group, (v) the short medial ramus of the pterygoid (our Ch. 10.0) and (vi) the medially expanded ilio-sacral sesamoid (our Ch. 24.1) optimize as synapomorphies of *Julianus*, whereas (iv) the reduced webbing between toes II and III (Ch. 59.1) and along the pre- and postaxial margins of toe IV (Ch. 60.0 and 61.0) are synapomorphies of the clade including *J. fontanarrosai*, *J. uruguayus*, and *J. pinimus*. We further consider that the bicolored iris with a golden upper half and dark brown to dark golden lower half (character not included in this study) is a putative synapomorphy of this clade (Ko-

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lenc et al., 2003; Faivovich et al., 2005; Baldo et al., 2019), as it does not occur in *J. camposseabrai* (Cândido et al., 2012: fig. 1), nor has it been described in *Ololygon* or most *Scinax* (the bicolored iris in *S. ruberoculatus* has a reddish upper half and gray lower half; Ferrão et al., 2018b).

Julianus fontanarrosai is morphologically most similar to its sister taxon (100% jackknife), *J. pinimus* (Fig. 26), and is known from Misiones and Corrientes in northeastern Argentina, and a few localities in Rio Grande do Sul, southern Brazil (Baldo et al., 2019). These two species were diagnosed thoroughly by Baldo et al. (2019) based on external morphology including female SVL, head shape, color pattern of iris, hand and toe discs, hidden surfaces of thighs, several osteological characters, and vocalizations. UPDs among *J. fontanarrosai* and *J. pinimus* are 1.7–1.9% (Appendix S10: Table 18).

Several authors raised doubts about the validity of *Julianus pinimus* and suggested that it could be a junior synonym of *J. uruguayus* given their similarity (Langone, 1990; Kwet, 2001; Kolenc et al., 2003; Eterovick and Sazima, 2004). However, new observations reported by Baldo et al. (2019) on several specimens of *J. pinimus* and *J. uruguayus*, including types and topotypic specimens, osteology, tadpoles, and advertisement calls corroborated that both are valid and distinguishable species. Baldo et al. (2019) presented a detailed comparison between these species. Besides the diagnostic morphological characters, UPDs between *J. pinimus* and *J. uruguayus* are 3.7–4.4% (Appendix S10: Table 18).

Other relevant literature. Bokermann and Sazima (1973: tadpole and vocalization of *Julianus pinimus*); Langone (1990: taxonomy of *J. uruguayus*); Kwet and Di Bernardo (1999: natural history of *J. pinimus*); Kwet et al. (2010: natural history of *J. pinimus*); Novaes and Zina, 2016 (vocalizations of *J. camposseabrai*); Baldo et al. (2019: tadpoles and vocalizations of *J. fontanarrosai*, *J. pinimus*, and *J. uruguayus*).

Scinax Wagler, 1830

Type species. *Hyla aurata* Wied, 1821 by subsequent designation of Stejneger (1907).

Garbeana Miranda-Ribeiro, 1926. Type species: *Garbeana garbei* Miranda-Ribeiro, 1926, by monotypy. Synonymy with *Hyla* by Lutz and Kloss (1952); see also Duellman (1970b).

Sister taxon. *Julianus*.

Diagnosis. This genus is well supported (100% jackknife) and delimited by molecular evidence and three phenotypic synapomorphies. These include (1) pars externa plectri distally expanded (Ch. 19.0, with instances of homoplasy in Cophomantini and *Xenohyla truncata*); (2) intercalary elements between ultimate and penultimate phalanges not mineralized (Ch. 26.0, with instances of homoplasy in

Ololygon and some outgroups, such as *Xenohyla truncata*, and Cophomantini); and (3) presence of the slip of the m. flexor brevis profundus digiti IV inserting on metatarsal V (Ch. 120.1, with one reversal in the *Scinax squalirostris* group).

Species assigned to *Scinax* can be further differentiated from those of other genera of Scinaxini by the combination of presence of pectoral fold (absent in most species of *Ololygon*; single exception the *O. agilis* group); single or bilobate externally evident vocal sac (internal in most species of *Ololygon*); papillae on the posterior labium of the same size as those in the lateral margins in tadpoles (larger in *Julianus*); lack of keratinized and colored plates on the sides of the lower jaw-sheath of tadpoles (present in *Julianus*); presence of anterior process of the suprascapula (absent in *Ololygon*); presence of the slip of the m. extensor digitorum inserting on metacarpal IV (absent in *Ololygon*). Furthermore, in most *Scinax* the m. depressor mandibulae has an origin from the dorsal fascia that covers the suprascapula (without an origin from the dorsal fascia in most species of *Julianus* and *Ololygon*; also absent in *S. staufferi* and polymorphic in *S. cruentomma* and *S. exiguus*). When the pectoral fold is absent in *Scinax* (the *S. squalirostris* group), the single, externally evident vocal sac, the anterior process of the suprascapula, and the m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula differentiate this group from all species of *Ololygon*.

Characterization. (1) SVL males 15.7–48.7 mm, SVL females 20.8–53.0 mm; (2) pectoral fold absent or present (Ch. 45.0 or 45.1); (3) vocal sac externally evident (Ch. 63.0); (4) vocal sac subgular, single or bilobate, reaches or not the level of the pectoral fold or region; (5) snout rounded, sub-elliptical with a pointed tip, elongate pointed, or elongate acuminated in dorsal view; (6) rounded or pointed tubercles in the lower lip absent or present; (7) dorsal skin smooth, shagreen, rugose, with scattered tubercles, or densely covered with tubercles; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching subarticular tubercle, midlength of the penultimate phalanx, or base of disc (Ch. 59.1, 59.2, or 59.3); (10) epidermal projections in the nuptial pad absent or present (Ch. 64.0 or 64.1); (11) spicules[11] in the nuptial pad, inner margin of arm, and pectoral region in males absent or present; (12) pectoral glands in males absent or present (Ch. 47.0 or 47.1); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze, silvery, reddish,

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11 Luna et al. (2018) described spicule-shaped papillary epidermal projections (PEPs) on the nuptial pad of *Scinax fuscovarius*. We observed the same spicules on the internal surface of the arm and pectoral region in this species and *S. x-signatus* (Araujo-Vieira et al., 2020b). For the current study, we considered the presence or absence of these spicules simply for taxonomy but did not include it as a transformation series in the phylogenetic analysis because the homology of the spicules with other PEPs requires further study. For this reason, we considered PEPs to be absent in *S. fuscovarius*, *S. x-signatus*, and *Scinax* sp. 26. Although the histological structure of the spicules was studied in detail in the context of the nuptial pad, it has not been studied in the other regions where they occur (Araujo-Vieira et al., 2020b).

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or bicolor, with or without blotches perpendicular above and below the pupil and/or a dark or reddish median streak on the sides of the pupil; (15) dorsal pattern uniform, with irregular blotches of different size, stripes, or spots; (16) hidden surfaces of thighs uniform, barred or with other markings; (17) physiological chlorosis absent or present (Ch. 158.0 or 158.1); (18) eyes of the tadpole visible or not visible ventrally (Ch. 146.0 or 146.1); (19) oral disc terminal, subterminal, or ventral (Ch. 143.0, 143.1, or 143.2); (20) posterior margin of the folded oral disc straight (Ch. 136.1); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent or present (Ch. 137.0, 137.1 or 137.2); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal or subparallel the main body axis (Ch. 148.0 or 148.1); (25) vent tube medial or dextral at the margin of the ventral fin or above the margin of the ventral fin (Ch. 145.0 or 145.1); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds or streams (Ch. 155.0 or 155.1); (28) advertisement calls with 1, 2–3, or 10–18 notes/call; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV present or absent (Ch. 91.0 or 91.1); (31) m. depressor mandibulae with or without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0 or 71.1); (32) m. depressor mandibulae with or without an origin from the tympanic annulus (Ch. 72.0 or 72.1); (33) chromosome pair 1 metacentric (Ch. 152.0); and (34) NOR in chromosome pairs 3, 8, or 11, proximal or distal (Ch. 153.2, 153.9, 152.12, or 152.13).

Contents. Seventy-four recognized species: 73 species assigned to 13 species groups and one species unassigned to any group. 28 UCSs; 10 CCSs.

Distribution. Tropical Mexico through Central America, including Trinidad and Tobago, and Saint Lucia in the Lesser Antilles, to extreme northern Peru west of the Andes, including the Galapagos islands (introduced); east of the Andes through South America southwards to Uruguay and central Argentina (Frost, 2023).

Comments. One of the phenotypic synapomorphies of the redefined *Scinax*, the presence of the slip of the m. flexor brevis profundus digiti IV inserting on metatarsal V (our Ch. 120.1; see also Burton, 2004), was previously considered a synapomorphy of *Scinax* sensu Faivovich et al. (2005). Another character-state present in most species of *Scinax*, the vent tube positioned above the margin of the ventral fin, was considered the single synapomorphy of the former *S. ruber* clade (our Ch. 145.0; Faivovich, 2002; Faivovich et al., 2005). See discussion on Section "*Julianus, Ololygon,* and *Scinax* sensu Duellman et al. (2016)" regarding this character-state.

Two additional phenotypic synapomorphies proposed for the former *Scinax ruber* clade by Faivovich (2002) require comments. They are arytenoids with a dorsal prominence developed over the pharyngeal margin (our Ch. 38.0) and lateral m. dorsometatarsalis distalis digiti V absent (our Ch. 132.0). On our most parsimonious trees, the arytenoids with a dorsal prominence developed over the pharyngeal margin (Ch. 38.0) optimize ambiguously and could be a synapomorphy of a large internal clade of *Scinax* or it could have evolved independently several times (Appendix S9). The absence of the lateral m. dorsometatarsalis distalis digiti V (Ch. 132.0) is plesiomorphic in relation to the presence of this muscle, being its presence a synapomorphy of *Ololygon*, with some instances of homoplasy in *S. constrictus*, *S. pedromedinae*, Sphaenorhynchini, and other outgroups.

Trewavas (1933) reported in *Scinax ruber* (as *Hyla rubra*) a rod of cartilage supporting each end of the vocal cords. Almost all species of *Scinax* and *Julianus* have this cartilaginous structure in the vocal cords (Ch. 41.1); exceptions are the species included in the *S. rostratus* group (as redefined here, see below) and *J. camposseabrai*. It optimizes as a synapomorphy of the sister taxon of the *S. rostratus* group (with instances of homoplasy in an internal clade of *Julianus* and in *Ololygon argyreornata*).

Within *Scinax*, we redefined the *S. rostratus* group of Faivovich (2002) to include *S. acuminatus* and *S. quinquefasciatus*, and further recognized 12 new species groups: the *S. auratus*, *S. boesemani*, *S. cruentomma*, *S. danae*, *S. elaeochroa*, *S. eurydice*, *S. funereus*, *S. fuscomarginatus*, *S. fuscovarius*, *S. granulatus*, *S. nasicus*, and *S. squalirostris* species group. Only one species remains unassigned to any species group, *S. pachycrus* (Figs. 27–40).

The conflicts among MPTs within *Scinax* are restricted to conspecific terminals and the interspecific relationships of an internal clade of the *S. rostratus* group and several species of the *S. cruentomma* group that collapse in a polytomy in the strict consensus (Fig. 19). The interspecific relationships are generally well supported (jackknife > 90%) or moderately supported (jackknife > 70%), but those of several species are poorly supported (< 50–65% jackknife). All these relationships are discussed in detail below in the sections dedicated to each species group.

The *Scinax rostratus* group

Sister taxon. The clade including all other species of *Scinax*.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular evidence and three phenotypic synapomorphies. These include (1) slip from ulnare of the m. extensor brevis superficialis digiti IV not inserted on the tendon of m. extensor brevis medius digiti IV (Ch. 105.0, with instances of homoplasy in *Julianus uruguayus*, the *Scinax squalirostris* group, and other species of *Scinax*, such as *S. boesemani*, *S. fuscomarginatus*, and *S. fuscovarius*); (2) P-3 on the margin of the oral disc (Ch. 137.1, with one known instance of homoplasy in *Sphaenorhynchus dorisae*, not included in this study; see Araujo-Vieira et al., 2019:485); and (3) terminal oral disc

(Ch. 143.2, with at least one reversal to subterminal oral disc in the clade including *S. constrictus*, *S. nebulosus*, and related candidate species, Ch. 143.1).

Moreover, species in this group differ from other species of *Scinax* by the combination of the rounded or elongate pointed snout in dorsal view (sub-elliptical with a pointed tip in the *S. auratus* group, elongate acuminated in the *S. squalirostris* group, rounded in all other species groups); single or bilobate vocal sac (mostly single, enlarged, reaching the level of the pectoral fold in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); lack of spicules in the nuptial pad, inner margin of arm, and pectoral region in males (present in the *S. fuscovarius* group); lack of pectoral glands in males (present in the *S. fuscovarius* and *S. nasicus* groups, and some species of the *S. funereus* group); and tadpoles with P-3 placed on the margin of the posterior labium or the labial arm (inside the oral disc in all other species of *Scinax* except for a clade of the *S. auratus* group).

Characterization. (1) SVL in males 20.8–48.7 mm, females 28.2–53.0 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single or bilobate, does not reach the level of the pectoral fold; (5) snout rounded or elongate pointed in dorsal view, with or without a terminal triangular skin flap or tubercle; (6) rounded or pointed tubercles in the lower lip absent or present; (7) dorsal skin smooth, shagreen, with scattered tubercles or densely covered with tubercles; (8) postaxial webbing of toe I reaching the margin of the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the base of the disc (Ch. 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in the nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands absent in males (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris light gray, tan, or bronze, with or without a median horizontal and perpendicular dark streak; (15) dorsal pattern with stripes, or irregular blotches, sometimes marbled; usually with a dark triangular mark between the eyes, whose apex is pointed backwards; (16) hidden surfaces of thighs uniform, marked with bold dark and light mottling, or broad vertical bars; (17) physiological chlorosis absent (polymorphic in *Scinax quinquefasciatus*; Ch. 158.0); (18) eyes of the tadpole visible ventrally (Ch. 146.1); (19) oral disc terminal or subterminal (Ch. 143.1 or 143.2); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm or margin of posterior labium supporting P-3 (Ch. 137.1 or 137.2); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis subparallel to the main body axis (Ch. 148.1); (25) vent tube medial or dextral, above or at the margin of the ventral fin (Ch. 145.0 or 145.1); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with one note/call, note duration 180–2,900 ms, and 4–90 pulses per note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent or present (Ch. 91.0 or 91.1); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 metacentric (Ch. 152.0); (34) NOR in chromosome pairs 8 or 11, proximal or distal (Ch. 153.9, 153.12, or 153.13).

Contents. Twelve recognized species: *Scinax acuminatus* (Cope, 1862a), *Scinax boulengeri* (Cope, 1887); *Scinax constrictus* Lima et al., 2005; *Scinax garbei* (Miranda-Ribeiro, 1926); *Scinax jolyi* (Lescure and Marty, 2000); *Scinax kennedyi* (Pyburn, 1973); *Scinax nebulosus* (Spix, 1824); *Scinax pedromedinae* (Henle, 1991); *Scinax proboscideus* (Brongersma, 1933); *Scinax quinquefasciatus* (Fowler, 1913), *Scinax rostratus* (Peters, 1863); and *Scinax sugillatus* (Duellman, 1973). Three CCSs, *Scinax* spp. 6–8; six UCSs, *Scinax* spp. 0–5.

Distribution. Lowlands of Central America from eastern Honduras southeastwards; in South America: Pacific lowlands of Colombia and Ecuador southwards to northwestern Peru, Galapagos Islands (introduced), Caribbean lowlands, Guianas, Orinoco and Amazon basins southward to Bolivia, lower Amazon region to northeastern and central Brazil, Paraguay, Bolivia, and northern Argentina (e.g., Duellman, 1972b; Cei, 1980; Duellman and Wiens, 1993; Rodríguez and Duellman, 1994; De la Riva et al., 2000; Lescure and Marty, 2000; Duellman, 2001; McCranie and Wilson, 2002; Lima et al., 2005; Köhler, 2011; Weiler et al., 2013; Ron et al., 2018; Barrio-Amorós et al., 2019).

Comments. The *Scinax rostratus* group was first defined by Duellman (1972b) based on overall similarities in the external morphology of adults and larvae, osteology, behavior, and call parameters. Although the monophyly of this group had not been tested until the early 2000s (Faivovich, 2002), it was the most distinct group within *Scinax* as formerly defined. Our results show that *S. acuminatus* and *S. quinquefasciatus* are closely related to the former *S. rostratus* group. However, contrary to previous results (Wiens et al., 2010; Duellman et al., 2016; Jetz and Pyron, 2018; Ron et al., 2018), *S. quinquefasciatus* is well supported (100% jackknife) as the sister taxon of *S. acuminatus* plus the remaining species of the *S. rostratus* group (Figs. 27–28). Therefore, our results corroborated the monophyly of *S. acuminatus* and the former *S. rostratus* group (99% jackknife) recovered by Faivovich (2002). Following these topological results and the molecular and phenotypic evidence that delimits this whole clade, we redefined the former *S. rostratus* group to include *S. acuminatus* and *S. quinquefasciatus*.

The adult external morphology of *Scinax quinquefasciatus* certainly does not resemble the typical external morphology associated with the former *S. rostratus* group, particularly in head shape, dermal ornamentations, and color pattern. The larva of *S. quinquefasciatus*

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is still undescribed, but we examined larvae from Guayas, Ecuador (QCAZ A-60994). These tadpoles share with larvae of other species of the *S. rostratus* group the terminal oral disc (evolves to subterminal position, Ch. 143.1, in the clade including at least *S. constrictus*, and related candidate species; state unknown in *S. nebulosus*). Furthermore, they share with *S. acuminatus* P-3 ½ the length of P-2 and its placement on the margin of the oral disc, which we assume to be an intermediate step in the evolution of the labial arm. These are the only two species in Scinaxini that present this character-state, otherwise only known to occur, homoplastically, in *Sphaenorhynchus dorisae* (Sphaenorhynchini; not included in our analyses; see Araujo-Vieira et al., 2019: 485) within Hylinae. In the remaining species of the *S. rostratus* group with known larvae, P-3 is directly placed on the labial arm.

Scinax acuminatus also shares some phenotypic traits with species placed in the former *S. rostratus* group that could provide additional evidence supporting their monophyly. Magrini et al. (2011) reported that some values of the call parameters of *S. acuminatus* (combined call duration and number of pulses per call) mostly resemble those of the larger species in the *S. rostratus* group. The call of *S. quinquefasciatus*, however, still retains the multipulsed structure with lower number of pulses per call (Ron et al., 2018) that is common in many species of *Scinax*.

Furthermore, Alcalde et al. (2011) reported that larvae of *Scinax acuminatus* share with *S. boulengeri* the straight labial teeth with cusps weakly developed or absent, the cornua trabeculae with long and narrow free portions, the processus muscularis acute and posteriorly directed, and m. subcualis rectus I with two slips (Fabrezi and Lavilla, 1992; Vera Candioti, 2007; Vera Candioti and Altig, 2010). These characters require further study in other species of the *S. rostratus* group, and *Scinax* in general; the taxonomic distribution reported by Alcalde et al. (2011) in the few studied Scinaxini suggest that at least some character-states (e.g., the morphology of the labial teeth) are likely to be synapomorphies of the *S. rostratus* group or one of its internal clades.

In the analysis of Faivovich (2002), the clade including *Scinax acuminatus* and the former *S. rostratus* group was delimited by six phenotypic synapomorphies: (i) slip of the lateral m. lumbricalis brevis digiti V originating from the lateral corner of the flexor plate absent (our Ch. 85.0); (ii) posterior gap in the larval oral disc (our Ch. 134.1); (iii) P-3 placed on the margin of the oral disc (our Ch. 137.1); (iv) reduction of P-3 to ½ the length of P-2 (our Ch. 138.1); (v) terminal position of the oral disc (our Ch. 143.2); and (vi) intestinal coiling axis subparallel to the main body axis (our Ch. 148.1). Our analysis corroborated (i) and (ii) as synapomorphies of this now internal clade of the redefined *S. rostratus* group; (iii) and (v) are synapomorphies of the redefined *S. rostratus* group; (iv) is plesiomorphic for Scinaxini; and (vi) optimizes ambiguously: it could be a synapomorphy of *Julianus* + *Scinax*, or had arisen independently in *Julianus* and the *S. rostratus* group.

Faivovich (2002) inferred that the former *Scinax rostratus* group was delimited by 11 synapomorphies:

(i) overlapping of the otic plate and the crista parotica due to a broad otic plate (our Ch. 5.2); (ii) juxtaposed inner margins of the vomers (our Ch. 12.1); (iii) nonfenestration of the cartilaginous plate of the oblique cartilage (our Ch. 15.0); (iv) pointed tubercle on heel (our Ch. 52.1); (v) absence of lateral m. dorsometacarpalis indicis distalis (our Ch. 97.0); (vi) presence of lateral m. dorsometatarsalis hallucis distalis (our Ch. 126.1); (vii) lateral margins of the oral disc discontinued with its posterior portion (our Ch. 135.1); (viii) third posterior labial tooth row placed on the labial arm (our Ch. 137.2); (ix) third posterior tooth row reduced to ¼ the length of the second row (our Ch. 138.2); (x) absence of keratinized spurs behind the lower jaw-sheath (our Ch. 142.0); and (xi) and head-down calling position (our Ch. 156.1). Our analysis corroborated several of these as synapomorphies of this now internal clade of the redefined *S. rostratus* group; exceptions are (ii), (v), and (vi). Vomers with juxtaposed inner margins (ii) optimize ambiguously because they are also present in *Julianus*. The lateral m. dorsometacarpalis indicis distalis (v) is, in fact, absent in the species of the *S. rostratus* group, but also in most species of Scinaxini and several outgroups and, therefore its absence is plesiomorphic for Scinaxini. The presence of the lateral m. dorsometatarsalis hallucis distalis (vi) is a synapomorphy of the clade including *S. acuminatus* and the remaining species of the *S. rostratus* group, with instances of homoplasy in the sister taxon of the *Ololygon agilis* group and in *Julianus camposseabrai*.

McDiarmid and Altig (1990) described the labial arm projection as a modification of the distal posterior tooth row of the oral disc in tadpoles. It gives support to P-3 and provides partial, independent movement from the rest of the oral disc. The presence of a labial arm has long been considered a synapomorphy of the *Scinax rostratus* group (Faivovich, 2002; Faivovich et al., 2005). This structure has also been observed in tadpoles of four species in the *S. auratus* group (*S. auratus*, *S. cuspidatus*, *S. crospedospilus*, and *S. juncae*; Heyer et al., 1990; Alves and Carvalho-e-Silva, 2002; Alves et al., 2004; Mercês and Juncá, 2012), and in *Scarthyla goinorum* (McDiarmid and Altig, 1990). Based on our phylogenetic hypothesis, the presence of a labial arm (Ch. 137.2) evolved independently three times in Hylinae: once in *Scarthyla goinorum* (P-3 inside the oral disc in *S. vigilans*; Ch. 137.0) and twice in *Scinax*. In the latter it evolved in an internal clade of the *S. rostratus* group (*S. boulengeri*, *S. garbei*, *S. nebulosus*, *S. pedromedinae*, *S. rostratus*, *S. sugillatus*; still unknown in all candidate species related to these, but presumably present) from the condition in which the third posterior tooth row sits on the margin of the oral disc (Ch. 137.1), as occurs in *S. acuminatus* and *S. quinquefasciatus*. The other independent origin of the labial arm in *Scinax* optimizes ambiguously on the ancestral node of the clade that includes *Scinax* sp. 11 and *S. cretatus* plus *S. auratus*, *S. crospedospilus*, *S. cuspidatus*, and *S. juncae*, because the tadpoles of *S. cretatus* and *Scinax* sp. 11 remain unknown. If tadpoles of *S. cretatus* and *Scinax* sp. 11 were found to have a labial arm, it would optimize as a synapomorphy of the clade includ-

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ing *S. auratus*, *S. cretatus*, *S. crospedospilus*, *S. cuspidatus*, *S. juncae*, and *Scinax* sp. 34. Regardless, the labial arm in this clade, unlike the case of the *S. rostratus* group, could have evolved from the character-state in which P-3 is inside the margins of the oral disc (Ch. 137.0).

In species of Scinaxini whose larval oral musculature has been studied (*Ololygon aromothyella*, *O. berthae*, *Scinax acuminatus*, *S. boulengeri*, *S. nasicus*, and *S. sugillatus*; McDiarmid and Altig, 1990; Vera Candioti et al., 2004; Vera Candioti, 2007; Alcalde et al., 2011), the m. mandibulolabialis is composed of two slips, the mm. mandibulolabialis inferior and superior, both of which originate from the ventromedial region of Meckel's cartilage. The well-developed inferior slip inserts in the posterior labium and the valleys between P-1–P-2 and P-2–P-3. In tadpoles of *S. boulengeri* and *S. sugillatus*, this well-developed inferior slip extends anteriad nearly to the tip of the labial arm at level of the P-3 row (McDiarmid and Altig, 1990; Vera Candioti, 2007).

The contraction of the m. mandibulolabialis causes the teeth to rotate distally at an angle that allows them to meet the substrate (Taylor et al., 1996). Furthermore, this muscle would be involved in the movements of the suctorial tube, at least in retraction in some species without labial teeth (i.e., *Dendropsophus nanus*). McDiarmid and Altig (1990) inferred that in tadpoles with labial arm the contraction of this muscle might result in powerful movements of this structure. In preserved specimens and presumably in live specimens when they are not feeding, the oral disc is folded or closed by the labial arm (e.g., McDiarmid and Altig, 1990; Mercês and Juncá, 2012).

The interspecific relationships among species of the *Scinax rostratus* group are generally well resolved and supported (> 90% jackknife), except for the poorly supported (< 52% jackknife) relationships of *S. constrictus* + *Scinax* sp. 4, and the unresolved relation of *Scinax* sp. 1, *Scinax* sp. 2, and the clade including *S. constrictus*, *S. nebulosus*, and related candidate species (Fig. 27). In general, our results for the *S. rostratus* group are congruent with those of Duellman et al. (2016) obtained with more reduced character and taxon sampling; exceptions are the position of *S. acuminatus* as mentioned earlier, and the positions of *S. rostratus* as sister taxon of *S. proboscideus* and that of *S. garbei* as sister species of *S. jolyi*, both with low support (bootstrap with RaxML < 40%) in the results of Duellman et al. (2016). Further, Duellman et al. (2016: 29) erroneously suggested that *S. pedromedinae* did not belong to the *S. rostratus* group, but their results clearly show this species placed within this group.

Overall, the optimal topologies for the *Scinax rostratus* group recover *S. quinquefasciatus* and *S. acuminatus* as the well-supported, successive sister taxa of two major clades; one includes the smaller species *S. nebulosus*, *S. constrictus*, *S. pedromedinae*, and several lineages associated with the former, all of which have a relatively small SVL (males 20.8–29.9 mm, females 27.5–39.4 mm; Duellman and Wiens, 1993; Lima et al., 2005); the other clade includes all larger species of the group (males 30.0–48.7 mm, females 36.5–53.0 mm; Duellman, 1970a,

1972b; Duellman and Wiens, 1993). These are structured in a well-supported pectinate series with four clades of northwestern South America/Mesoamerican species, with *S. garbei* and two lineages of Amazonian candidate species nested in different parts of the topology.

Scinax quinquefasciatus is known for Galapagos Islands (introduced), and the Pacific basin of Ecuador, southwestern Colombia, and extreme northwestern Peru (Ron et al., 2018; Armijos-Ojeda et al., 2021). Our analyses included samples from Guayas, Manabi, and Esmeralda in Ecuador, and from Tumbes, in Peru (Fig. 27; see Appendix S1). Samples from Colombia were not available. Complete 16S sequences are only available for the Peruvian sample, so no information on intraspecific UPDs is available.

Scinax acuminatus[12] is distributed in central Brazil (Mato Grosso and Mato Grosso do Sul), Paraguay, Bolivia, and northern Argentina (e.g., Cei, 1980; De la Riva et al., 2000; Weiler et al., 2013). Our analyses included specimens from Argentina (Corrientes and Santa Fé), Brazil (Mato Grosso), and Paraguay (Ñeembucú); samples from Bolivia were unavailable (Fig. 27). UPDs among our samples are 0.0–1.0% (Appendix S10: Table 19).

Scinax pedromedinae is widely distributed in the western Amazon basin, from northern Bolivia to Colombia (Duellman and Wiens, 1993; De la Riva et al., 2000; Hoogmoed and Avila-Pires, 2011; Melo-Sampaio and Souza, 2015). Our study included a sample from 15 km E Cusco Amazónico, Peru, which is the locality of some paratypes of this species, and ≈40 km ENE from the type locality ("Tres Chimbadas am Rio Tambopata, Departamento Madre de Dios, Peru"; Henle, 1991), two samples from Porto Velho, Rondônia, Brazil, and one sample from Leticia, Amazonas, Colombia. Our results recover these as monophyletic, with the specimen of Cusco Amazónico as the sister group of the other samples (Fig. 27). UPDs between this specimen and those from Porto Velho and Leticia are 4.9–5.8%, while the UPDs between samples of the last two localities are 2.1–2.3% (Appendix S10: Table 20). Based on these UPDs between material close to the type locality and the specimens from Brazil and Colombia, we consider that the included populations from these two countries belong to a UCS, *Scinax* sp. 0. We are not aware of diagnostic characters separating these lineages. Considering the wide distribution traditionally considered for *S. pedromedinae*, our results indicate the need for a thorough study of the populations associated with this species.

Scinax nebulosus is currently distributed throughout southeastern Venezuela, Guianas, and the lower Amazon region to northeastern Brazil, and also in Amazonian Bolivia (De la Riva et al., 2000; Lescure and Marty, 2000; Ouboter and Jairam, 2012; Barrio-Amorós et al., 2019), whereas

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12 The type series of this species includes two syntypes (USNM 5843 and 102700), both adult males. One of them (USNM 5843) approximately corresponds in size with the description provided by Cope (1862a) and the taxon to which this name has historically been applied throughout its distribution. The other specimen (USNM 102700) is *Scinax nasicus*. In order to stabilize the application of the name to the taxon to which it has historically been applied, we designate USNM 5843 as lectotype of *Hyla acuminata* Cope, 1862a.
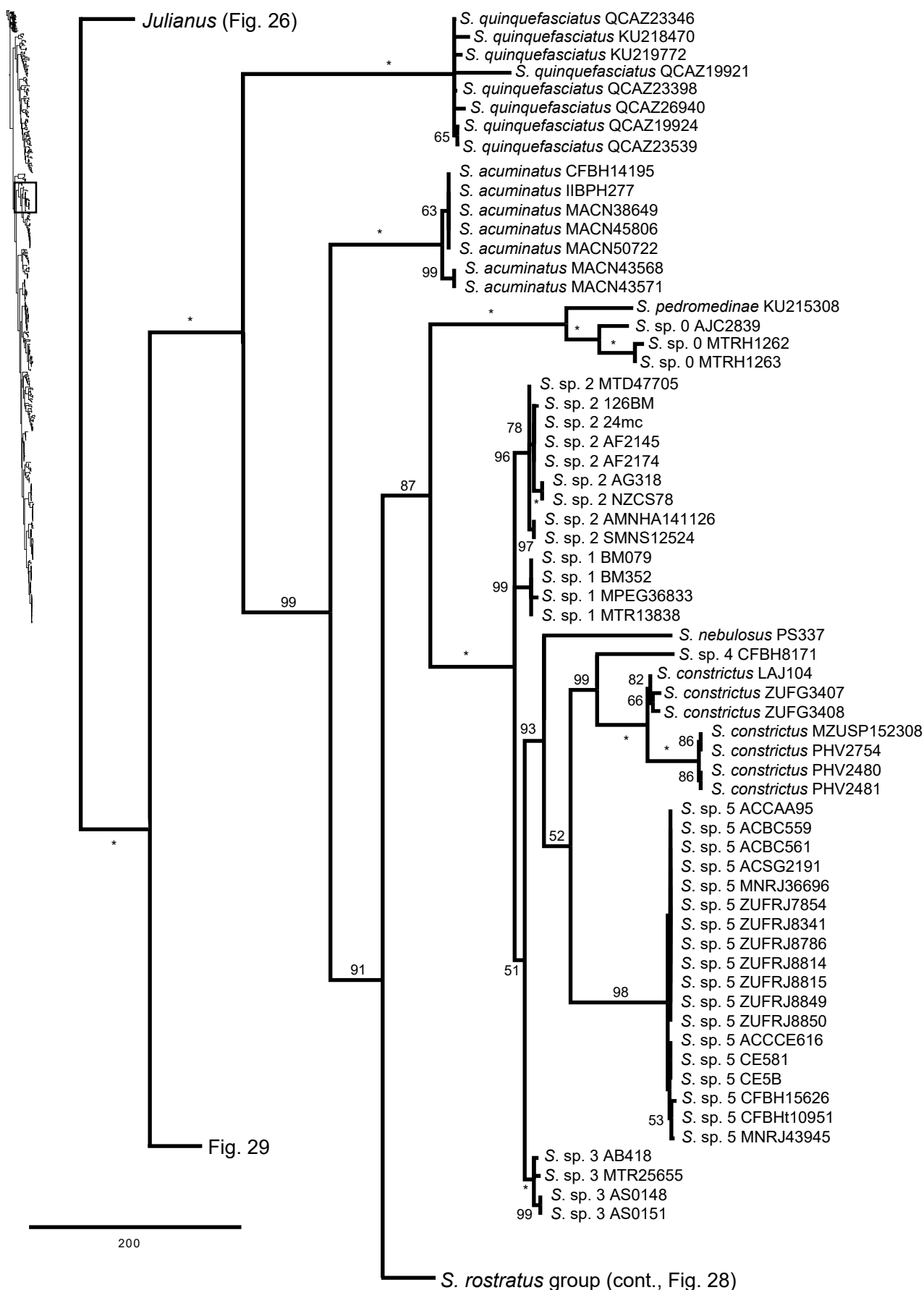
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Figure 27. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 8 of 21: The *Scinax rostratus* group, part 1 of 2. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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S. constrictus, the species morphologically most similar to *S. nebulosus* (Lima et al., 2005), is restricted to some localities in the states of Goiás, southeastern Tocantins, Minas Gerais, and Mato Grosso do Sul, central Brazil (Vaz-Silva et al., 2020). Our results indicate that *S. constrictus* and *S. nebulosus*[13] are nested within five distinct lineages that are currently referred to as *S. nebulosus* (Fig. 27).

Six lineages correspond to populations that have been associated with *Scinax nebulosus*. Of these, one is associated with the name *S. nebulosus*, and five are considered UCSs (Fig. 27). UPDs between these UCSs and *S. constrictus* and *S. nebulosus* are 4.8–10.2% (Appendix S10: Table 20). The six lineages are: (1) a lineage from Pará, represented by one specimen (PS 337) from the Municipality of Ananindeua, distant ≈12 km NE from the type locality in the "pirarucu" pond of the Museu Goeldi, Belém, Brazil (holotype of *Hyla egleri* Lutz, 1968b, designated neotype of *Hyla nebulosa* by Hoogmoed and Gruber, 1983), for which we apply the name *S. nebulosus*; (2) *Scinax* sp. 1, from Amapá and Pará, Brazil, with localities along the rivers Tapajos, Xingu, and Amapari; (3) *Scinax* sp. 2 from French Guiana, for which the name *Hyla cynocephala* Duméril and Bibron, 1841 is available; (4) *Scinax* sp. 3 (referred to *Scinax* sp. A by Jansen et al., 2011) from Bolivia; (5) *Scinax* sp. 4 represented by a single specimen (CFBH 8171) from northeastern Tocantins, Brazil; and (6) *Scinax* sp. 5 from Piauí to Alagoas, northeastern Brazil. *Scinax constrictus* is represented by specimens from Goianópolis and Palmeiras, Goiás (the latter is the type locality; Lima et al., 2005), and Barra do Garças, Mato Grosso, Central Brazil. The tadpole of *S. nebulosus* was described based on individuals from Cabo de Santo Agostinho, Pernambuco, Brazil (Gomes et al., 2014), and therefore could belong to *Scinax* sp. 5. In the same way, the phylogeographic study of Carnaval (2002) most likely corresponds to this same UCS.

Advertisement calls possibly belonging to *Scinax* sp. 3 were described by De la Riva et al. (1994, as *S. nebulosus*) from Puerto Almacén, Bolivia, and considered overall similar to those of *S. nebulosus* from Belém, Pará, Brazil, described by Duellman (1972b; as *Hyla egleri*) and Duellman and Pyles (1983; as *Ololygon egleri*). Hödl (1977) described calls of a species identified as *Hyla egleri* from Manaus, Amazonas, Brazil; it is unclear to which of the lineages recognized here it corresponds. He reported

a primary note and a secondary shorter note that differ in temporal and spectral values from those reported for *Scinax* sp. 3 and *S. nebulosus*. Lescure and Marty (2000) briefly described the calls of *Scinax* sp. 2 (as *S. nebulosus*), whose parameters also overlap with those of *Scinax* sp. 3 and *S. nebulosus*.

According to the original description, *Scinax constrictus* differs from *S. nebulosus* in the smaller size, presence of discrete cloacal flap (reported as an anal flap), presence of small tubercles on the lower jaw, and call parameters (dominant frequency, call duration, and number of notes; see Lima et al., 2005). Our observations on the type series of *S. constrictus* and the neotype of *S. nebulosus* showed that the diagnostic characters used to distinguish *S. constrictus* from *S. nebulosus* vary intraspecifically or overlap in both species. The size of adults and call parameters overlapped as was already evident from the original description (see Lima et al., 2005), the cloacal flap present in *S. constrictus* is similar to that of *S. nebulosus* and the remaining species of *Scinax*, as well as the small tubercles on the lower jaw, which are also present in *S. nebulosus* (reported as absent or indistinct by Lima et al., 2005). Further, the dorsolateral dermal constriction on the shoulders in adults and the two separate tubercles above the cloaca in females of *S. constrictus* also occur in males and females of *S. nebulosus*. Santos et al. (2019) suggested that the absence of submarginal papillae could differentiate tadpoles of *S. constrictus* from those of *S. nebulosus* (Gomes et al., 2014; therefore, very likely corresponding to *Scinax* sp. 5, see above). However, these same authors state that submarginal papillae occur in some of the larvae of *S. constrictus*, calling into question their suggestion.

Despite the questionable phenotypic evidence supporting their distinctiveness, the UPDs between these species (*Scinax nebulosus* PS 337 distant ≈16 km NE from the type locality in Pará, Brazil) and *S. constrictus* (including topotypic specimens) are 6.1–7.1% (Appendix S10: Table 20). Therefore, our results indicate that *S. constrictus* and *S. nebulosus* are a complex of apparently cryptic species that require a detailed taxonomic revision. The lack of a clear diagnosis between *S. constrictus* and *S. nebulosus* is the reason why we consider as UCSs all the lineages within which these two species are nested.

In the clade of the "large" species of the *Scinax rostratus* group, the sister taxon of the pectinate series is a clade composed of two lineages of *S. boulengeri* A and B and *S. sugillatus* (Fig. 28). *Scinax boulengeri* has "Nicaragua" as its type locality (Cope, 1887). We did not include Nicaraguan specimens of *S. boulengeri*, but only three samples from Costa Rica and Honduras; a flawed representation of its range considering its distribution throughout Central America from Honduras to Panama, the Choco, and the eastern flank of the Cordillera Central to Caldas in Colombia (Ruiz-Carranza et al., 1996; Savage, 2002; Lynch and Suárez-Mayorga, 2004; McCranie, 2007; Sunyer et al., 2009, 2014; Köhler, 2011). Our results indicate that these three samples belong to two different lineages that are not monophyletic (Fig. 28), as *S. sugillatus* is nested among them, although with moderate support

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13 This is congruent with the results of Freitas et al. (2020), who identified three lineages under the name *Scinax nebulosus*, one of which corresponds to *S. constrictus*. GenBank accessions are not informed in the publication. We located the 16S sequences produced for that study in GenBank, but not the COI sequences. Unfortunately, it is not possible to associate the information provided in the text of Freitas et al. (2020) with that annotated on the 16S sequences. For that reason, we did not include these in our definitive data set. A preliminary analysis, however, indicates that besides *S. constrictus*, their lineages correspond to those that we identified as *Scinax* spp. 3 and 5 (results not shown). Freitas et al. (2022) reported a number of lineages under the name *S. nebulosus*; it is unclear if one of them (they included samples from Goiás) corresponds to *S. constrictus*. Since the authors did not inform GenBank accession numbers, we do not have direct evidence to compare the lineages of their paper with those inferred in the present study.
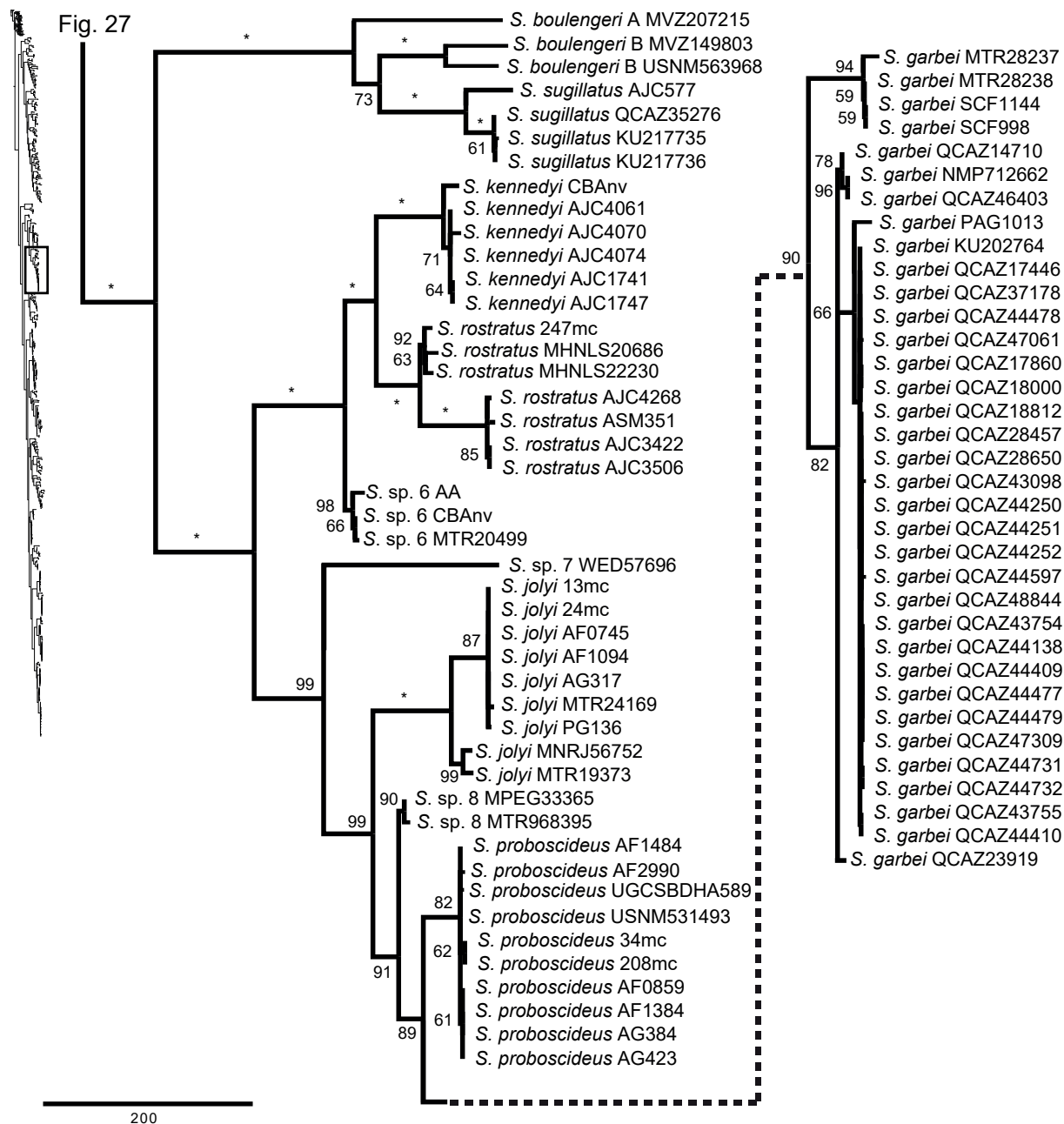
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Figure 28. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 9 of 21: The *Scinax rostratus* group, part 2 of 2. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency. Dashed lines connecting parts of the tree are not proportional to branch-lengths.

(73% jackknife). The lineage named *S. boulengeri* A is represented by one specimen from Costa Rica (Guanacaste) and differs in UPDs of 6.1−6.5% from the other lineage that we named *S. boulengeri* B (Appendix S10: Table 21). This lineage includes specimens from Limón, Costa Rica, and Gracias a Dios, Honduras, that differ in UPD of 2.0% (Appendix S10: Table 21). The name *S. boulengeri* could correspond to any of these lineages, as the lineage from Honduras and Costa Rica presumably includes populations distributed in Nicaragua, and the lineage from Guanacaste is only 17 km S from Nicaragua. A densely sampled taxonomic study of *S. boulengeri* from Costa Rica, Honduras, and Nicaragua is required to establish clearly with which of these lineages the name should be associated.

Scinax sugillatus was described for populations originally considered *S. boulengeri* from Chocoan Ecuador and Colombia (Duellman, 1972b, 1973). We included one specimen from Los Ríos, Ecuador (≈20 km S from the type locality), two specimens from Manabi, Ecuador (≈100 km NW from the type locality), and one specimen from Darien, Panama (≈950 km N from the type locality). The latter was originally identified as *S. boulengeri*, and we did not see the voucher. Considering the monophyly (Fig. 28) and low UPDs between *S. sugillatus* from Ecuador (1.3−1.4%; Appendix S10: Table 21) and this specimen, we tentatively consider it conspecific. *Scinax sugillatus* is known from several localities in Choco, Colombia, being the northernmost record in the area of Quibdó, Chocó

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(Lynch and Suárez-Mayorga, 2004), about 500 km S from the record in Panama. The required taxonomic reassessment of *S. boulengeri* could surely affect the notions of species limits with *S. sugillatus*.

The sister taxon of *Scinax kennedyi* + *S. rostratus* is *Scinax* sp. 6 (Fig. 28), a CCS represented by specimens from Orocué, Casanare (Colombia), Puerto Ayacucho, Amazonas (Venezuela), and Reserva Biologica Ilha de Maracá, Roraima (Brazil), three localities that span nearly 1,100 km. The UPD between the specimens Puerto Ayacucho and Reserva Biológica Ilha de Maracá[14] is 1.2% (Appendix S10: Table 22). Photographs of the specimen from Puerto Ayacucho show a very dark dorsal coloration and a densely tuberculate dorsum, without the very conspicuous pattern and smooth skin occurring in *S. kennedyi*, whose type locality[15] is ≈165 km SW from Orocué. *Scinax* sp. 6 differs in UPDs of 3.6–5.8% from *S. kennedyi* and *S. rostratus* (Appendix S10: Table 22).

We included six specimens of *Scinax kennedyi* from three localities in Casanare and Meta, Colombia and one in Barinas, Venezuela (Fig. 28). UPDs among these samples are 0.0% (Appendix S10: Table 22). Our sampled locality in Colombia (Sabanalarga, Casanare) is 140 km NW from the type locality, and the locality in Venezuela (Barinas, Caño Caimán) is ≈480 km NE. Our voucher specimen from Venezuela (see Barrio-Amorós et al., 2019: fig. 176B) and other specimens collected with it lack the posterior extension of the interocular triangular blotch, but have the characteristic irregular black bars separated by dull orange on the hidden surfaces of thighs. So far, *S. kennedyi* has been known in Venezuela from nine specimens from Puerto Ayacucho identified by Rivero (1961) as *S. boulengeri* (as *Hyla*) but considered by Pyburn (1973) to be *S. kennedyi*. These specimens should be reevaluated, as they could be the CCS *Scinax* sp. 6. Similarly, several specimens reported as *S. kennedyi* from eastern Orocué and Vichada (Colombia) by Acosta-Galvis (2018) could correspond to *Scinax* sp. 6. Lopes and Giaretta (2022) reported similar calls for topotypes of *S. kennedyi* and specimens from Roraima (Brazil). The identity of these latter requires corroboration, considering the occurrence of *Scinax* sp. 6 in Roraima as reported earlier.

Pyburn (1973) noted the similarity between *Scinax kennedyi* and *S. rostratus*, in the smooth dorsum and the lack of pointed tubercles along the margin of the lower jaw, and stressed that the latter was a much larger species. The UPDs between these species are 2.4–4.2% (Appendix S10: Table 22). Lopes and Giaretta (2022) reported

some differences in call structure between *S. kennedyi* and specimens of *S. rostratus* from Guaraúnos, Sucre (Venezuela; about 400 km E Caracas, the type locality).

Our specimens of *Scinax rostratus* are recovered as two sister lineages (Fig. 28). One includes the three available specimens from Venezuela, that span up to 500 km (from Falcón to Bolívar), and the other lineage includes the four available specimens from Colombia (from the Magdalena Valley, in Cundinamarca, Meta, and Santander). The UPDs between both lineages are 2.7–3.2% (Appendix S10: Table 22). We are not aware of phenotypic differences between them. Considering that the minimum distance between our sampled localities for both lineages is 600 km, we prefer to recognize them as a single species, pending a much denser geographic sampling. The name *S. rostratus* is associated with the lineage from Venezuela (type locality "Caracas"; Peters, 1863). An important weakness of our sampling of *S. rostratus* is the lack of specimens from NE Colombia and Panama; specimens from these areas would allow us to determine if they are related to the lineage of the Colombian populations. A positive association would imply that the name *Hyla foliamorta* Fouquette, 1958 (type locality "7 miles northwest Miraflores Locks, Canal Zone, on the west bank of the Gaillard Cut"), currently a synonym of *S. rostratus* (see Rivero, 1968a), might be available to that lineage.

The third clade in the pectinate series includes *Scinax jolyi* and *S. proboscideus* nested among three lineages that had been identified as *S. garbei*, two of which are here considered CCS (*Scinax* sp. 7 and 8) because of their phylogenetic position (Fig. 28). All these lineages form a well-supported clade (99% jackknife), where *Scinax* sp. 7, *S. jolyi*, and *Scinax* sp. 8 are successive sister taxa (93 and 99% jackknife) of *S. garbei* + *S. proboscideus*.

Scinax garbei is widespread throughout the middle and upper Amazon basin in Venezuela, Colombia, Ecuador, Peru, Bolivia, and Brazil (Duellman, 1972b; Rodríguez and Duellman, 1994; Barrio-Amorós, 1998; De la Riva et al., 2000; Silva and Costa-Campos, 2014). Unfortunately, our study lacks tissue samples from Bolivia and Venezuela and large areas of its distribution in Brazil; however, we included several samples from Ecuador, two localities from Acre and Mato Grosso, Brazil, and two from Peru. Our results recover a lineage including the populations of *S. garbei* from SW Brazil, W Peru, Ecuador, and Colombia, and show that the specimens from SE Peru and Mato Grosso represent two separate lineages that are not monophyletic (Fig. 28).

The lineage that includes the populations of *Scinax garbei* from SW Brazil, W Peru, Ecuador, and Colombia shows relatively low UPDs, 0.2–2.1% (Appendix S10: Table 23). Considering the relative proximity of these populations to the Rio Juruá[16], we consider that this lineage is

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14 The fragment of the 16S sequence of the specimen from Orocué, Casanare (Colombia) is very short, so we excluded it from the UPD calculation. However, when the alignment is trimmed so only comparable fragments of the three available samples of *Scinax* sp. 6 are included, the UPD between the sample from Orocué and those from Venezuela and Brazil is 2.8% (data not shown).

15 The type locality of *Scinax kennedyi* was reported as "110 mi. ESE Puerto Gaitán, Departamento de Meta, Colombia" by Pyburn (1973). Eric Smith (personal comm.) informed us that according to W.F. Pyburn's field notes, the type locality of this species should be corrected to Finca El Carmen, 14 road miles east of Los Kioskos, along road from Puerto Gaitán to Mapiripán, Meta, Colombia, 245 m elev., 03°26'47.17"N, 072°02'15.27"W.

16 The type locality of *Scinax garbei* was established as "Rio Juruá" by Miranda-Ribeiro (1926), and Bokermann (1966a) restricted it to "Rio Juruá, Eirunepé, Amazonas." Ihering (1904) reported that the collector, E. Garbe, reached San Felippe (former name of Eirunepé) after 23 d of navigation from Manaus. There are ≈740 km (airline) from the river Solimões to Eirunepé along the Rio Juruá; in the absence

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the one to which the name *S. garbei* should tentatively be applied (Fig. 28).

Our lineage from SE Peru, the CCS that we call *Scinax* sp. 7, is 15 km E from Puerto Maldonado, Madre de Dios, Peru, and was included in the analysis of Frost et al. (2006); this population was identified as *S. garbei* by Duellman and Salas (1991) and Duellman (2005). This sample is the only one from SE Peru available for our study and differs in UPDs of 4.7–6.6% from its closely related species (*S. garbei*, *S. jolyi*, *S. proboscideus*, *Scinax* sp. 8; Fig. 28; Appendix S10: Table 23). We are not certain if the other populations of SE Peru currently associated with *S. garbei* (Duellman and Wiens, 1993) belong to this lineage. *Scinax epacrorhinus* (Duellman, 1972b) described from Pilcopata, Cuzco, Peru, 250 km WSW from where our only sample of *Scinax* sp. 7 was collected, was distinguished from *S. garbei* mainly by the presence of a fleshy proboscis and call parameters (note duration, number of notes, and number of pulses). Subsequently, Duellman and Wiens (1993) synonymized *S. epacrorhinus* with *S. garbei*. They argued that the development of the fleshy proboscis is variable, with some Ecuadorian and Peruvian specimens of *S. garbei* having a larger projection than some *S. epacrorhinus* from Peru. Furthermore, they judged that the call differences between the two species represent geographic variation within a single species, based on comparisons with calls from one specimen of *S. garbei* from SE Peru (Tambopata; > 40 km SW from the locality of *Scinax* sp. 7, Puerto Maldonado) that had overlapping parameters with the calls of *S. epacrorhinus*. To add uncertainty to this scenario, Duellman (2005) described calls of *S. garbei* from Puerto Maldonado (and which presumably belong to *Scinax* sp. 7) as having notes of 1.1–1.4 s, much longer than those described for Ecuador (0.16–0.26 s; Duellman and Wiens, 1993) and *S. garbei* from Pilcopata and Tambopata (0.5–0.7 s; Duellman and Wiens, 1993). Future studies should determine how many lineages associated with *S. garbei* besides *Scinax* sp. 7 occur in SE Peru and adjacent Bolivia, and if *S. epacrorhinus* is an available name for one of them.

The other CCS, *Scinax* sp. 8, is from Apiacás, Mato Grosso, Brazil, and is the sister taxon of *S. proboscideus* + *S. garbei* (Fig. 28). It differs from its closely related species in UPDs of 2.7–6.6% (Appendix S10: Table 23). Our lack of material from Manaus or adjacent areas makes it uncertain whether *Hyla lutzi* Melin, 1941 (type locality: "Vicinity of Manáos and Rio Uaupés"; Melin, 1941) is an available name for this lineage. Considering this generally deficient sampling and the comments made earlier for *Scinax* sp. 7, a thorough study of these and *S. garbei* throughout its wide distribution is required to properly clarify the taxonomy of these species.

The recent study by Lopes et al. (2020) reported some differences in calls from specimens from different populations originally assigned to *Scinax garbei*. They inferred that these belong to three different lineages, which seem to correspond to our *Scinax* sp. 7 (their "*S. garbei* Southwestern"), *Scinax* sp. 8 (their "*S. garbei* Brazil"), and *S. garbei* (their "*S. garbei* Northwestern"). They reported spectral and temporal differences, some of which overlap, but their study constitutes a starting point for a detailed study of call variation in these three species.

Scinax jolyi has been known so far from coastal lowland forests in Suriname, French Guiana and adjacent Brazil (Lescure and Marty, 2000; Ouboter and Jairam, 2012; Vacher et al., 2020). Our results revealed that two specimens misidentified as *S. garbei* from localities on the Purus and Amazonas Rivers, Brazil, ≈1900 and ≈950 SW, respectively, from the known area of distribution of *S. jolyi*, belong to this species (Fig. 28). This result is corroborated by the study of the voucher specimens, which match the description of Lescure and Marty (2000), including the characters that were mentioned differentiating it from *S. garbei* (see comments below regarding this species). Our study also included samples from different localities in French Guiana and adjacent Brazil (Amapá). UPDs between these and those from the localities on the Purus and Amazonas Rivers are 1.2% (Appendix S10: Table 23). Taucce et al. (2022) suggested that records associated with *S. garbei* from Amapá (Silva and Costa-Campos, 2014, 2018; Ferreira-Lima et al., 2017) likely correspond to *S. jolyi*; this requires corroboration.

Scinax proboscideus occurs in the Guianas and adjacent Brazil (Lescure and Marty, 2000; Ouboter and Jairam, 2012; Cole et al., 2013; Taucce et al., 2022). From this poorly known species, we included samples from French Guiana and Guyana; it differs from its sister species, *S. garbei* in UPDs of 2.4–3.2% (Fig. 28; Appendix S10: Table 23).

Other relevant literature. Rivero (1968a; vocalizations of *Scinax rostratus*); León (1969: vocalizations and tadpole of *S. boulengeri*; it is unclear to which of the lineages identified here they correspond; vocalizations and tadpole of *S. rostratus*, the latter as *Hyla foliamorta*; the tadpoles were misidentified as suggested by McDiarmid and Altig, 1990, and corroborated by Hero and Mijares-Urrutia, 1995); Duellman (1970a: vocalizations and tadpole of *S. boulengeri*; it is unclear if it corresponds to one of the lineages identified here; vocalizations and tadpole of *S. rostratus*, the latter as *Hyla foliamorta*; the larvae were misidentified as suggested by McDiarmid and Altig, 1990, and corroborated by Hero and Mijares-Urrutia, 1995); Duellman (1970b: vocalization of *S. garbei*); Campbell and Telford (1971: vocalization of *S. boulengeri* from Panama; it is unclear if it corresponds with one of the lineages identified here); Duellman (1971: vocalizations of *S. quinquefasciatus*); Duellman (1972b: vocalizations of *S. garbei*, *S. nebulosus*, *S. proboscideus*, *S. sugillatus* [as *Hyla boulengeri*, see Duellman, 1973], an unidentified lineage associated with *S. garbei* [as *Hyla epacrorhina*, see discussion above]); Duellman (1973: vocalizations of *S. sugillatus*); Pyburn

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of any specific indication associating this locality with the holotype of *S. garbei*, the type locality of this species should be considered Rio Juruá, Amazonas, Brazil. This correction might or might not be relevant to the taxonomy of this species, depending on how many lineages associated with this name are revealed along the area traversed by this long river. For more details on the itinerary of Garbe in the Juruá, see Ihering (1904) and Garbe (2018).

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(1973: vocalization of *S. kennedyi*); Duellman (1978: tadpole and vocalizations of *S. garbei*); Jungfer (1986: natural history of *S. boulengeri* from Panama, it is unclear if it corresponds with one of the lineages identified here); McDiarmid and Altig (1990: tadpole of *S. sugillatus*); Duellman and Wiens (1993: vocalization of *S. pedromedinae*); De la Riva et al. (1994: vocalizations of *Scinax* sp. 3 [as *S. nebulosus*], and *S. garbei* from Bolivia; it is unclear if the latter corresponds with the lineages associated with that name here); Mercolli et al. (1994: natural history and tadpole of *S. acuminatus*); Bevier (1995, 1997a,b: physiology of *S. boulengeri* from Panama; it is unclear if it corresponds with one of the lineages identified here); Hero and Mijares-Urrutia (1995: tadpole of *S. rostratus*); Ressel (1996: physiology of *S. boulengeri* from Panama; it is unclear if it corresponds with one of the lineages identified here); Lescure and Marty (2000: natural history and vocalizations of *Scinax* sp. 2, as *S. nebulosus*, and *S. proboscideus*); Sandoval (2000: tadpole of *S. acuminatus*); Costa et al. (2004: spermatozoid of *S. constrictus*, as *S. rostratus*); Lima et al. (2005: vocalization of *S. constrictus*); Duellman (2005: tadpole and vocalization of *S. pedromedinae*; natural history and vocalization of *Scinax* sp. 7, as *S. garbei*); Prado et al. (2005: reproductive biology of *S. acuminatus*); Lima et al. (2006: natural history of populations identified as *S. garbei* from the outskirts of Manaus, Brazil; it is unclear if it corresponds with one of the lineages identified here); Vera Candioti (2007: tadpole of *S. boulengeri* from Panama; it is unclear if it corresponds with one of the lineages identified here); Magrini et al. (2011: vocalizations of *S. acuminatus*); Gomes et al. (2014: tadpole likely of *Scinax* sp. 5, as *S. nebulosus*); Targueta et al. (2018: karyotype of *S. constrictus*); Santos et al. (2019: tadpole of *S. constrictus*); Schiesari et al. (2022: tadpole identified as *S. garbei* from Central Amazonia; it is unclear if it corresponds with one of the lineages identified here).

The *Scinax auratus* group

Sister taxon. The clade including the *Scinax boesemani*, *S. cruentomma*, *S. danae*, *S. elaeochroa*, *S. eurydice*, *S. funereus*, *S. fuscomarginatus*, *S. fuscovarius*, *S. granulatus*, *S. nasicus*, and *S. squalirostris* groups, and *S. pachycrus*.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data and a single phenotypic synapomorphy: exoccipital bones ventrally fused (Ch. 9.0, with instances of homoplasy in *Ololygon*, *Scinax exiguus*, *S. pachycrus*, and an internal clade of the *S. granulatus* group).

Moreover, species in this group differ from other species of *Scinax* by the combination of sub-elliptical snout with a pointed tip in dorsal view (rounded, elongate pointed, or elongate acuminated in all other species of *Scinax*); single, subgular vocal sac, does not reach the level of the pectoral fold (enlarged, reaching the level of the pectoral fold or region in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); lack of spicules in nuptial pad, inner margin of arm, and pectoral region in males (present in the *S. fuscovarius* group); lack of pectoral glands in males (present in the *S. fuscovarius* and *S. nasicus* groups, and some species of the *S. funereus* group); and dorsal pattern with irregular dark blotches, or light or dark dorsal continuous or broken stripes, sometimes delimiting a central darker area (silvery white dorsolateral stripe in the *S. squalirostris* group; dark dorsolateral band in the *S. fuscomarginatus* group).

Characterization. (1) SVL in males 20.6–35.0 mm, females 22.3–38.0 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single, does not reach the level of the pectoral fold; (5) snout sub-elliptical with a pointed tip; (6) rounded tubercles in the lower lip absent or present; (7) dorsal skin smooth, shagreen, or with scattered tubercles; (8) postaxial webbing of toe I reaching subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching subarticular tubercle (Ch. 59.1); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pad, inner margin of arm, and pectoral region in males absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.1); (14) iris red or bronze, with a median horizontal dark streak; (15) dorsal pattern with irregular dark blotches, or light or dark dorsal continuous or broken stripes, sometimes delimiting a central darker area, together with an interocular stripe; (16) hidden surfaces of thighs uniform dark or with blotches; (17) physiological chlorosis absent or present (Ch. 158.0 or 158.1; see below); (18) eyes of the tadpole visible or not visible ventrally (Ch. 146.0 or 146.1); (19) oral disc subterminal (Ch. 143.0); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent or present (Ch. 137.0 or 137.2); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis subparallel or orthogonal/suborthogonal to the main body axis (Ch. 148.0 or 148.1); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with 1 note/call, note duration 120–2,070 ms, and 4–152 pulses per note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent or present (Ch. 91.0 or 91.1); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 metacentric (Ch. 152.0); and (34) NOR in chromosome pair 3, or 11, proximal (Ch. 153.2 or 153.10).

Contents. Eight recognized species: *Scinax alter* (Lutz, 1973a); *Scinax auratus* (Wied, 1821); *Scinax cuspidatus* (Lutz, 1925); *Scinax cretatus* Nunes and Pombal, 2011; *Scinax crospedospilus* (Lutz, 1925); *Scinax juncae* Nunes and Pombal, 2010; *Scinax imbegue* Nunes et al., 2012;

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and *Scinax tymbamirim* Nunes et al., 2012. One CCS, *Scinax* sp. 11; two UCSs, *Scinax* spp. 9–10.

Distribution. Northeastern and southeastern Brazil from Paraíba to Rio Grande do Sul (e.g., Izecksohn and Carvalho-e-Silva, 2001; Lima and Skuk, 2006; Santana et al., 2009; Protázio et al., 2011).

Comments. Similarities among the species included in this group were already noticed by Lutz (1973a) and more recent studies (e.g., Mercês and Juncá, 2012; Nunes et al., 2012; Nogueira et al., 2015a). In the results of Duellman et al. (2016), the position of *Scinax crospedospilus*, the single species of this group included by these authors, is congruent with our analyses. It was found as sister taxon of a clade including most species of *Scinax*, excepting the redefined *S. rostratus* group (including *S. acuminatus* and *S. quinquefasciatus*).

The internal relationships of the *Scinax auratus* group are generally well supported (≥ 80% jackknife; Fig. 29). *Scinax alter* was described (as *Hyla rubra orientalis*, then replaced by *Hyla rubra altera* Lutz, 1973a) by Lutz (1968b) as a subspecies of *S. ruber* for specimens from Ribeirão Crubixá-Mirim, Municipality of Santa Leopoldina, Espírito Santo, Brazil. Some studies treated this species as a synonym of *S. ruber* (Duellman, 1977; Duellman and Wiens, 1992), but it is currently considered a valid species distinguished from *S. ruber* by size and color pattern differences (Lutz, 1973a; Carvalho-e-Silva and Peixoto, 1991; Nunes et al., 2012), among other phenotypic characters.

Pombal et al. (1995a,b) commented that there were likely several species under the name *Scinax alter*, based on differences in size, color pattern, and call parameters among its populations (Lutz, 1973a). This was corroborated in the study of Nunes et al. (2012), who reviewed and redelimited the species. *Scinax alter* as formerly recognized was partitioned into three species: *S. alter*, *S. imbegue*, and *S. tymbamirim*. *Scinax alter* is notably similar to *S. imbegue* and *S. tymbamirim*, and is commonly confused with them, as a result of the intraspecific variation in the external morphological characters used by Nunes et al. (2012) to differentiate these species: presence and morphology of metacarpal and tarsal tubercles, and finger and toe discs diameter. Our observation of type material of these three species showed that both inner and outer metacarpal tubercles of *S. imbegue* are morphologically indistinguishable from those of *S. alter* (*vs*. lower metacarpal tubercle in *S. imbegue*; Nunes et al., 2012); the tarsal region in *S. alter* and *S. imbegue* have round, low, small tubercles in the ventrolateral surface of the tarsi and low tubercles next to the tibiotarsal articulation, as well as *S. tymbamirim* (*vs*. smooth tarsal region in *S. imbegue* and presence of a single tarsal tubercle in *S. tymbamirim*; Nunes et al., 2012). Furthermore, although the finger and toe discs in *S. tymbamirim* are slightly smaller than those of *S. alter* and *S. imbegue*, the diameters of finger and toe discs overlapped between these species (Nunes et al., 2012: Table 2). Tadpoles of *S. imbegue* and *S. tymbamirim* are unknown. The only reported characters that

differentiate these three species are some call parameter differences like pulse duration, interval between pulses, and pulse rate (Pombal et al., 1995b; Nunes et al., 2012).

Our results show that *Scinax alter* and *S. imbegue* are well-supported lineages (≥ 99% jackknife; Fig. 29). The NORs placed in the long arm of chromosome pair 3 (Ch. 153.2) could be a synapomorphy of this group, with at least one instance of homoplasy with *S. staufferi* (Anderson, 1991), but this character-state is solely known for *S. alter* (Cardozo et al., 2011) and *S. auratus* B (Ch. 153.11, plesiomorphic condition for Scinaxini) in this group (Cardozo et al., 2011; Nogueira et al., 2015a).

The lineage that we associate with *Scinax alter* includes specimens that have traditionally been considered this species (Nunes et al., 2012) from several localities in southeastern Bahia, Espírito Santo, eastern Minas Gerais, and Rio de Janeiro (Fig. 29). Although we do not have topotypes (type locality: Ribeirão Crubixá Mirim, Santa Leopoldina, Espírito Santo, as amended by Nunes et al., 2012), we have specimens from several localities surrounding the type locality (Santa Teresa, Marechal Floriano, Aracruz), including one (Santa Teresa) distant only ≈24 km NW from the type locality. The inclusion of specimens from the southern part of its distribution (São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul; Nunes et al., 2012) will allow an in-depth exploration of the limits with *S. imbegue*, *S. tymbamirim*, and the candidate species *Scinax* spp. 9–10.

Specimens associated with the name *Scinax tymbamirim* are recovered in two distantly related lineages (Fig. 29). One lineage from Praia dos Naufragados, Florianópolis, Santa Catarina (≈23 km S from its type locality; Nunes et al., 2012), for which we applied the name *S. tymbamirim*; and the other, including populations from Bertioga (CFBH 10515, referred material in the original description of *S. tymbamirim*; Nunes et al., 2012) a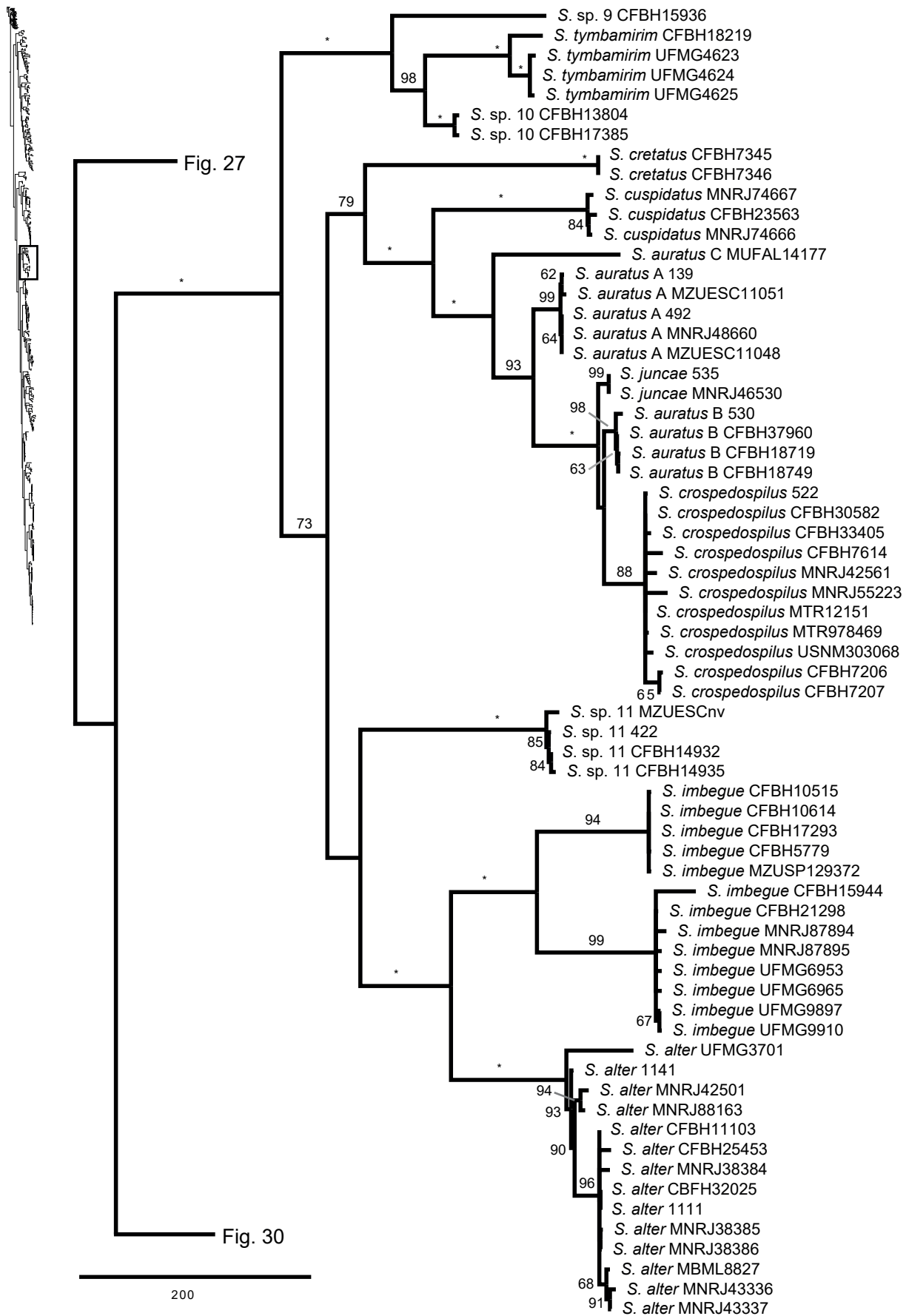nd Ubatuba, both in São Paulo, and Paraty in Rio de Janeiro, is one of the clades that we associate with *S. imbegue* (Fig. 29; see below). Further, two other distinct lineages referred to as *Scinax* sp. 9 (Cananéia, São Paulo) and *Scinax* sp. 10 (Mongaguá and Peruíbe, São Paulo) are sympatric with *S. imbegue* and *S. tymbamirim* (Nunes et al., 2012). Therefore, we could have at least two unrelated species that had been associated with *S. imbegue* and *S. tymbamirim*, which we consider UCSs based on their phylogenetic position and the taxonomic confusion surrounding these species. *Scinax* spp. 9–10, and *S. tymbamirim* have UPDs of 3.7–4.1%, and the two UCSs differ by 3.4–10.9% from all remaining species of the *S. auratus* group (Appendix S10: Table 24).

The lineage with which we associate *Scinax imbegue* includes two sister clades (Fig. 29). One with specimens from São Bento do Sul and Rancho Queimado, both in Santa Catarina, Brazil (distant ≈75 km N and ≈93 km S from its type locality, respectively; Nunes et al., 2012), and Iguape in São Paulo (CFBH 15944, referred material in the original description; Nunes et al., 2012). The other clade includes populations from Bertioga (CFBH 10515, referred material in the original description of *S. tymbamirim*; Nunes et al., 2012) and Ubatuba, both in São Paulo, and Paraty in Rio

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Figure 29. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 10 of 21: The *Scinax auratus* group. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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de Janeiro. UPDs between both clades are 1.5–1.7%, with the smaller UPD being between the samples from Iguape and Bertioga, two localities ≈175 km apart (same UPDs with the sample from Paraty; Appendix S10: Table 24).

Scinax sp. 11 is poorly supported (< 50% jackknife) as the sister taxon of the clade including *S. auratus*, *S. cretatus*, *S. crospedospilus*, *S cuspidatus*, and *S. juncae* (Fig. 29). *Scinax* sp. 11 is morphologically most similar to *S. cuspidatus* and differs in UPDs of 6.2–10.2% from all remaining species of the group (Appendix S10: Table 24). We have samples of this candidate species from Linhares, Espírito Santo, and Uruçuca, Bahia, Brazil. We are not aware of any diagnostic phenotypic character for this species but consider it CCS based on its cladistic distance from *S. cuspidatus*.

The clade composed of *Scinax auratus*, *S. cretatus*, *S. crospedospilus*, *S. cuspidatus*, and *S. juncae* is moderately supported (79% jackknife) and delimited by molecular evidence and a single phenotypic synapomorphy: the presence of tubercles in the lower lip (Ch. 53.1, with some instances of homoplasy in the sister taxon of *S. quinquefasciatus* in the *S. rostratus* group, *S. pachycrus*, two species of *Ololygon*, and an internal clade of the *O. catharinae* group). These rounded, flattened tubercles are positioned on each side of the lower lip at the level of the articulation between the mentomeckelian and dentary bones (a combination of Ch. 54.0—synapomorphy of the sister taxon of *S. rostratus* group—and Ch. 55.0, plesiomorphic for Scinaxini). Furthermore, we consider as putative synapomorphies of this clade the presence of a posterior gap in the row of marginal papillae of the oral disc (Ch. 134.1); lateral margins of the oral disc discontinued of its posterior portion (Ch. 135.1); P-3 placed on the labial arm (Ch. 137.2); and P-3 reduced to ¼ the length of P-2 (Ch. 138.2). All these transformations have instances of homoplasy in the sister taxon of *S. acuminatus* in the *S. rostratus* group. In the *S. auratus* group these character-states optimize ambiguously on the nodes immediately above and below *S. cretatus* and *Scinax* sp. 11, because their tadpoles are still unknown. However, it is relevant to mention that the tadpoles described by Alves et al. (2004) assigned to *S. auratus* are from Quebrangulo, Alagoas, Brazil. Considering that *S. auratus* and *S. cretatus* are sympatric in that locality (Nunes and Pombal, 2011), the identity of these larvae requires confirmation.

The morphology of the labial arm is somewhat different between the species of the *Scinax auratus* and *S. rostratus* groups. In some tadpoles of the *S. auratus* group (*S. auratus*, *S. crospedospilus*, and *S. juncae*; Heyer et al., 1990; Alves and Carvalho-e-Silva, 2002; Alves et al., 2004; Mercês and Juncá, 2012), the labial arm seems to be proportionally larger than in those of the *S. rostratus* group (Hero and Mijares-Urrutia, 1995: fig. 2; Mercês and Juncá, 2012: fig. 1D, E). Moreover, tadpoles of *S. juncae* have two pairs of enlarged cylindrical papillae on the sides of the labial arm, somewhat similar to what has been observed in tadpoles of *S. crospedospilus* (Heyer et al., 1990: fig. 22).

Scinax cretatus (CFBH 7345–7346, referred material in the original description; see Nunes and Pombal, 2011) is the sister taxon of the remaining species of this clade,

followed by *S. cuspidatus* as the sister taxon of the remaining species, that are well supported (100% jackknife; Fig. 29). These include *S. crospedospilus* (including CFBH 7206–7207 from Queluz, São Paulo distant ≈55 km WSW from its type locality in Campo Belo, Itatiaia, Rio de Janeiro; Bokermann, 1966a), *S. juncae* (MNRJ 46530, referred material in the original description; Nunes and Pombal, 2010), and three non-monophyletic lineages associated with *S. auratus* (*S. auratus* A, B, and C; Fig. 29).

Scinax cuspidatus was described originally from the city of Rio de Janeiro (Lutz, 1925) and subsequently reported for Espírito Santo (Bokermann, 1966b), Bahia (Silvano and Pimenta, 2001), and Alagoas (Lima and Skuk, 2006). We included specimens from the type locality (Rio de Janeiro; Lutz, 1925) and a nearby locality. The recognition of the phenotypically close *Scinax* sp. 11 (Fig. 29) based on specimens from Espírito Santo and Bahia indicates the need to reassess the taxonomic status of the populations associated with *S. cuspidatus*.

Scinax auratus was described for Santa Inês, Bahia, Brazil ("*S.* Agnés"; Wied, 1821); the holotype was considered lost (Bokermann, 1969; see also Vanzolini and Myers, 2015), and Duellman and Wiens (1992) designated a neotype from Maracás, Bahia, Brazil. Unfortunately, tissue samples of topotypes of *S. auratus* were unavailable for comparisons, but our optimal topologies recovered three unrelated lineages currently named *S. auratus* (Fig. 29). *Scinax auratus* A is represented by specimens from Candeias, Nazaré, and Jequié, central and eastern Bahia, the latter being ≈60 km SE from the type locality of the neotype of *S. auratus*. *Scinax auratus* B includes specimens from Aurelino Leal, Porto Seguro, and Uruçuca, southeastern Bahia, distant from the type locality ≈145 km SE (Aurelino Leal) and 360 km SSE (Porto Seguro). *Scinax auratus* C is represented by one individual from Catolé, Maceió, Alagoas, ≈670 km NE from the type locality of *S. auratus*. These three lineages have UPDs of 2.8–6.0 (Appendix S10: Table 24). However, this is still a limited representation of the widespread distribution of *S. auratus*, which occurs through eastern Bahia and Sergipe to Paraíba, Brazil (Bokermann, 1969; Duellman and Wiens, 1992; Protázio et al., 2011; Santana et al., 2009), and therefore more samples from throughout its distribution are needed, including topotypes. We did not find phenotypic diagnostic characters that distinguish these lineages from the topotypic *S. auratus* (Duellman and Wiens, 1992).

Scinax auratus was associated with the former *Hyla ruber* group (sensu Dunn, 1933) by Bokermann (1969). Lutz (1973a) pointed out that *S. auratus* and *S. cuspidatus* are morphologically similar and called them "smooth-skinned forms with pointed snout." Duellman and Wiens (1992) assigned *S. cuspidatus* and *S. crospedospilus* to their *S. x-signatus* group, without mentioning any diagnostic character for this group, whereas *S. auratus* was considered unassigned to any group. Pombal et al. (1995b) assigned *S. auratus*, *S. crospedospilus*, and *S. cuspidatus* to the *S. ruber* group as defined by them; Faivovich et al. (2005) placed these species in their *S. ruber* clade but considered them unassigned to any group. Subsequently,

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based on minor differences in size, dorsal color pattern, and call parameters, Nunes and Pombal (2011) excluded *S. cuspidatus* from what they called the "*S. auratus* complex," composed of *S. auratus*, *S. cretatus*, and *S. juncae*. Our results rejected the monophyly of the "*S. alter* complex" proposed by Nunes et al. (2012) for *S. alter*, *S. imbegue*, and *S. tymbamirim*, because *S. auratus*, *S. cuspidatus*, *S. crospedospilus*, and *S. juncae* are nested among those species (Fig. 29).

Lutz (1973a) commented on the variation in the dorsal color pattern in *Scinax auratus* that occur in the coastal area of Bahia, Brazil, and in the last few years, two new species previously confused with that species have been described: *S. cretatus* and *S. juncae* (Nunes and Pombal, 2010, 2011). Adults of both species are morphologically similar to *S. auratus*, but the species differ in adult and larval morphological characters (unknown tadpoles for *S. cretatus*) and call parameters (Alves et al., 2004; Nunes et al., 2007; Nunes and Pombal, 2010; Mercês and Juncá, 2012). Confusions persist, as some of the specimens that Nogueira et al. (2022) identified as *S. juncae* are recovered as *S. auratus* B (a specimen from Camacan, Bahia, NOG530) and *S. crospedospilus* (a specimen from Porto Seguro, Bahia, NOG538) in our results (Fig. 29).

The taxonomy of *Scinax crospedospilus* has rarely been addressed in the literature (e.g., Lutz, 1973a) and it has not been diagnosed from the closely related *S. auratus* and *S. juncae*, from which it seems to differ in SVL, dorsal color pattern, and advertisement call structure (see also Bokermann, 1969; Heyer et al., 1990; Duellman and Wiens, 1992; Bevier et al., 2008; Nunes and Pombal, 2010; Magrini et al., 2011). We included specimens of *S. crospedospilus* from several localities in São Paulo, Rio de Janeiro, Espírito Santo, and Bahia (see also Silveira et al., 2020), including one (Queluz, São Paulo) that is only 40 km SW from the type locality (Campo Belo, Itatiaia, Rio de Janeiro; Bokermann, 1966a). The UPDs for these samples are 0.0–1.8% (Appendix S10: Table 24). We note that UPDs between *S. crospedospilus*, *S. auratus* B, and *S. juncae* are quite reduced, being 0.6–1.8%. We do not doubt the identification of our voucher specimens; as the sample of *S. juncae* is a referred specimen of Nunes and Pombal (2010) and the others are topotypes, we examined most specimens of *S. crospedospilus* and, as stated above, *S. auratus* B is not distinguishable from *S. auratus* A. The relatively low UPDs could be the result of different evolutionary processes or indicate problems with the taxonomic knowledge of these species, which is a general issue for the group, as discussed above.

Other relevant literature. Bokermann (1969: vocalizations of *S. auratus*); Heyer et al. (1990: tadpole and vocalizations of *S. crospedospilus*); Alves and Carvalho-e-Silva (2002: tadpoles of *S. alter* and *S. cuspidatus*); Alves et al. (2004: tadpole of *S. auratus*); Bevier et al. (2008: vocalizations of *S. crospedospilus* and *S. juncae*, as *S. auratus*); Nunes et al. (2007: vocalization of *S. auratus* from Feira de Santana, Bahia; it is unclear with which of the lineages identified here it should be associated); Nunes and Pombal (2010, 2011: vocalizations of *S. cretatus* and *S. juncae*); Magrini et al. (2011: vocalizations of *S. crospedospilus*); Cardozo et al. (2011: karyotypes of *S. alter* from a specimen Ubatuba, São Paulo, and one also identified as this species from Rancho Queimado, Santa Catarina that could be *S. tymbamirim*); Nunes et al. (2012: vocalizations of *S. alter*, *S. imbegue*, and *S. tymbamirim*); Abrunhosa et al. (2014: vocalizations and natural history of *S. cuspidatus*); Domingos et al. (2015: natural history of *S. cuspidatus*); Nogueira et al. (2015a: karyotype *S. auratus* from Jequié, Bahia; it is unclear with which of the lineages identified here it should be associated); Pederassi et al. (2022: vocalizations of *S. crospedospilus*).

The *Scinax squalirostris* group

Sister taxon. The clade including the *Scinax boesemani*, *S. cruentomma*, *S. danae*, *S. elaeochroa*, *S. eurydice*, *S. funereus*, *S. fuscomarginatus*, *S. fuscovarius*, *S. granulatus*, and *S. nasicus* groups, and *S. pachycrus*.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular evidence and eight phenotypic synapomorphies: (1) pectoral fold absent (Ch. 45.0, also absent in most species of *Ololygon*); (2) and (3) preaxial and postaxial webbing of toe IV reaching at most proximal half of antepenultimate phalanx (Chs. 60.0 and 61.0, both with many instances of homoplasy in internal clades of *Julianus*, *Ololygon*, and *Scinax*); (4) m. interhyoideus reaching posteriorly the anterior edge of the m. pectoralis esternalis (Ch. 78.3, with instances of homoplasy in *S. fuscomarginatus*, *S. cruentomma*, and *Dendropsophus elegans*); (5) Burton's ligament absent (Ch. 88.0, with one instance of homoplasy in *O. humilis*); (6) slip of the m. abductor indicis brevis dorsalis inserting on prepollex present (Ch. 95.1, with instances of homoplasy in some species of the *S. granulatus* group, and in *S. alter* and *S. quinquefasciatus*); (7) ulnare slip of the m. extensor brevis superficialis digiti IV inserting on tendon of m. extensor brevis medius digiti IV absent (Ch. 105.0, with some instances of homoplasy in *Julianus uruguayus*, the *S. rostratus* group, and other species of *Scinax*, such as *S. boesemani*, *S. fuscomarginatus*, and *S. fuscovarius*); and (8) slip of m. flexor brevis profundus digiti IV inserting on metatarsal V absent (Ch. 120.0).

Optimizations of intercalary elements between ultimate and penultimate phalanges completely mineralized (Ch. 26.2, also completely mineralized in *Julianus uruguayus*, *Scinax fuscomarginatus*, and some species of *Ololygon*), and internal buttresses of the arytenoids absent (Ch. 39.0, also absent in *S. oreites*, *O. agilis*, and *O. melanodactyla*) are ambiguous, but could be other synapomorphies of this group, depending on the character-states still unknown in *S. squalirostris*.

Furthermore, species of this group differ from all other species of *Scinax* by the combination of elongate acuminated snout in dorsal view (elongate pointed in most species of the *S. rostratus* group; sub-elliptical with a pointed tip in the *S. auratus* group; rounded in all other species groups); vocal sac enlarged, reaching the level of

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the pectoral region (not reaching the pectoral fold in the *S. auratus*, *S. boesemani*, *S. danae*, *S. elaeochroa*, *S. funereus*, *S. fuscovarius*, *S. granulatus*, *S. nasicus*, and *S. rostratus* groups, and *S. pachycrus*); lack of spicules in nuptial pad, inner margin of arm, and pectoral region (present in the *S. fuscovarius* group); lack of pectoral glands in males (present in the *S. fuscovarius* and *S. nasicus* groups, and in some species of the *S. funereus* group); dorsal pattern with dorso-lateral silvery white stripes (uniform, with large irregular blotches, dark stripes or spots in all other groups); absence of physiological chlorosis (present in the *S. boesemani* and *S. elaeochroa* groups, some species of the *S. auratus*, *S. cruentomma*, and *S. funereus* groups); and tadpoles with P-3 inside the oral disc (in the margin of the labium or supported by a labial arm in the *S. rostratus* group and some species of the *S. auratus* group).

Characterization. (1) SVL in males 24.0–29.0 mm, females 20.6–27.6; (2) pectoral fold absent (Ch. 45.0); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single, enlarged, reaches the level of the pectoral region; (5) snout elongate acuminated in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth, shagreen, or with scattered tubercles; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the midlength of the penultimate phalanx (Ch. 59.1); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze with a brown streak; (15) dorsal pattern with silvery white dorsolateral stripes; (16) hidden surfaces of thighs uniform; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole visible ventrally (Ch. 146.1); (19) oral disc subterminal (Ch. 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with 10–18 notes/call, note duration 20–30 ms, and 3–12 pulses per note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent (Ch. 91.0); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 metacentric (Ch. 152.0); and (34) NOR in chromosome pair 11, proximal (Ch. 153.12).

Contents. One recognized species: *Scinax squalirostris* (Lutz, 1925). One UCS, *Scinax* sp. 13.

Distribution. Southeastern Brazil from Rio de Janeiro to Rio Grande do Sul, and westwards to Mato Grosso and western Bolivia. Eastern Argentina from Formosa and Misiones to Buenos Aires, eastern Paraguay, and Uruguay (e.g., Cei, 1980; Brandão et al., 1997; De la Riva et al., 2000; Achaval and Olmos, 2003; Eterovick and Sazima, 2004; Canelas and Bertoluci, 2007; Uetanabaro et al., 2007; Faria et al., 2013; Weiler et al., 2013; Vaz-Silva et al., 2020).

Comments. In the results of Faivovich (2002), *Scinax* sp. 13 (as *S. squalirostris*) is nested within a poorly supported clade composed of *S. cruentomma*, *S. exiguus* (referred to as *Scinax* sp. 2), *S. fuscomarginatus*, *S. nasicus*, and *S. staufferi*. In the results of Duellman et al. (2016), *Scinax* sp. 13 (as *S. squalirostris*) is the well-supported (bootstrap with RaxML = 93%) sister taxon of a large clade that includes most species of *Scinax*, except for *S. crospedospilus* (our *S. auratus* group) and the members of the *S. rostratus* group as redefined here. In our results (Fig. 30), the position of *S. squalirostris* is congruent with that recovered by Duellman et al. (2016).

Scinax squalirostris Lutz (1925) was described based on specimens from Fazenda do Bonito, Serra da Bocaina, São José do Barreiro, São Paulo, Brazil. We included tissue samples or sequences available in Genbank from different localities in northeast and central-eastern Argentina, Uruguay, southeastern and central Brazil, including topotypes, and southern Paraguay. Samples from Bolivia were unavailable.

Our results show two distinct, well-supported clades associated with *Scinax squalirostris* (Fig. 30), differing in UPDs of 4.9–7.1% (Appendix S10: Table 25). One of these includes specimens collected very close to the type locality of the nominal species (see below), and the other is considered as the UCS *Scinax* sp. 13, because we are not aware of diagnostic characters. The former of these clades has an internal polytomy with four clades (Fig. 30), including specimens from populations of (1) Distrito Federal, Brazil; (2) central Minas Gerais, Brazil; (3) Goiás and Minas Gerais; and (4) São Paulo (including São José do Barreiro, ≈6.2 km NW from the type locality of *S. squalirostris*), Paraná, Rio Grande do Sul, Santa Catarina, and adjacent Argentina (Misiones). Unfortunately, for clades 1 and 2 there are no 16S sequences available. For clades 3 and 4, UPDs indicate a borderline situation regarding the arbitrary threshold of 3% to distinguish UCSs (Appendix S10: Table 25), as they differ in 2.7–3.5%. While the deeply nested position of the topotypes in clade 4 allows us to associate it with the name *S. squalirostris*, considering the UPDs and the available evidence, it is unclear if the name should be applied to the other three clades as well, and therefore, we provisionally treat these as such until the problem is clarified.

Faria et al. (2013) reported differences in acoustic parameters from *Scinax squalirostris* from Congonhas do Norte, Minas Gerais, Brazil, with other populations (mostly from our clade 4, but also from UCS *Scinax* sp. 13, see below). Samples from Congonhas do Norte were not available for this study, and geographically this popula-
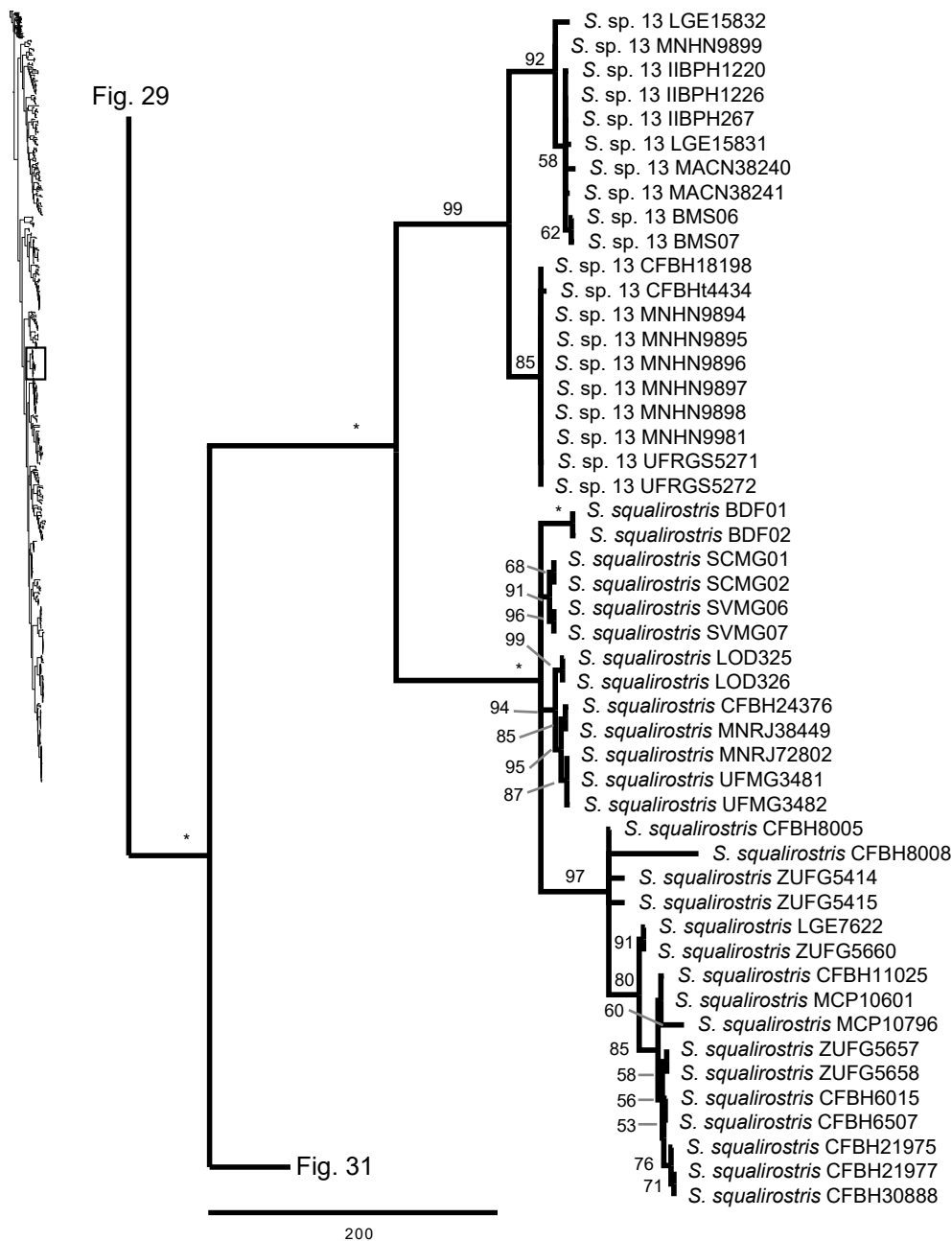
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Figure 30. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 11 of 21: The *Scinax squalirostris* group. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

tion could belong to our clades 2 or 3. Pezzuti et al. (2021) noticed differences in larval morphology including LTRF and coloration between tadpoles from the type locality (Bokermann, 1967b) and Itabirito, Minas Gerais. Further studies will determine if these apply to all populations recovered in our clade 3.

Pombal et al. (2011) pointed out that differences in the acoustic parameters (call duration, number of pulses, pulse duration, and pulse repetition rate) of *Scinax squalirostris* from Brazil (Cristalina, Goiás; Pombal et al., 2011) and Bolivia (La Paz; De la Riva et al., 2002) may indicate the existence of more than one species. Furthermore, they noted that SVL and morphology are variable among populations, which could suggest a species complex. Faria

et al. (2013) and Giaretta et al. (2020) corroborated the observations of Pombal et al. (2011) that the individuals from Cristalina, Goiás differ in acoustic parameters, having a single multipulsed note/call, whereas all other populations have 10–18 notes/call. We did not include tissue samples from this locality, but given its proximity to Brasilia, these could well belong to the same population. Morphological information on the voucher specimen of the call remains unpublished, and as the relationships of this putative different species are still unknown, we did not consider the characteristics of its call in the diagnosis of the *S. squalirostris* group.

Scinax sp. 13 is a UCS that includes specimens from localities in Entre Ríos and Misiones, Argentina, in Artigas,

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Maldonado, Rivera, Rocha, and San José, Uruguay, Mato Grosso do Sul, Rio Grande do Sul, and SW Santa Catarina, Brazil, and Itapuá and Ñeembucu, Paraguay. These are recovered in two clades, one including the specimens from Mato Grosso do Sul, Paraguay, and Argentina, and the other including the specimens from Santa Catarina to Uruguay (Fig. 30). The UPDs between these two clades are 1.0–1.5% (Appendix S10: Table 25) and based on these relatively low values and the absence of other diagnostic characters, we consider them as a single species. The available names for this lineage are *Hyla evelynae* Schmidt, 1944 (type locality: Hacienda Álvarez, 15 km northeast of San Carlos, Uruguay), *Hyla leucotaenia* Burmeister, 1861 (Type locality: "Bei Paraná, in den Gebüschen am Ufer der Lagunen" [Paraná, Entre Ríos], Argentina; see Pinheiro et al., 2014), and possibly *Hyla lindneri* Müller and Hellmich, 1936 (Type locality: "Junca Viejo," Formosa, Argentina[17]). We did not include sequences of topotypes of these available names; however, their type localities are roughly within the extreme points that we sampled in Argentina, central Brazil, and Uruguay. We very likely consider that the valid available name for this lineage would be *Hyla leucotaenia* in the case that additional evidence supports its distinctiveness from *S. squalirostris*.

The results of Faria et al. (2013) indicated that call parameters (call duration, pulses per call, and pulse rate) of individuals from northeastern and southeastern Rio Grande do Sul, which correspond to *Scinax* sp. 13, overlapped with those of *S. squalirostris* from the type locality in Serra da Bocaina (São Paulo). This suggests that there are no discernible acoustic differences between *Scinax* sp. 13 and *S. squalirostris*.

Other relevant literature. Lutz (1952, 1973a: taxonomy of *S. squalirostris*); Gallardo (1961a: taxonomy of *S. squalirostris*); Barrio (1962, 1963: vocalizations of *Scinax* sp. 13, as *S. squalirostris*); Bokermann (1967b: tadpole of *S. squalirostris*); Haddad et al. (1988: vocalizations of *S. squalirostris*); Basso (1990: natural history of *Scinax* sp. 13, as *S. squalirostris*); Pombal et al. (1995b, 2011: vocalizations of *S. squalirostris*); Kwet and Di Bernardo (1999: natural history of *S. squalirostris*); Alcalde and Rosset (2003: tadpole of *Scinax* sp. 13, as *S. squalirostris*); Costa et al. (2004: spermatozoid of *S. squalirostris*); Alcalde (2005: tadpole of *Scinax* sp. 13, as *S. squalirostris*); Kwet et al. (2010: natural history of *S. squalirostris*); Faria et al. (2013: vocalizations of *S. squalirostris*); Giaretta et al. (2020: vocalizations of *S. squalirostris*); Abreu-Jardim et al. (2021: phylogeography); Pezzuti et al. (2021: tadpole of *S. squalirostris*). Boelter et al. (2022: phenotypic variation in tadpoles of *S. squalirostris* and *Scinax* sp. 13, all consid-

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17 Restricted to "Formosa, Formosa, Argentina" by Lavilla (1992). Considering the itinerary of the German expedition to the Gran Chaco in 1926 (Müller and Hellmich, 1936), and the fact that Hellmich (1960) employs both spellings, "Junca" and "Yuncá," "Junca Viejo" as employed by Müller and Hellmich (1936) is clearly a misspelling of Yunká Viejo. This toponym (meaning "old Yunká") is a reference, still in use locally and in maps, to the original location of Fortín Yunká, the former name of the locality currently named Sargento Primero Leyes, Patiño, Formosa, Argentina.

ered as the former); Pederassi et al. (2022: vocalizations of *S. squalirostris*).

The *Scinax fuscomarginatus* group

Sister taxon. The *Scinax cruentomma* + *S. elaeochroa* groups.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data. No phenotypic synapomorphies are recovered for this group. Synapomorphies that optimize ambiguously are the pars externa plectri mediodistally expanded (Ch. 19.1, with instances of homoplasy in *Scinax* sp. 13 of the *S. squalirostris* group, and the *S. granulatus* group) and cardiac process of the cricoid subcylindrical, slightly wider than adjacent parts of the ring (Ch. 35.4, with instances of homoplasy in *Ololygon belloni*, *O. kautskyi*, *O. luizotavioi*, and *O. perpusilla*). These character-states are still unknown in *S. madeirae* and *S. villasboasi*.

The species included in this group further differ from all other species of *Scinax*, except for the *S. cruentomma* and *S. squalirostris* groups, by having an enlarged, single vocal sac that reaches the level of the pectoral fold. The dorsal pattern with a single, thick, dark dorsolateral stripe on a light background arising from the eyelid differentiates species of this group from those in the *S. cruentomma* and *S. squalirostris* groups. Furthermore, the rounded snout in dorsal view differentiates species of this group from those in the *S. squalirostris* group (elongate acuminated snout).

Characterization. (1) SVL in males 15.7–26.7 mm, females 22.1–26.3 mm (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac enlarged, subgular, single, reaching the level of the pectoral fold; (5) snout rounded in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the subarticular tubercle, midlength of the penultimate phalanx, or base of the disc (Ch. 59.1, 59.2, or 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands absent in males (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze; (15) dorsal pattern with one dark, thick dorsolateral stripe on a clear background, sometimes with a vertebral line; (16) hidden surfaces of thighs uniform, pale; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole visible ventrally (Ch. 146.1); (18) oral disc subterminal (Ch. 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent (Ch. 150.1); (27) oviposition in ponds (Ch. 155.0);

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(28) advertisement call with 1 note/call, note duration 154–1277 ms, pulses per note unreported; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent (Ch. 91.0); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair (Ch. 152.0); and (34) NOR in chromosome pair 11, proximal (Ch. 153.12).

Contents. Three recognized species: *Scinax fuscomarginatus* (Lutz, 1925); *Scinax madeirae* (Bokermann, 1964b); and *Scinax villasboasi* Brusquetti et al., 2014.

Distribution. Eastern Venezuela and savannas of Guiana and southern Suriname; Brazil; eastern Bolivia, Paraguay, and northeastern Argentina (e.g., Ouboter and Jairam, 2012; Cole et al., 2013; Weiler et al., 2013; Brusquetti et al., 2014; Barrio-Amorós et al., 2019).

Comments. The monophyly of the *Scinax fuscomarginatus* group with the *S. cruentomma* and *S. elaeochroa* groups is poorly supported (62% jackknife). The phylogenetic position of *S. fuscomarginatus* is unresolved in the results of Duellman et al. (2016); in those of Ferrão et al. (2016), the position of the *S. fuscomarginatus* group is congruent with ours.

After years of controversy (Lutz, 1925, 1926; Gaige, 1929; Cochran, 1952; Bokermann, 1966a; Lutz, 1973a; Hoogmoed and Gorzula, 1979; Duellman and Wiens, 1992; De la Riva et al., 1994, 1997; Cardoso and Pombal, 2010; Pombal et al., 2011), Brusquetti et al. (2014) revised the taxonomic identity of *Scinax fuscomarginatus* and its related species (*S. lutzorum* Woitovicz-Cardoso and Pombal, 2010, *S. parkeri* [Gaige, 1929], *S. pusillus* Pombal et al., 2011, and *S. trilineatus* [Hoogmoed and Gorzula, 1979]) using phenotypic (adult and larval external morphology and advertisement calls) and molecular evidence (16S and COI sequences). As a result, they resurrected *S. madeirae* (Bokermann, 1964b), described a new species, *S. villasboasi*, for specimens from Serra do Cachimbo, Pará, Brazil, and considered *S. lutzorum*, *S. parkeri*, *S. pusillus*, and *S. trilineatus* junior synonyms of *S. fuscomarginatus* (Lutz, 1925). For a review of the taxonomic history of the *S. fuscomarginatus* group, see Brusquetti et al. (2014). Our taxon sampling of this group (61 specimens) is represented mostly by sequences (40 specimens) produced by Brusquetti et al. (2014), some sequences taken from Jansen et al. (2011), two from Ferrão et al. (2016), and seven new samples (see Appendix S1). Our results (Fig. 31) differ from those of Brusquetti et al. (2014) in that *S. villasboasi* is recovered with low support (59% jackknife) as the sister taxon of *S. fuscomarginatus* instead of the sister taxon of *S. madeirae*. The internal relationships of *S. fuscomarginatus* are congruent with those of Brusquetti et al. (2014).

Scinax fuscomarginatus includes six lineages as proposed by Brusquetti et al. (2004: fig. 3; reported as B1 to B6 subclades). The relationships of these lineages within *S. fuscomarginatus* are well supported (Fig. 31). The UPDs between the six lineages are 2.2–8.3% (Appendix S10: Table 26), similar to those of Brusquetti et al. (2014: Table 4). Although these UPDs would indicate that each lineage corresponds to candidate species, Brusquetti et al. (2014) did not find morphological or bioacoustic characteristics that allow differentiate them from *S. fuscomarginatus*, and for that reason they are considered here DCLs.

Brusquetti et al. (2014) hypothesized that the relatively high sequence divergences within *Scinax fuscomarginatus* were the result of geographic distance. Some authors reported call and morphological differences among populations of *S. fuscomarginatus*, suggesting that it is a species complex (Toledo and Haddad, 2005; Cardoso and Pombal, 2010). Recently, Ferrão et al. (2016) pointed out that their *Scinax* sp. 2 (INPAH 34670, 34676) can be distinguished morphologically and bioacoustically from its closest sister species *S. fuscomarginatus* (Brusquetti et al., 2014) by snout shape, dorsal coloration pattern of tibia, and note duration and dominant call frequency. In our analysis, their *Scinax* sp. 2 is nested within the lineage including the specimens from Bolivia (Fig. 31). If these morphological differences referred by Ferrão et al. (2016) are corroborated, *Hyla parkeri* Gaige, 1929 (type locality Buenavista, Santa Cruz, Bolivia) is available for that lineage; other names are available for several other lineages as well (Hoogmoed and Gorzula, 1979; Pombal et al., 2011; Brusquetti et al., 2014).

Recently, Estupiñán et al. (2016) recorded UPDs for COI (10.9%) in *Scinax fuscomarginatus* (four individuals) from Rio Marmelos, Manicoré, Amazonas, Brazil. We could not include these sequences in our analysis because they sequenced the subunit II region of COI, a portion that does not overlap with our sequences (subunit I region).

Other relevant literature. Bokermann (1967c: vocalizations of *Scinax fuscomarginatus*) Hoogmoed and Gorzula (1979: taxonomy of *S. fuscomarginatus*, as *Ololygon trilineata*); Duellman and Pyles (1983: vocalizations of *S. fuscomarginatus*, as *Ololygon parkeri*); De la Riva et al. (1994: vocalizations of *S. fuscomarginatus*, as *S. parkeri*); Pombal et al. (1995a, 2011: vocalizations of *S. fuscomarginatus*); Prado et al. (2005: reproductive biology of *S. fuscomarginatus*); Toledo and Haddad (2005: reproductive biology of *S. fuscomarginatus*); Rossa-Feres and Nomura (2006: tadpole of *S. fuscomarginatus*); Cardozo et al. (2011: karyotype of *S. fuscomarginatus*); Franco-Belussi et al. (2012: visceral pigmentation in *S. fuscomarginatus*); Brusquetti et al. (2014: vocalizations of *S. fuscomarginatus* and *S. madeirae*); Jansen et al. (2016: vocalizations of *S. fuscomarginatus*); Lira et al. (2020: vocalization of *S. fuscomarginatus*); Pezzuti et al. (2021: tadpole of *S. fuscomarginatus*); Pederassi et al. (2022: vocalizations of *S. fuscomarginatus*).

The *Scinax elaeochroa* group

Sister taxon. The *Scinax cruentomma* group.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data. No phenotypic character

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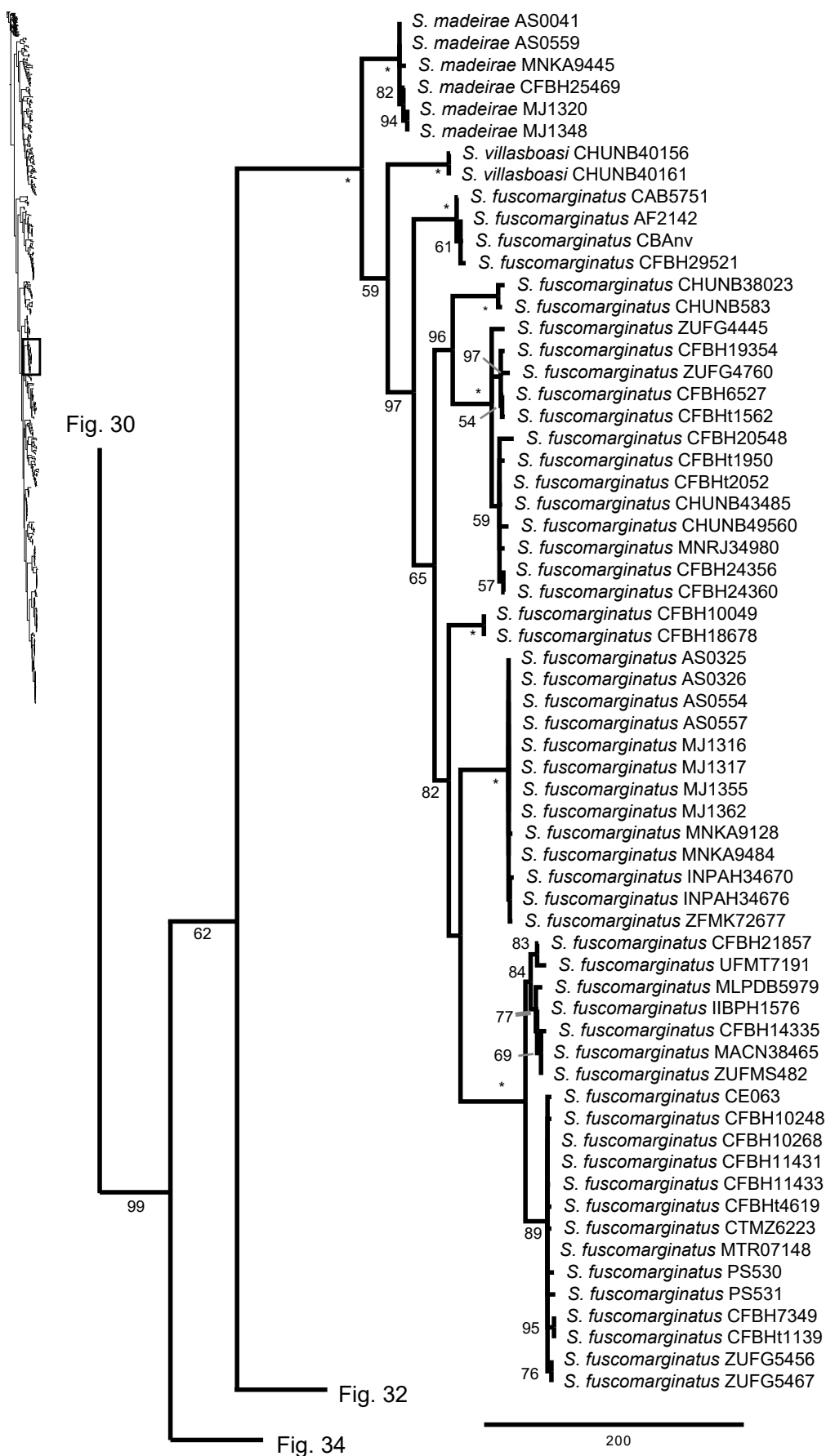
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Figure 31. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 12 of 21: The *Scinax fuscomarginatus* group. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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included in our analysis optimizes as a synapomorphy of this group. The species included in this group differ from all other species of *Scinax* by the combination of rounded snout in dorsal view (elongate pointed in most species of the *S. rostratus* group, elongate acuminated in the *S. squalirostris* group, sub-elliptical with a pointed tip in the *S. auratus* group); single, subgular vocal sac, that does not reach the level of the pectoral fold (enlarged, reaching the level of the pectoral fold or region in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); lack of spicules in the nuptial pad, inner margin of arm, and pectoral region (present in the *S. fuscovarius* group); lack of pectoral glands in males (present in the *S. fuscovarius* and *S. nasicus* groups, and in some species of the *S. funereus* group); hidden surfaces of thighs uniform pale or with small dark blotches (uniform, grey or brown or black in the *S. danae* group and most of the *S. funereus* group; if pale, with horizontal yellow markings); presence of physiological chlorosis (absent in the *S. danae*, *S. eurydice*, *S. fuscomarginatus*, *S. fuscovarius*, *S. granulatus*, *S. rostratus*, and *S. squalirostris* groups, some species of the *S. auratus*, *S. cruentomma*, and *S. funereus* groups, and *S. pachycrus*); and tadpoles with P-3 inside the oral disc (in the margin of the labium or supported by a labial arm in the *S. rostratus* group and some species of the *S. auratus* group).

Characterization. (1) SVL 26.3–37.7 mm, females 33.2–36.4; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single, does not reach the level of the pectoral fold; (5) snout rounded in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth, shagreen, or with scattered tubercles; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching midlength of the penultimate phalanx or base of the disc (Ch. 59.2 or 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze to orange yellow, with or without a median horizontal dark streak, and dark reticulations; (15) dorsal pattern with irregular blotches, sometimes with stripes; (16) hidden surfaces of thighs uniform, with or without dark reticulation; (17) physiological chlorosis present (Ch. 158.1); (18) eyes of the tadpole visible or not visible ventrally (Ch. 146.0 or 146.1); (19) oral disc subterminal (Ch. 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with 1 note/call, note

duration 80–470 ms, and 3–11 pulses/note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent (Ch. 91.0); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 metacentric (Ch. 152.0); and (34) NOR in chromosome pair 11, proximal (Ch. 153.12).

Contents. Three recognized species: *Scinax caprarius* Acosta-Galvis, 2018; *Scinax elaeochroa* (Cope, 1875); and *Scinax tsachila* Ron et al., 2018. One UCS, *Scinax* sp. 15.

Distribution. Caribbean lowlands from Nicaragua to western Panama; Pacific lowlands in Costa Rica and Panama; Pacific lowlands and Andean slopes (up to 1,500 m) of Colombia and Ecuador; and Sub-Andean forests in the middle part of the valley of the Rio Magdalena, Colombia (e.g., Duellman, 1970a; Savage, 2002; Sunyer et al., 2009; Köhler, 2011; Acosta-Galvis, 2018; Ron et al., 2018).

Comments. *Scinax caprarius* is the sister taxon of a well-supported clade (100% jackknife) including *S. elaeochroa*, *S. tsachila*, and a UCS, *Scinax* sp. 15 (Fig. 32). *Scinax caprarius* and *S. tsachila* were previously associated with *S. elaeochroa* and *S. quinquefasciatus*, respectively (Acosta-Galvis, 2018; Ron et al., 2018), and share with *S. elaeochroa* the occurrence of physiological chlorosis.

The type locality of *Scinax elaeochroa* ("east foot of mountains near Sipurio") is Cantón de Talamanca, Limón, Costa Rica (Savage, 1974). This species is distributed from the Caribbean lowlands of Nicaragua and Costa Rica to extreme western Panama (Savage and Heyer, 1969; Duellman, 1970a; Savage, 2002; Ron et al., 2018). Our analyses included specimens of *S. elaeochroa* from the Atlantic coast in Costa Rica and Panama, including one sample from Cahuita, Limón, Costa Rica (MVZ 149784), distant ≈15 km ENE from the type locality. *Scinax elaeochroa* was historically associated with populations recorded along the Pacific basin of Colombia (Ruiz-Carranza et al., 1996; Lynch and Suárez-Mayorga, 2004; Acosta-Galvis, 2018). Ron et al. (2018) pointed out that specimens from the Pacific basin of Colombia referred to *S. elaeochroa* need to be reassessed to corroborate their identity and that they are more likely to be *S. caprarius*, *S. quinquefasciatus*, *S. tsachila*, or an unnamed species; Pinto-Erazo et al. (2020) recently reported *S. tsachila* for southern Colombia.

Scinax sp. 15 differs in UPDs of 2.9–3.2% from its sister taxon, *S. tsachila* (Fig. 32), and 4.8% from *S. elaeochroa* (Appendix S10: Table 27). *Scinax* sp. 15 is represented by a single specimen from Los Algarrobos, Chiriquí, Panama. The study of the voucher specimen indicates that *Scinax* sp. 15 corresponds with what has been identified as *S. elaeochroa* from the Pacific coast of Panama and, very likely, neighboring Costa Rica. The name *Hyla dulcensis* Taylor, 1958 (type locality "Golfito, [Cantón de Golfito,] Puntarenas province, Costa Rica") distant ≈75 km ESE from

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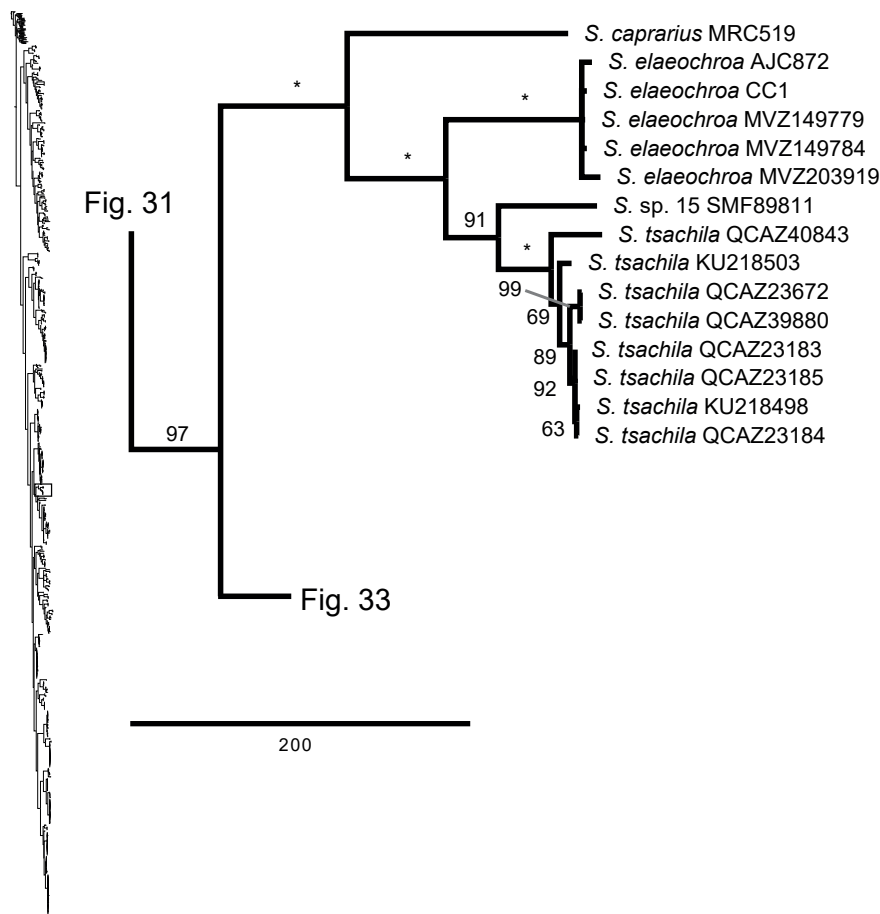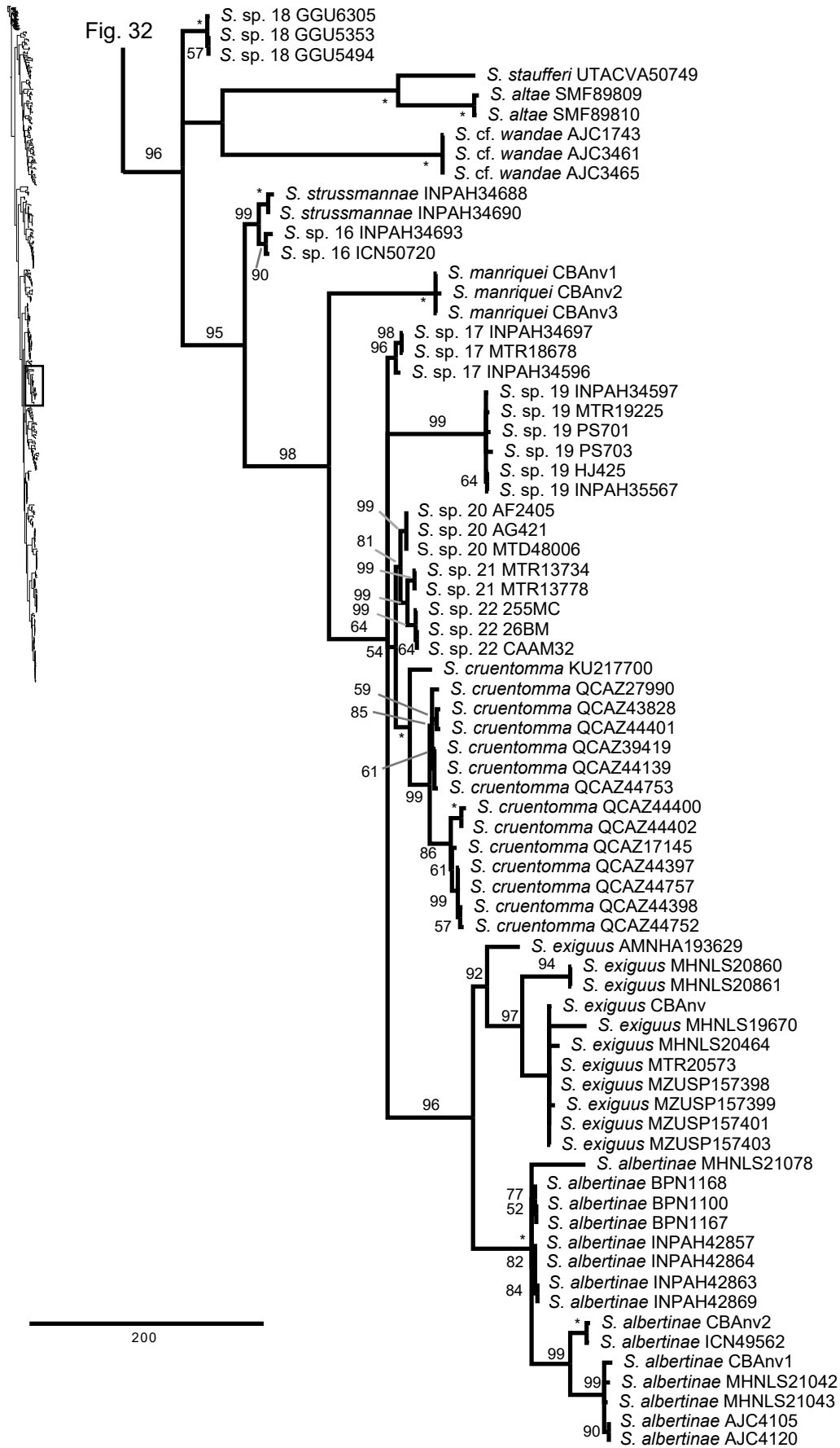
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Figure 32. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 13 of 21: The *Scinax elaeochroa* group. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

Los Algarrobos—considered a synonym of *S. elaeochroa* by Duellman (1966)—could be available for *Scinax* sp. 15. Ron et al. (2018) considered the possibility that *Hyla dulcensis* could be an available name for *S. tsachila* but discarded it based on the occurrence in the former of an interocular mark characteristic of most *S. elaeochroa* and absent in most *S. tsachila*. Nevertheless, Ron et al. (2018: fig. 9) depict three specimens of *S. tsachila*, out of 10, presenting the same interocular mark attributed to *S. elaeochroa* (Ron et al., 2018: fig. 8G). Considering this uncertain evidence, we consider *Scinax* sp. 15 as a UCS.

The *Scinax elaeochroa* group is well supported (97% jackknife) as the sister taxon of the *S. cruentomma* group (Fig. 32). This clade is delimited solely by molecular evidence.

Other relevant literature. Starrett (1960: natural history and tadpole of *Scinax elaeochroa*); Duellman (1967a,b: vocalization and chorus structure of *S. elaeochroa*); León (1969: vocalizations and tadpole of *S. elaeochroa*); Duellman (1970a, 2001: account, vocalizations and tadpole of *S. elaeochroa*); Duellman and Pyles (1983: vocalizations of *S. elaeochroa*); Donnelly and Guyer (1994: reproductive biology of *S. elaeochroa*); Acosta-Galvis (2018: vocalizations and tadpole of *S. caprarius*); Ron et al. (2018: vocalizations of *S. tsachila*).

The *Scinax cruentomma* group

Sister taxon. The *Scinax elaeochroa* group.

Diagnosis. This group is well supported (96% jackknife) and delimited by molecular data. We are not aware of any phenotypic synapomorphy. The species included in this group differ from all other species of *Scinax*, with the exception of those in the *S. fuscomarginatus* and *S. squalirostris* groups for having single or weakly bilobate enlarged vocal sac that reaches the level of the pectoral fold (not reaching the level of the pectoral fold in the *S. auratus*, *S. boesemani*, *S. danae*, *S. funereus*, *S. fuscovarius*, *S. granulatus*, *S. nasicus*, and *S. rostratus* groups, and *S. pachycrus*). Furthermore they differ from all species of *Scinax* by the combination of rounded snout in dorsal view (sub-elliptical with a pointed tip in the *S. auratus* group; elongate pointed in most species of the *S. rostratus* group, elongate acuminated in the *S. squalirostris* group); lack of spicules in nuptial pad, inner margin of arm, and pectoral region (present in the *S. fuscovarius* group); lack of pectoral glands in males (present in the *S. fuscovarius* and *S. nasicus* groups, and in some species of the *S. funereus* group); dorsal pattern uniform, with irregular blotches, or stripes (silvery white dorsolateral stripes in the *S. squalirostris* group; thick, dark dorsolateral stripe arising from

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the eyelid in the *S. fuscomarginatus* group); and tadpoles with P-3 inside the oral disc (in the margin of the labium or supported by a labial arm in the *S. rostratus* group and some species of the *S. auratus* group).

Characterization. (1) SVL males 18.0–30.0 mm, females 20.8–32.5 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac enlarged, subgular, single or weakly bilobate that reaches the level of the pectoral fold; (5) snout rounded in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth, shagreen, or with scattered tubercles; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the subarticular tubercle, midlength of the penultimate phalanx, or base of the disc (Ch. 59.1, 59.2, or 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pads, inner margin of arms, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze, with or without a median horizontal red streak; (15) dorsal pattern uniform, with irregular blotches, or stripes; (16) hidden surfaces of thighs uniform, light or dark; (17) physiological chlorosis absent or present (Ch. 158.0); (18) eyes of the tadpole visible ventrally (Ch. 146.1); (19) oral disc subterminal or ventral (Ch. 143.0 or 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with 1 note/call, note duration 97–1,638 ms, and 23–108 pulses/note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent (Ch. 91.0); (31) m. depressor mandibulae with or without an origin from the dorsal fascia that covers the suprascapula (Ch. 71.0 or 71.1); (32) m. depressor mandibulae with or without an origin from the tympanic annulus (Ch. 72.0 or 72.1); (33) chromosome pair 1 metacentric (Ch. 152.0); and (34) NOR in chromosome pair 11, proximal (Ch. 153.12).

Contents. Twelve recognized species: *Scinax albertinae* Ferrão et al., 2022; *Scinax altae* (Dunn, 1933); *Scinax baumgardneri* (Rivero, 1961); *Scinax blairi* (Fouquette and Pyburn, 1972); *Scinax cruentomma* (Duellman, 1972a); *Scinax exiguus* (Duellman, 1986); *Scinax karenanneae* (Pyburn, 1993); *Scinax lindsayi* Pyburn, 1992; *Scinax manriquei* Barrio-Amorós et al., 2004; *Scinax staufferi* (Cope, 1865); *Scinax strussmannae* Ferrão et al., 2018a; and *Scinax wandae* (Pyburn and Fouquette, 1971). Four CCSs, *Scinax* spp. 16–19; three UCSs *Scinax* spp. 20–22.

Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, Guyana, Colombia, Ecuador, Peru, and western Brazil (e.g., Duellman, 1970a; Pyburn, 1993; Rodríguez and Duellman, 1994; Barrio-Amorós, 1998; Lescure and Marty, 2000; Lynch, 2006b; Köhler, 2011; Cole et al., 2013; Carvalho et al., 2015a; Araujo-Vieira, 2016; Ferrão et al., 2018a).

Comments. In the results of Faivovich (2002), *Scinax cruentomma* and *S. staufferi* were recovered with *S. fuscomarginatus*, *S. nasicus*, *S. squalirostris*, and *S. exiguus* (as *Scinax* sp. 2) in a poorly supported clade (Bremer support 1) with one phenotypic synapomorphy: esophageal process of the cricoid ring absent in males. Although all those species are not recovered as a monophyletic group in our analyses, *S. cruentomma*, *S. exiguus*, *S. staufferi* (*S. cruentomma* group), and *S. fuscomarginatus* (*S. fuscomarginatus* group) are closely related (Fig. 33).

Our phylogenetic hypothesis shows a basal polytomy that includes *Scinax* sp. 18, a poorly supported clade (< 50% jackknife) including *S.* cf. *wandae* as the sister taxon of *S. altae* + *S. staufferi*, and a clade (95% jackknife) with *S. strussmannae* + *Scinax* sp. 16 as the sister taxon of the remaining species of the group (Fig. 33). These are well supported (98% jackknife) and include *S. manriquei* as the sister taxon of a poorly supported clade (64% jackknife) that includes a polytomy with two species (*Scinax* spp. 17 and 19) and two clades. One of these is well supported (96% jackknife) and includes *S. albertinae* and *S. exiguus*. The other clade is poorly supported (54% jackknife) and includes *S. cruentomma* and three candidate species, *Scinax* spp. 20–22.

Scinax staufferi (UTA A-50749) was included in previous phylogenetic analyses of Hylidae (Faivovich et al., 2005; Duellman et al., 2016). In the results of Duellman et al. (2016), this species was recovered as the sister species of *S. elaeochroa* (81% bootstrap with RaxML), a result congruent with ours. The analysis by Ferrão et al. (2022: Appendix 1) based on 16S sequences is also partially congruent.

Scinax sp. 18 is a CCS from Loreto, Peru, that is phenotypically similar to *S. strussmannae* but differs from it mainly in vocalizations (L.A.G. Gagliardi-Urrutia, personal comm.). UPDs between this CCS and all other species of the *S. cruentomma* group are 7.5–11.6% (Appendix S10: Table 28).

Scinax altae, a species described from Panama (Summit, Canal Zone; Dunn, 1933), was considered by León (1969) and Duellman (1970a) a subspecies of *S. staufferi* restricted to Panama, while the nominal subspecies was considered distributed from northwestern Costa Rica to Mexico. Subsequently, Duellman (2001) raised *S. altae* to species status. Our single specimen of *S. staufferi*, from Guatemala (Teculután, Zacapa) shows a UPD of 3.0% from our two specimens of *S. altae* from Panama (Los Algarrobos; Appendix S10: Table 28). Considering that 1,000 km (airline) separates both localities, a much denser sampling of these two species will be necessary to corroborate the distinctiveness of the latter species, as suggested by Duellman (2001).

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Figure 33. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 14 of 21: The *Scinax cruentomma* group. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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Scinax strussmannae and *Scinax* sp. 16 (*Scinax* sp. 1 and *Scinax* sp. 4 of Ferrão et al., 2016, respectively; see Appendix S10) are from nearby localities in Amazonas, Brazil (see Ferrão et al., 2016: fig. 1A, B). UPDs among these species are 4.1–5.8% (Appendix S10: Table 28). Further, Ferrão et al. (2016) stated that *S. strussmannae* (as *Scinax* sp. 1) differs morphologically from *Scinax* sp. 16 (as *Scinax* sp. 4) in SVL, supernumerary tubercles, and dorsal coloration. Although in the original description of *S. strussmannae* Ferrão et al. (2018a) did not report any morphological difference between this species and the sister candidate species *Scinax* sp. 16 (their *Scinax* sp. 4), we tentatively consider it a CCS. We included one sample of *Scinax* sp. 16 from Leticia, Colombia. The UPD with the sample from Amazonas, Brazil, is 2.6% (Appendix S10: Table 28). *Scinax strussmannae* shares with *S. cruentomma* and *Scinax* sp. 18 (also probably with our *Scinax* sp. 16 and *Scinax* sp. 19; see Ferrão et al., 2016) the presence of a median horizontal red streak in the iris.

Scinax manriquei was described from Mesa Quintero, Guaraque, Mérida, Venezuela (Barrio-Amorós et al., 2004), and reported to occur in the Andes of Venezuela (Mérida and Táchira) and adjacent Colombia (Norte de Santander; Barrio-Amorós et al., 2019). We included specimens from Merida and Táchira, the one from Táchira being only 30 km SW from the type locality, and their 16S sequences are identical (UPDs 0%; Appendix S10: Table 28). The description of the call of *S. manriquei* provided by Barrio-Amorós et al. (2004) differs considerably from the known calls of the *S. cruentomma* group, and the scale of the accompanying audiospectrogram precludes clear comparisons with those available in the literature. We consider plausible that the description corresponds to a sequence of advertisement (first and perhaps second note) and aggressive calls (notes 3–6), but this requires corroboration.

Some specimens identified as *Scinax cruentomma* and *S. wandae* from different localities were included in molecular analyses focused on the study of frog diversity in restricted areas (Salducci et al., 2002, 2005; Fouquet et al., 2007a,b; Guarnizo et al., 2015; Ferrão et al., 2016). Despite the context of a poor representation of species diversity of *Scinax*, they suggested the presence of candidate species. In a study of some species of *Scinax* from a region in the south of the Amazon River in Amazonas and Rondônia, Brazil, Ferrão et al. (2016) recognized a *S. wandae* clade (> 0.95 Bayesian posterior probability), based on their molecular results generated from 16S sequences. This clade included distinct lineages of *S. cruentomma* from Brazil, *S. wandae* from Colombia (Guarnizo et al., 2015), and three candidate species that they recognized as *Scinax* sp. 1 (*S. strussmannae*; Ferrão et al., 2018a), *Scinax* sp. 4 (our *Scinax* sp. 16), and *Scinax* sp. 7 (our *Scinax* sp. 19; see Appendix S10) from Brazil.

Ferrão et al. (2016) did not provide a diagnosis for their *Scinax wandae* clade, only mentioning some diagnostic characters for the candidate species (their *Scinax* sp. 1, *Scinax* sp. 4, and *Scinax* sp. 6) that they inferred from their results. Our results show that the *S. wandae* clade as de-

fined by Ferrão et al. (2016) is paraphyletic concerning *S. exiguus* and *S. manriquei* (Fig. 33). The latter two species occur, respectively, nearly 1,300 and 1,800 km N from the geographic area in which Ferrão et al. (2016) did their study.

Scinax wandae was described based on specimens from 12–18 km NNE of Villavicencio, Meta, Colombia (Pyburn and Fouquette, 1971). The results of Guarnizo et al. (2015) and Ferrão et al. (2016) indicated that at least two different lineages were included under the name *S. wandae*. Tissue samples were unavailable from the type locality of *S. wandae* (12 km NNE Villavicencio, Meta, Colombia) or anywhere significantly nearby. Originally, we included in this study samples of *S. wandae* from several localities in Colombia and Venezuela. As in previous studies, these were recovered as two separate lineages (Fig. 33), one of which was recovered as the sister taxon of *S. altae* and *S. staufferi* (< 50% jackknife), and included specimens from San Juan de Arama, Meta, Colombia (≈110 km SW from the type locality of *S. wandae*). The other lineage, recovered as the sister taxon of *S. exiguus* (96% jackknife), included specimens from Sabanalarga, Casanare, Colombia (≈85 km NE from the type locality of *S. wandae*) as well as specimens from Puerto Ayacucho, Amazonas, Venezuela (≈700 km ENE from its type locality), and localities from Alto Orinoco, Amazonas, Venezuela (≈1050 km ESE from its type locality) to as far as Guyana and Suriname (up to W Sipalwini; ≈1800 km W from its type locality). Based on our observations on the lack of clear diagnostic characters, and the lack of tissues from the type locality of *S. wandae*, we found no evidence to provide a definitive association of that name with one of these two lineages, and we are not aware of diagnostic phenotypic character distinguishing them from topotypic *S. wandae* nor if these lineages in any way show variation consistent with that already noticed by Pyburn and Fouquette (1971) in size between their type series and referred specimens collected 7 km S from the type locality, and in Puerto López, Meta, ≈70 km ESE.

For this paper, we are applying the name *Scinax* cf. *wandae* to the lineage represented solely by specimens from San Juan de Arama; for the other lineage, which is represented by specimens from Sabanalarga, Casanare, other localities in Colombia, Venezuela, Guyana, Suriname, and Brazil, we are applying the recently coined name *S. albertinae* Ferrão et al., 2022 (Fig. 33; see below). The correct application of the name *S. wandae* to one of these lineages will be solved when the type locality is prospected, and the diversity of the *Scinax* species is assessed and compared with the type series—it could well be that the two lineages identified here occur in the type locality.

Ferrão et al. (2022) described *Scinax albertinae* from Novo Airão, Amazonas, Brazil, for a small clade that we recover nested within the widespread lineage that includes the specimens Sabanalarga, Casanare, Colombia (≈85 km NE from the type locality of *S. wandae*). Their phylogenetic analysis, based on 16S mtDNA, included as *Scinax* sp. Clade 72 the same samples that we included from Guyana and Suriname (BPN 1100, 1167–1168). Fer-

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rão et al. (2022) reported UPDs of 1.4% between these samples and *S. albertinae*, stressing that they could not see vouchers from Guyana and Suriname, but could well belong to *S. albertinae*. The samples from Sabanalarga, Casanare, Colombia included by Ferrão et al. (2022) as *S. wandae* were recovered by them as the sister taxon of the clade including *Scinax* sp. Clade 72 and *S. albertinae*. Our observations and the UPDs within this lineage (0.4–3.4%; Appendix S10: Table 28) are coincident with UPDs reported by Ferrão et al. (2022) between their *Scinax* sp. Clade 72, *S. albertinae*, and the sequences they considered *S. wandae* are most reasonably interpreted as a single species broadly distributed in the northwestern Amazon basin, from Colombia and Brazil to Suriname (Fig. 33).

The characters considered diagnostic between *Scinax albertinae* and *S. wandae* provided by Ferrão et al. (2022) deserve a detailed examination. These authors differentiated *S. albertinae* and *S. wandae* based on "the absence of a well-defined and continuous dark dorsolateral stripe, maximum SVL 25.5 mm in males, white nuptial pad present in breeding males, *canthus rostralis* straight and bilobate vocal sac (well-defined and continuous dark dorsolateral stripe always present, maximum SVL 26.9 mm in males, nuptial pad absent, *canthus rostralis* rounded, and single vocal sac; Pyburn and Fouquette, 1971)." The combination of the information provided by Pyburn and Fouquette (1971) and our observations on a paratopotype of *S. wandae* (KU 131717) and some vouchers (see Appendices 1 and 2) indicate that *S. wandae* does have a white (i.e., uncolored; Luna et al., 2018) nuptial pad, the *canthus rostralis* does not look different from that of the many specimens shown by Ferrão et al. (2022), the SVL ranges of males of both species broadly overlap (21.6–25.4 mm in *S. albertinae*, 23.4–26.9 mm in *S. wandae*), and the vocal sacs of both *S. albertinae* and *S. wandae* are externally identical, although due to a lack of dissections we cannot specify if they correspond to what we called a weakly bilobate vocal sac in this study (see footnote 3, above).

Ferrão et al. (2022) further mentioned some differences in vocalizations between *Scinax albertinae* and *S. wandae* as reported by Pyburn and Fouquette (1971). However, as shown by Ferrão et al. (2022: Table 3) the spectral and temporal parameters of the vocalizations of *S. albertinae*, and *S. wandae* from San Martín, Meta, Colombia, broadly overlap, while they are both continuous with the values reported by Pyburn and Fouquette (1971), although keeping in mind that these were obtained with very different technology to the one available today. We also note that the unvouchered call associated with *S. wandae* from San Martín, Meta could correspond to specimens from the lineages *S. albertinae* or *S.* cf. *wandae*. In all, the only difference that would seem to persist between the type series of *S. wandae* and *S. albertinae* is the occurrence of a dark dorsolateral stripe in the former. Considering that the two type series are separated by ≈1600 km, this color pattern difference requires a thorough study throughout the broad distribution of this lineage before it could be considered a diagnostic character.

Scinax exiguus is known from the northern part of the Gran Sabana (drainage of the Río Caroní), Bolívar, Venezuela, and from Boa Vista, Pacaraíma, and Tepequém, Roraima, Brazil (Martins, 1998; Araujo-Vieira, 2016; Carvalho et al., 2017; Barrio-Amorós et al., 2019). We included specimens from Pacaraíma, Roraima, Brazil; Maripa (lower Caura River), Cerro Guanay, Parque Nacional Canaima, and Santa Elena de Uairén (topotypes), Bolívar; and Isla de Piñate (confluence of the Orinoco and Ventuari rivers), Amazonas, Venezuela. UPDs among these are 0.0–2.0% (Appendix S10: Table 28). These specimens indicate a much wider distribution than previously thought, extending from the Gran Sabana to the Amazonian region, and suggest the need for a reassessment of the variation in this species.

The type locality of *Scinax cruentomma* is Santa Cecilia on the Río Aguarico, Provincia Sucumbíos, Ecuador (Duellman, 1972a), and this species has been also reported in Brazil, Colombia, and Peru (Zimmerman and Rodrigues, 1990; Duellman and Wiens, 1993; Lynch, 2005; Malambo-L and Madrid-Ordóñez, 2008; França and Venâncio, 2010; Bernarde et al., 2011; Carvalho et al., 2015b). Our molecular dataset includes several sequences from Ecuador, one of which is nearly topotypic (KU 217700, from 17 NE from the type locality), and only two sequences (INPAH 34696 and 34697 from Ferrão et al., 2016) from two localities separated by 300 km in Amazonas, Brazil, and ca. 900 km SE from the closest represented localities in Ecuador. As such, our sampling is poor in terms of the wide distribution of this species.

Our analysis recovered all specimens of *Scinax cruentomma* from Ecuador as a single lineage, which is poorly supported as the sister of a moderately supported (81% jackknife) clade including *Scinax* spp. 20–22 (Fig. 33). The lineage including the two specimens from Brazil (INPAH 34596 and 34697), identified by Ferrão et al. (2016) as *S. cruentomma*, here called *Scinax* sp. 17, has unresolved relationships (Fig. 33), being recovered alternatively as the sister taxon of *Scinax* sp. 19, or the clade including *S. albertinae* and *S. exiguus*. The two terminals of *Scinax* sp. 17 are represented only by sequences for 16S produced by Ferrão et al. (2016: Table S1), which differ in UPDs of 3.3–4.2% from *S. cruentomma* KU 217700 (Appendix S10: Table 28). We are not aware of characters differentiating this lineage from *S. cruentomma*; considering its phylogenetic position and the UPDs, we consider it a CCS. Carvalho et al. (2015b) reported calls of *S. cruentomma* from 800 km N from the closest locality where *Scinax* sp. 17 was collected. Those calls showed some minor differences with topotypic *S. cruentomma*. *Scinax* sp. 17 and the populations identified as *S. cruentomma* throughout its distribution require a thorough taxonomic study.

Scinax sp. 19 is a lineage with individuals from the Brazilian localities of Carajás, Pará, and nearby localities in Amazonas and Porto Velho, Rondônia (*Scinax* sp. 6 of Ferrão et al., 2016). Its relationships are unresolved in the strict consensus (Fig. 33), as it is recovered alternatively, as the sister taxon of *Scinax* sp. 17 or the clade including *Scinax* spp. 20–22, and *S. cruentomma*. UPDs between this

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candidate species and *S. cruentomma* are 3.2–4.4% (Appendix S10: Table 28). Furthermore, Ferrão et al. (2016) observed that *Scinax* sp. 19 differs from *S. cruentomma* by supernumerary tubercles on finger II, outer metatarsal tubercle shape, shape of *canthus rostralis*, and relative size of finger discs. For this reason, we consider it a CCS.

The three candidate species, *Scinax* spp. 20–22, are from the Guianas, and adjacent Amapá, Brazil. Considering the limited or total lack of information about them, they are considered as UCSs. *Scinax* sp. 20 is represented by three specimens from Iwokrama (Guyana), Sipalwini (Suriname), and Maripasoula (French Guiana), and *Scinax* sp. 21 by two specimens from Serra do Navio, Amapá, Brazil. We have no information regarding the morphology of the voucher specimens of these two lineages. *Scinax* sp. 22 (*Scinax* sp. 1 from Lescure and Marty, 2000:176; see also Fouquet et al., 2007a) is represented by specimens from Camopi, Roura, and Saint Élie (French Guiana) and seems to differ from the other species of the group at least by the black barred pattern on a bluish background in the hidden surfaces of the thighs. The scarce available data (Lescure and Marty, 2000:364) suggest that the advertisement call is much shorter than in *S. exiguus* and *S. wandae* (Duellman, 1972a, 1986; Pyburn and Fouquette, 1971). *Scinax* sp. 22 is also likely to be present in adjacent Brazil (Amapá), as the locality in Camapi (Montagne de Cacao) is only 10 km from the frontier between both countries. UPDs between *Scinax* spp. 20–22 are 3.3–4.4%, and UPDs between these and *S. cruentomma* are 2.6–5.2% (Appendix S10: Table 28).

Specimens identified as *Scinax cruentomma* have also been reported from French Guiana (Lescure and Marty, 2000; Salducci et al., 2002, 2005; Fouquet et al., 2007a,b). In our analyses, tissue samples identified as *S. cruentomma* from French Guiana (Salducci et al., 2005; Fouquet et al., 2007a,b), including the sequence used by Duellman et al. (2016) produced by Fouquet et al. (2007a), are recovered as a distinct lineage, *Scinax* sp. 30, only distantly related to the *S. cruentomma* group, and closely related to *S. danae* (Fig. 36).

Our study of specimens of the type series of *Scinax baumgardneri* (Rivero, 1961), *S. blairi* (Fouquette and Pyburn, 1972), *S. karenanneae* (Pyburn, 1993), and *S. lindsayi* Pyburn, 1992 indicate that they should be included tentatively in this group based on the character combinations mentioned in the diagnosis. *Scinax baumgardneri* has a subgular, enlarged vocal sac that reaches the level of the pectoral fold. Barrio-Amorós et al. (2019) stated that *S. lindsayi* could be a junior synonym of *S. baumgardneri*. Our comparison of paratypes of both indicates that they are distinct species, as the vocal sac of *S. lindsayi* is weakly bilobate, as described by Pyburn (1992), as is also in *S. karenanneae* (Pyburn, 1993). Our study of paratypes of these latter two species corroborates these observations, and they would be the only two species of *Scinax* having a vocal sac that combines reaching the pectoral fold and being weakly bilobate; as more specimens become available, a study of its anatomy would be quite relevant for our understanding of vocal sac structure and evolution in *Scinax*. Considering that *S. baumgardneri*, *S. blairi*, *S. kare-*

nanneae, and *S. lindsayi* are poorly known and have not been diagnosed in the context of the newly recognized *S. cruentomma* group, any attempt to study the CCSs and UCSs recognized here for this group necessarily needs to consider them.

Other relevant literature. León (1969: vocalizations of *Scinax altae* and *S. staufferi*; tadpole of *S. staufferi*); Duellman (1970a: vocalizations and tadpole of *S. staufferi*); Pyburn and Fouquette (1971: vocalization of *S. wandae*); Duellman (1972a: tadpole and vocalization of *S. cruentomma*); Fouquette and Pyburn (1972: vocalization of *S. blairi*); Duellman (1978: natural history of *S. cruentomma*); Duellman and Pyles (1983: vocalizations of *S. cruentomma*); Duellman (1986: vocalization of *S. exiguus*); Anderson (1991: karyotypes of *S. staufferi*); Pyburn (1992: vocalization of *S. lindsayi*); Cardozo et al. (2011: comment on the interpretation of Anderson, 1991); Pombal et al. (2011: vocalization assigned to *S. wandae*, unclear if it corresponds to one of the lineages identified here); Carvalho et al. (2017: vocalization of *S. exiguus*); Ferrão et al. (2018a: vocalization of *S. strussmannae*); Schiesari et al. (2022: tadpole of *S. cruentomma*).

The *Scinax eurydice* group

Sister taxon. The *Scinax granulatus* group.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data. No phenotypic synapomorphies are known. The species included in this group can be differentiated from other species of *Scinax* by rounded snout in dorsal view (sub-elliptical with a pointed tip in the *S. auratus* group; elongate pointed in most species of the *S. rostratus* group, elongate acuminated in the *S. squalirostris* group); single or weakly bilobate vocal sac that does not reach the pectoral region (single or weakly bilobate enlarged vocal sac that reaches the level of the pectoral fold or region in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); lack of spicules in nuptial pad, inner margin of arm, and pectoral region in males (present in the *S. fuscovarius* group); lack of pectoral glands in males (present in the *S. fuscovarius* and *S. nasicus* groups, and in some species of the *S. funereus* group); dorsal pattern with large irregular blotches, sometimes with X-shaped mark composed of one or two pairs of inverted parentheses-like blotches (two irregular longitudinal stripes arising from an interocular marking in some species of the *S. granulatus* group; silvery white dorsolateral stripes in the *S. squalirostris* group; a dark lateral stripe in the *S. boesemani* group and in *S. pachycrus*); the absence of physiological chlorosis (present in the *S. boesemani* and *S. elaeochroa* groups, and in some species of the *S. auratus*, *S. cruentomma*, and *S. funereus* groups); tadpoles with P-3 inside the oral disc (in the margin of the labium or supported by a labial arm in the *S. rostratus* group and some species of the *S. auratus* group); and advertisement call composed of 2–3 notes (a single note or 10–18 notes/call in all other groups of *Scinax*).

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Characterization. (1) SVL males 35.2–52.3 mm, SVL females 33.2–48.6 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single or weakly bilobate, does not reach the level of the pectoral fold; (5) snout rounded in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin shagreen, rugose, or with scattered tubercles; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the base of the disc (Ch. 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze, with a dark median horizontal streak; (15) dorsal pattern with large irregular blotches, sometimes with X-shaped marks composed of one or two pairs of inverted parentheses-like blotches, with or without light splotches; (16) hidden surfaces of thighs with irregular light blotches; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole visible ventrally (Ch. 146.1); (19) oral disc subterminal (Ch. 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with 2–3 notes/call, note duration 17–32.3 ms (first note) and 20–38 ms (second note), and 4–6 (first note) and 5–7 (second note) pulses/note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent (Ch. 91.0); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 metacentric (Ch. 72.0); and (34) NOR in chromosome pair 11, proximal or distal (Ch. 153.12 or 153.13).

Contents. Three recognized species: *Scinax castroviejoi* De la Riva, 1993; *Scinax eurydice* (Bokermann, 1968); *Scinax sateremawe* Sturaro and Peloso, 2014. Four UCSs, *Scinax* spp. 12, 14, 23–24.

Distribution. The Andes in central Bolivia, 1,100–1,900 m a.s.l., in Santa Cruz and Cochabamba; western Amazon basin in Brazil (Amazonas), and northeastern and southeastern Brazil, from Paraíba to São Paulo (De la Riva, 1993; Köhler, 2000; Sturaro and Peloso, 2014; Menezes et al., 2016).

Comments. In this species group *Scinax sateremawe* + *Scinax castroviejoi* are recovered as the sister taxon (100% jackknife) of the remaining species, where *Scinax* sp. 24 is the sister taxon of *S. eurydice* and related lineages

(Fig. 34). *Scinax castroviejoi*, *S. eurydice*, and related UCSs share a similar advertisement call that includes 2–3 notes/call, as already noticed by Novaes and Zina (2016; two notes in *S. castroviejoi* and *S. eurydice*, three notes in *Scinax* sp. 23; De la Riva, 1993; De la Riva et al., 1994; Pombal et al., 1995b; Köhler, 2000; Magrini et al., 2011; Mângia et al., 2017). Calls remain unknown for *S. sateremawe*.

The type locality of *Scinax eurydice* is Fazenda Santo Onofre, 10 km east of Maracás, Bahia, Brazil (Bokermann, 1968), and the species is distributed from Paraíba to São Paulo, Brazil (Menezes et al., 2016). Recently, Menezes et al. (2016), based on a species tree and population assignment methods using mitochondrial (ND2) and nuclear (RAG1, β-fibint7, and 28S) genes, suggested that *S. eurydice* is a complex of species. Their results supported the existence of two major clades corresponding to northern and southern populations, each one composed of two clades. Our analyses did not include tissue samples from their northernmost clade composed of populations from Alagoas, Pernambuco, and Paraíba, Brazil. However, our results, at least in terms of molecular divergence, corroborate their suggestion for the existence of one northern lineage composed mostly of populations from central-eastern Bahia (including topotypic specimens; Bokermann, 1968) and the two southern lineages (Fig. 34). Our results also suggested the presence of two additional lineages represented by specimens from southern Bahia and from northern Rio de Janeiro, respectively. UPDs between these five lineages are 2.2–5.5% (Appendix S10: Table 29). Based on these distances and our topology, we associate the northern lineage that we recovered with *S. eurydice*, and consider the other four as UCSs.

The relationships between *Scinax eurydice* and all related UCCs are well supported (Fig. 34). *Scinax* sp. 24 is the sister taxon of *S. eurydice* and all other UCSs. It is represented by one specimen from Santa Cruz Cabrália, southern Bahia, Brazil. *Scinax* sp. 12 is represented by specimens from Santa Maria Madalena, in NE Rio de Janeiro, Brazil. The lineage that we associate with *S. eurydice* includes specimens from its type locality and from other localities in central-eastern Bahia, Brazil, and corresponds with the NE2 clade of Menezes et al. (2016). *Scinax* sp. 14 includes specimens from Juiz de Fora, E Minas Gerais and Petrópolis, Rio de Janeiro, possibly corresponding with the SE1 clade of Menezes et al. (2016). *Scinax* sp. 23 is represented by specimens from several localities from NE São Paulo, Minas Gerais, Espírito Santo, and SE Bahia, and corresponds with the SE2 clade of Menezes et al. (2016). It should be noted that this lineage is sympatric with *S.* sp. 14 and possibly with *S. eurydice*. We included a single sample of *Scinax* sp. 23 from Bahia, produced by Vacher et al. (2020).

Although Menezes et al. (2016) referred to phenotypic evidence (body size and shape, color patterns, and calls) allowing to differentiate the lineages associated with *Scinax eurydice*, these remain unpublished. The only differences among lineages that we are aware of involve the advertisement calls and cytogenetics. There are two notes in the calls described from Paraíba (Mângia et al.,

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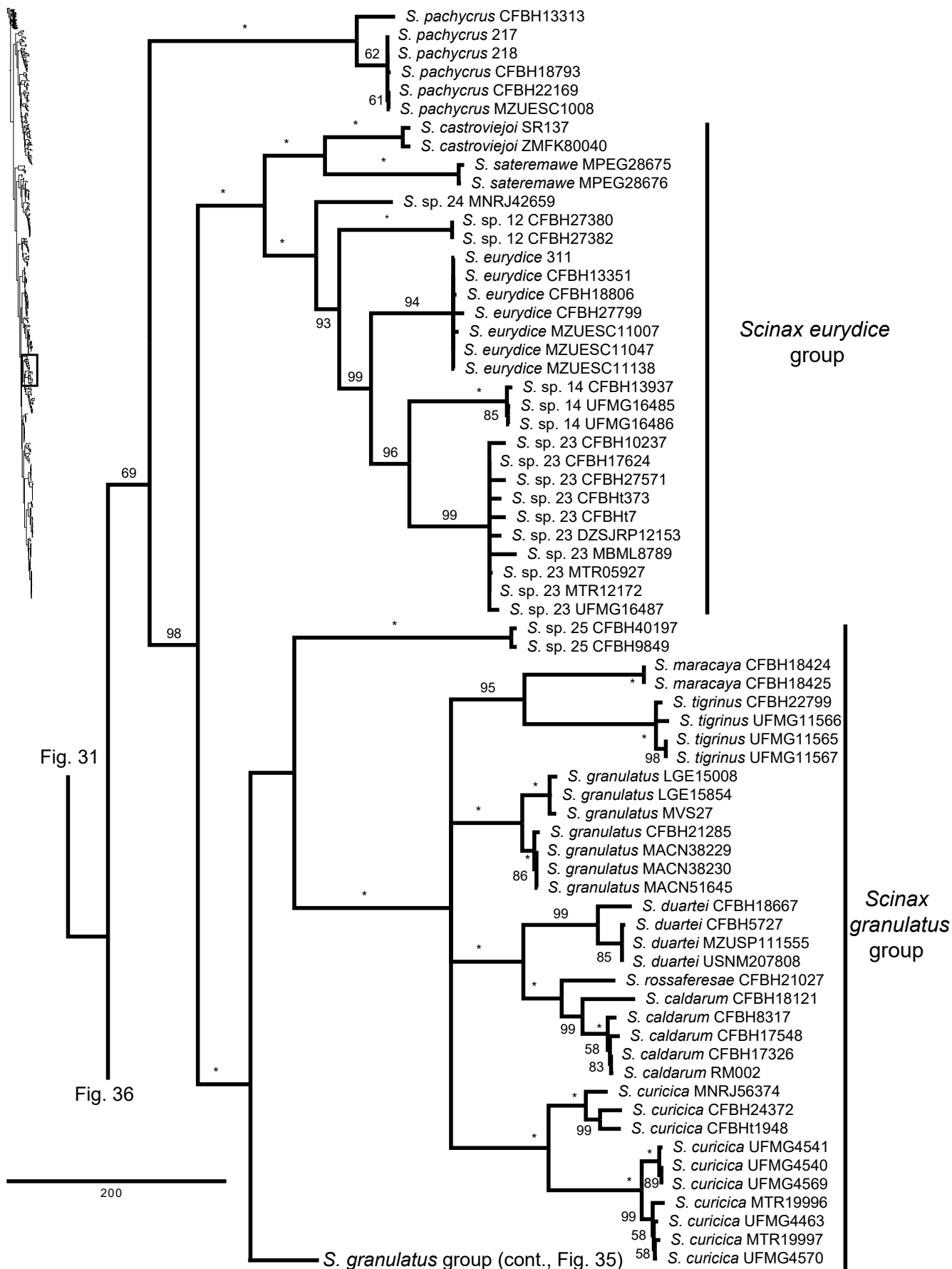
Figure 34. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 15 of 21: *Scinax pachycrus*, the *S. euridyce* group, and the *S. granulatus* group, part 1 of 2. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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2017; NE1 clade of Menezes et al., 2016) and Bahia (*S. eurydice*; Novaes and Zina, 2016), and three notes in calls from Espírito Santo (Pombal et al., 1995b) and São Paulo (Magrini et al., 2011); the latter corresponds to the UCS *Scinax* sp. 23. Cardozo et al. (2011) reported NORs in terminal position in chromosome pair 13 on male specimens that correspond to UCS *Scinax* sp. 23, noticing that one female had the NOR in proximal position. Nogueira et al. (2015a) reported the NOR in proximal (interstitial) position in the same chromosome in specimens corresponding to *S. eurydice*. Nogueira et al. (2015a) further noticed differences in the distribution of C-bands, being these centromeric in what we call *Scinax* sp. 23 and mostly telomeric in *S. eurydice*. The taxonomic distribution of these cytogenetic characters requires additional studies in the *S. eurydice* group.

We included sequences of a specimen that we identified as *Scinax castroviejoi* based on the description of adult morphology and advertisement call by De la Riva (1993) and De la Riva et al. (1994). This specimen (ZFMK 80040) was collected on the road to San Onofre, Chapare, Cochabamba, Bolivia, 245 km NW (airline) from the type locality of *S. castroviejoi* (Laguna de Bermejo, 1,130 m, Provincia Florida, Departamento Santa Cruz, Bolivia). Köhler (2000) reported calls of specimens collected with the sequenced specimen, and they have the same structure as that described for *S. castroviejoi*, with two short notes/call. These specimens have a weakly bilobate vocal sac and they lack pectoral glands, as mentioned for the type series by De la Riva (1993). Furthermore, they lack spicules in the nuptial pad, inner margin of arm, and pectoral region. All these characters differentiate this species from the widespread *S. fuscovarius*, with which it is syntopic[18]. The type series of *S. castroviejoi* included specimens from the type locality (holotype and seven paratypes), and other three paratypes from Argentina (Arroyo Los Naranjos, 9.3 km SSW Perico del Carmen, 1,230 m, Jujuy). De la Riva et al. (2000) advanced the possibility that the latter could correspond to *S. fuscovarius*. Our study of photographs of the paratypes[19] from the type locality (MNK 509–510) and those from Argentina (KU 160423–160425) indicate that the latter belongs to *S. fuscovarius*, as evidenced by the presence of pectoral glands and the occurrence of spicules in the nuptial pad, inner margin of arm, and pectoral region in the two male paratypes (KU 160423–160424). De la Riva et al. (2000) reported *S. castroviejoi* from the area near Apolo, Departamento La Paz, Bolivia, but this record needs corroboration.

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18   We included in our analyses a specimen of *Scinax fuscovarius* (ZFMK 60430; identified as *S. castroviejoi* by Köhler, 2000) from the type locality of *S. castroviejoi*, Laguna de Bermejo, Provincia Florida, Departamento Santa Cruz, Bolivia (De la Riva, 1993).

19   We also studied photographs of the type series from Bolivia formerly housed in the Centro de Estudios Tropicales (CET) that were transferred to the collection of Estación Biológica de Doñana (EBD; both in Sevilla, Spain). Unfortunately, before the transfer (Urdiales, personal comm.), the holotype and four paratypes (formerly CET A600–605, currently EBD 37255–60) suffered significant dehydration that limits the information that can be gathered from these specimens. It is evident, however, that they lack pectoral glands.

Scinax sateremawe is known from Maués, Amazonas, Brazil (Sturaro and Peloso, 2014). This species and *S. castroviejoi* share the weakly bilobate vocal sac, which is peculiar, showing one discrete lobe on each side, somewhat similar to the vocal sac of *Julianus camposseabrai*. Unfortunately, no material of these two species was available for dissection and study of the submandibular musculature.

The monophyly of *Scinax pachycrus* and the clade including the *S. eurydice* + *S. granulatus* groups is poorly supported (69% jackknife) by molecular data and by the NOR placed in distal position in chromosome pair 11 (Ch. 153.13; homoplastic in *S. acuminatus*, and several outgroups such as *Aplastodiscus perviridis*, *Trachycephalus typhonius*, *Triprion petasatus*, and *Smilisca baudinii*; Cole, 1974; Cardozo et al., 2011; Gruber et al., 2012; Nogueira et al., 2015b, 2016; Suárez et al., 2020), a character still known for very few species in this clade.

The monophyly of the *Scinax eurydice* and *S. granulatus* groups (Fig. 34) is well supported (98% jackknife) and delimited by molecular data and one phenotypic synapomorphy: tendon of insertion of lateral m. lumbricalis brevis digiti IV adhered to the fascia of m. flexor brevis profundus digiti IV (Ch. 84.0, with instances of homoplasy in *Julianus camposseabrai*, *J. uruguayus*, few species of *Scinax*, such as *S. nasicus* and *S. quinquefasciatus*, and at least *Tepuihyla rodriguezi*; this character-state optimizes as present in most species of *Ololygon*).

Other relevant literature. De la Riva (1993: vocalization of *Scinax castroviejoi*); De la Riva et al. (1994: vocalization of *S. castroviejoi*); Pombal et al. (1995b: vocalization of *S.* sp. 23, as *S. eurydice*); Köhler (2000: account and vocalization of *S. castroviejoi*); Wogel et al. (2000: tadpole that we tentatively associate with *S.* sp. 14); Hartmann et al. (2005: visual signaling in *S.* sp. 23, as *S. eurydice*); Cardozo et al. (2011: karyotype of *S.* sp. 23, as *S. eurydice*); Magrini et al. (2011: vocalization of *S.* sp. 23, as *S. eurydice*); Nogueira et al. (2015b: karyotype of *S. eurydice*); Novaes and Zina (2016: vocalization of *S. eurydice*); Mângia et al. (2017: vocalization of *S. eurydice*; it is unclear to which of the lineages identified here, if any, it belongs); Dubeux et al. (2020: tadpole of *S. eurydice*; it is unclear to which of the lineages identified here, if any, it belongs).

The *Scinax granulatus* group

Sister taxon. The *Scinax eurydice* group.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data. No phenotypic synapomorphies are known. The species included in this group can be differentiated from other species of *Scinax* by the combination of rounded snout in dorsal view (elongate pointed in most species of the *S. rostratus* group, elongate acuminated in the *S. squalirostris* group, and sub-elliptical with a pointed tip in the *S. auratus* group); single or weakly bilobate vocal sac that does not reach the level of the pectoral fold (enlarged, reaching the level of the pectoral fold

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or region in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); lack of spicules in nuptial pad, inner margin of arm, and pectoral region in males (present in the *S. fuscovarius* group); lack of pectoral glands in males (present in the *S. fuscovarius* and *S. nasicus* groups, and in some species of the *S. funereus* group); dorsal pattern uniform, or with large irregular blotches, sometimes with X-shaped mark composed of one or two pairs of inverted parentheses-like blotches, or with two irregular longitudinal stripes arising from an interocular marking (dorsolateral stripes never arising from an interocular marking in the *S. auratus*, *S. fuscomarginatus*, and *S. squalirostris* groups, and some species of the *S. cruentomma* group; a dark lateral stripe in *S. pachycrus* and *S. boesemani*); lack of physiological chlorosis (present in the *S. boesemani* and *S. elaeochroa* groups, and in some species of the *S. auratus*, *S. cruentomma*, and *S. funereus* groups); tadpoles with P-3 inside the oral disc (in the margin of the labium or supported by a labial arm in the *S. rostratus* group and some species of the *S. auratus* group); and advertisement call with a single note (two or three notes in the *S. eurydice* group).

Characterization. (1) SVL in males 22.5–43.0 mm, females 24.2–51.0 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single or weakly bilobate that does not reach the level of the pectoral fold; (5) snout rounded or acuminate; (6) tubercles in the lower lip absent; (7) dorsal skin smooth, shagreen, with scattered tubercles, or densely covered with tubercles; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the subarticular tubercle, midlength of the penultimate phalanx, or base of the disc (Ch. 59.1, 59.2, or 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in the nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands absent in males (Ch. 47.0 or 47.1); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze, with a dark median horizontal streak; (15) dorsal pattern uniform, with irregular dark blotches, or with two irregular longitudinal stripes arising from an interocular marking; (16) hidden surfaces of thighs with light reticulate pattern, large spots or irregular blotches; (17) physiological chlorosis absent (Ch. 158.1); (18) eyes of the tadpole visible or not visible ventrally (Ch. 146.0 or 146.1); (19) oral disc subterminal or ventral (Ch. 143.0 or 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae in the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent (Ch. 150.0); (27) oviposition in ponds or streams (Ch. 155.0); (28) advertisement call with 1 note/call, note duration 80–4,500 ms, and 4–43 pulses/note; (29) anteri-

or process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent or present (Ch. 91.0 or 91.1); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 metacentric (Ch. 152.1); and (34) NOR in chromosome pair 11, distal (Ch. 153.13).

Contents. Sixteen recognized species: *Scinax cabralensis* Drummond et al., 2007; *Scinax caldarum* (Lutz, 1968b); *Scinax curicica* Pugliese et al., 2004; *Scinax dolloi* (Werner, 1903); *Scinax duartei* (Lutz, 1951); *Scinax granulatus* (Peters, 1871); *Scinax haddadorum* Araujo-Vieira et al., 2016; *Scinax hayii* (Barbour, 1909); *Scinax maracaya* (Cardoso and Sazima, 1980); *Scinax montivagus* Juncá et al., 2015; *Scinax perereca* Pombal et al., 1995a; *Scinax rogerioi* Pugliese et al., 2009; *Scinax rossaferesae* Conte et al., 2016; *Scinax rupestris* Araujo-Vieira et al., 2015b; *Scinax tigrinus* Nunes et al., 2010; *Scinax tropicalia* Novaes-e-Fagundes et al., 2021. One CCS, *Scinax* sp. 25; two UCSs, *Scinax* spp. 28–29.

Distribution. Northeastern, southeastern, and central Brazil, from Ceará to Rio Grande do Sul; Uruguay; and eastern Argentina, from Misiones to Buenos Aires (e.g., Bokermann, 1967d; Heyer et al., 1990; Achaval and Olmos, 2003; Eterovick and Sazima, 2004; Nunes et al., 2010; Agostini and Roesler, 2011; Magrini et al., 2011; Vega et al., 2011; Juncá et al., 2015; Araujo-Vieira et al., 2016; Conte et al., 2016; Novaes-e-Fagundes et al., 2021).

Comments. Few species of this newly recognized species group were included in previous phylogenetic analyses (*Scinax granulatus*, *S. hayii*, *S. maracaya*, and *S. perereca* in the analysis of Faivovich, 2002; *S. duartei* and *S. hayii* in the analyses of Wiens et al., 2010 and Duellman et al., 2016; *S. granulatus*, *S. perereca*, and *Scinax* sp. 25 in the analysis of Malleret et al., 2022), and only Malleret et al. (2022) recovered them as monophyletic. Our results (Figs. 34, 35) recovered this group with two major clades that are well supported (100% jackknife), and one clade (*S. cabralensis* + *S. rogerioi*) and two species (*S. rupestris* and *Scinax* sp. 25) whose relationships with these major clades are poorly supported (< 50% jackknife).

Scinax sp. 25 is the sister taxon of well-supported clade (100% jackknife) with a polytomy that includes *S. granulatus*, *S. curicica*, and two well-supported clades (Fig. 34). One of these (100% jackknife) includes *S. duartei* as the sister taxon of *S. rossaferesae* and *S. caldarum*. And the other clade (98% jackknife) includes *S. maracaya* + *S. tigrinus*. There are some character-states that optimize ambiguously in our most parsimonious trees because they are still unknown in *S. curicica*, *S. rossaferesae*, *Scinax* sp. 25, and *S. tigrinus*, and could be putative synapomorphies of *Scinax* sp. 25 and its sister taxon, or a less inclusive clade. These are the fontanelle partially exposed (Ch. 2.1; fontanelle partially exposed through a

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keyhole-shaped fenestra in *S. maracaya*, Ch. 2.2), the pars externa plectri mediodistally expanded (Ch. 19.1), and the presence of three internal buttresses of the arytenoids (Ch. 40.1; with a reversal to one single internal buttress in *S. maracaya*, Ch. 40.0).

Scinax rupestris and *S. cabralensis* + *S. rogerioi* (100% jackknife) are poorly supported, successive sister taxa of a well-supported clade (100% jackknife) structured as a pectinate series with *S. haddadorum*, *S. tropicalia*, and *S. montivagus* + *Scinax* sp. 28, as successive sister taxa of a clade of larger species (*S. dolloi*, *S. hayii*, *S. perereca*, and one UCS, *Scinax* sp. 29; Fig. 35). The internal relationships are generally well supported (≥ 90% jackknife); an exception is the moderately supported (70% jackknife) position of *S. montivagus* + *Scinax* sp. 28 as the sister taxon of the clade including *S. dolloi*, *S. hayii*, *S. perereca*, and *Scinax* sp. 29.

The clade including the larger species is well supported (99% jackknife; Fig. 35) and has two phenotypic synapomorphies: (1) presence of the slip from element Y of the m. extensor brevis medius III (Ch. 100.1, also present in *Julianus uruguayus*, most species of *Ololygon*, and some other species of *Scinax*) and (2) presence of ulnare slip of m. extensor brevis superficialis digiti IV inserting on tendon of m. extensor brevis medius digiti IV (Ch. 105.1).

Pugliese et al. (2009) recognized four species for what they called the *Scinax duartei* complex (*S. caldarum*, *S. curicica*, *S. duartei*, and *S. rogerioi*) based on overall similarities in the dorsal color pattern. Our results showed that this complex is not monophyletic, since *S. maracaya*, *S. rossaferesae*, and *S. tigrinus* are nested among the first three species, and *S. granulatus* is more closely related to all of these than *S. rogerioi* (Figs. 34–35). Malleret et al. (2022) considered that some populations that had been associated with *S. granulatus* (Wachlevski and Rocha, 2010) from coastal areas in SW Santa Catarina and NE Rio Grande do Sul, Brazil, were a different species, based on poorly detailed phenotypic differences (only a supralabial stripe is mentioned). They tested this hypothesis using a dataset of cytochrome b and RAG1 sequences of several populations of the putative new species and *S. granulatus*, using different species delimitation methods. These corroborated the distinctiveness of populations of the new species from *S. granulatus*, and Malleret et al. (2022) considered them as candidate species, *Scinax* sp. D, both parts of what they called the *S. granulatus* complex. These two species were recovered as monophyletic in a reduced phylogenetic study also including *S. fuscovarius*, *S. nasicus*, *S. perereca*, and *S. ruber*, rooted with *Ololygon catharinae*.

Our study included two samples of the candidate species detected by Malleret et al. (2022), here labeled *Scinax* sp. 25. Our results indicate that it is the sister taxon of *S. granulatus* plus a clade including several other species, thus rejecting the monophyly of what Malleret et al. (2022) considered the *S. granulatus* species complex (Fig. 34). On the basis of its phylogenetic relationships, we consider it a CCS. UPDs between this species and all other species of the *S. granulatus* group are 6.2–10% (Appendix S10: Table 30).

The type locality of *Scinax granulatus* is in Porto Alegre, Rio Grande do Sul, Brazil (Peters, 1871), and the species is widely distributed from northeastern Argentina south to Buenos Aires and north to Uruguay and Rio Grande do Sul, Santa Catarina, and Paraná in Brazil (Kwet, 2001; Achaval and Olmos, 2003; Moresco et al., 2009; Vega et al., 2011; Weiler et al., 2013). Our analyses included specimens from disjunct localities in Tijucas do Sul (Paraná, Brazil), and Misiones, Entre Ríos, and Buenos Aires (Argentina). We recovered two sister lineages (Fig. 34) with UPDs of 2.3–2.5%; one lineage includes the specimens from Paraná (Brazil) and Misiones (Argentina), and the other lineage those from Entre Ríos and Buenos Aires (Argentina) and Rio Grande do Sul (Brazil; Appendix S10: Table 30). Malleret et al. (2022) identified these same two lineages and a third one, including populations from SE Rio Grande do Sul and NE Uruguay. Unfortunately, their study appeared too late in the process of writing the present manuscript and their sequences could not be included in our analyses. Our observations of specimens found no phenotypic characters that could distinguish the two lineages of *S. granulatus* that we identified (see also Kwet, 2001). Nevertheless, if shown to be different, the name *Hyla eringiophila* Gallardo, 1961a (type locality: Bella Vista, Buenos Aires, Argentina) is available for the lineage including the populations from Buenos Aires.

Scinax duartei was described by Lutz (1951) from Itatiaia, Rio de Janeiro, Brazil (type locality), and further studied by Bokermann (1967d) who reported on specimens from Serra da Bocaina and Campos do Jordão, São Paulo, and Serra do Cipó, Minas Gerais, Brazil. Bokermann (1967d) commented about geographic variation in the SVL for these different populations of *S. duartei* and the need for a revision. A year later, Lutz (1968b) described *S. caldarum* as a subspecies of *S. duartei* from Poço de Caldas, Minas Gerais, Brazil. Subsequently, Fouquette and Delahoussaye (1977) considered it a valid species, and Andrade and Cardoso (1991) further described its vocalization and larva. Unaware of the latter contribution, Duellman and Wiens (1992) considered *S. caldarum* to be a junior synonym of *S. duartei*. Pombal et al. (1995b) considered it to be a valid species and placed it in the former *S. ruber* group. Faivovich et al. (2005) considered it to be unassigned to any species group. *Scinax caldarum* differs from *S. duartei* in SVL (Bokermann, 1967d; Lutz, 1968b, 1973a) and call parameters (call duration and call and pulse rates; Magrini and Giaretta, 2010; Magrini et al., 2011).

Subsequent studies recognized differences among the populations previously referred to *Scinax duartei*. Two different species previously associated with this name were described: *S. curicica* (Serra do Cipó, Minas Gerais, Brazil; Pugliese et al., 2004) and *S. rogerioi* (Chapada dos Veadeiros, Goiás, Brazil; Pugliese et al., 2009). Our results showed that *S. curicica* includes two well-supported clades (Fig. 34). One of these includes the populations from central Minas Gerais, including a topotypic specimen. The other clade includes populations from the northern Espinhaço Mountain Range, southwestern Bahia (Mucugê,

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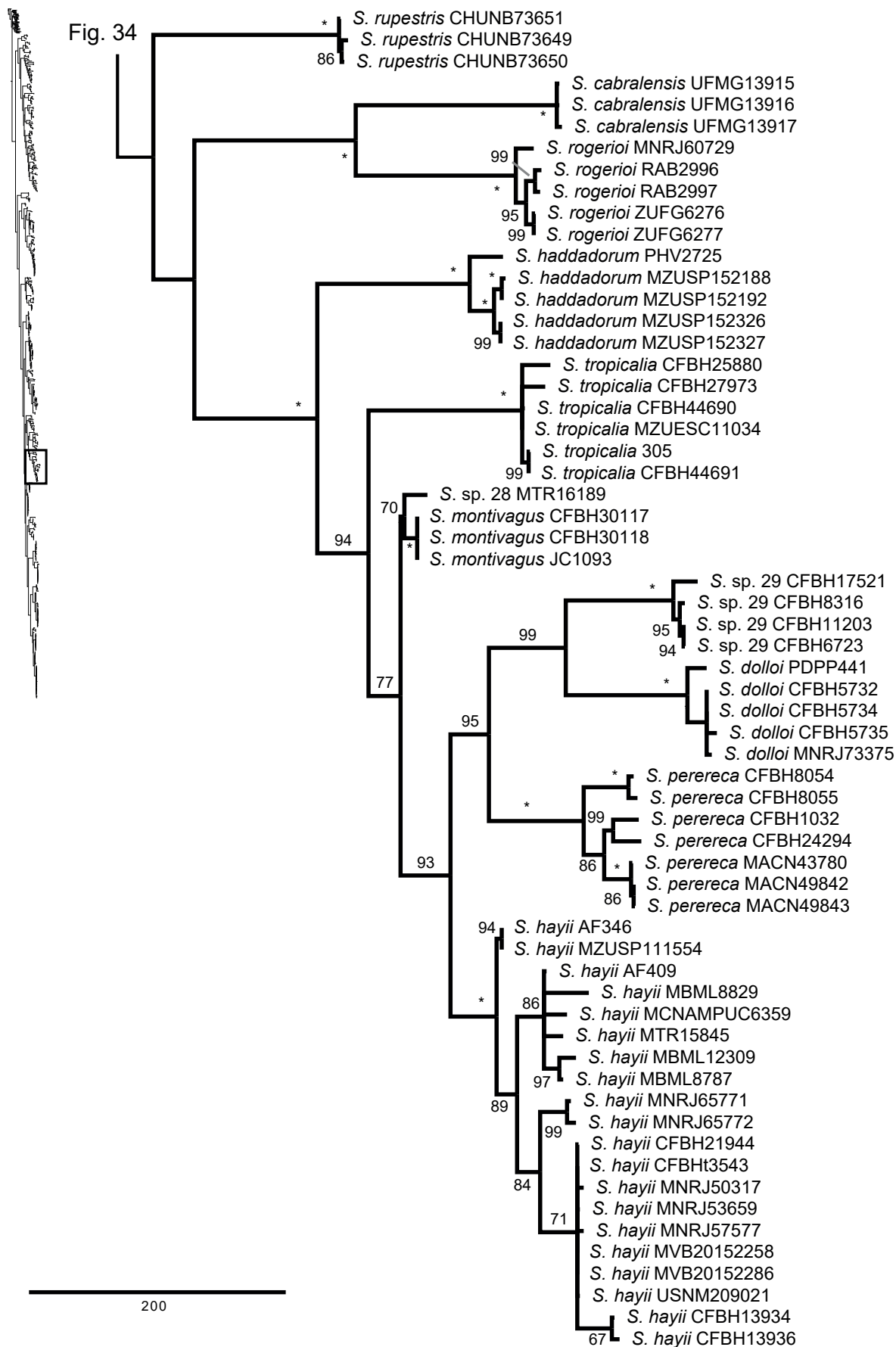
Figure 35. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 16 of 21: The *Scinax granulatus* group, part 2 of 2. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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Piatã, and Rio de Contas, in the Chapada Diamantina region). These populations are distant ≈260 km NNE from the closest locality in Serranópolis de Minas, also at the Espinhaço where *S. curicica* has been reported in Minas Gerais (Leite et al., 2008). The UPDs between these two clades are 2.5–3.2% (Appendix S10: Table 30). So far, no differences in morphology or advertisement call could be found between these two clades (FSFL and VGDO, personal obs.), and for these reasons, we tentatively consider that they correspond to a single species.

Bokermann (1967d) mentioned that specimens of *Scinax duartei* from Campos do Jordão (São Paulo, Brazil) are smaller (SVL of males and females 27–36 mm, *n* = 32) than those from the type locality (SVL of males and females 29–36 mm, *n* = 9). Further, Magrini et al. (2011) based on differences in call duration (200 ms at Campos do Jordão *vs.* mean of 547 ms in *S. duartei* from the type locality) pointed out that the population from Campos do Jordão could be a different species. Our single specimen from this locality (CFBH 8317) is recovered as the sister taxon of the topotypes of *S. caldarum* (Morro do Ferro, Poços de Caldas, Minas Gerais, Brazil; Fig. 34). Besides the low UPDs (0.5%) between them (Appendix S10: Table 30), the call parameters (call duration, dominant frequency, number of pulses per call, and call rate) reported by Bokermann (1967d) for specimens from Campos do Jordão are within the range of the topotypic recordings of *S. caldarum* reported by Magrini and Giaretta (2010:123). This indicates that the population of Campos do Jordão belongs to *S. caldarum*.

Specimens identified as *Scinax duartei* from Serra da Bocaina (São Paulo, Brazil) in general have two irregular dorsal dark stripes arising from an interocular marking concealed by the background color, the region between the dorsal and lateral dark stripes much lighter than the other dorsal regions, the lateral dark stripe reaching the inguinal region, and fore- and hindlimbs without transversal bars (Bokermann, 1967d; Lutz, 1968b, 1973a; Pugliese et al., 2004). However, these loose value as diagnostic characters when compared with large samples of *S. caldarum*, *S. curicica*, *S. duartei*, and *S. rogerioi*. Our study (Fig. 34) recovered the sample from Serra da Bocaina (CFBH 18121) as the sister taxon of the two included populations of *S. caldarum* (see above), differing in UPDs of 1.7–1.8% (Appendix S10: Table 30). The shorter UPDs correspond to the topotypic specimens, and the larger to that from Campos do Jordão, ≈100 km W. Based on the lack of clear diagnostic characters and the relatively low UPDs, we consider that the populations from Serra da Bocaina identified as *S. duartei* correspond to *S. caldarum*. The association of these populations with *S. caldarum* extends its known distribution ≈220 km SE from its type locality in Poços de Caldas in Minas Gerais, Brazil (Ferrante et al., 2019).

Scinax rossaferesae is known only from a few localities in open areas of the highlands in eastern Paraná, Brazil (Conte et al., 2016). In the original description, it was considered more similar to *S. granulatus*, *S. maracaya*, and *S. tigrinus* based on dorsal pattern and vocalization. Our results do not recover these monophyletic, although relatively closely related (Fig. 34). Interestingly, none of these species were ever considered minimally similar to the other most closely related species, *S. caldarum*, *S. curicica*, and *S. duartei*. UPDs between *S. rossaferesae* and its sister taxon, *S. caldarum* are 2.3–3.0% (Appendix S10: Table 30).

Nunes et al. (2010) differentiated *Scinax tigrinus* from *S. maracaya* based on color patterns and some morphological characters. Bang and Giaretta (2016) questioned some of these differences based on their study of additional samples from other localities. These authors also showed that these allopatric species have very similar advertisement calls that overlap in all parameters. Our results recover both species as sister taxa (Fig. 34; 95% jackknife), with UPDs of 5.4–5.7% (Appendix S10: Table 30).

Scinax cabralensis, *S. rogerioi*, and *S. rupestris* are small-sized species (combined SVL, males 21.9–32.6 mm, females 24.2–34.5 mm; Drummond et al., 2007; Pugliese et al., 2009; Araujo-Vieira et al., 2015b) that inhabit "Campos Rupestres" and plateaus in the Cerrado of central Brazil. *Scinax rupestris* is represented in our study by topotypes, whereas for *S. cabralensis* the samples are from Buenópolis, Serra do Cabral, Minas Gerais, Brazil, ≈25 km NW from its type locality (Joaquim Felício, Minas Gerais, Brazil; Drummond et al., 2007). Although *S. rupestris* is morphologically similar to *S. cabralensis* (Araujo-Vieira et al., 2015b), they are not monophyletic (Fig. 35). Their UPDs with the closely related species of the *S. granulatus* group are 6.6–11.4% (Appendix S10: Table 30). Our study included topotypes of *S. rogerioi* (Chapada dos Veadeiros, Goiás), and one specimen from Catas Altas, Minas Gerais, ≈820 km SE. This broad distribution was already recognized when the species was described (Pugliese et al., 2009), and the authors reported no differences in morphology or advertisement calls from these extreme points. UPDs between our samples from both localities are 0.3–0.7% (Appendix S10: Table 30).

Scinax haddadorum is another Cerrado inhabitant, superficially similar to *S. rupestris*, but differs in some morphological characters and calls (Araujo-Vieira et al., 2016; Bang et al., 2017). Notably, this species from central Brazil is well supported (100% jackknife) as the sister taxon of a clade including species with a much more eastern distribution, including areas of Cerrado and Atlantic Forest (Fig. 35).

The recently described *Scinax tropicalia*, previously misidentified in collections as *S. hayii* or *S. x-signatus*, has a very interesting distribution, being known from Bahia and Ceará, Brazil (Novaes-e-Fagundes et al., 2021). We included a paratopotype (Campus UESC, Bahia) and paratypes and referred specimens from other localities in Bahia and Ceará. Relationships among all these terminals are unresolved (Fig. 35). UPDs among the samples from Bahia are 0.2–1.4%, the same UPDs between them and the sample from Ceará (Appendix S10: Table 30). *Scinax tropicalia* differs in 3.6–7.3% from the species of its sister group (Appendix S10: Table 30).

Scinax montivagus, a species currently known to occur only in Chapada Diamantina, Bahia, was considered

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more similar to *S. cabralensis* and *S. rupestris* (Juncá et al., 2015). We included samples from Mucugê, in Chapada Diamantina, where some of the referred specimens of the original description were collected. Our results show *S. montivagus* to be only distantly related to *S. cabralensis* and *S. rupestris*, being instead the sister taxon of *Scinax* sp. 28, from Serra Bonita, Camacan, Bahia (Fig. 35), from which it differs in UPDs of 4.8% (Appendix S10: Table 30). We are not aware of phenotypic differences between them, and for that reason *Scinax* sp. 28 is considered an UCS.

The type locality of *Scinax hayii* is Petrópolis, Rio de Janeiro, Brazil (Barbour, 1909), and the species occurs from Espírito Santo to Santa Catarina, southeastern Brazil (Heyer et al., 1990; Magrini et al., 2011; Santos and Martins, 2017). We included tissue samples from different localities in Rio de Janeiro (including topotypes), Minas Gerais, Espírito Santo, and São Paulo. Tissue samples from Santa Catarina were unavailable. Our results show that individuals identified as *S. hayii* from São José do Barreiro and Campos do Jordão (both in São Paulo), and Camanducaia (Minas Gerais), belong to a distinct lineage from that including topotypes of *S. hayii* (Fig. 35). This candidate species, *Scinax* sp. 29, is recovered as the sister taxon of *S. dolloi* and differs from its closely related species (*S. dolloi*, *S. hayii*, and *S. perereca*) in UPDs of 4.6–6.6% (Appendix S10: Table 30). While *Scinax* sp. 29 differs from *S. hayii* in the pattern of hidden surfaces of thighs (large yellow blotches in *S. hayii*) and smaller male SVL, we are not aware of any diagnostic phenotypic character that distinguishes it from *S. dolloi*, and for that reason, it is considered an UCS.

Lutz (1973a) mentioned that individuals of *Scinax hayii* from Serra da Bocaina (São Paulo, Brazil) are smaller and with different color patterns on the hidden surfaces of thighs than topotypes. Calls of *S. hayii* have been recorded from the type locality (Santos and Martins, 2017; Santos et al., 2021), Bocaina de Minas (Minas Gerais, Brazil; Pederassi et al., 2022)[20], Poços de Caldas (Minas Gerais; Andrade and Cardoso, 1991), and Itapeva (Minas Gerais; Magrini et al., 2011)[21], and three localities in São Paulo, Boracéia (Heyer et al., 1990), Jundiaí (Pombal et al., 1995b), and Atibaia (Magrini et al., 2011). Most call parameters (call duration, pulses per call, pulse rate) overlapped in these recordings, but Santos and Martins (2017) noted that calls from the type locality, Boracéia, and Poços de Caldas had a narrower frequency range (1.1–3.4 kHz; Heyer et al., 1990) than calls from Atibaia, Jundiaí, and Itapeva (0.49–6.4 kHz; Pombal et al., 1995b; Magrini et al., 2011). Additional call recordings from different localities along the distribution range of *S. hayii* would allow a better evaluation of these call differences. In the same

way, the populations identified as *S. hayii* from Poços de Caldas, Minas Gerais, from where larvae and calls were described (Andrade and Cardoso, 1991), require further study to clarify if they correspond to *Scinax* sp. 29.

Pombal et al. (1995a) described *Scinax perereca* from Riberão Branco, in southeastern São Paulo, Brazil, and reported it as well from nearby localities. Subsequently, this species was reported in northeastern São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, Brazil, and in Misiones, Argentina (Faivovich and Carrizo, 1999; Machado et al., 1999; Kwet, 2001; Magrini and Giaretta, 2010). Our study included samples from nearby the type locality, and Santa Catarina, and Misiones. UPDs among them are 0.7–2.2%, with the largest UPD (2.0–2.2%) between the nearly topotypic samples and that from Campos Novos, Santa Catarina (Appendix S10: Table 30).

Pezzuti et al. (2021) described tadpoles of *Scinax* aff. *perereca* from Barão de Cocais, Catas Altas, and Ouro Branco, in Minas Gerais. Our study included sequences of *S. hayii* from nearby Santa Bárbara and Santana do Riacho. It is very likely that the specimens that were considered *S.* aff. *perereca* correspond to *S. hayii*. The identity of specimens reported as *Scinax* aff. *perereca* in Minas Gerais by Galdino et al. (2008) from Belo Horizonte and by Lacerda et al. (2009) from Araponga and Fervedouro requires corroboration, but they also likely correspond to *S. hayii*.

Hyla dolloi was treated as a "doubtful species" by Lutz (1973a) and was subsequently considered a "name not associated with any known species" by Duellman *in* Frost (1985). After studying the two syntypes (IRSNB 6481, two individuals), Faivovich et al. (2005) considered *Hyla dolloi* to be a valid species of *Scinax*. They established the combination *Scinax dolloi* (Werner, 1903) and included it in the *S. ruber* clade of Faivovich (2002). The type locality of *S. dolloi* was originally referred to as "Brasilien" by Werner (1903), then corrected to "Haut Maringa, Brésil" by Lang (1990), and recently restricted to "the Village of Maringá (about 2219'S, 4435'W; ca. 1,130 m a.s.l.; WGS84 datum), Itatiaia, in the Mantiqueira Mountain Range, Rio de Janeiro, southeastern Brazil" by Caramaschi et al. (2013). Our analyses recover the topotypes of *S. dolloi* and specimens from Funil (Rio Preto, Minas Gerais, distant ≈84 km ENE from its type locality) as a distinct lineage (Fig. 35). UPDs between this species and *S. hayii*, *S. perereca*, and *S.* sp. 29 are 4.8–6.2% (Appendix S10: Table 30). Santos et al. (2021) recently described the advertisement calls of topotypes of *S. dolloi* and compared them with those from topotypes of *S. hayii* and *S. perereca*, reporting in general overlapping parameters, but some continuous differences in pulses per note, pulse rate, and pulse duration.

Other relevant literature. Barrio (1962: vocalization of *Scinax granulatus*, as *Hyla strigilata eringiophila*); Bokermann (1967b: tadpole of *S. hayii*); Bokermann (1967d: tadpole and vocalization of *S. duartei*); Lutz (1973a: accounts of *S. caldarum*, *S. duartei*, and *S. hayii*); Cardoso and Sazima (1980: tadpole and vocalization of *S. maracaya*); Haddad et al. (1988: vocalization of *S. maracaya*); Basso (1990:

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20 Bocaina de Minas (Minas Gerais) is ≈25 km NE from the type locality of *Scinax dolloi* (Maringá, Itatiaia, Rio de Janeiro). The identity of the recorded specimens requires corroboration.

21 Itapeva (Minas Gerais) is only ≈20 km WNW from Monte Verde, Camanducaia (Minas Gerais), from where we have samples of *Scinax* sp. 029. The identity of the recorded specimens requires corroboration.

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natural history of *S. granulatus*); Heyer et al. (1990: tadpole and vocalization of *S. hayii*); Andrade and Cardoso (1991: vocalization and tadpole of *S. caldarum* and one species identified as *S. hayii* that could correspond to *Scinax* sp. 29); Pombal et al. (1995a,b: vocalization of *S. duartei*, *S. hayii*, and *S. perereca*); Echeverria (1997b: tadpole of *S. granulatus*, as *Hyla strigilata eringiophila*); Langone and Cardoso (1997: tadpole of *S. granulatus*, as *Scinax eringiophila*); Alves and Carvalho e Silva (1999: tadpole of *S. hayii*); Pugliese and Bastos (2001: tadpole of *S. perereca*); Alcalde and Rosset (2003: tadpole of *S. granulatus*); Kwet (2001: vocalization of *S. granulatus* and *S. perereca*); Alcalde (2005: tadpole of *S. granulatus*); Kwet et al. (2010: natural history of *S. granulatus* and *S. perereca*); Barros et al. (2011: visual communication in *S. maracaya*); Cardozo et al. (2011: karyotypes of *S. granulatus*, *S. perereca*, and *Scinax* sp. 29 as *S. hayii*); Araujo-Vieira et al. (2015b: tadpole and vocalizations of *S. rupestris*); Conte et al. (2016: vocalization of *S. rossaferesae*); Bang and Giaretta (2016: vocalizations of *S. maracaya* and *S. tigrinus*); Bang et al. (2017: vocalizations of *S. haddadorum* and *S. rupestris*); Ferrante et al. (2019: natural history of *S. caldarum*); Lopes et al. (2019: vocalization of *S. montivagus*); Pezzuti et al. (2021: tadpoles of *S. curicica*, *S. maracaya*, *S. rogerioi*, and *S. hayii* as *S.* aff. *perereca*); Pederassi et al. (2022: vocalizations of *S. hayii* and *S. rogerioi*).

The *Scinax danae* group

Sister taxon. The *Scinax boesemani* group.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data. No phenotypic synapomorphies are known for this group. Treefrogs in this group can be differentiated from all other species of *Scinax* by the combination of rounded snout in dorsal view (elongate pointed in most species of the *S. rostratus* group, elongate acuminated in the *S. squalirostris* group, and sub-elliptical with a pointed tip in the *S. auratus* group); weakly bilobate vocal sac, not reaching the level of the pectoral fold (mostly single, enlarged vocal sac reaching the level of the pectoral fold in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); lack of pectoral glands in males (present in the *S. fuscovarius* and *S. nasicus* groups, and in some species of the *S. funereus* group); absence of physiological chlorosis (present in the *S. boesemani* and *S. elaeochroa* group, most species of the *S. funereus* group, some species of the *S. auratus* and *S. cruentomma* groups); dorsal coloration pattern without stripes (dorsal stripes present in the *S. auratus*, *S. fuscomarginatus*, *S. squalirostris* groups, and some species of the *S. cruentomma* group; a dark lateral stripe in the *S. boesemani* group and *S. pachycrus*); hidden surfaces of thighs uniform, brown (with bars or blotches in the *S. auratus*, *S. eurydice*, *S. fuscovarius*, *S. nasicus*, and *S. rostratus* groups, and several species of the *S. granulatus* group); and tadpoles with P-3 inside the oral disc (in the margin of the labium or supported by a labial arm in the *S. rostratus* group and some species of the *S. auratus* group).

Characterization. (1) SVL males 22.6.9–27.4 mm, SVL females 25.4–29.5 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, weakly bilobate, does not reach the level of the pectoral fold; (5) snout rounded in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth or shagreen; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching midlength of the penultimate phalanx or base of the disc (Ch. 59.2 or 59.3); (10)–(11) unknown; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (48.0); (14) iris bronze, golden or bicolored silvery gray and bronze, with a median horizontal reddish streak; (14) dorsal pattern with irregular dark blotches, with or without light splotches; (16) hidden surfaces of thighs uniform, brown; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole not visible ventrally (Ch. 146.0); (19) oral disc ventral (Ch. 143.0); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent (Ch. 150.0); (27) oviposition unknown, apparently in ponds or small streams; (28) advertisement call with 1 note/call, note duration 134–331 ms, and 10–23 pulses per note; (29)–(34) unknown.

Contents. Two recognized species: *Scinax danae* (Duellman, 1986); *Scinax ruberoculatus* Ferrão et al., 2018b. One CCS, *Scinax* sp. 30.

Distribution. Amazon basin in Brazil, French Guiana, Guyana, Suriname, and Venezuela.

Comments. This species group includes *Scinax danae* as the sister taxon of a clade including *S. ruberoculatus* and *Scinax* sp. 30 (Fig. 36), a candidate species from French Guiana and Suriname (referred to as *S. cruentomma* in Salducci et al., 2005; Fouquet et al., 2007a; and Ferrão et al., 2016). The *S. danae* group is poorly supported (< 50% jackknife) as the sister taxon of the *S. boesemani* group (Fig. 36).

  Scinax danae is known for the cloud forests of Venezuela (Duellman, 1986). This species was assigned to the former *S. staufferi* group (sensu Fouquette and Delahoussaye, 1977). Morphologically it has been considered reminiscent of *S. boesemani*, from which it differs in SVL, dorsal color pattern, and call structure (Duellman, 1986), and, apparently, absence of physiological chlorosis. Duellman (1986) described the vocal sac of *S. danae* as single subgular, but the study of two paratypes (KU 167089–167090) and photographs indicates that it is weakly bilobate.

  Scinax ruberoculatus is known from Amazonas, Amapá and Mato Grosso, Brazil (Ferrão et al., 2018b;

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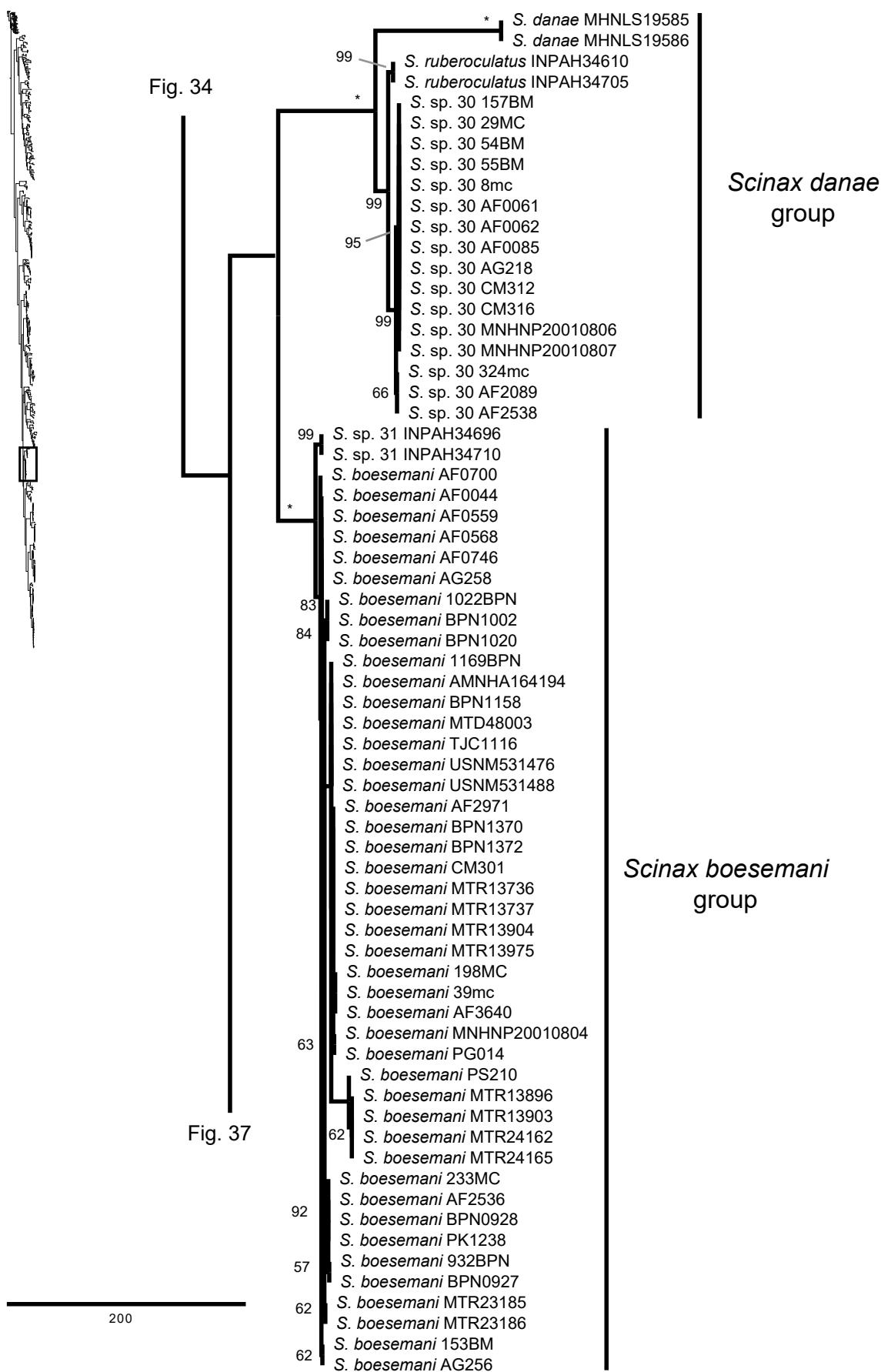
Figure 36. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 17 of 21: The *Scinax danae* and *S. boesemani* groups. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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Camera et al., 2019; Figueiredo et al., 2021). Our analysis included only samples from Amazonas. This species is characterized by the presence of a bicolored iris (reddish upper and grey lower; Ferrão et al., 2018a). The only character employed by Ferrão et al. (2018b) to differentiate *S. ruberoculatus* from *S. danae* was the smaller body size in females (SVL *S. ruberoculatus* 25.4–27.5 mm; SVL *S. danae* 27.8–29.5 mm; Duellman, 1986), which are nearly continuous. Although they did not mention it, the bicolored iris seems to differentiate both species.

Scinax sp. 30 was associated with *S. cruentomma* by Fouquet et al. (2007a) based on the description presented by Lescure and Marty (2000:172). Lescure and Marty (2000) associated this population with *S. cruentomma* mainly by having the iris with a median horizontal red streak in adults, a characteristic only known for *S. cruentomma* at that time (iris with a median horizontal red streak in *S. strussmannae*; Ferrão et al., 2018a). However, Fouquet et al. (2007a) have pointed out that this species does not seem to correspond to *S. cruentomma*, and Carvalho et al. (2015b) reported important differences with the vocalizations of that species from localities in Western Amazonia. Our results corroborated that this lineage from French Guiana and Suriname is distantly related to *S. cruentomma*. Vacher et al. (2020) identified this species as *S. ruberoculatus*, although both differ in UPDs of 4.5–5.3% (Appendix S10: Table 31). In this paper we consider *Scinax* sp. 30 a CCS because it differs from *S. ruberoculatus*, its sister taxon (Fig. 36), in that it apparently lacks a bicolored iris (Lescure and Marty, 2000; present in *S. ruberoculatus*; Ferrão et al., 2018b), and it is larger (Lescure and Marty, 2000 report a maximum size of 30 mm, without further details; SVL in males of *S. ruberoculatus* 22.6–25.9 mm, females 25.4–27.5 mm; Ferrão et al., 2018b). From *S. danae* it differs apparently in size (SVL in males 24.5–27.4 mm, females 28.8–29.5 mm; Duellman, 1986). Furthermore, reported call parameters of *Scinax* sp. 30 differ from those of the other two species (Duellman, 1986; Lescure and Marty, 2000; Ferrão et al., 2018b). Since the three species have not been considered closely related before this study, their diagnostic characters in general, should be reevaluated. One of the records of *Scinax* sp. 30 is from southern Suriname, 25 km N of the border with Brazil, so it is expected that this species will occur in this country as well.

Other relevant literature. Duellman (1986: vocalization of *S. danae*); Lescure and Marty (2000: natural history and vocalization of *Scinax* sp. 30, as *S. cruentomma*); Ferrão et al. (2018b: vocalization and tadpole of *S. ruberoculatus*); Figueiredo et al. (2021: vocalization of *S. ruberoculatus*).

The *Scinax boesemani* group

Sister taxon. The *Scinax danae* group.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data. No phenotypic synapomorphies are known for this group. Treefrogs in this group can be differentiated from all other species of *Scinax* by the combination of rounded snout in dorsal view (elongate pointed in most species of the *S. rostratus* group, elongate acuminated in the *S. squalirostris* group, and sub-elliptical with a pointed tip in the *S. auratus* group); weakly bilobate vocal sac, not reaching the level of the pectoral fold (mostly single, enlarged vocal sac reaching the level of the pectoral fold in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); lack of pectoral glands in males (present in the *S. fuscovarius* and *S. nasicus* groups, also in some species of the *S. funereus* group); lack of spicules in nuptial pads, inner margin of arms, and pectoral region in males (present in the *S. fuscovarius* group); presence of physiological chlorosis (absent in the *S. danae*, *S. eurydice*, *S. fuscomarginatus*, *S. fuscovarius*, *S. granulatus*, *S. rostratus*, and *S. squalirostris* groups, some species of the *S. auratus*, *S. cruentomma*, and *S. funereus* groups, and *S. pachycrus*); dorsal coloration pattern with a dark lateral stripe (dorsal stripes present in the *S. auratus*, *S. fuscomarginatus*, *S. squalirostris* groups, and some species of the *S. cruentomma* group); hidden surfaces of thighs uniform (with different patterns of transverse bars or blotches in the *S. auratus*, *S. elaeochroa*, *S. eurydice*, *S. fuscovarius*, *S. nasicus*, and *S. rostratus* groups, several species of the *S. granulatus* group).

Characterization. These treefrogs are characterized by (1) SVL in males 29.4–41.2 mm, females 37.2–43.8 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, weakly bilobate, does not reach the level of the pectoral fold; (5) snout rounded; (6) tubercles in the lower lip absent; (7) dorsal skin smooth or shagreen; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing between toe II reaching the base of disc (Ch. 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pads, inner margin of arms, and pectoral region in males absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze, with a median diffuse dark streak; (15) dorsal pattern with spots and splotches, a dark lateral stripe reaching up to midbody; (16) hidden surfaces of thighs uniform; (17) physiological chlorosis present (Ch. 158.1); (18)–(26) tadpole unknown; (27) oviposition in ponds and small streams (Ch. 155.0 or 155.1); (28) advertisement call with 1 note/call, note duration 130–310 ms, and pulses per note unreported; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent or present (Ch. 91.0 or 91.1); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 metacentric (Ch. 152.1); and (34) NOR in chromosome pair 8, proximal (Ch. 153.9).

Contents. *Scinax boesemani* (Goin, 1966). One UCS, *Scinax* sp. 31.

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Distribution. *Scinax boesemani* is distributed through Guyana, Suriname, French Guiana, Venezuela, and the northern Amazon basin of Brazil (Goin, 1966; Lescure and Marty, 2000; Fouquet et al., 2007b; Ouboter and Jairam, 2012; Cole et al., 2013).

Comments. Our samples of *Scinax boesemani* are recovered in two well-supported clades (Fig. 36). One includes the specimens INPAH 34696 and 34710 (Amazonas, Brazil) that Ferrão et al. (2016) referred to as *Scinax* sp. 5. These authors stated that they differ from *S. boesemani* in dorsal and ventral color pattern, although this was not evident in our study of the preserved vouchers. These samples differ in UPDs of 3.1–3.7% (Appendix S10: Table 32) from the other specimens of *S. boesemani* and for this reason we consider them as UCS. The clade that we associate with *S. boesemani* includes specimens from populations from Suriname, French Guiana, and Brazil, all of which have relatively low sequence divergence (0.0–1.9%; Appendix S10: Table 32). We do not have topotypic specimens (type locality: near Zanderij, Suriname District, Suriname; Goin, 1966), but instead, we have samples from localities in Suriname distant 100 km SW (Road to Apura; 932BPN), and 100 km SE (Nassau; AF 2536) from the type locality, and these are deeply nested within the other specimens. Although de Sá et al. (1997) described tadpoles of this species, the lack of evidence supporting the identification made us consider it undescribed, as done by Faivovich (2002). This was corroborated recently by Schiesari et al. (2022), who provided a description of new larval material, pointing out several differences from that of de Sá et al. (1997). Unfortunately, the publication of Schiesari et al. (2022) was too late to be included in our phenotypic data set, and we direct the reader to that article.

Other relevant literature. Hödl (1977: vocalization); Duellman (1986, 1997: vocalization, natural history); de Sá et al. (1997: tadpole); Lescure and Marty (2000: vocalization, natural history); Lima et al. (2006: natural history); Kok and Kalamandeen (2008: natural history); Nogueira et al. (2015b: cytogenetics); Sanches et al. (2019: natural history); Schiesari et al. (2022: tadpole).

The *Scinax funereus* group

Sister taxon. The *Scinax fuscovarius* + *S. nasicus* groups.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data. No phenotypic synapomorphies are known for this group. Treefrogs in this group can be differentiated from all other species of *Scinax* by the combination of rounded snout in dorsal view (elongate pointed in most species of the *S. rostratus* group, elongate acuminated in the *S. squalirostris* group, and sub-elliptical with a pointed tip in the *S. auratus* group); single or weakly bilobate vocal sac that does not reach the pectoral region (mostly single, enlarged, reaching the level of the pectoral fold or region in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); lack of spicules

in nuptial pads, inner margin of arms, and pectoral region in males (present in the *S. fuscovarius* group); dorsal pattern uniform, with irregular dark blotches or spots (dorsal stripes present in the *S. auratus*, *S. fuscomarginatus*, and *S. squalirostris* groups; a dark lateral stripe in the *S. boesemani* group and *S. pachycrus*); hidden surfaces of thighs uniform, dark or light, with irregular or horizontal blotches (with different patterns of transverse bars or blotches in the *S. auratus*, *S. elaeochroa*, *S. eurydice*, *S. fuscovarius*, *S. nasicus*, and *S. rostratus* groups, several species of the *S. granulatus* group); and tadpoles with P-3 inside the oral disc (in the margin of the labium or supported by a labial arm in the *S. rostratus* group and some species of the *S. auratus* group). Furthermore, the species of this group differ from those in the *S. danae* group by the presence of physiological chlorosis or, when absent, by the occurrence of light color in the hidden surfaces of thighs with horizontal markings. They differ from the species of the *S. boesemani* and *S. elaeochroa* group by the uniform dark color (gray, brown, or black) in the hidden areas of thighs, or when the color is light, by the absence of physiological chlorosis (present in the *S. boesemani* and *S. elaeochroa* groups).

Characterization. (1) SVL males 27.9–37.5 mm, SVL females 30.2–39.3 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single or weakly bilobate that does not reach the level of the pectoral fold; (5) snout rounded in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth, shagreen, or densely covered with tubercles; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the base of the disc (Ch. 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands absent or present in males (Ch. 47.0 or 47.1); (13) inguinal glands absent (Ch. 48.1); (14) iris orange, bronze, golden, or bicolor silvery gray and bronze, with a median horizontal dark streak; (15) dorsal pattern uniform, with irregular dark blotches or spots; (16) hidden surfaces of thighs uniform, or with horizontal or irregular blotches; (17) physiological chlorosis absent or present (Ch. 158.0 or 158.1); (18) eyes of the tadpole visible or not visible ventrally (Ch. 146.0 or 146.1); (19) oral disc subterminal or ventral (Ch. 143.0 or 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with 1 note/call, note duration 70–338 ms, and 16–42 pulses/note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip

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of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent or present (Ch. 91.0 or 91.1); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); and (33)–(34) unknown.

Contents. Six recognized species: *Scinax chiquitanus* (De la Riva, 1990); *Scinax funereus* (Cope, 1874); *Scinax ictericus* Duellman and Wiens, 1993; *Scinax iquitorum* Moravec et al., 2009; *Scinax onca* Ferrão et al., 2017; and *Scinax oreites* Duellman and Wiens, 1993. One UCS, *Scinax* sp. 32.

Distribution. Amazon basin in Bolivia, Brazil, Ecuador, Peru, and montane forest on the eastern slopes of the Peruvian Andes (e.g., De la Riva, 1990; Gonzales-Álvarez and Reichle, 2004; Melo-Sampaio and Souza, 2015; Ferrão et al., 2017; Chávez, 2018).

Comments. In the morphological analyses of Faivovich (2002), *Scinax ictericus* and *S. oreites* were not monophyletic because *S. ictericus* was placed as the sister taxon of all other species of the former *S. ruber* clade, and *S. oreites* was placed in a poorly supported clade together with *S. granulatus* (as *S. eringiophila*), *S. maracaya*, and *S. elaeochroa* (Faivovich, 2002). Duellman et al. (2016) recovered *S. chiquitanus*, *S. funereus*, *S. ictericus*, and *S. oreites* as a poorly supported (bootstrap with RAxML < 50%) monophyletic group, the sister taxon of a clade including *S. fuscovarius*, *S. nasicus*, *S. ruber*, and *S. x-signatus*—the latter from French Guiana—congruent with our results.

The *Scinax funereus* group is composed of two main clades (Fig. 37). One of these includes *S. ictericus* as the sister taxon of *S. funereus*, *S. iquitorum*, and *S. onca* (99% jackknife), and the other includes *S. oreites* as the sister taxon of *S. chiquitanus* and one UCS, *Scinax* sp. 32 (99% jackknife). The occurrence of physiological chlorosis is a synapomorphy of the first clade (Ch. 158.1; *S. funereus*, Duellman, 1971; *S. ictericus*, Melo-Sampaio and Souza, 2015: fig. 5A; *S. iquitorum*, Moravec et al., 2009; *S. onca*, Ferrão et al., 2017: fig. 5B, D, E and Chávez, 2018: fig. 1B, D), that is homoplastic with the *S. cruentomma* + *S. elaeochroa* groups, the *S. boesemani* group, *S. cuspidatus*, *S. quinquefasciatus* (polymorphic), and *Scinax* sp. 37 (polymorphic).

Scinax ictericus was described from Cuzco Amazónico, Madre de Dios, Peru (Duellman and Wiens, 1993), and is known to occur in several other localities of southeastern Peru. Subsequently, it was reported in adjacent Bolivia (Gonzales-Álvarez and Reichle, 2004), Brazil (Melo-Sampaio and Souza, 2015), and Colombia (Suárez-Mayorga, 1999; Medina-Rangel et al., 2019). We only included topotypes and samples from a nearby locality.

Scinax funereus has been recorded from the western Amazon basin, from Colombia to southeastern Peru and Brazil (Duellman and Wiens, 1993; Lynch, 2005; Bernarde et al., 2011; Ramalho et al., 2016). Our samples of *S. funereus*, from localities distant up ≈1,000 km, are recovered monophyletic (Fig. 37) but with low support (54% jackknife). Within this species, there are two clades differing in UPDs of 2.1–2.2% (Appendix S10: Table 33). One includes samples from Napo in Ecuador, Loreto in Peru, and Acre in Brazil (UPDs between localities for which 16S is available is 1.5%), while the other includes specimens from two localities in Pastaza and Orellana, Ecuador. The study of the vouchers indicates that these two clades correspond to two different species, as the inner mucosae of the vocal sac are fused in the clade with samples from Ecuador, Peru, and Brazil, and unfused in the clade restricted to Ecuador. We do not have topotypic samples of *S. funereus* (type locality: "Moyabamba, Peru"; Cope, 1874), and thus it is uncertain with which of these two clades it could be associated. For this reason, we refer to the lineages as *S. funereus* A and *S. funereus* B. Furthermore, we lack samples from Colombia. Once topotypes are included, it could be tested whether the names currently included in the synonymy of *S. funereus* (Duellman, 1971) are available for any of these clades. These names are *Hyla depressiceps* Boulenger, 1882 (type locality: "Ecuador"; Boulenger, 1882) and *Hyla rubra inconspicua* Melin, 1941 (type locality: Roque, San Martín, Peru). Read and Lopes (2020) described calls of *S. funereus* from Napo and Orellana, Ecuador, and reported no differences between them. As the taxonomic status and distribution of the two lineages identified here are clarified, it will be possible to associate previous references in the literature with each of them. UPDs between the relatively similar *S. funereus* A and B, *S. iquitorum*, and *S. onca* (Moravec et al., 2009; Ferrão et al., 2017) are 2.1–6.1% (Appendix S10: Table 33).

Scinax oreites was described from the eastern Andean slopes in Peru (type locality 8 km NNE Balzapata, Provincia Bongará, Departamento Amazonas, Peru; Duellman and Wiens, 1993), based on specimens from several points around the type locality, and two localities ≈550 km SW in Pasco. We included samples from two specimens collected close to the type locality (16S available only for one of these) and from two localities in Pasco, Peru. The UPD between these is 0.5% (Appendix S10: Table 33).

Scinax chiquitanus is known from Beni, Cochabamba, La Paz, Pando, and Santa Cruz in Amazonian Bolivia, Madre de Dios, Peru (Duellman and Salas, 1991; Duellman and Wiens, 1993; De la Riva et al., 2000), and for a locality in Porto Velho, Rondônia, Brazil (Ferrão et al., 2016). Ferrão et al. (2016) commented, without additional details, that the morphology and advertisement call of *S. chiquitanus* from Brazil are similar to those from Bolivia. Our results recovered *S. chiquitanus* from Bolivia and Brazil in a clade with low UPDs (0.4–1.3%; Appendix S10: Table 33).

De la Riva et al. (2000) suggested that Peruvian populations of *Scinax chiquitanus* may not be conspecific with the Bolivian populations, because males have a color pattern (with dark blotches and dorsolateral stripes; see Duellman and Wiens, 1993: fig. 2) which differs markedly from that of Bolivian males, which otherwise present little variation (without dark blotches or stripes; see De la Riva et al., 2000:111). However, Duellman and Wiens (1993) reported that recordings of males from Tambopata, Peru and Puerto Almacén, Bolivia (type locality of *S. chiquitanus*) only showed differences in the note repetition rate,

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which are 20–36 notes/min in calls recorded at Tambopata and 45 notes/min in those recorded at Puerto Almacén. Tissue samples from Peru were not available for our analyses; therefore, future studies should include samples and revise the taxonomic status of the Peruvian population of *S. chiquitanus*.

    Scinax chiquitanus is the sister taxon of *Scinax* sp. 32 (Fig. 37), known from five localities in Orellana, Ecuador (see localities in Appendix S1). UPDs between both species are 4.2–5.0% (Appendix S10: Table 33). However, we are not aware of any diagnostic character distinguishing this candidate species from *S. chiquitanus*, and for this reason, it is considered a UCS.

Other relevant literature. Duellman (1971: taxonomy of *Scinax funereus*); Duellman (1978: tadpole and vocalization of *S. funereus*); Duellman (2005: natural history of *S. chiquitanus*); Duellman and Wiens (1993: vocalization
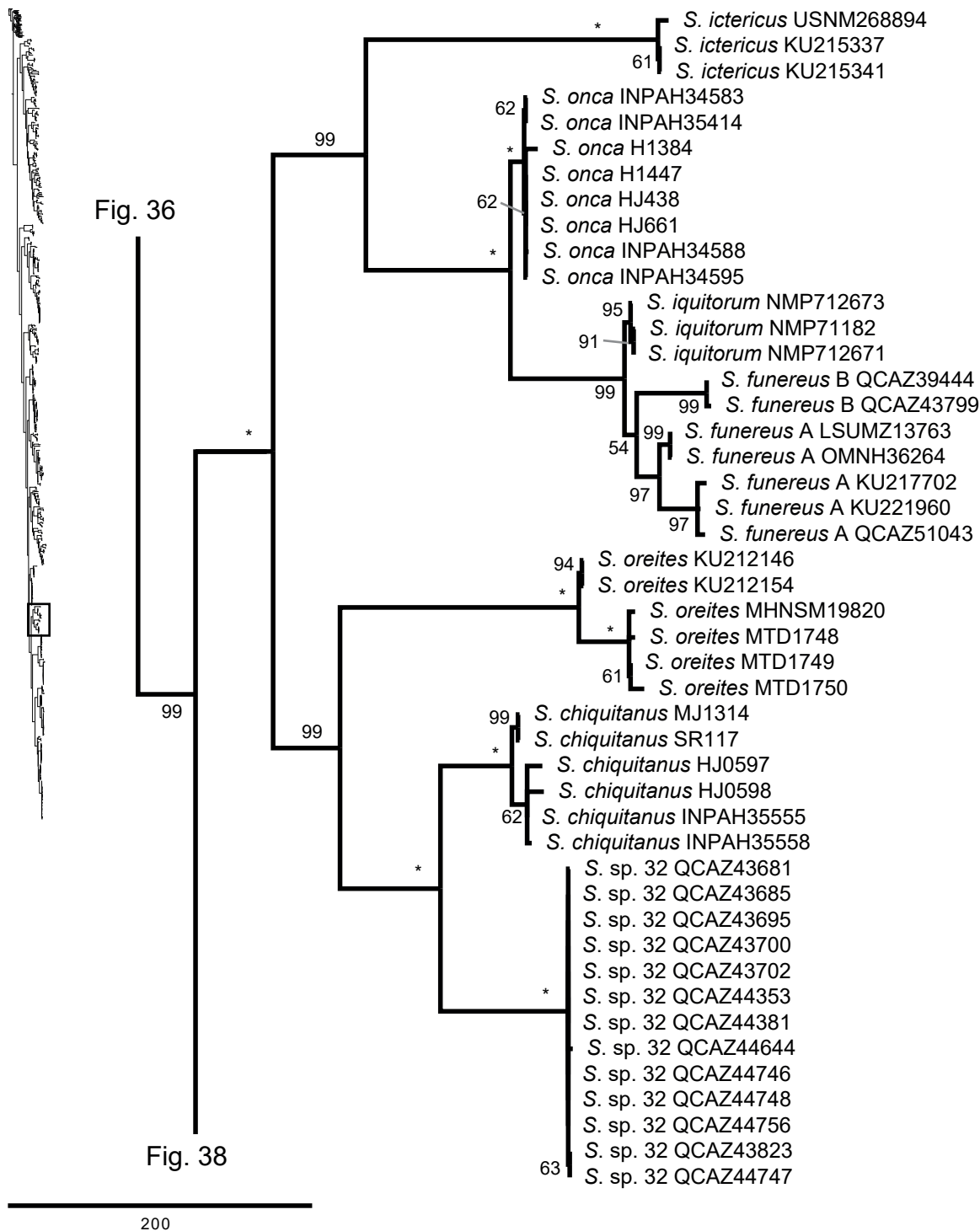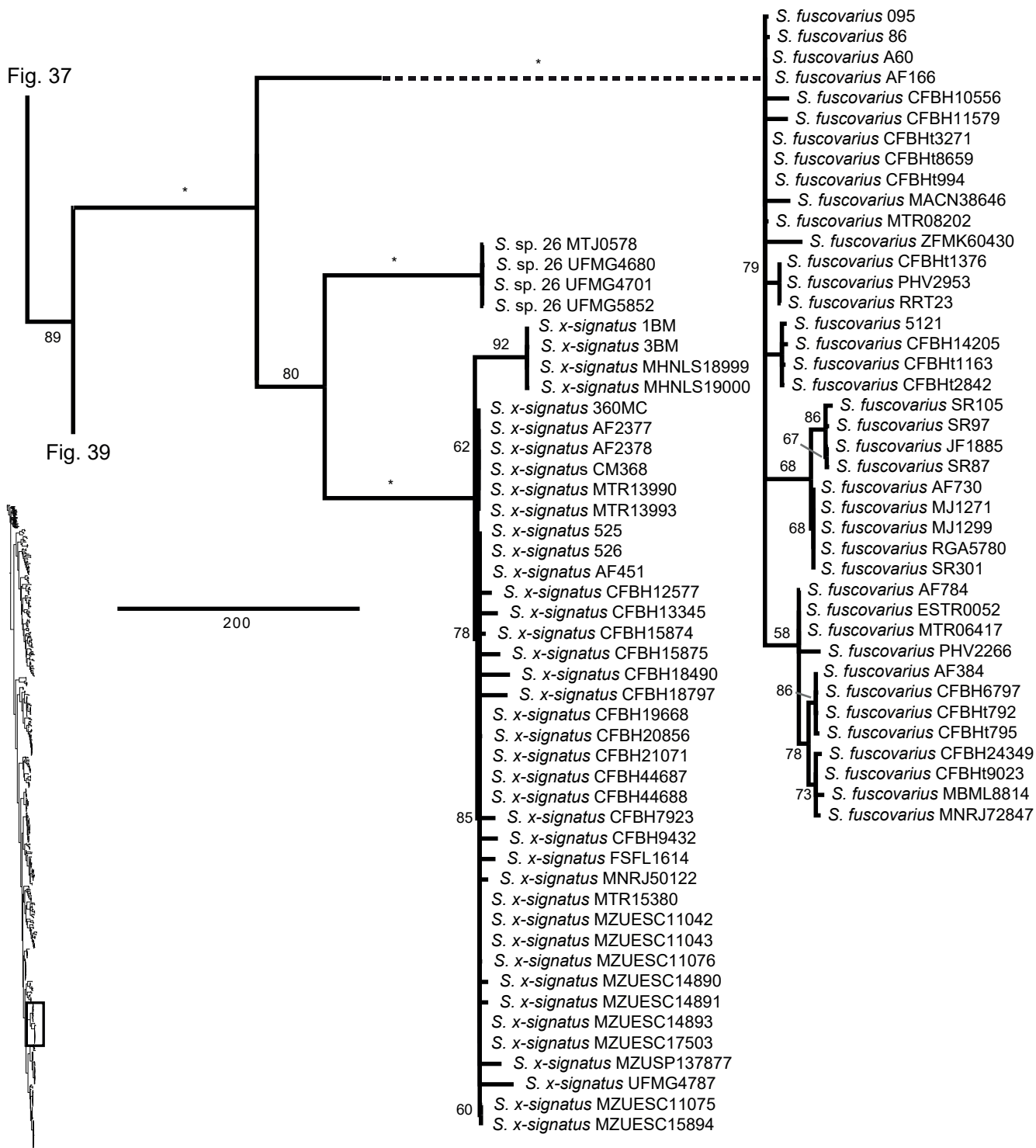

Figure 37. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 18 of 21: The *Scinax funereus* group. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency.

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of *S. chiquitanus*, *S. ictericus*, and *S. oreites*; tadpoles of the latter two); De la Riva et al. (1994: vocalization of *S. chiquitanus*); Duellman (2005: natural history and vocalization of *S. chiquitanus*); Ferrão et al. (2017: vocalization and tadpole of *S. onca*); Read and Lopes (2020: vocalization of *S. funereus*).

The *Scinax fuscovarius* group

Sister taxon. The *Scinax nasicus* group.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data and one phenotypic synapomorphy, glandular acini in the medial region of the forearm present (Ch. 49.1, with instances of homoplasy in some internal clades of *Ololygon*).

Treefrogs in this group can be differentiated from all other species by the combination of rounded snout in dorsal view (elongate pointed in most species of the *Scinax rostratus* group, elongate acuminated in the *S. squalirostris* group, and sub-elliptical with a pointed tip in the *S. auratus* group); weakly bilobate vocal sac that does not reach the level of the pectoral fold (mostly single, enlarged, reaching the level of the pectoral fold or region in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); presence of spicules[22] in nuptial pad, inner margin of arm, and pectoral region in males (absent in all other species of *Scinax*); presence of pectoral glands in males (absent in all species of the *S. auratus*, *S. boesemani*, *S. cruentomma*, *S. danae*, *S. elaeochroa*, *S. eurydice*, *S. fuscomarginatus*, *S. rostratus*, and *S. squalirostris* groups, in some species of the *S. funereus* group, and in *S. pachycrus*); dorsal pattern with large irregular blotches, sometimes with X-shaped mark composed of one or two pairs of inverted parentheses-like blotches (stripes in the *S. fuscomarginatus* and *S. squalirostris* groups, and some species of the *S. cruentomma*, *S. granulatus*, and *S. rostratus* groups, lateral stripe in *S. boesemani* group and *S. pachycrus*); and tadpoles with P-3 inside the oral disc (in the margin of the labium or supported by a labial arm in the *S. rostratus* group and some species of the *S. auratus* group).

***Characterization.*** (1) SVL in males 37.0–47.0 mm, females 42.0–48.0 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac, subgular, weakly bilobate, does not reach the level of the pectoral fold; (5) snout rounded in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth, with scattered tubercles; (8) postaxial webbing of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the base of disc (Ch. 59.3); (10) epidermal projections in the nuptial pad absent (Ch. 64.0); (11) spicules in nuptial pad and pectoral region present; (12) pectoral glands in males present (Ch. 47.1); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze, with a median horizontal dark streak; (15) dorsal pattern with irregular dark blotches; (16) hidden surfaces of thighs with irregular blotches; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole visible ventrally (Ch. 146.1); (19) oral disc subterminal (Ch. 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with 1 note/call, note duration 110–187 ms, and 7–10 pulses/note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent or present (Ch. 91.0 or 91.1); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 metacentric (Ch. 152.0); and (34) NOR in chromosome pair 11, proximal (Ch. 153.12).

Contents. Two recognized species: *Scinax fuscovarius* (Lutz, 1925) and *Scinax x-signatus* (Spix, 1824). One UCS, *Scinax* sp. 26.

Distribution. Northeastern, southeastern, and southwestern Brazil, Paraguay, Bolivia, northern Argentina, and northeastern Uruguay (e.g., Arrieta and Maneyro, 1999; Achaval and Olmos, 2003; Baldo and Rosset, 2005; Canelas and Bertoluci, 2007; Eterovick and Sazima, 2004; Juncá, 2006; Cruz et al., 2009; Silva et al., 2010; Weiler et al., 2013).

Comments. *Scinax fuscovarius* is widely distributed, and our results show all included specimens in a single lineage with relatively little genetic divergence between extremes of its wide distribution (e.g., UPDs of 1.0% between populations from Espírito Santo, Brazil, and Salta, Argentina, distant ≈2,600 km; Appendix S10: Table 34). We included specimens from very distant localities in southeastern Brazil, northern Argentina, and Bolivia (Fig. 38); tissue samples of specimens from Paraguay were unavailable. Although we do not have samples from the type localities of the two junior synonyms of *S. fuscovarius*, *Hyla megapodia* Miranda-Ribeiro, 1926 (type locality: Porto Esperidião and Caceres, Mato Grosso; Miranda-Ribeiro, 1937) and *Hyla trachythorax* Müller and Hellmich, 1936 [type locality: "Apa-Bergland (San Luis)" and "Apa-Bergland, Centurion (San Luis)"] these fall within the polygon of our sampled localities, being ca. 70 and 150 km respectively from our closest localities (RGA 5780, UHE Guaporé, Jauru, Mato Grosso, and CFBH 14205, Bonito, Mato Grosso do Sul), not much in the context of the broad distribution of this species. The sequences from these points do not

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22 See footnote 11. This character, when properly studied, will likely be shown to be a phenotypic synapomorphy of the *Scinax fuscovarius* group.

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differ particularly from all other samples of *S. fuscovarius* (Appendix S10: Table 34). This sequence similarity, the study of type material (*Hyla megapodia*), and the detailed descriptions and accompanying illustrations of *Hyla trachythorax* (the type series is lost; Glaw and Franzen, 2006) reinforce and corroborate the status of these two names as junior synonyms of *S. fuscovarius*, as originally suggested by Lutz (1973a) and followed by several authors for one

or the two names (Cei, 1980; Almeida and Cardoso, 1985; Duellman and Wiens, 1992; Lavilla, 1992; De la Riva et al., 2000; Faivovich et al., 2005).

Araujo-Vieira et al. (2020b) recently reviewed the taxonomic history of *Scinax x-signatus* and designated a neotype consistent with the figure and information of the lost type specimen provided by Spix (1824) and Peters (1872a). Furthermore, Araujo-Vieira et al. (2020b)

Figure 38. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 19 of 21: The *Scinax fuscovarius* group. The taxonomy and the species groups shown are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency. Dashed lines connecting parts of the tree are not proportional to branch-lengths.

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corroborated the identification as *S. x-signatus* of several samples available in GenBank from Amapá, Bahia, Ceará, and Pernambuco (Brazil), French Guiana (lineages *S. ruber* E and G of Fouquet et al., 2007a,b), and the oceanic islands of Martinique and Fernando de Noronha. Besides samples from all the localities included by Araujo-Vieira et al. (2020b), our dataset included samples from Venezuela (Caracas) and Alagoas, Maranhão, Paraíba, Piauí, Sergipe, and Rio Grande do Norte (Brazil). Our results recover all of these as a well-supported clade (100% jackknife), where the specimens from Kurou (French Guiana) and Caracas (Venezuela) are the sister lineage of all other samples, including some from French Guiana (Montravel), whose monophyly is poorly supported (Fig. 38). UPDs between both clades are 0.8–1.1% (Appendix S10: Table 34).

We still lack samples from Colombia, Suriname, Guyana, and some Brazilian states where several populations have been assigned to *Scinax x-signatus* (e.g., Lynch and Suárez-Mayorga, 2011; Ouboter and Jairam, 2012; Cole et al., 2013); the corroboration of its occurrence in Venezuela and French Guiana suggests that the species likely occurs in Guyana and Suriname. It is expected that the recent designation of a neotype for this species will facilitate the reassessment of all populations to which the name has been applied throughout its wide distribution (Araujo-Vieira et al., 2020b).

Our analyses showed that several specimens misidentified as *Scinax x-signatus* were *S. eurydice*, *S. ruber*, *S. similis*, or *S. fuscovarius*. Several specimens from Colombia and central-west Venezuela to which the name *S. x-signatus* has been applied (Rivero, 1969; Gorzula and Señaris, 1999; Acosta-Galvis, 2000; Lynch, 2006b; Ugueto and Rivas-Fuenmayor, 2010) belong to a distinct lineage that is only distantly related to *S. x-signatus*. That lineage here named *Scinax* sp. 33 is well supported (100% jackknife) as the sister taxon of *S. similis* in the *S. nasicus* group (Fig. 39).

Our results corroborate the occurrence of a UCS from Brazil, as revealed by Araujo-Vieira et al. (2020b), *Scinax* sp. 26, that is well supported (80% jackknife) as the sister taxon of *S. x-signatus* (Fig. 38). UPDs between these lineages are 6.1–7.6% (Appendix S10: Table 34). *Scinax* sp. 26 is represented by a specimen from Januária, Minas Gerais, as reported by Araujo-Vieira et al. (2020b), to which we add specimens from Caitité and Jacaraci, southwestern Bahia. The variation of *S. x-signatus* throughout its distribution needs to be better understood to produce a reasonable diagnosis of *Scinax* sp. 26.

Other relevant literature. Cochran (1955: account of *Scinax fuscovarius*); Rivero (1969: taxonomy of *S. x-signatus*); Lutz (1973a: accounts of *S. fuscovarius* and *S. x-signatus*); Cei (1980: account of *S. fuscovarius*); Almeida and Cardoso (1985: spermatozoid of *S. fuscovarius*); Abe and Neto (1991: physiology of *S. fuscovarius*); Echeverria and Montanelli (1992: tadpole of *S. fuscovarius*); De la Riva et al. (1994: vocalization of *S. fuscovarius*); Pombal et al. (1995b: vocalization of *S. fuscovarius*); Fabrezi and Vera (1997: tadpole of *S. fuscovarius*); Oliveira and Andrade (1997: ova-

ries and fat bodies of *S. fuscovarius*); Oliveira and Vicentini (1998: testes and fat bodies of *S. fuscovarius*); Alves and Carvalho e Silva (1999: tadpole of *S. fuscovarius*); Kasahara et al. (2003: karyotype of *S. fuscovarius*); Rossa-Feres and Nomura (2006: tadpole of *S. fuscovarius*); Cardozo et al. (2011: karyotype of *S. fuscovarius*); Nogueira et al. (2015b: karyotype of a species identified as *S. x-signatus*; requires corroboration); Kwet and Di Bernardo (1999: account of *S. fuscovarius*); Köhler (2000: account and vocalization of *S. fuscovarius*); Oliveira et al. (2003: testicles of *S. fuscovarius*); Kwet et al. (2010: account of *S. fuscovarius*); Franco-Belussi et al. (2012: visceral pigmentation in *S. fuscovarius*); Novaes and Zina (2016: vocalization of *S. x-signatus*); Goldberg et al. (2018: geographic variation in *S. fuscovarius*); Araujo-Vieira et al. (2020b: vocalization of *S. x-signatus*, and comments to most previous publications referring to this species and that require corroboration of the identification); Lira et al. (2020: vocalization of *S. fuscovarius*); Quinzio and Goldberg (2021: tadpole of *S. fuscovarius*).

The *Scinax nasicus* group

Sister taxon. The *Scinax fuscovarius* group.

Diagnosis. This group is well supported (100% jackknife) and delimited by molecular data and a single phenotypic synapomorphy: m. interhyoideus with a medial raphe (Ch. 74.1, with instances of homoplasy in *Julianus camposseabrai*, *Scinax perereca*, *S. tsachila*, the *S. rostratus* group, and some internal clades of *Ololygon*). A putative phenotypic synapomorphy of this group is the palatine reduced to ¾ of the *planum antorbitale* (Ch. 14.1, also reduced in *Julianus uruguayus*, *S. chiquitanus*, and *S. rogerioi*); however, the taxonomic distribution of this character-state is still unknown for *S. ruber* and closely related candidate species.

Treefrogs in this group can be differentiated from all other species of *Scinax* by the combination of rounded snout in dorsal view (elongate pointed in most species of the *S. rostratus* group, elongate acuminated in the *S. squalirostris* group, and sub-elliptical with a pointed tip in the *S. auratus* group); single vocal sac that does not reach the level of the pectoral fold (enlarged reaching the level of the pectoral fold or region in the *S. cruentomma*, *S. fuscomarginatus*, and *S. squalirostris* groups); lack of spicules in nuptial pads, inner margin of arms, and pectoral region in males (present in the *S. fuscovarius* group); presence of pectoral glands in males (absent in all species of the *S. auratus*, *S. boesemani*, *S. cruentomma*, *S. danae*, *S. elaeochroa*, *S. eurydice*, *S. fuscomarginatus*, *S. rostratus*, and *S. squalirostris* groups, in some species of the *S. funereus* group, and *S. pachycrus*); and tadpoles with P-3 inside the oral disc (in the margin of the labium or supported by a labial arm in the *S. rostratus* group and some species of the *S. auratus* group).

Characterization. (1) SVL in males 29.4–41.2 mm, females 37.2–43.8 mm; (2) pectoral fold present (Ch. 45.1);
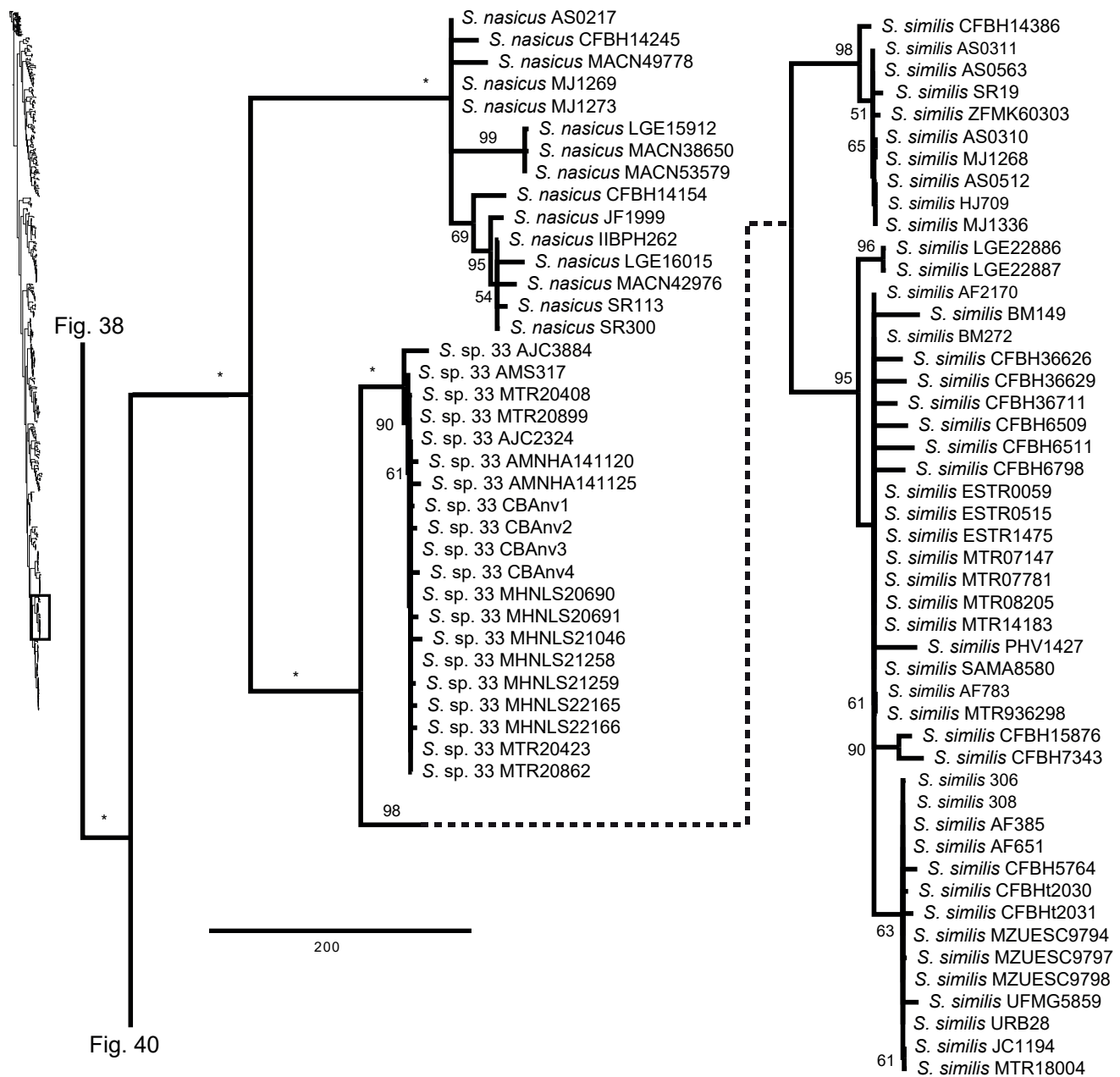
Figure 39. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 20 of 21: The *Scinax nasicus* group, part 1 of 2. The taxonomy and the species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency. Dashed lines connecting parts of the tree are not proportional to branch-lengths.

(3) vocal sac externally evident (Ch. 63.1); (4) vocal sac subgular, single, does not reach the level of the pectoral fold; (5) snout rounded in dorsal view; (6) tubercles in the lower lip absent; (7) dorsal skin smooth or shagreen; (8) postaxial webbing between of toe I reaching the subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the subarticular tubercle, midlength of the penultimate phalanx, or base of the disc (Ch. 59.1, 59.2, or 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males present (Ch. 47.1); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze, with a median horizontal dark streak; (15) dorsal pattern with irregular dark blotches or dorsolateral stripes with dark borders; (16) hidden surfaces of thighs with irregular light blotches; (17) physiological chlorosis absent (polymorphic in *Scinax* sp. 37; Ch. 158.0); (18) eyes of the tadpole visible ventrally (Ch. 146.0); (19) oral disc subterminal (Ch. 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae in the posterior labium of the same size as those in the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with 1 note/call, note duration

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42–225 ms; and 4–14 pulses/note; (29) anterior process of the suprascapula present (Ch. 20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent or present (Ch. 91.0 or 91.1); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with an origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 metacentric (Ch. 152.0); and (34) NOR in chromosome pair 11, proximal (Ch. 153.12).

Contents. Three recognized species: *Scinax nasicus* (Cope, 1862a); *Scinax ruber* (Laurenti, 1768); and *Scinax similis* (Cochran, 1952). Six UCSs, *Scinax* spp. 27, 33–37.

Distribution. Eastern Panama through coastal northern South America; Amazon basin of Brazil, Bolivia, Peru, Colombia, and Ecuador; Guianas; Trinidad and Tobago, and St. Lucia. Central, northeastern, and southern Brazil; eastern Bolivia; Paraguay; northern Uruguay; and northern and central Argentina (e.g., Murphy, 1997; Izecksohn and Carvalho-e-Silva, 2001; Achaval and Olmos, 2003; Lever, 2003; Cole et al., 2013; Weiler et al., 2013; Guarnizo et al., 2015; Schulze et al., 2015).

Comments. In the phylogenetic results of Faivovich (2002), *Scinax nasicus* and *S. ruber* were distantly related. Molecular phylogenetic analyses found *S. nasicus* closely related to *S. ruber*; however, *S. similis* was recovered distantly related to these species (Wiens et al., 2006, 2010; Pyron and Wiens, 2011; Duellman et al., 2016). Other molecular studies including these species were restricted mainly to species delimitation (Salducci et al., 2005; Fouquet et al., 2007a,b, 2012; Jansen et al., 2011; Guarnizo et al., 2015; Ferrão et al., 2016; Lyra et al., 2017; Vacher et al., 2020). Our analyses recovered a clade including six lineages of *Scinax ruber* as the sister taxon of a clade with *S. nasicus*, *S. similis*, and *Scinax* sp. 33 (Figs. 39–40). *Scinax nasicus* was described from an unknown locality, somewhere along the drainages of the Paraná and Paraguay Rivers in Brazil, northeastern Argentina, and southern Paraguay (Cope, 1862a). It is widely distributed throughout Paraguay, northern and central Argentina, Uruguay, eastern Bolivia, and central and southern Brazil (Lutz, 1973a; Cei, 1980; De la Riva et al., 2000; Carezzano and Cabrera, 2010; Jansen et al., 2011; Santos et al., 2011; Weiler et al., 2013; Dalmolin et al., 2017). According to Jansen et al. (2011), there are two Bolivian lineages referred to *S. nasicus* (*S.* cf. *nasicus* and *S. nasicus* A) that differ in mitochondrial DNA (UPDs > 3.0%) and phenotypic characters (larval and adult morphology, and bioacoustics). Our results show that their *Scinax* cf. *nasicus* (MJ 1269, 1273, AS 0217) is nested with all our specimens of *S. nasicus* (Fig. 39). Besides the low UPDs (UPDs 0.2–0.9%; Appendix S10: Table 35), these specimens are phenotypically (larval and adult morphology, and bioacoustics) similar to *S. nasicus* (De la Riva, 1993; Kehr and Dure, 1995; Vera Candioti et al., 2004; Vera Candioti, 2007; Jansen et al., 2011; Schulze et al., 2015). Further, our results corroborate Jansen et al.'s (2011) sug-

gestions that their *S. nasicus* A (MJ 1268, 1336, AS 0310, 0311, 0512, 0563) from Bolivia is a different species; it corresponds to *S. similis* in our analyses (Fig. 39; see below).

The type locality of *Scinax similis* is in Manguinhos, in the city of Rio de Janeiro, Rio de Janeiro, Brazil (Cochran, 1952) and is currently known from Brazilian localities in Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Goiás, and Brasília as well in northeast Argentina (Corrientes and Misiones) and Paraguay (Itapúa, Misiones; e.g., Izecksohn and Carvalho-e-Silva, 2001; Rödder et al., 2007; Weiler et al., 2013; Vaz-Silva et al., 2020). Our results, however, indicate that *S. similis* has a much wider distribution also occurring in the Brazilian states of Minas Gerais, Alagoas, Ceará, Mato Grosso, Tocantins, Maranhão, and Pará, reaching southern Suriname in the north, but also extending westwards to Bolivia, from where we included specimens from several localities in Santa Cruz and Beni (Fig. 39).

The wide distribution of *Scinax similis* includes Atlantic Forest, Caatinga, Cerrado, and Amazon basin. The latter is reached in northern Mato Grosso, Pará (Brazil), and Suriname, but also in the southwest of Bolivia. The populations from central Mato Grosso and Bolivia are recovered as a lineage that is the sister clade of all other populations from the Atlantic Forest, Caatinga, and Amazon basin. UPDs between both clades are 2.0–2.9% (Appendix S10: Table 35). We are not aware of any phenotypic evidence distinguishing these two clades. Our results indicate that *S. nasicus* A from Jansen et al. (2011) corresponds to the lineage of *S. similis* from central Mato Grosso and Bolivia (Fig. 39). This association is further supported by comparing available information on vocalizations (Jansen et al., 2011; Bilate and Lack, 2011) and larvae (Alves and Carvalho e Silva, 1999; Schulze et al., 2015). Our results represent a remarkable extension in our knowledge of the distribution of *S. similis* and show it to be one of the most broadly distributed species in the genus.

Scinax sp. 33 is the sister taxon (100% jackknife) of *S. similis* (Fig. 39) and differs in UPDs of 2.8–5.6% (Appendix S10: Table 35). This lineage is mostly composed of populations from Guyana, Venezuela, and northwest Colombia, treated as *S. ruber* by Guarnizo et al. (2015), as *S.* cf. *x-signatus* by Cole et al. (2013), and as *S. x-signatus* by Barrio-Amorós et al. (2019: figs. 179b, c). Given that we are not aware of any diagnostic phenotypic character that distinguishes this candidate species from its relatives and the UPDs, we consider it a UCS. We note that the smaller UPDs (2.8–2.9%) between *Scinax* sp. 33 and *S. similis* involve specimens of *S. similis* from disparate areas in the Brazilian states of Goiás, Maranhão, Mato Grosso, and Pará.

The name *Scinax ruber* has been widely applied to multiple populations found in the Amazon basin of Brazil, Bolivia, Peru, Colombia, Ecuador, Guianas, eastern Panama east through coastal northern South America, Trinidad and Tobago, and St. Lucia (e.g., Murphy, 1997; Lever, 2003; Cole et al., 2013; Guarnizo et al., 2015; Schulze et al., 2015). Several authors have suggested, on the basis of phylogenetic molecular analyses, that *S. ruber* includes multiple species along its distribution (Fouquet

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et al., 2007b; Jansen et al., 2011; Guarnizo et al., 2015; Ferrão et al., 2016). For example, Fouquet et al. (2007b) reported six distinct lineages under the name *S. ruber* in French Guiana, forming a paraphyletic group concerning their specimens of *S. cruentomma* and *S. x-signatus* (see Appendix S11).

Our results revealed six well-supported (≥ 90% jackknife) distinct lineages under the name *Scinax ruber* throughout its wide distribution (Fig. 40), one of which includes topotypes (Paramaribo, Suriname; Duellman and Wiens, 1993). UPDs between the six lineages of *S. ruber* are 2.7–8.3% (Appendix S10: Table 36). Besides UPDs between these lineages, some authors have reported the presence of adult and larval morphological and bioacoustic differences that may diagnose them. As discussed below we associate the name *Scinax ruber* (Laurenti, 1768) with one of the lineages and consider all others as UCSs, *Scinax* spp. 27, 34–37, pending a study of their variation and possible phenotypic diagnostic characters.

Duellman and Wiens (1993) pointed out adult morphological (size, dorsal and posterior surfaces of the thighs color pattern) and bioacoustic (pulse rate and dominant frequency) differences between populations found in Peru (possibly our *Scinax* sp. 27) and Ecuador (our *Scinax* sp. 37). De la Riva et al. (1994) indicated that the calls of populations from Venezuela (Rivero, 1969) differ markedly (call durations and dominant frequency) from recordings of Bolivian populations (De la Riva et al., 1994). Furthermore, Schulze et al. (2015) mentioned larval differences regarding the SVLs and LTRFs for tadpoles described in Brazil, Colombia, Ecuador, and Trinidad and Tobago (Kenny, 1969; Duellman, 1978; Hero, 1990; Lynch, 2006a; Lynch and Suárez-Mayorga, 2011).

Scinax sp. 34 and sp. 35 are the sister taxon of the remaining lineages (Fig. 40) and include specimens from the Magdalena valley, and Amazonia, in Colombia, respectively, Colombia mostly taken from Guarnizo et al. (2015). UPDs between these two lineages and *S. ruber* and its most closely related UCSs are 4.5–8.3% (Appendix S10: Table 36). Future work should determine if any of these lineages (most likely *Scinax* sp. 34) correspond with what was identified as *S. ruber* in Panama (León, 1969; Duellman, 1970a; Campbell and Telford, 1971).

Our results corroborate the suggestions by Guarnizo et al. (2015) that there are three lineages under the name *Scinax ruber* in Colombia. These are represented by *Scinax* sp. 33 (AJC 2324 and 3884) and *Scinax* spp. 34–35, with the former being the sister taxon of *S. similis* and only distantly related to the other two lineages (Fig. 40). *Scinax* sp. 36 is represented by two specimens from localities in northwest Bolivia (Riberalta and Puerto Barrador, Beni). UPDs between this UCS and *S. ruber*, *Scinax* sp. 27 and sp. 37 are 2.9–5.3% (Appendix S10: Table 36). *Scinax* sp. 37 includes specimens from several localities in Ecuador. UPDs between this UCS, *S. ruber*, and *Scinax* sp. 27 are 2.7–5.0% (Appendix S10: Table 36).

We consider as *Scinax ruber* the lineage that includes a topotype of this species (Paramaribo, Suriname; Duellman and Wiens, 1992). It is represented in our study by specimens from Venezuela (Bolívar), Guyana, Suriname, French Guiana (lineage *S. ruber* C of Fouquet et al., 2007a), and the island of Martinique (Fig. 40). In this way, this species is mostly restricted to coastal regions in northeastern South America, as suggested by Barrio-Amorós et al. (2019) based on the results of Fouquet et al. (2007a).

The sister lineage of *Scinax ruber* is *Scinax* sp. 27 (Fig. 40). UPDs between these are 2.7–4.4% (Appendix S10: Table 36). The smaller UPDs (2.7–2.9%) involve specimens of *Scinax* sp. 27 from disparate areas, in the Brazilian states of Amapá, Amazonas, Pará, and Rondônia. *Scinax* sp. 27 is a widely distributed lineage including specimens from several localities in Pando and Santa Cruz (Bolivia), Amapá, Amazonas, Pará, Rondônia, Tocantins (Brazil), French Guiana, Loreto and Madre de Dios (Peru), Suriname, and Amazonas (Venezuela).

Scinax sp. 27 includes the specimens from French Guiana that Fouquet et al. (2007a) considered as *S. ruber* lineages A and B, and *S. x-signatus*; the specimens that Jansen et al. (2011) considered as the Bolivian *S. ruber* F lineage; and the specimens of the Brazilian Amazonia that Ferrão et al. (2016) considered lineages *S. ruber* F and PM (see Appendix S11). *Scinax x-signatus* of Fouquet et al. (2007a) was possibly misidentified as noted by Ferrão et al. (2016). Likewise, *S. ruber* E from French Guiana of Fouquet et al. (2007a) is recovered as *S. x-signatus* in our analyses (see Appendix S11 and Fig. 38). Ferrão et al. (2016) mentioned that their lineages *S. ruber* F and *S. ruber* PM (Ferrão et al., 2016: fig. 3H) are distinguished from each other by snout shape. We were unable to corroborate this variation in these individuals. However, our results showed that two specimens (AS 0224, 0225) from Bolivia correspond to *Scinax* sp. 27, as do the specimens of the lineage *S. ruber* PM of Ferrão et al. (2016). UPDs between their *S. ruber* F and *S. ruber* PM is < 2.5% (Appendix S10: Table 36). Morphological differences between their putative *S. ruber* lineages require a thorough comparison and an evaluation in the context of the intraspecific variation of *Scinax* sp. 27.

Notably missing from our analyses are samples from populations commonly identified as *Scinax ruber* from northern Colombia, eastern Panama, Trinidad and Tobago, and several areas of the Amazon basin, particularly in Peru. It remains to be elucidated if these could represent different lineages from those identified here or not.

There are several available names in the synonymy of *Scinax ruber*, some of which could be applied to the UCSs *Scinax* sp. 27 and spp. 34–37, pending a careful reassessment of the type specimens. If the addition of specimens from Venezuela and Trinidad and Tobago indicates that they are nested in *S. ruber*, then *Hyla lineomaculata* Werner, 1899 (type locality: "Arima, Trinidad") and *Hyla robersimoni* Donoso-Barros, 1965 (type locality: "pajonales de la península de Paria," Estado de Sucre, Venezuela) would be corroborated as junior synonyms of that species (Barrio-Amorós and Ortiz, 2015). *Hyla conirostris* Peters, 1863 (type locality: "Suriname") could be a junior synonym of *Scinax ruber* (Laurenti, 1768) or an available name for *Scinax* sp. 27.

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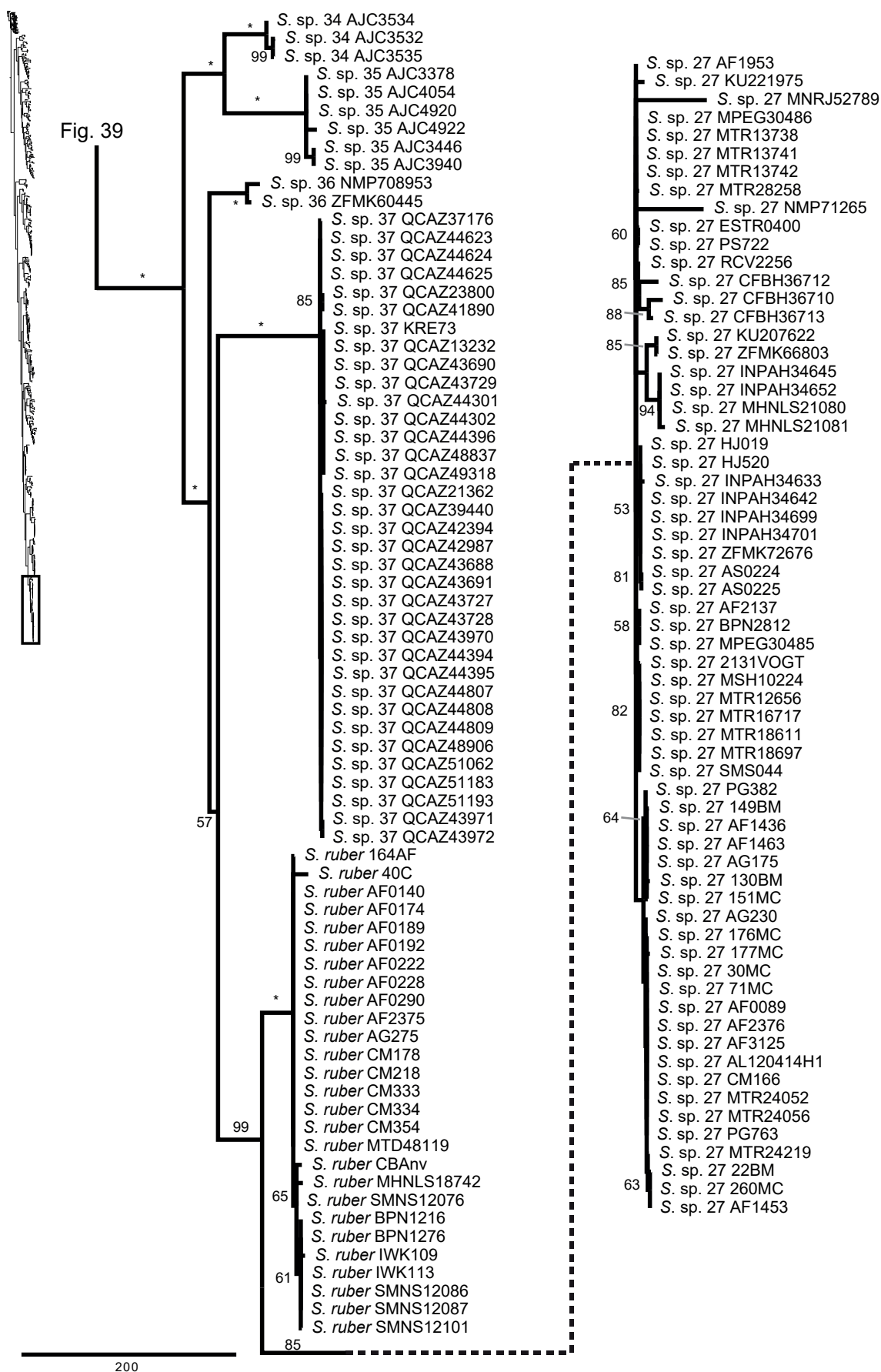
Figure 40. Strict consensus of the most parsimonious trees from the total evidence analysis in TNT considering gaps as a fifth state, part 21 of 21: The *Scinax nasicus* group, part 2 of 2. The taxonomy and species groups are those recognized in this study. The upper left inset indicates the section of the complete cladogram shown in the figure. Values around nodes are jackknife absolute frequencies. Nodes lacking values have frequencies < 50%. An asterisk (*) indicates 100% frequency. Dashed lines connecting parts of the tree are not proportional to branch-lengths.

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The holotype of *Hyla lateristriga* Spix, 1824 (type locality not stated, but Brazil by implication) is quite faded, but undoubtedly belongs to a species of *Scinax*. Spix's (1824) figure and the comments by Peters (1872a) indicate a strong similarity with *S. ruber*. The type locality of *H. lateristriga* was not mentioned by Spix (1824). Considering that his trip to the Amazon basin in Brazil reached almost the frontier with Peru (Vanzolini, 1981), covering mostly the areas from which we have samples of *Scinax* sp. 27, and not the areas from where we have samples of *S. ruber*, it is likely that *H. lateristriga* is the name that should be applied to *Scinax* sp. 27.

Hyla rubra huebneri Melin, 1941 (type localities: "Taracuá, Rio Uaupés," "S[ão]. Gabriel, Rio Negro," and "vicinity of Manáos," Amazonas, Brazil) has been considered a synonym of *Scinax ruber* (e.g., Cochran and Goin, 1970; Duellman, 1977; Duellman and Wiens, 1992, 1993). However, Lutz (1973a) applied this name to a heterogeneous group of frogs from the Amazon basin. The syntypes of this species require thorough study to determine the status of this *nomem* and whether it can be associated with any of the UCSs identified here.

Scytopis alleni Cope, 1870 (Type localities: "Pebas," Loreto, Peru, and "Para, Brazil" = Pará, Brazil; restricted to Pará, Brazil, by lectotype designation of Duellman and Wiens, 1992) was considered a synonym of *Hyla rubra* by Boulenger (1882) and Duellman (1977). Duellman and Wiens (1993) stated that the syntype ANSP 2159 ("Pebas, Equador") is a female "in structure and coloration" as *Scinax ruber* in the Upper Amazon basin of Ecuador and Peru. The syntype ANSP 1519 ("Para, Brazil") is a somewhat desiccated male and identifiable as a "*rubra*-type of *Scinax*". In this specimen, Fouquette and Delahoussaye (1977) described what they called a "*catharinae*-type" spermatozoid and placed the species in the former *Ololygon catharinae* group (as recognized by them). Based on this information, Duellman and Wiens (1993) designated ANSP 1519 as the lectotype of *Scytopis alleni*. Considering the type locality, if a positive association can be made with fresh specimens, this name is likely another one available for *Scinax* sp. 27.

Boulenger (1882) considered *Scytopis cryptanthus* Cope, 1874 (type locality: "Nauta," Departamento Loreto, Peru) a synonym of *Hyla rubra*, without further comments. This was followed by Nieden (1923), Cochran and Goin (1970), Duellman (1977), and Duellman and Wiens (1992, 1993). The type specimen was reported to be lost by Duellman (1977) and it seems safe to assume that everyone that considered it a synonym of *Hyla rubra* did so without looking at the type specimen, following the description provided by Cope (1874). Indeed, his description seems congruent with that of populations historically associated with *S. ruber*, including all UCSs recognized here, and therefore could be another available name for *Scinax* sp. 27.

Other relevant literature. Kenny (1969: tadpole of *Scinax ruber* from Trinidad and Tobago; it is unclear if it corresponds with one of the lineages identified here); Rivero (1969: vocalization and taxonomy of *S. ruber*); Campbell and Telford (1971: vocalizations of *S. ruber* from Panama; it is unclear if it corresponds with one of the lineages identified here); Duellman, 1978 (vocalization likely of *Scinax* sp. 37, as *Hyla rubra*); Bourne (1992, 1993: reproductive biology of *S. ruber*); De la Riva et al. (1994: vocalization likely of *Scinax* sp. 27 or 36, as *S. ruber*); Kehr and Dure (1995: tadpole of *S. nasicus*); Fabrezi and Vera (1997: tadpole of *S. nasicus*); Yanosky and Dixon (1997: ecology of *S. nasicus*); Lajmanovich et al. (1998: tadpole of *S. nasicus*); Peltzer and Lajmanovich (1999: feeding ecology *S. nasicus*); Alves and Carvalho e Silva (1999: tadpole of *S. similis*); Lajmanovich (2000: larval ecology of *S. nasicus*); Lescure and Marty (2000: natural history and vocalization of *S. ruber*); Vera Candioti et al. (2004: tadpole of *S. nasicus*); Alcalde (2005: tadpole of *S. nasicus*); Duellman (2005: vocalizations likely of *Scinax* sp. 27 or 36, as *S. ruber*); Prado et al. (2005: reproductive biology of *S. nasicus*); Lima et al. (2006: natural history likely of *Scinax* sp. 27); Vera Candioti (2007: tadpole of *S. nasicus*); Bilate and Lack (2011: vocalization of *S. similis*); Cardozo et al. (2011: karyotypes of *S. nasicus* and *S. similis*); Franco-Belussi et al. (2012: visceral pigmentation in *S. similis*); León et al. (2019: vocalization of *S. nasicus*); Pederassi et al. (2022: vocalizations of *S. similis*); Schiesari et al. (2022; tadpole of *S. ruber* from Central Amazonia, possibly corresponds to *Scinax* sp. 27).

Species unassigned to any group

***Scinax pachycrus* (Miranda-Ribeiro, 1937).** *Scinax pachycrus* is considered unassigned to any group, as its monophyly with the *S. eurydice* + *S. granulatus* groups is poorly supported (Fig. 34). It can be differentiated from all other species of Scinaxini by having longer hindlimbs in relation to the SVL, acuminate snout in dorsal view, and a dark lateral stripe from the snout extending posteriorly to the groin. This species is characterized by (1) SVL in males 30.2–32.4 mm, females 31.2–33 mm; (2) pectoral fold present (Ch. 45.1); (3) vocal sac externally evident (Ch. 63.1); (4) vocal sac, subgular, weakly bilobate, does not reach the level of the pectoral fold; (5) snout rounded; (6) rounded tubercles in the lower lip present; (7) dorsal skin smooth, with scattered tubercles; (8) postaxial webbing of toe I reaching distal margin of subarticular tubercle (Ch. 58.1); (9) postaxial webbing of toe II reaching the base of the disc (Ch. 59.3); (10) epidermal projections in the nuptial pad present (Ch. 64.1); (11) spicules in nuptial pad, inner margin of arm, and pectoral region absent; (12) pectoral glands in males absent (Ch. 47.0); (13) inguinal glands absent (Ch. 48.0); (14) iris bronze, with a median horizontal dark streak; (15) dorsal pattern with few irregular blotches or spots, and with a dark postorbital lateral stripe; (16) hidden surfaces of thighs uniform; (17) physiological chlorosis absent (Ch. 158.0); (18) eyes of the tadpole visible ventrally (Ch. 146.1); (19) oral disc subterminal (Ch. 143.1); (20) posterior margin of the folded oral disc straight (Ch. 136.0); (21) papillae on the posterior labium of the same size as those in

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the lateral margins (Ch. 140.0); (22) labial arm supporting P-3 absent (Ch. 137.0); (23) keratinized dark plates on the sides of the lower jaw-sheath absent (Ch. 151.0); (24) intestinal coiling axis orthogonal/suborthogonal to the main body axis (Ch. 148.0); (25) vent tube above the margin of the ventral fin (Ch. 145.0); (26) golden/yellow spots or large frontal band between the eyes and the nostrils absent in larvae (Ch. 150.0); (27) oviposition in ponds (Ch. 155.0); (28) advertisement call with 1 note/call; note duration 140–530 ms; 13–48 pulses per note; (29) anterior process of the suprascapula present (20.1); (30) slip of the m. extensor digitorum inserting on the metacarpophalangeal joint of digit IV absent (Ch. 91.0); (31) m. depressor mandibulae with an origin from the dorsal fascia that covers the suprascapula (Ch. 71.1); (32) m. depressor mandibulae with origin from the tympanic annulus (Ch. 72.1); (33) chromosome pair 1 (Ch. 152.0); (34) NOR in chromosome pair 11, distal (Ch. 153.13).

This singular species occurs in Northeastern Brazil from Rio Grande do Norte to southern Bahia (e.g., Lutz, 1973a; Juncá, 2006). We only had available samples from Sergipe (Itabaiana) and Bahia (Caetité and Maracás), the former being ≈280 km SW from the type locality (Poção, Pernambuco). UPDs among our samples are 0.2–1.4% (Appendix S10: Table 37). *Hyla pickeli* Lutz and Lutz, 1938 (Type locality: "Tapera, State of Pernambuco," Brazil), from the coastal region of Pernambuco, is a junior synonym (Bokermann, 1966a).

Other relevant literature. Miranda-Ribeiro (1955: lectotype designation); Carneiro et al. (2004: tadpole and vocalization); Nogueira et al. (2015b: cytogenetics); Novaes and Zina (2016: vocalization); Araújo et al. (2019, 2020: natural history); Dubeux et al. (2020: tadpole).

Conservative estimate of species diversity

Several taxonomic studies based on external morphology and vocalizations have suggested the existence of multiple undescribed species confused with common, widespread species in Scinaxini (e.g., Bokermann, 1967c; Lutz, 1973a; Pombal et al., 1995b; Nunes et al., 2012). Furthermore, studies using molecular data have pointed to unnamed diversity throughout this tribe (e.g., Fouquet et al., 2007a,b; Ferrão et al., 2016; Menezes et al., 2016).

Our results indicate six confirmed candidate species of *Ololygon* based on phenotypic differences (*Ololygon* spp. 7, 8, 14, 15, 16, and 18) and five confirmed candidate species of *Scinax* (*Scinax* spp. 6, 16, 18, 19, and 30). To these, we add the ten candidate species considered confirmed because they were not sister to the nominal species from which they could not be distinguished phenotypically, including four *Ololygon* (*Ololygon* spp. 1, 11, 17, and 19) and five *Scinax* (*Scinax* spp. 7, 8, 11, 17, and 25). Additionally, we identified 37 unconfirmed candidate species (9 *Ololygon* and 28 *Scinax*), giving a total of 57 candidate species.

The recognition of 57 candidate species represents an increase of 44.2% of the currently described diversity of Scinaxini. This increase corroborates previous studies showing that anuran species richness is underestimated in the Neotropics (e.g., Fouquet et al., 2007a,b, 2021; Funk et al., 2012; Gehara et al., 2014; Guarnizo et al., 2015; Lyra et al., 2016; Moraes et al., 2022). The study of other anuran groups will show if the percentage of inferred candidate species is within the bounds of other anuran clades.

The candidate species in our study were heuristically detected on the basis of cladogram topology, UPDs of 3.0% (16S rRNA) as a threshold (Fouquet et al., 2007a), and/or diagnostic phenotypic characters (e.g., mostly external morphology of adults and larvae and vocalizations). The use of thresholds for species delimitation has been criticized (e.g., Grant et al., 2006; Baker et al., 2009; Padial et al., 2009; Collins and Cruickshank, 2013), stressing among other things, how unreasonable it is to expect a stable, consistent value among different lineages (e.g., see the UPDs among different species of *Rhinella* in the study of Pereyra et al., 2021). From this perspective, it should be noted that UPDs among some pairs of phenotypically diagnosed sister species of Scinaxini (e.g., *Scinax caldarum* and *S. rossaferesae*) are less than 3.0% (2.4–3.1%; Appendix S10: Table 30), indicating that our estimation of candidate species is conservative and suggesting that several of the conspecific lineages we identified (e.g., in *S. granulatus*, *S. similis*, *S. rostratus*, and *S. squalirostris*) might be heterospecific. However, large intraspecific UPDs do occur in some species of Scinaxini: Brusquetti et al. (2014) recognized conspecific lineages of *S. fuscomarginatus* with much larger UPDs, as high as 9.8%. As long as there is no additional evidence to consider them as distinct species, these UPDs should serve as a reminder of their strictly heuristic value.

Another source of additional candidate species stems from the fact that in six cases where we identified different lineages, it was not clear with which, if any, should the population of the type locality be associated, and so we were left with some lineages that we called *Ololygon* or *Scinax* species A, B, etc. In two of these cases, these names designate lineages that are not even monophyletic (*S. auratus* A, B, and C; *S. boulengeri* A and B). It seems reasonable to assume that at least three of these represent additional candidate species, with the conservative assumption that topotypes will be shown to be associated with one of the different identified lineages for each species.

Our results relied mainly on the use of DNA sequences for identifying candidate species, and this effort will accelerate the discovery of unnamed diversity in Scinaxini. However, we note that our assessment of unconfirmed candidate species stems from a combination of time constraints and a generally conservative approach. Therefore, we expect that as studies continue on the vouchers and associated data (vocalizations, larvae) and the species with which they have been confused, it will be possible to corroborate many of the unconfirmed candidate species inferred in this study as new species. Although there has

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been an extreme emphasis on cryptic diversity (e.g., Ferrão et al., 2016; Menezes et al., 2016), the fact remains that most described species of Scinaxini are not cryptic; only in the worst cases, they may be challenging to differentiate based on morphology alone.

FINAL COMMENTS

One of the wonders of systematic and taxonomic practice is that one can spend years studying a particular group without noticing any informative variation in the studied character systems. And suddenly, when the group is considered already barren and devoid of informative characters, a change of perspective reveals a new source of evidence for the study of its taxonomy and evolutionary history. This pattern is seen in Scinaxini by the study of Luna et al. (2018) that found spicules in the nuptial pads of *Scinax fuscovarius*, which in turn allowed a better diagnosis of *S. x-signatus* (Araujo-Vieira et al., 2020b), or the recent report of differences in pupil shape in some species of *Ololygon* (Cervino et al., 2021: Appendix S2). Our phylogenetic results will be useful in the study of multiple character systems such as call evolution and its correlation with laryngeal morphology, sexual selection (Bastos and Haddad, 1999), tadpole evolution (Pezzuti et al., 2016), chromosome evolution (Cardozo et al., 2011), thermal physiology (Abe and Neto, 1991), miniaturization, and others. Furthermore, they provide an essential framework for a thorough approach to the wide range of questions about Neotropical biogeography that could be addressed with Scinaxini. Despite our efforts in amassing a large dataset, several sections of our phylogenetic hypothesis remain poorly supported. These include many clades in the *Ololygon catharinae* group, which suggest that our knowledge of its diversity may still be quite incomplete. As a consequence of our efforts, several unknown taxonomic problems were exposed and now await solutions. The systematics and taxonomy of Scinaxini will keep interested herpetologists busy for many years to come.

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NOTE ADDED IN PROOF

Photographs of voucher specimen AJC 3461 identified as *Scinax* cf. *wandae* by Guarnizo et al. (2015) and in the present paper show that it is morphologically similar to *S. cruentomma*, implying that that lineage should be considered a candidate species, clearly different from *S. wandae*. Similarly, the Colombian and Venezuelan specimens associated with *S. albertinae* very likely correspond to *S. wandae*, reinforcing the need for a taxonomic study of these two species (as noted in the Discussion) to determine if the former is a junior synonym of the latter.

While the current article was in press, Abreu-Jardim et al. (2023) published a phylogeographic analysis of *Scinax squalirostris* based on the same dataset of Abreu-Jardim et al. (2021). Their results are consistent with the recognition of UCS *Scinax* sp. 13.

Similarly, Chávez et al. (2023) described a new species of *Scinax* from the middle Ucayali River in Peru, *S. pyroinguinis*. They presented a phylogenetic analysis based on a fragment of the 16S rRNA gene that placed it as the sister taxon of all other species in the *S. rostratus* group. The inclusion of the sequences of *S. pyroinguinis* in our dataset (unpublished data) recovered this species deeply nested in the *S. rostratus* group, where it is the sister taxon of the clade including *S. garbei*, *S. jolyi*, *S. proboscideus*, *Scinax* sp. 7, and *Scinax* sp. 8.

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ONLINE SUPPORT INFORMATION

The following Supporting Information is available for this article online:

Appendix S1. Voucher specimens, collection numbers, localities, GenBank accession numbers of mitochondrial and nuclear sequences employed in this study, and taxonomic authorities for some names in the main text.

Appendix S2. Voucher specimens examined for phenotypic characters and taxonomic purposes.

Appendix S3. Primers used in PCR amplification.

Appendix S4. List of the sources of phenotypic character-state scorings in the phenotypic data matrix.

Appendix S5. Partitions and models selected for the Maximum Likelihood analysis.

Appendix S6. Phenotypic data matrix.

Appendix S7. Strict consensus of the most parsimonious trees in Newick format.

Appendix S8. Results of the Maximum Likelihood analysis.

Appendix S9. List of phenotypic synapomorphies and individual optimization of all phenotypic characters.

Appendix S10. Tables of uncorrected pairwise distances (UPDs) for the 16S gene fragment for selected clades.

Appendix S11. Names used in this study for voucher specimens included in previous studies.

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