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The phylogeny of Dendropsophini (Anura: Hylidae: Hylinae)

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Abstract

The relationships of the hyline tribe Dendropsophini remain poorly studied, with most published analyses dealing with few of the species groups of *Dendropsophus*. In order to test the monophyly of Dendropsophini, its genera, and the species groups currently recognized in *Dendropsophus*, we performed a total evidence phylogenetic analysis. The molecular dataset included sequences of three mitochondrial and five nuclear genes from 210 terminals, including 12 outgroup species, the two species of *Xenohyla*, and 93 of the 108 recognized species of *Dendropsophus*. The phenomic dataset includes 46 terminals, one per species (34 *Dendropsophus*, one *Xenohyla*, and 11 outgroup species). Our results corroborate the monophyly of Dendropsophini and the reciprocal monophyly of *Dendropsophus* and *Xenohyla*. Some species groups of *Dendropsophus* are paraphyletic (the *D. microcephalus*, *D. minimus*, and *D. parviceps* groups, and the *D. rubicundulus* clade). On the basis of our results, we recognize nine species groups; for three of them (*D. leucophyllatus*, *D. microcephalus*, and *D. parviceps* groups) we recognize some nominal clades to highlight specific morphology or relationships and facilitate species taxonomy. We further discuss the evolution of oviposition site selection, where our results show multiple instances of independent evolution of terrestrial egg clutches during the evolutionary history of *Dendropsophus*.

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Introduction

With 1011 species, the new world treefrogs (Hylidae) are the most species-rich family of amphibians (species numbers from Frost, 2020, taxonomy from Faivovich et al, 2018). Knowledge of phylogenetic relationships of this family has steadily increased since the studies of Faivovich et al. (2005) and Wiens et al. (2005) laid a phylogenetic framework that has been mostly corroborated by later work (Duellman et al., 2016; Jetz and Pyron, 2018). The family includes three subfamilies (Hylinae, Pelodryadinae, and Phyllomedusinae), and seven tribes (Cophomantini, Dendropsophini, Hylini, Lophyohylini, Pseudini, Scinaxini, and Sphaenorhynchini) are recognized in the most species rich-subfamily, Hylinae (Faivovich et al., 2018). Although phylogenetic studies have been published for major groups such as Phyllomedusinae (Faivovich et al., 2010), the hyline tribes Cophomantini (Pinheiro et al., 2019; Lyra et al., 2020), Hylini (Faivovich et al., 2018), Lophyohylini (Blotto et al., 2020), Pseudini (Aguiar et al., 2007; Garda and Cannatella, 2007), and Sphaenorhynchini (Araújo-Vieira et al., 2019), some groups have lagged behind, such as Pelodryadinae, Dendropsophini, and Scinaxini. Although some studies have focused on species groups or putative clades of *Dendropsophus* (Fouquet et al., 2011; Motta et al., 2012; Caminer et al., 2017) and *Scinax* (Brusquetti et al., 2014; Baldo et al., 2019), so far there have been no thorough analyses of these tribes.

The group of small, mostly South American hylids known or suspected to have a diploid number of 30 chromosomes was long believed to be monophyletic (see Duellman and Cole, 1965). Although the monophyly of the "30-chromosome *Hyla*" had been recovered previously in analyses including few species (e.g. Salducci et al., 2002), the overwhelming problem of the paraphyly of *Hyla* prevented the resurrection of *Dendropsophus* Fitzinger, 1843 until the phylogenetic analysis of Faivovich et al. (2005).

Dendropsophus is a species-rich genus of Hylidae currently comprising 108 recognized species (Frost, 2020). These are highly variable in morphology (e.g. Duellman and Fouquette, 1968; Franco-Belussi et al., 2011), advertisement call (e.g. Martins and Jim, 2003; Martins and Jim, 2004), chromosome morphology (e.g. Gruber et al., 2005; Medeiros et al., 2013; Suarez et al., 2013), and reproductive behavior (e.g. Touchon and Warkentin, 2008). Misidentifications tend to accumulate in the literature (e.g. de la Riva and Duellman, 1997), and the taxonomy within *Dendropsophus* is generally regarded as difficult (Duellman, 1982; Gehara et al., 2014). Some phenomic synapomorphies or diagnostic characters for the genus and its species groups have been proposed (see Appendix S1 for more details), but most of them have yet to be tested in a quantitative context.

Faivovich et al. (2005) considered the tribe Dendropsophini to include the genera *Dendropsophus*, *Lysapsus* Cope, 1862, *Pseudis* Wagler, 1830, *Scarthyla* Duellman and de Sá, 1988, *Scinax* Wagler, 1830, *Sphaenorhynchus* Tschudi, 1838, and *Xenohyla* Izecksohn, 1998. Dendropsophini was the least supported of the tribes they recognized. While *Dendropsophus* is consistently found to be the sister taxon of *Xenohyla* (Faivovich et al., 2005; Wiens, 2006; Moen et al., 2009; Wiens et al., 2010; Pyron and Wiens, 2011; Duellman et al., 2016), the monophyly of this tribe has been both rejected (Wiens et al., 2006: supp. data; Pyron and Wiens, 2011) and corroborated (Wiens et al., 2010) by subsequent analyses, always with relatively low support.

In a reanalysis of GenBank sequences, Duellman et al. (2016) obtained Dendropsophini as non-monophyletic, with a clade including *Scarthyla, Lysapsus,* and *Pseudis* as the sister taxon of *Dendropsophus* + *Xenohyla,* whereas an unsupported clade (49% bootstrap, with RAxML) with *Scinax* + *Sphaenorhynchus* was distantly related. Duellman et al. (2016) restricted Dendropsophini (as Dendropsophinae) to *Dendropsophus* + *Xenohyla,* resurrected Pseudinae for *Scarthyla, Lysapsus,* and *Pseudis,* and erected Scinaxinae for *Scinax* + *Sphaenorhynchus*. While the redefinition of Dendropsophini was a reasonable step, the recognition of the hyline tribes as subfamilies and a formal taxon for the poorly supported *Scinax* + *Sphaenorhynchus* were challenged by Faivovich et al. (2018). These authors erected a separate tribe, Sphaenorhynchini for *Sphaenorhynchus*, and further recognized the tribes Cophomantini, Dendropsophini, Hylini, Lophyohylini Scinaxini, and Pseudini within the hylid subfamily Hylinae. Within Scinaxini, we consider *Julianus* Duellman et al., 2016 and *Ololygon* Fitzinger, 1843 as junior synonyms of *Scinax* Wagler, 1830 (see Lourenço et al., 2016). Throughout this paper we follow this taxonomic arrangement of hylids.

Relationships within *Dendropsophus* are unclear (e.g. Medeiros et al., 2013; Orrico et al., 2013). Since the 1960s, several species groups have been proposed, with discussions based mostly on external morphology and/or geography (e.g. Bokermann, 1964b; Duellman and Fouquette, 1968; Lutz, 1973b; Duellman and Trueb, 1983; Napoli and Caramaschi, 1998; Kaplan, 1999); however, little progress has been achieved, especially in understanding the relationships between and within these groups. Group relationships and composition are usually poorly supported and highly unstable (e.g. Jungfer et al., 2010; Fouquet et al., 2011; Motta et al., 2012; Medeiros et al., 2013; Rivera-Correa and Orrico, 2013; Peloso et al., 2016) and many of the putatively diagnostic characters are not unique to a given group (Faivovich et al., 2005).

Faivovich et al. (2005) divided *Dendropsophus* into nine groups: the *D. columbianus*, *D. garagoensis*, *D. labialis*, *D. leucophyllatus*, *D. marmoratus*, *D. microcephalus*, *D. minimus*, *D. minutus*, and *D. parviceps* groups. Note that Jungfer (2017) proposed that *Hyla labialis* Peters, 1863 should be considered a junior synonym of *Hyla molitor* Schmidt, 1857, and we refer to this group as the *D. molitor* group. Six species of the genus that were unavailable to Faivovich et al. (2005) and not assigned to any group in their original descriptions remained unassigned: *D. amicorum*, *D. battersbyi*, *D. haraldschultzi*, *D. stingi*, *D. tintinnabulum*, and *D. yaracuyanus*. Moreover, some species described more recently were only tentatively assigned to groups without phylogenetic analyses (Ortega-Andrade and Ron, 2013; Orrico et al., 2014). Subsequent contributions to Faivovich et al. (2005) provided DNA sequence data from previously unsampled species (Wiens et al., 2006; Moen et al., 2009; Jungfer et al., 2010; Wiens et al., 2010; Fouquet et al., 2011; Motta et al., 2012; Rivera-Correa and Orrico, 2013; Gehara et al., 2014; Peloso et al., 2016) or reviewed material assigned to widespread species (Caminer and Ron, 2014; Fouquet et al., 2015; Rivadeneira et al., 2018).

Duellman and Crump (1974) and Duellman and Trueb (1983) proposed the first phylogenetic hypotheses for species now referred to *Dendropsophus*, although those authors did not test the monophyly of the species groups. More recent papers on *Dendropsophus* phylogenetics are largely based on molecular data, although Faivovich et al. (2005) included data on foot musculature from Burton (2004) and Wiens et al. (2005) included many characters based on morphology (internal and external), life history and chromosome number for four species of *Dendropsophus*.

Earlier studies of the phylogeny of *Dendropsophus* were usually conducted as part of taxonomically broader phylogenetic analyses (Salducci et al., 2002, 2005) or as analyses of evolutionary trends, usually being re-analyses of available sequences in GenBank (Wiens et al., 2005, 2010; Moen et al., 2009; Moen and Wiens, 2009). Given that none of those studies was designed specifically to test relationships among species of *Dendropsophus*, characters were chosen to address different questions (i.e. broader treefrog diversity) and *Dendropsophus* sequences were not intensely produced or discussed. More recently, papers that addressed the internal relationships of *Dendropsophus* have become more common (Jungfer et al., 2010; Wiens et al., 2010; Fouquet et al., 2011; Pyron and Wiens, 2011; Motta et al., 2012; Medeiros et al., 2013; Rivera-Correa and Orrico, 2013; Peloso et al., 2016) and the inclusion of previously unanalyzed species has revealed that several groups recognized or proposed by Faivovich et al. (2005) are suspected to be paraphyletic (see Fouquet et al., 2011; Motta et al., 2012; Fouquet et al., 2015; Peloso et al., 2016). See Appendix S2 for a historical summary of currently recognized species groups.

Although most modern cladistic analyses that included species of *Dendropsophus* employed only DNA sequence data, other sources of evidence are equally valid and desirable, as even small phenomic matrices can have disproportionately large impacts on results (de Sá et al., 2014; Mirande, 2016; Sanchez-Pacheco et al., 2018). Indeed, the absence of non-DNA sequence data (with morphology, behavior, and chromosome numbers as the most striking examples) might be the weakest point of those analyses (as discussed by Faivovich et al., 2005). The exceptions are Burton (2004), Faivovich et al. (2005) [that included Burton's (2004) data], Wiens et al. (2005), and Araújo-Vieira et al. (2019). Medeiros et al. (2013) and Suarez et al. (2013) presented information on chromosome morphology but did not use it as additional evidence to test phylogenetic hypotheses.

Wiens et al. (2005) produced a matrix of osteological (n = 97), external adult (n = 19) and larval (n = 20) morphology, adult myology (n = 2), life history (n = 5), and chromosome number (n = 1) characters. They included four species in their morphological dataset (*Dendropsophus ebraccatus*, *D. koechlini*, *D. microcephalus*, and *D. nanus*) and DNA sequences of another 14 species in their more inclusive dataset (*D. aperomeus*, *D. bifurcus*, *D. carnifex*, *D. elegans*, *D. leali*, *D. leucophyllatus*, *D. marmoratus*, *D. minutus*, *D. parviceps*, *D. pelidnus*, *D. robertmertensi*, *D. sarayacuensis*, *D. sartori*, and *D. triangulum*). Faivovich et al. (2005) included Burton's (2004) matrix of characters from hylid foot musculature, which included data for 18 species of *Dendropsophus* (*D. bifurcus*, *D. carnifex*, *D. columbianus*, *D. ebraccatus*, *D. leali*, *D. leucophyllatus*, *D. marmoratus*, *D. microcephalus*, *D. minutus*, *D. molitor* as *D. labialis*, *D. nanus*, *D. parviceps*, *D. rhodopeplus*, *D. robertmertensi*, *D. sarayacuensis*, *D. sartori*, *D. schubarti*, and *D. triangulum*). Araújo-Vieira et al. (2019) used only four species of *Dendropsophus* in their study of phylogenetic relationships of *Sphaenorhynchus*: *D. elegans*, *D. microps*, *D. minutus,* and *D. sanborni* and produced a large phenomic character matrix of adult osteology (n = 106), adult external morphology (n = 26), larval external morphology (n = 14), adult myology (n = 44), adult internal anatomy (n = 1), natural history (n = 1), and chromosome number (n = 1) characters.

Goals of this paper

The internal relationships of *Dendropsophus* are still largely unexplored and little phenomic evidence has been used in phylogenetic analyses of the genus. Consequently, the goals of this study were to test the monophyly and internal relationships of *Dendropsophus* with an evidentially diverse dataset composed of genomic (DNA sequences) and phenomic (chromosome number; morphology; behavior) characters scored for a dense sample of *Dendropsophus* species and exemplar outgroup taxa. Based on our results, we propose taxonomic rearrangements in the composition of the species groups, including diagnoses and, when available, phenomic synapomorphies. We also discuss outstanding taxonomic problems and the evolution of oviposition site selection in *Dendropsophus*.

Materials and Methods

Conventions and abbreviations

GenBank (Clark, et al., 2016) accession numbers for new sequences produced for this project are listed in Appendix S3, as are the permanent collection numbers for voucher specimens or, if unavailable, the tissue-collection number or field voucher number for the sequences. Examined specimens are listed in Appendix S4. Throughout the paper, when referring to character numbers in the matrix, “c.” and “cs.” refer, respectively, to “character” and “character state”. Collection abbreviations are as follows: AL, Adolpho Lutz collection, Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brasil; ANSP, Herpetological Collection from the Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; CAB, Cinthia A. Brasileiro Field Number (to be deposited at CFBH); CBF, Colección Boliviana de Fauna, La Paz, Bolívia; CCT, Carla Cassini Field Tissue Number (to be deposited at CFBH); CFBH, Amphibian collection Célio F.B. Haddad, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; CFBHT, Tissue Collection of CFBH; CHUNB, Herpetological Collection of the Universidade de Brasília, Brasília, Brazil; UNICAMP, Coleção de Tecidos e Banco de Células de Anfíbios, Campinas, São Paulo, Brasil; CTMZ, Tissue Collection of Museu de Zoologia da Universidade de São Paulo; DL, Daniel Loebmann Field Series (to be deposited at CFBH); DZUFRJ, Collection of the Departamento de Zoologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil; FSFL, Felipe S. F. Leite Field Number (to be deposited at UFMG); ICN, Instituto de Ciencias Naturales, Bogotá, Colombia; JDL, John D. Lynch Field Series (to be deposited at ICN); JF, Julián Faivovich Field Series (to be deposited at MACN); JJ, Jorge Jim Collection (to be accessioned in MNRJ); JKfn, Jöern Köhler Field Number; JZ, Juliana Zina Field Number; KU, Herpetological Collection of the University of Kansas Biodiversity Institute, Lawrence, Kansas, USA; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MAR, Marco Rada Field Number; MNCN/ADN, Tissue and DNA Collection of Museo Nacional de Ciencias Naturales, Madrid, Spain; MCNAM, Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; MHUA, Museo de Herpetología de la Universidad de Antioquia, Medellin, Antioquia, Colombia; MNRJ, Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil; MPEG, Coleção de Herpetologia Osvaldo Rodrigues da Cunha, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil; MRC, Maurício Rivera-Correa Field Number; MTR, Miguel Trefault Rodrigues Field Number at USP; MZUFBA, Museu de Zoologia da Universidade Federal da Bahia, Salvador, Bahia, Brazil; MZUFV, Museu de Zoologia “João Moogen”, Universidade Federal de Viçosa, Minas Gerais, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil; NMP6V, National Museum, Prague, Czech Republic; PHV, Paula H. Valdujo Field Series; PS, Pablo Suárez Field Number; TG, Taran Grant Field Series; UFMT, Zoological Collection of the Universidade Federal do Mato Grosso, Cuiabá, Mato Grosso, Brazil; UNIRIO, Herpetological Collection of the Universidade Federal do Estado do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil; USP, Miguel Trefaut Rodrigues Collection at Departamento de Zoologia do Instituto de Biociências da USP; USNM, Smithsonian National Museum of Natural History, Washington, D.C., USA; WCAB, Werner C. A. Bokermann Collection, deposited in MZUSP; WED, William E. Duellman Field Numbers; ZFMK, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Cologne, Germany; ZUEC, Museu de História Natural, Universidade de Campinas, Campinas, São Paulo, Brazil.

Character definitions, coding, and scoring

Characters are understood as historical transformations series (see Grant and Kluge, 2004) described in terms of variables and character states as different values for these variables i.e. mutually exclusive conditions of a character (Grant and Kluge, 2004; Sereno, 2007). We scored the co-occurrence of different character states within a single terminal or species as ambiguities. We used YBYRÁ (Machado, 2015) and TNT v.1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016) to identify and plot unambiguously optimized synapomorphies shared across all optimal trees, generating color-coded boxes to indicate if an apomorphic state occurs only in the clade in question (non-homoplastic) or also occurs in other clades (homoplastic), and if it is shared by all terminals of the clade (unique) or is subsequently transformed into one or more different states within the clade (non-unique).

Taxon sampling

We included the two known species of *Xenohyla*. Due to the broad geographical distribution and taxonomic confusion of many species of *Dendropsophus* (e.g. Kaplan, 1994; Köhler and Lötters, 2001a; Hawkins et al., 2007; Ortega-Andrade and Ron, 2013; Caminer and Ron, 2014; Gehara et al., 2014; Fouquet et al., 2015; Rivadeneira et al., 2018) we took several steps to correctly associate terminals with available names. First, we examined type specimens (or photographs of type specimens) of 80 species of *Dendropsophus*. Second, we collected new topotypic material for 15 species. Third, we generated 12S and/or 16S DNA sequences for as many *Dendropsophus* specimens representing as many localities as possible and performed preliminary analyses to test taxonomic determinations and assess intraspecific variation. Specifically, we generated mitochondrial DNA sequences for 274 *Dendropsophus* specimens, downloaded all *Dendropsophus* sequences available in GenBank, aligned the sequences using MAFFT (Katoh et al., 2005) with default parameters, ran preliminary searches in TNT v. 1.5 (Goloboff et al., 2008), and calculated uncorrected pairwise distances with MEGA5 (Tamura et al., 2011). These preliminary analyses enabled us to select terminals representing the diversity of each lineage while limiting the total number of terminals included in our analysis.

Not all species were scored for phenomic characters. Since maximally divergent taxa within a given group provide a stronger test of its monophyly than do morphologically similar taxa (Prendini, 2001), we aimed to include multiple species per species group (including the *Dendropsophus decipiens* and *D. rubicundulus* clades) representing the most disparate morphologies within each group. Failure to include data from a given species is due mainly to one or more of the following reasons: (1) the species is only known from the holotype or type series and tissue samples were unavailable; (2) tissue samples or sequences lack reliable identification due to (2a) absence of voucher specimens or (2b) species-level assignment not being published as of 1 May 2016; (3) it was not possible to collect the species because (3a) the species occurs entirely in countries where it was not possible to obtain collection permits, or (3b) the species was not detected in recent field expeditions.

Sequences of different specimens were treated as independent terminals. The two exceptions are GenBank sequences for two individuals of *Dendropsophus elegans* (12S-DQ380355 from specimen LM 3135, and 16S-AF308124 and CytB-AF308103 from specimen MZUSP 95033) and two individuals of *D. bifurcus* (12S partial-DQ380350 from specimen KU 217514 and 12S partial-16S AY362975 from a specimen with no voucher) that were combined into single terminals representing the respective species.

Outgroup selection

Prior knowledge is used heuristically to perform a severe test of prior beliefs about ingroup evolution. Previous phylogenetic studies have obtained Dendropsophini as the poorly supported sister taxon of Pseudini (Wiens et al., 2010; Duellman et al., 2016) or Sphaenorhynchini (Faivovich et al., 2005). As such, we included species from the genera of these tribes as outgroup exemplars. Furthermore, we included some species of Scinaxini (*Scinax*) and Lophyohylini (*Phyllodytes luteolus* and *Itapotihyla langsdorffii*) as more distant outgroups.

The phenomic characters of *Sphaenorhynchus prasinus* were combined with sequences of *S. dorisae*, as were two individuals of *Itapotihyla langsdorffii* for one of the terminals representing the species (Appendix S3). Finally, after reviewing literature records and available material, we concluded that neither larval descriptions nor reliably identified larvae were available for *Phyllodytes luteolous*. Except for *P. gyrinaethes*, all *Phyllodytes* larvae are similar (Caramaschi et al., 1992; Peixoto et al., 2003; Vieira et al., 2009; Santos et al., 2019). Hence, we used *P. melanomystax* tadpoles to score *Phyllodytes* larval morphology.

Molecular data

Gene sampling was based on recent studies of *Dendropsophus* relationships (Faivovich et al., 2005; Wiens et al., 2005; Wiens, 2006; Moen and Wiens, 2009; Wiens et al., 2010; Pyron and Wiens, 2011). We sequenced the mitochondrial H-strand transcription unit 1 (H1), which includes 12S ribosomal (12S), tRNAval and 16S ribosomal (16S) sequences, generated in four to five fragments (approximately 2470 bp), fragments of cytochrome *b* using two primers pairs (CytB; 400–870 bp), the barcode fragment of cytochrome oxidase *c* subunit I (COI; 647 bp), and the nuclear genes rhodopsin (RHOD; 316 bp), tyrosinase (TYR; 532 bp), recombination activation gene 1 (RAG-1; 428 bp), proopiomelanocortin A (POMC; 522 bp), and seventh in absentia (SIA; 397 bp) were sequenced using the primers listed in Appendix S5.

DNA sequencing followed Faivovich et al. (2005), with minor modifications. Whole cellular DNA was extracted from frozen and ethanol-preserved tissues (usually liver or muscle) using the DNeasy (QIAGEN) isolation kit. DNA amplification was carried out in a 25 µL reaction using either puRe Taq Ready-To-Go PCR beads (Amersham Biosciences, Piscataway, NJ, USA) or Fermentas Master Mix (Thermo Fisher Scientific, Waltham, MA, USA) and conducted on M.J. Research PTC-100 and Axygen Maxygene thermocyclers.

Different thermocycling protocols were followed according to the primer pair. For most fragments, the PCR program included an initial denaturing step of 2 min at 94 °C followed by 35 cycles of amplification (94 °C for 30 s, 48–56 °C for 30 s, 72 °C for 2 min) and a final extension step at 72 °C for 10 min. For nuclear primers, the usual program comprised an initial denaturing step of 2 min at 94 °C followed by 35 cycles of amplification (94 °C for 30 s, 52–56 °C for 30 s, 60–72 °C for 2 min) and a final extension step at 60–72 °C for 10 min. Amplified PCR products were confirmed on 1.0%–1.5% agarose gels stained with either ethidium bromide or blue-green or gel-red loading dyes.

Subsequent steps followed either of two procedures:

1. PCR amplification products were desalted and concentrated using either Ampure (Agencourt Biosciences, Beverly, MA, USA) or GE GFX PCR purification kits and labelled with fluorescent-dye labels terminators (ABI Prism Big Dye Terminators v. 1.1 cycle sequencing kits; Applied Biosystems, Foster City, CA, USA). The labelled PCR products were cleaned using cleanSEQ (Agencourt Biosciences) and sequenced with an ABI 3730XL (Applied Biosystems) or;
2. Unpurified PCR products were sent to Macrogen Inc. (South Korea) for purification and sequencing using an ABI 3730XL.

Samples were sequenced in both directions to check for errors, although a few fragments could only be sequenced in one direction. Chromatograms were read and contigs made using the sequence editing software Sequencher 3.0 (Gene Codes, Ann Arbor, MI, USA). Final contigs were edited with BioEdit (Hall, 1999) or MEGA version 5 (Tamura et al., 2011).

For GenBank sequences (see Appendix S3), we selected outgroup and ingroup terminals for which the highest number of gene sequences were available. Multiple individuals of a given species with the same amount of available data were chosen in order to represent the distinct lineages identified previously [e.g. *Dendropsophus minutus* A and B lineages of Jansen et al. (2011)].

Unused sequences

In addition to the sequences used in our analysis, four more gene fragments are available in GenBank for species of *Dendropsophus*, including one mitochondrial (a fragment of the NADH dehydrogenase subunit I, ND1; 1295 bp), and three nuclear (Cellular myelocytomatosis exons 2 and 3, C-myc2 and 3; approximately 460 bp each, and 28S ribosomal RNA ribosomal, 713–757 bp) loci. We excluded these sequences because they were available for only nine, six, six, and 16 species, respectively, and we did not include data scored for fewer than 20 species.

Phenomic data

General procedures. We examined 1778 specimens (1685 adults and 93 larvae), representing both ingroup (1607) and outgroup (171) taxa (Appendix S4). Phenomic character observations were coded into a data matrix using Mesquite (Maddison and Maddison, 2010). Skeletal characters were scored from cleared and double-stained specimens (Taylor and Van Dyke, 1985) or dry skeletons. Dissections were made with the aid of Nikon SMZ 800 or SMZ 1500 stereomicroscopes. Photographs were taken using the Nikon NIS-Elements D program and a Nikon Digital camera DS-Fi1 attached to an SMZ 1500.

Anatomical terminology is based on numerous publications depending on the character system. We followed Duellman (1970) for external morphology, Trueb (1973, 1993) for cranial and postcranial osteology, Fabrezi (1992) for carpal osteology, Fabrezi (1993) for tarsal osteology, Trewavas (1933) for larynx morphology, Jurgens (1971) for nasal cartilages morphology, Luna et al. (2018) for nuptial pad morphology, Gaupp (1896) for other regions of the body, and Altig and McDiarmid (1999) for external larval morphology. We use phenomic in the sense of O'Leary et al. (2013). Anatomical characters were coded only on the basis of gross dissection, which is potentially problematic for glandular characters. Although granular and mucous glands are distributed over most of the skin, specialized acini can form clusters of more or less well-individualized units (Toledo and Jared, 1995). Although histochemistry and light and electron microscopy can provide much more information about these glandular clusters than simple observation under a dissection microscope, it is still possible to recognize some of these clusters and often propose specific functions for them (e.g. Noble, 1927). Here, the presence of these clusters was established by external observation or by gross dissection.

The final phenomic matrix included 201 characters: 101 adult cranial osteological, three myological, 59 adult external morphological, one karyological, 21 larval external morphological, 14 adult visceral, one of natural history, and one biochemical characters (see Appendix S6 for details; an additional copy can be found at: http://morphobank.org/permalink/?P3755).

Phylogenetic analysis

General procedures. Polymorphisms were treated as ambiguities for both morphological and molecular datasets (the latter, using standard IUPAC codes). Discrepancies between our and previously published observations were scored as polymorphisms unless we were able to correct the published account by examining the same voucher specimen(s).

We used BLAST (Altschul et al., 1997) to compare new sequences with those in GenBank to check for contamination and other errors (e.g. tissue mislabelling or voucher misidentification). As an initial procedure to check for errors (i.e. tissue mislabelling, voucher misidentification, or errors in morphological matrix scoring), sequences were aligned with CLUSTALW using MEGA version 5 (Tamura et al., 2011). These alignments of each independent fragment and the morphological matrix were subjected to quick analyses by using 200 random addition sequence Wagner builds (RAS) plus three rounds of tree bisection reconnection (otherwise default options) run in TNT v. 1.5 (Goloboff et al., 2008) treating gaps as missing data. Mesquite v. 3.03 (Maddison & Maddison 2010) and Sequence Matrix v.1.7.8 (Vaidya et al., 2010) were used for file conversion (e.g. FASTA to TNT) and concatenation. Results of the quick analyses guided sequence and voucher identification checking.

Final phylogenetic analyses. For the complete dataset, we included 210 terminals, sampling 12 outgroup species, the two species of *Xenohyla*, and 93 of the 108 recognized species of *Dendropsophus*. The phenomic dataset includes 46 terminals, one per species (34 *Dendropsophus*, one *Xenohyla* and 11 outgroup species); all other terminals have only molecular data. All species in this dataset are represented by conspecific sequences in the molecular matrix—with two exceptions for the outgroups (see Appendix S3 for a cross-reference). Phenomic character assessment resulted in 201 transformation series (i.e. characters) that are listed and discussed in Appendix S6. A complete matrix is provided in Appendix S7.

The most taxonomically complete fragment is 16S rRNA, which is available for 205 terminals (97.5%). The least complete fragment is POMC, available for only 62 terminals (30.5%). Some species (e.g. *D. decipiens*) are represented by more than one terminal in the molecular dataset. The most complete of them (i.e. the individual terminal with the greatest number of available sequences) was associated with morphological data. Correspondence between terminals included in the phenomic and molecular partitions are given in Appendix S3.

We performed a total evidence (i.e. character congruence) analysis (Kluge, 1989, 2004) of the DNA sequences and phenomic characters using the parsimony optimality criterion and applying equal weights to all transformations. We treated each sequenced individual as a separate terminal and associated the phenomic data coded for the corresponding species as a whole with only one terminal. Trees were rooted using *Phyllodytes luteolus*. On the basis of the arguments of Padial et al. (2014; see also Kluge and Grant, 2006; Grant and Kluge, 2009), we employed tree-alignment (e.g. Sankoff, 1975; Wheeler, 1996; Varón and Wheeler, 2012; Varón and Wheeler, 2013) in POY v.5.1.1 (Wheeler et al., 2015), which tests hypotheses of nucleotide homology dynamically by optimizing unaligned DNA sequences directly onto alternative topologies (Kluge and Grant, 2006; Grant and Kluge, 2009; Wheeler et al., 2015) while simultaneously optimizing prealigned transformation series (e.g. morphology) as standard matrices. All computer-intensive analyses were run on Ace, a high-performance computing cluster at Universidade de São Paulo composed of 12 quad-socket AMD Opteron 6376 16-core 2.3-GHz CPU, 16 MB cache, 6.4 GT/s compute nodes (= 768 cores total), eight with 128 GB RAM DDR3 1600 MHz (16 × 8 GB), two with 256 GB (16 × 16 GB), and two with 512 GB (32 × 16 GB), and QDR 4× InfiniBand (32 GB/s) networking.

Our analyses included several steps. First, using the standard direct optimization algorithm (Wheeler, 1996), we ran six 12 h searches using 704 CPUs (= 8448 CPU-hours each, total = 50 688 CPU-hours) using the command *search*, which implements a driven search composed of RAS, Subtree Pruning and Regrafting (SPR) and Tree Bisection and Reconnection (TBR) branch swapping (RAS + swapping, Goloboff, 1996), Parsimony Ratcheting (Nixon, 1999), Tree Fusing (Goloboff, 1999), alternating between the specified optimization algorithm (standard direct optimization in this case) and static-approximation, which searches using the implied alignment of the best tree in memory.

Next, we calculated the cost of the optimal tree from the previous analyses using the approximate iterative pass algorithm (Wheeler, 2003b) and generated the implied alignment for the best tree in memory (Wheeler, 2003a). Finally, to corroborate the length reported by POY and search for better and/or additional trees given the implied alignment, we performed an additional driven search of the implied alignment in TNT v.1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016), stopping once a stable consensus had been reached five times independently (command line: xmult = level 10 chklevel 5 consense 5).

We calculated Goodman-Bremer (GB) values (Goodman et al., 1982; Bremer, 1988; Bremer, 1994; Grant and Kluge, 2008) in TNT v.1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016) using the implied alignment and the parameters specified in the bremer.run macro (for details see Goloboff et al., 2008; macro available at http://www.lillo.org.ar/phylogeny/tnt/). Shorter suboptimal trees might be found by calculating the optimal tree-alignment for each visited topology, but time requirements would be prohibitive unless searches were extremely superficial. Moreover, Padial et al. (2014) found that using the implied alignment to estimate support overestimates GB values considerably less than when GB is calculated using a MAFFT v.7 (Katoh and Standley, 2013) similarity-alignment due to topology-specific placement of gap characters.

Results

The length of the single most-parsimonious tree (MPT) found in POY was 31344 steps. The driven search of the implied alignment in TNT failed to find shorter trees but increased the number of MPTs to five, one of which is shown in Figs 1–4. A complete list of phenomic transformations is shown in Appendix S8. Topological conflict is restricted to two clades: the first includes multiple specimens of *Dendropsophus meridianus* and *D. pseudomeridianus*; the other is within the clade composed of *D. anataliasiasi*, *D. sanborni*, and *D. elianeae*.

Scinax is the sister taxon of all other taxa, and Pseudini is sister taxon of the clade including Sphaenorhynchini + Dendropsophini. All genera whose monophyly was tested were recovered as monophyletic (Fig. 1).

The *Dendropsophus microcephalus*, *D. minimus*, *D. parviceps* groups, and the *D. rubicundulus* clade, are not monophyletic as presently defined (sensu Faivovich et al., 2005) are not monophyletic. The *D. microcephalus* group is polyphyletic, as the *D. decipiens* clade (sensu Faivovich et al., 2005) and *D. ozzyi* are more closely related to other clades in *Dendropsophus*. The *D. parviceps* group is not monophyletic as the monophyletic *D. garagoensis* group is nested within it, and *D. ruschii* is more closely related to *D. ozzyi*. The *D. minimus* group is polyphyletic, with *D. riveroi* nested within the *D. microcephalus* group, and *D. miyatai* in a clade that is the sister taxon of the *D. leucophyllatus* group as currently defined.

The remaining recognized groups are monophyletic. The clade including *Dendropsophus ruschii* + *D. ozzyi,* here recognized as the *D. ruschii* group, is the sister taxon of a pectinate series including all remaining species groups of *Dendropsophus* (Fig. 2). This is followed by the former *D. decipiens* clade of Faivovich et al. (2005), here recognized as the *D. decipiens* group. Our results revealed important genetic diversity within this group, with samples labelled as *D. decipiens* recovered as paraphyletic with respect to samples of *D. haddadi* and *D. oliveirai*. Ferreira et al. (2015) did not associate *D. bromeliaceus* with any species group, but our results firmly places it within the *D. decipiens* group.

The *Dendropsophus decipiens* group is followed by a clade that includes the bulk of the paraphyletic *D. parviceps* group and a clade that includes the other groups (Fig. 2). The *D. parviceps* group is paraphyletic with respect to the *D. garagoensis* group, which is the sister taxon of a clade composed of *D. pauiniensis* + *D. koechlini*. *Dendropsophus praestans* is the sister taxon of the remaining species of the *D. garagoensis* group, as suggested previously by Kaplan (1999). Moreover, *D. schubarti* (currently assigned to the *D. parviceps* group) plus *D. miyatai* and *D. haraldschultzi* (both currently assigned to the *D. microcephalus* group) form the newly recognized *D. haraldschultzi* clade, which is sister taxon of the *D. leucophyllatus* group as currently defined (Fig. 3)—we consider these two aforementioned clusters of taxa as clades within a more broadly defined *D. leucophyllatus* group.

The clade including the bulk of the *Dendropsophus parviceps* group is followed by a clade including the *D. columbianus* and *D. molitor* groups, and a clade that includes the other groups. The *D. molitor* group includes two clades: one composed of *D. pelidnus* and *D. meridensis*, and another composed of *D. luddeckei* and *D. molitor*. In the *D. columbianus* group, *D. norandinus* is the sister taxon of *D. carnifex* and a clade composed of *D. columbianus* and *D. bogerti*, with *D. columbianus* paraphyletic with respect to *D. bogerti* (Fig. 2).

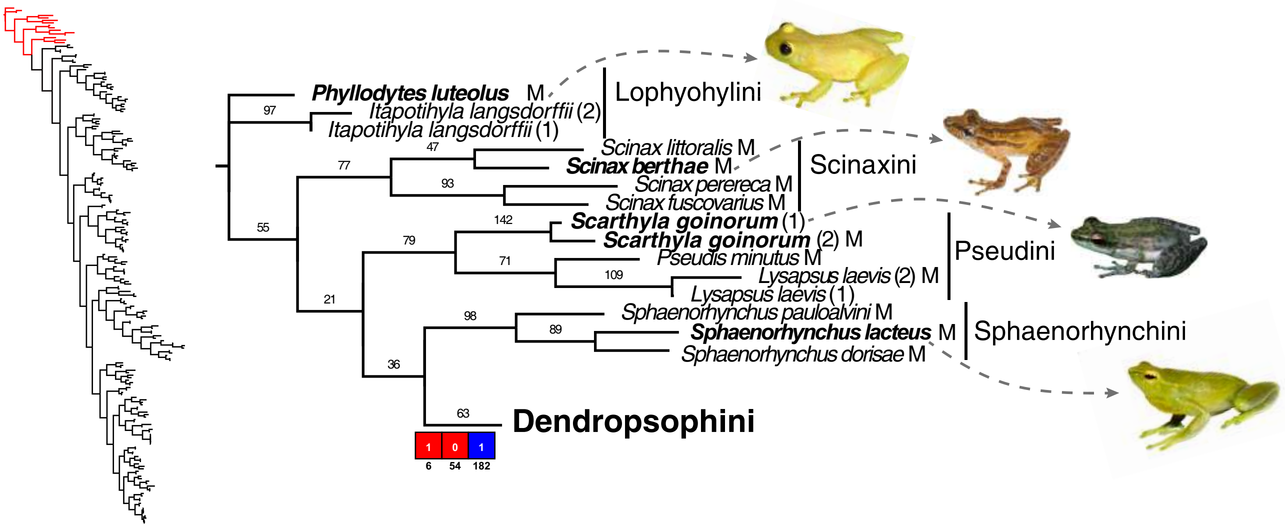

Fig. 1. Section of one of the five equally optimal hypotheses found in POY—Outgroup relationships. Tree shows proportional branch-lengths (from one of the most parsimonious trees), unsupported nodes collapsed, all supported nodes labelled with Goodman-Bremer values, and selected nodes labelled with unambiguously optimized phenomic synapomorphies (red square = unique, homoplastic; blue square = non-unique, homoplastic; character number below squares; plesiomorphic-apomorphic character-states inside squares). Information on phenomic character and character states can be found in Appendix S6. See Figs 2–4 for the other sections of the tree (Photos by PLVP, Thiago Pezzutti, TG, and Fernando Ayala. Boldface names correspond to the species depicted to represent each nominal clade. Frogs not to scale.)

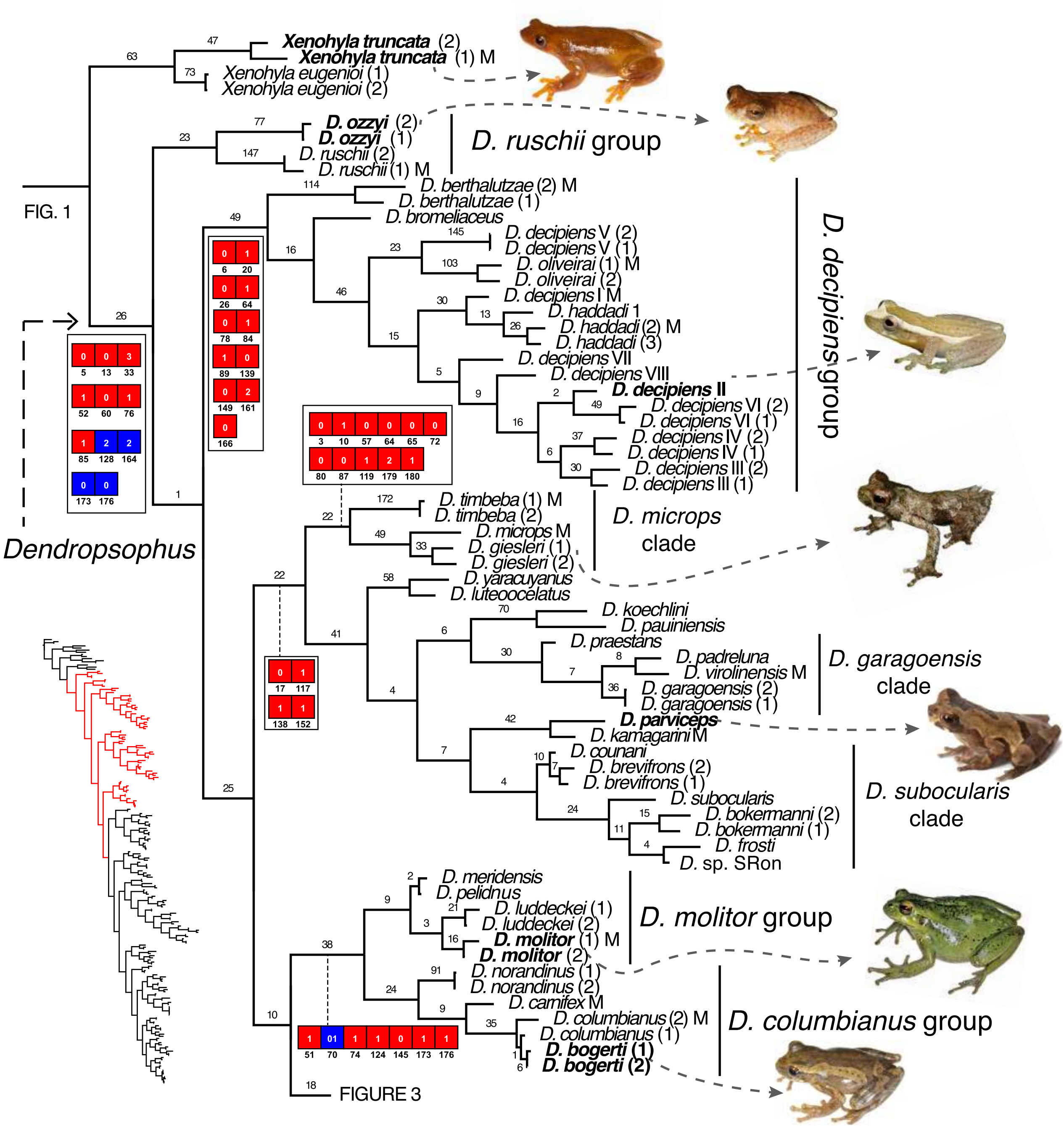

Fig. 2. Section of one of the five equally optimal hypotheses found in POY—*Xenohyla* and *Dendropsophus* (partial): *Dendropsophus ruschii*, *D. decipiens*, *D. parviceps*, *D. molitor*, and *D. columbianus* groups. Tree shows proportional branch-lengths (from one of the most parsimonious trees), all supported nodes labelled with Goodman-Bremer values, and selected nodes labelled with unambiguously optimized phenomic synapomorphies (red square = unique, homoplastic; blue square = non-unique, homoplastic; character number below squares; plesiomorphic-apomorphic character-states inside squares). Information on phenomic character and character states can be found in Appendix S6. See Figs. 1 and 3–4 for the other sections of the tree. (Photos by PLVP, Santiago Ron, William Duellman, MRC. Boldface names correspond to the species depicted to represent each nominal clade. Frogs not to scale.)

The clade composed of the *Dendropsophus columbianus* + *D. molitor* groups is followed by the *D. marmoratus* group and a clade that include the other groups. In the *D. marmoratus* group, *D. nahdereri* is recovered as sister taxon of the remaining species, which are recovered in two clades. One includes *D. seniculus* as sister taxon of a clade including *D. novaisi* + *D. dutrai*, two very similar species (see Gomes and Peixoto, 1996), with *D. novaisi* being

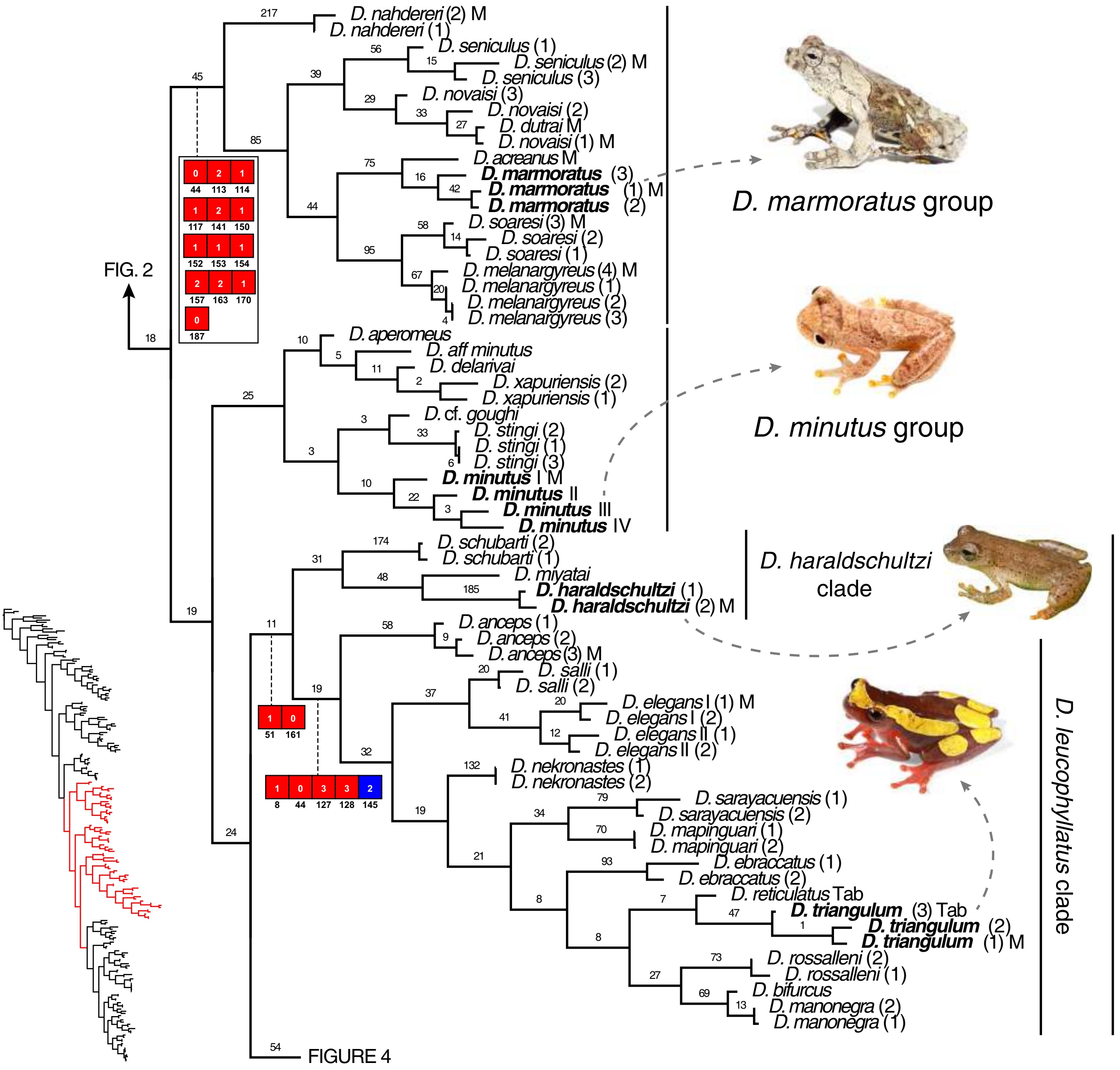

Fig. 3. Section of one of the five equally optimal hypotheses found in POY—*Dendropsophus marmoratus*, *D. minutus*, and *D. leucophyllatus* groups. Tree shows proportional branch-lengths (from one of the most parsimonious trees), all supported nodes labelled with Goodman-Bremer values, and selected nodes labelled with unambiguously optimized phenomic synapomorphies (red square = unique, homoplastic; blue square = non-unique, homoplastic; character number below squares; plesiomorphic-apomorphic character-states inside squares). Information on phenomic character and character states can be found in Appendix S6. See Figs. 1–2 and 4 for the other sections of the strict consensus tree. (Photos by Diego Quirola, Juan Carlos Sánchez, PLVP, Santiago Ron. Boldface names correspond to the species depicted to represent each nominal clade. Frogs not to scale.)

paraphyletic with respect to *D. dutrai*. The other clade is composed of two species pairs: *D. acreanus* + *D. marmoratus,* and *D. melanargyreus* + *D. soaresi* (Fig. 3).

The *Dendropsophus marmoratus* group is followed by the *D. minutus* group, and a clade that includes the other groups. The *D. minutus* group includes two major clades. The first is composed of a pectinated series including *D. aperomeus*, *D.* aff. *minutus*, *D. delarivai*, and *D. xapuriensis*. The second is composed of several lineages of *D. minutus* as the sister clade of *D. stingi* and *D.* cf. *amicorum* (Fig. 3).

The sister taxon of the *Dendropsophus minutus* group includes two major clades. One is composed of the herein newly recognized *D. haraldschultzi* clade, *D. anceps*, and the *D. leucophyllatus* group as currently

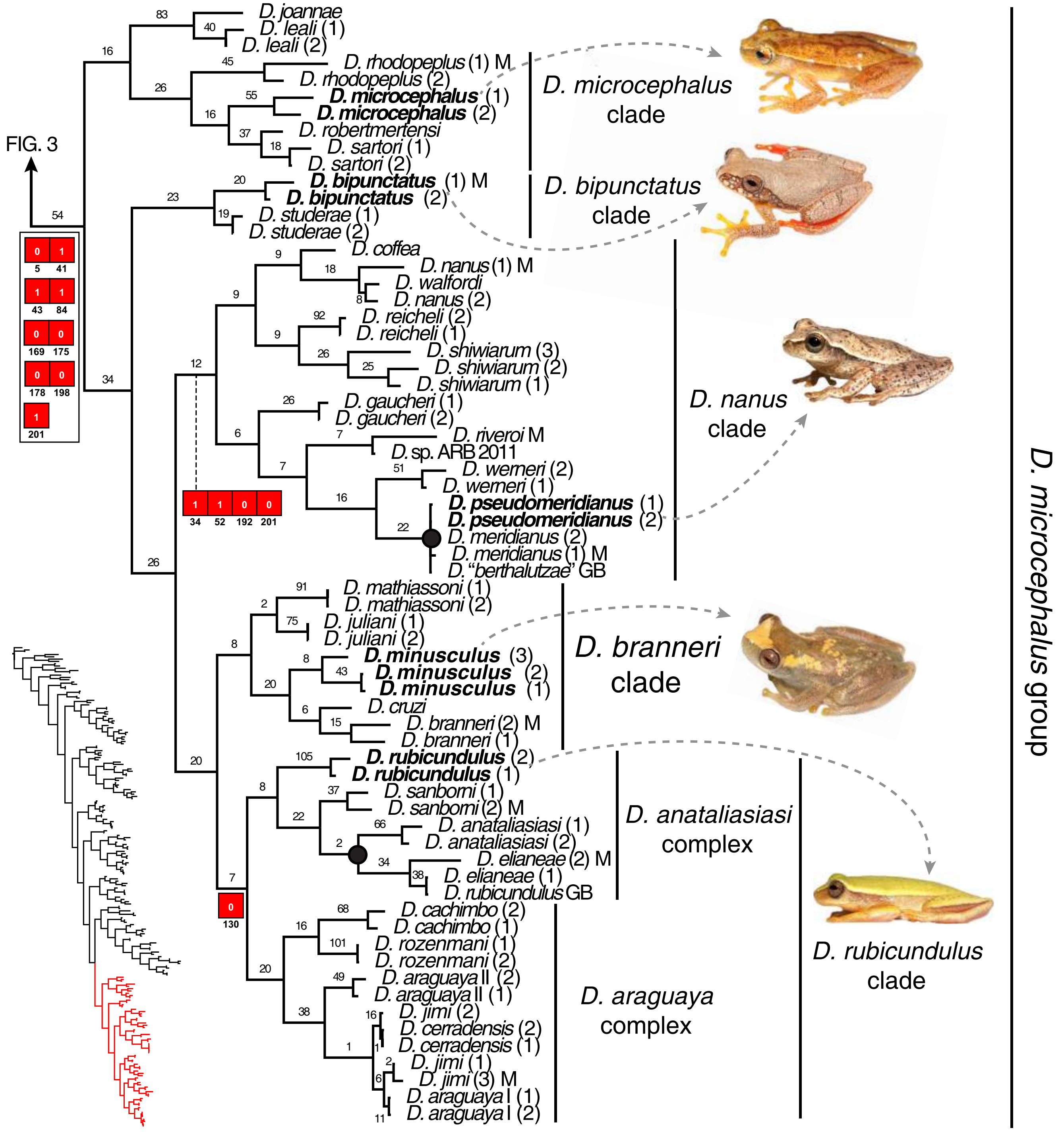

Fig. 4. Section of one of the five equally optimal hypotheses found in POY—*Dendropsophus microcephalus* group. Tree shows proportional branch-lengths (from one of the most parsimonious trees), unsupported nodes collapsed, black circles indicate nodes that collapse in the consensus, all supported nodes labelled with Goodman-Bremer values, and selected nodes labelled with unambiguously optimized phenomic synapomorphies (red square = unique, homoplastic; blue square = non-unique, homoplastic; character number below squares; plesiomorphic-apomorphic character-states inside squares). Information on phenomic character and character states can be found in Appendix S6. See Figs 1–3 for the other sections of the strict consensus tree. (Photos by PLVP, Rodrigo Tinoco. Boldface names correspond to the species depicted to represent each nominal clade. Frogs not to scale.)

understood. The other clade corresponds to the bulk of what has been assigned to the *D. microcephalus* group. The *D. haraldschultzi* clade and *D. anceps* are heretofore considered members of a redefined *D. leucophyllatus* group (for details see below). *Dendropsophus anceps* is the sister taxon of a pectinate series that includes one clade composed of the reciprocally monophyletic *D. salli* and *D. elegans*, followed by *D. nekronastes*, a clade that includes *D. sarayacuensis* and *D. mapinguari*, *D. ebraccatus*, *D. reticulatus* and *D. triangulum* (as a clade), and *D. rossalleni*, which is sister of a clade composed of *D. bifurcus* and *D. manonegra* (Fig. 3).

The bulk of what is currently recognized as the *Dendropsophus microcephalus* group is monophyletic (Fig. 4). The group includes the *D. rubicundulus* clade of Faivovich et al. (2005), which is recovered as paraphyletic with respect to *D. sanborni*. This group is divided in to a pectinate series of five clades. The first comprises a clade with *D. joannae* + *D. leali* that is sister of a clade that includes *D. rhodopeplus* as sister of the *D. microcephalus* clade (*D. microcephalus*, *D. robertmertensi* + *D. sartori*). The second includes two species with the dark brown dorsum: *D. bipunctatus* and *D. studerae*. The third includes 10 brownish yellow species arranged in two clades, the first arranged as one clade composed of the reciprocally monophyletic *Dendropsophus reichlei* and *D. shiwiarum*, which is sister of a clade composed of *D. coffea*, *D. nanus*, and *D. walfordi*, being *D. coffea* sister of the non-reciprocally monophyletic samples of *D. nanus* and *D. walfordi*, and the second forming the pectinate series of *D. gaucheri*, *D. riveroi*, *D. werneri*, and the non-reciprocally monophyletic samples of *D. pseudomeridianus* and *D. meridianus* (one of those being previously misidentified as D. berthalutzae in literature). The fourth is composed of five species with bluish green tints (especially in the male vocal sacs) in living specimens. This fourth clade is internally divided into two clades: one composed of *D. mathiassoni* + *D. juliani* and the other of *D. minusculus* as sister of *D. cruzi* and *D. branneri*. The last clade is equivalent to the *D. rubicundulus* clade of Faivovich et al. (2005) with the inclusion of *D. sanborni*. This clade has two internal clades: one composed of *D. anataliasiasi*, *D. elianeae*, *D. sanborni*, and *D. rubicundulus*, the other in which samples of *D. cachimbo* and *D. tritaeniatus* form a clade sister of a clade that has *D. araguaya* II as sister of the non-reciprocally monophyletic samples of *D. araguaya* I, *D. jimi*, and *D. cerradensis* (see Fig. 4).

With the exception of the *Dendropsophus ruschii* group, and a particular situation with the *D. minutus* group, phenomic synapomorphies are known for all newly recognized species groups—these are listed and discussed below.

Discussion

The monophyly of Dendropsophini and Dendropsophus

The monophyly of Dendropsophini (sensu Faivovich et al., 2005) has been the most controversial among the tribes of Hylidae. While some analyses have recovered this tribe as monophyletic (Wiens et al., 2005; e.g. Moen and Wiens, 2009), others have not (e,g, Pyron and Wiens, 2011). Our taxon sampling was not designed to provide a stringent test of the relationships of Dendropsophini sensu, e.g. Faivovich et al. (2005) with other hylines. Nevertheless, we recover *Dendropsophus* as sister to *Xenohyla* in accordance to the recent redefinition of Dendropsophini (Duellman et al., 2016; Faivovich et al., 2018; Araújo-Vieira et al., 2019).

Araújo-Vieira et al. (2019) recovered five phenomic synapomorphies for *Dendropsophus* + *Xenohyla* (character states for the clade given in brackets): Absence of black lateral line in adults [cs.108(0)]; absence of ornamentation on the ventral surfaces of adults [cs.118 (0)]; absence of internal dermal ornamentation on tarsus [cs.122(0)]; [cs.148(1)] presence of a medial raphe of the *m. intermandibularis*; [cs.176(1)] presence of the *m. flexor teres hallucis*. None of these characters were scored in our dataset.

Xenohyla and *Dendropsophus* (i.e. Dendropsophini) share three unique phenomic synapomorphies in our results: posterior margin of frontoparietals reaching or slightly covering epiotic eminences [cs.6(1)], presence of processus prenasalis medius [cs.54(0)], and the frontally positioned larval nostrils [cs.182(1)] (Fig. 1). While the first two are not clearly related to any behaviour or evolutionary trend, the frontally positioned larval nostrils [cs.182(1)] are found only in these genera within our dataset and may be related to predatory behaviour in these larvae.

Captive tadpoles of *Xenohyla truncata* actively consumed another tadpole (species unknown; VGDO pers. obs.) and tadpoles of *Dendropsophus minutus* are known to be active predators (Peixoto and Gomes, 1997). Dias et al. (2019) noted that larvae of *Dendropsophus decipiens* have a combination of buccopharyngeal character states that suggests a less specialized predator (within carnivore or omnivore diets) than the tadpoles of *D. microcephalus* and *D. nanus*. Nevertheless, intestinal anatomy of *D. nanus* larvae suggests that this species is a macrophagous carnivore (Vera Candioti et al., 2004). Thus, a broader interpretation of these data is that the ancestor of Dendropsophini underwent a larval ecological shift from bottom-scraping to active mid-water predation. Also, the shift from laterally ovoid larval bodies—like those of *D. ruschii* and the *D. decipiens* group (see Bokermann, 1963b; Weygoldt and Peixoto, 1987; Pugliese et al., 2000;

Lourenço-de-Moraes et al., 2012)—to a more triangular shape [c.166], like those found in the *D. leucophyllatus* and *D. microcephalus* groups (see Duellman, 1970 figures), are indicative of increased specialization in mid-water predation during the evolutionary history of the tribe.

Although a general reduction of the number of elements in the buccopharyngeal cavity has been suggested as a putative synapomorphy for the clade composed of *Dendropsophus*, *Lysapsus*, *Pseudis*, *Scarthyla*, *Scinax*, and *Sphaenorhynchus* (Dendropsophini sensu Faivovich et al., 2005), its individual elements vary in shape, presence, and taxonomic distribution. The buccopharyngeal cavity of larval *Dendropsophus* is almost unexplored, but some elements as the absence of lingual papillae may be a synapomorphy of *Dendropsophus* or Dendropsophini (see Dias et al., 2019).

It is remarkable that *Xenohyla* presented no phenomic synapomorphies. Izecksohn (1996) hypothesized that *Xenohyla* was related to *Scinax* and, especially, *Sphaenorhynchus*, on the basis of multiple morphological similarities. This resemblance is reflected in our results through the many homoplastic character states shared between these genera. Faivovich et al. (2005) understood the limb emergence scars to be pectoral glands (like those found in many *Dendropsophus*; see c.160 discussion in Appendix S6) and rejected them as a synapomorphy of *Xenohyla* (corroborated herein), but highlighted two possible synapomorphies for *Xenohyla*, discussed below: the presence of a small, transverse process on the urostyle, and frugivory.

We have found transverse processes on the urostyles in *Dendropsophus melanargyreus* (unilateral, left present) and *D. nahdereri* (bilateral). We have found little variation in urostyles and the uniqueness and non-bilaterality of those with processes suggest that they might be teratologies. Herein, we took a cautionary approach and treated the urostyle transverse processes as a teratology—however, we recognize that a study focusing on this variation is needed.

As far as we are aware, *Xenohyla truncata* is the only known amphibian to actively include a large proportion of fruits in its diet (da Silva et al., 1989; da Silva and de Britto-Pereira, 2006), but diet is entirely unknown for *Xenohyla eugenioi*. We have not scored this character in the present contribution because food habit in *Dendropsophus* is mostly unknown and biased to the *D. microcephalus* group (see Gutiérrez-Cárdenas et al., 2013), which are indeed carnivorous. Therefore, frugivory remains a potential synapomorphy of *Xenohyla*, but a broader understanding of hylid diet is needed to adequately test this assumption.

Both species of *Xenohyla* exude a strong, curry-like smell (and flavour; VGDO, JF and PLVP pers. obs.). Carvalho et al. (2008) studied skin secretions of *Xenohyla truncata* and found only *N*-phenyl-acetamide (which is odourless). These authors suggested that such chemical content might be a consequence of groundwater pollution. We did not score this character in our matrix because, unfortunately, the condition of other Dendropsophini species is unknown—in fact, frog volatile compounds are nearly unknown in general (see Brunetti et al., 2015). Nevertheless, we emphasize that the presence of compound(s) responsible for the curry odour and flavour might be a synapomorphy for *Xenohyla*, as we are unaware of its presence in any other hylid species.

Eleven character states optimized as synapomorphies of *Dendropsophus*: Posterior third of medial margins of frontoparietals slender, not expanding medially more than the medial edge of the epiotic eminescences, leaving nearly all tectum synoticum exposed [cs.5(0)]; operculum dorsally not visible [cs.13(0)]; palatines medially reaching the level of vomer dentigerous process [cs.33 (3)]; crista subnasalis with a bicapitate ventral edge [cs.52(1)]; anterior process of hyoid absent [cs.60(0)]; arytenoids with inner longitudinal ridges [cs.76(1)]; posterior margins of the arytenoids clearly passing cricoid ring in lateral view [cs.85(1)]; webbing insertion between fingers IV and V (scored on IV) short, reaching the subarticular tubercle III level [cs.128(2)]; a 2n = 30 chromosomal complement [cs.164(2)]; the lack of anterior labial tooth rows (ALTR) [cs.173(0)]; and the presence of two posterior labial tooth rows (PLTR) [cs.176(1)]—apart from 164(2), all with many instances of secondary modifications.

Araújo-Vieira et al. (2019) found 13 synapomorphies for *Dendropsophus*. Given their small taxonomic sample, it is remarkable that of those, six are directly concordant with our results: widely separated frontoparietals, anterior end of the quadratojugal that does not contact the maxilla, absence of the anterior process of hyale, absence of anterior larval teeth rows, the presence of two posterior tooth rows (although their [cs.141(0)] refers to "one or two posterior tooth rows"), and the 2n = 30 chromosome complement. Of the remaining seven, four are from the muscular character systems (*m. intermandibularis* juxtaposes the posterior margin of the *m. submentalis* medially [their cs.147(2)]; well-developed anterior development of the *m. interhyoideus* [their cs.151(2)]; posterior extension of the fold of the *m. interhyoideus* reaches the posterior margin of the *m. pectoralis sternalis* [their cs. 152(4)]; absence of a *pars dorsalis* of the *m. sternohyoideus* [their cs. 161(0)]) that was not explored in the present contribution. The three remaining were not reviewed in our material (presence of a cartilaginous lamina that extends from cartilaginous plate to the inferior margin of the oblique cartilage [their 62(1)]; submarginal papillae of the oral disc absent [their cs. 135(0)]); absence of a gap in the first PLTR [cs 142(0)].

Our results support the findings of Suarez et al. (2013) and Araújo-Vieira et al. (2019), where the 2n = 30 chromosome complement is indeed a synapomorphy of *Dendropsophus*, as long has been suggested in the literature. To date, the only other hylid recorded to have 2n = 30 is *Litoria angiana* (Duellman, 1967; Catroli and Kasahara, 2009), but this state also occurs in other anurans [e.g. *Pristimantis paulodutrai* (see Siqueira et al., 2008), *Pipa parva* (Morescalchi, 1981), and *Indirana* sp. (Vences et al., 2000)]. Given that most other hylines have a chromosome complement of 2n = 24 or less, *Dendropsophus* is an excellent model to study chromosome evolution and homeology (Suarez et al., 2013).

Faivovich et al. (2005) suggested a 1/2 labial tooth row formula as a synapomorphy of *Dendropsophus* following Duellman and Trueb (1983) and Wogel et al. (2000). Our topological results corroborate the loss of P3 as a synapomorphy of this clade [cs.176(1)], but reject the presence of only A1 as a synapomorphy, instead indicating that the complete loss of the ALTR [cs.173(0)] is a synapomorphy of *Dendropsophus* (as suggested by Araújo-Vieira et al., 2019). We found that the ALTR re-evolved three times within the genus: (i) *D. anceps*, (ii) *D. minutus*, and (iii) the *D. columbianus* + *D. molitor* groups. Even within these groups, information in the literature for species not included in our morphological matrix highlights both the presence [e.g. *D. stingi* (see Kaplan, 1994)] and absence [e.g. *D. norandinus* (see Rivera-Correa and Gutiérrez-Cárdenas, 2012)] of the ALTR.

PLTR number varies greatly within *Dendropsophus*. *Dendropsophus elegans*, *D. microps*, *D. nahdereri*, *D. oliveirai*, *D. ruschii*, and *D. soaresi* have a single PLTR, whereas *D. anceps* has three. For the moment, the only clade for which the number of PLTR is a synapomorphy is the *D. columbianus* + *D. molitor* group [cs.176 (1), in which the presence of two PLTR is synapomorphic. *Dendropsophus* larvae are understudied and this scenario might be overturned with the addition of more data especially for internal clades of the *D. decipiens* and the *D. minutus* groups.

The literature is not clear regarding the labial tooth row (LTR) number of some species of *Dendropsophus*. For example, Kaplan and Ruiz-Carranza (1997) reported that *D. padreluna* and *D. virolinensis* have ALTR but give a contradictory LTR formula of "0/02" for these species, and material of those species examined for the present study lacked ALTR.

Kaplan (2017) also found tooth ridges on the anterior labium of three species of the *Dendropsophus microcephalus* group. Although he states that labial tooth rows are absent and that there is only one labial ridge, it is possible to see in his figure 2a,c, dark areas in the labial ridges that could correspond to labial teeth.

At least one study (Thibaudeau and Altig, 1988) suggested that LTR may appear and then atrophy during tadpole development. The tadpole of *Dendropsophus minutus* has been described at least five times (Bokermann, 1963b; Duellman, 1978; Cei, 1980; Heyer et al., 1990; Rossa-Feres and Nomura, 2006). According to Gehara et al.'s.(2014) results, other descriptions (e.g. Kenny, 1969; Duellman, 1978; Hero, 1990) might have been based on misidentified specimens. However, two studies (Rossa-Feres and Nomura, 2006; Ballen, 2018) report intraspecific variation in the number of LTR, thus suggesting that ALTR might vary ontogenetically. Therefore, the homology of individual LTRs deserves further investigation.

The presence of inner longitudinal ridges in the arytenoids [cs.76(1)] is a novelty in anuran anatomy. To date, no study of the anuran larynx has described such ridges. Comprehensive studies of these cartilages (e.g. Trewavas, 1933; Lambiris, 1994) made no references to such structures. Faivovich (2002) scored variation of the internal buttresses, which are transverse rather than longitudinal ridges. Assuming that the laryngeal morphology affects the sounds produced (e.g. Schmidt, 1965; Wilczynski et al., 1993), the diversity of sounds produced by *Dendropsophus* species (see Duellman, 1978; Cardoso and Haddad, 1984; Orrico et al., 2014) suggests that a more thorough study of laryngeal morphology is merited.

Faivovich et al. (2005) suggested the extreme reduction of the quadratojugal as a synapomorphy of *Dendropsophus*. We have found large variation in the morphology of this bone. The most unusual one was the "floating" quadratojugal of *Sphaenorhynchus*, lacking contact with either the squamosal or maxilla. In most *Dendropsophus*, the quadratojugal is absent or extremely reduced (see details on the character list); however, in the *D. decipiens* group, *D. haraldschultzi*, and females (but not in males) *D. elegans* the quadratojugal was present and in contact with both the squamosal and maxilla. Given our topology, the absence or extremely reduced quadratojugal [cs.18(0)] is ambiguously optimized due to the position of the *D. ruschii* group. Although we lack this information for *D. ozzyi*, any character state in that species would still result in an ambiguous optimization.

Species group monophyly and relationships

Faivovich et al. (2005) recognized nine species groups in *Dendropsophus* and assigned most species not included in their dataset to some of these groups based on previous associations by several authors. With our expanded taxon sampling, we retrieved some of those species groups paraphyletic, corroborating previous studies (Fouquet et al., 2011; Motta et al., 2012; Rivera-Correa and Orrico, 2013). Given this is the largest and most complete study of *Dendropsophus* phylogeny, we propose a new taxonomic arrangement for the genus based on our results. We recognize nine species groups and within three of them (i.e. *D. leucophyllatus*, *D. microcephalus*, and *D. parviceps* groups) we suggest some nominal clades to highlight specific morphological characteristics or particular relationships. Groups are listed successively according to the optimal topology shown in Figs 2–4.

The Dendropsophus ruschii *Group*

Characterization, diagnosis, and support. There are no phenomic synapomorphies for this group. For genomic synapomorphies see Appendix S8. For nodal support values, see Fig. 2. Species of this group have no conspicuous shared characteristics except for calls being composed of short thrilled notes with 3–5 pulses each (no secondary notes) and the fact that both are small species (SVL 18.5–27.9 mm for males and 26.7–29.0 mm for females; Orrico et al., 2014; Weygoldt and Peixoto, 1987).

Content (2 species). *Dendropsophus ozzyi* Orrico et al., 2014; *D. ruschii* (Weygoldt and Peixoto, 1987).

Distribution. The group has a disjunct distribution, with one species (*Dendropsophus ruschii*) found in the Atlantic Forest of Southeastern Brazil (states of Minas Gerais and Espírito Santo) and the other known from scattered localities in Amazonia, Madeira-Tapajós interfluvium at the border between the states of Amazonas and Pará (Brazil).

Comments. The group comprises two very different species that share no obvious phenomic similarities apart from those shared with other species of *Dendropsophus*. Note that those include the short-trilled calls (found in the *Dendropsophus decipiens* and *D. microcephalus* groups) and the small size (found in the *Dendropsophus decipiens*, *D. parviceps*, *D. minutus* and *D. microcephalus* groups and the *D. haraldschultzi* clade).

The Dendropsophus decipiens *Group*

Characterization, diagnosis, and support. This group has 11 phenomic synapomorphies, all with some degree of homoplasy: Posterior margin of frontoparietals not reaching epiotic eminences [cs.6(0)]; quadratojugal in contact with maxilla [cs.20(1)]; dentigerous processes of the vomers with scattered, unaligned teeth [cs.26(0)]; subretangular anterolateral process of hyoid [cs.64(1)]; arytenoids without internal buttresses [cs.78(0)]; cricoid esophageal margin in esophageal view straight [cs.84 (1)]; two distal prepolical elements [cs.89(1)]; pelvic girdle without melanin deposits [cs.139(0)]; ulnar fold absent [cs.149(0)]; pectoral glands arranged as scattered acini [cs.161(2)]; Larval body shape anteriorly abruptly ending, rounded, or oval in lateral view [cs.166(0)] (Fig. 2). For nodal support values see Fig. 2. For genomic synapomorphies see Appendix S8. Apart from the proposed phenomic synapomorphies, all species of the *Dendropsophus decipiens* group are small (combined SVLs range from 13.0–21.4 mm for males and 18.0–24.0 mm for females) with a brownish or pale yellow dorsum (which in most species also exhibits a frame-like pattern with paler interorbital and dorsolateral bands) and calls composed of short thrills with 4–6 pulses with no secondary notes. Thighs are creamy white.

Content (5 species). *Dendropsophus berthalutzae* (Bokermann, 1962a); *D. bromeliaceus* Ferreira et al., 2015; *D. decipiens* (Lutz, 1925); *D. haddadi* (Bastos and Pombal, 1996); *D. oliveirai* (Bokermann, 1963c).

Distribution. All species are found in the Atlantic Forest, north of the southern border of state of Paraná (Brazil).

Comments. Faivovich et al. (2005) found their single sample of the *Dendropsophus decipiens* clade to be nested within the *D. microcephalus* group. However, examination of the voucher specimen CFBH 5418 revealed that the terminal was actually a *D. meridianus* specimen (Fig. 4) misidentified as *D. berthalutzae*. Our results show that the former *D. decipiens* clade, recognized here as the *D. decipiens* group, is one of the earliest diverging clades within *Dendropsophus*.

One interesting synapomorphy of this group is the absence of melanin deposits in the lymphatic hearts at the pelvic girdle [cs.139(0)]. In most *Dendropsophus* species, a pair of black spots can be seen externally by transparency in faded specimens. Dissections indicated that these black blotches seem to be the lymphatic hearts colored by a black substance that we assume to be melanin. Species of *Sphaenorhynchus* and the *Dendropsophus decipiens* group are the exceptions; black lymphatic hearts were absent in all analyzed specimens, both in life and preservative. We are unaware of the physiological role of such deposits or why they are absent in these taxa.

Tadpoles of *Dendropsophus berthalutzae, D. decipiens, D. haddadi,* and *D. oliveirai* have round bodies in lateral view [cs.166(0)] and are considerably different from tadpoles of the *D. microcephalus* group (see Pugliese et al., 2000; Carvalho-e-Silva et al., 2003; Lourenço-de-Moraes et al., 2012). Larvae of the species of the *D. microcephalus* group have an elongate body in lateral view [cs.166(2)] and oral disk without marginal papillae [cs.169(0)], whereas larvae of the *D. decipiens* group have round bodies [cs.166(0)] and marginal papillae [cs.169(1)]. In our dataset, a round larval body [cs.166(0)] is a synapomorphy of the *D. decipiens* group.

Terminals identified as *Dendropsophus decipiens* and *D. haddadi* (including topotypes of the latter) prior to our phylogenetic analyses were recovered as paraphyletic with respect to each other and *D. oliveirai*. We were not able to obtain topotypic specimens of *D. decipiens*. Nevertheless, *D. decipiens* was described from specimens collected "at wetlands near Rio de Janeiro" (Lutz, 1925) and it seems that more species of this clade occur in the municipality of Rio de Janeiro (Izecksohn and Carvalho-e-Silva, 2001). Our nearest collected specimen (CFBH 22230) is from the municipality of Seropédica, Rio de Janeiro, 50 km airline from Rio de Janeiro. This specimen matches the original description of *D. decipiens* and we consider it to be a representative of this taxon (*D. decipiens* I in the tree; Fig. 2). Additional data (e.g. morphology and vocalizations) are required to determine how many species occur in this clade.

The Dendropsophus parviceps *Group*

Characterization, diagnosis, and support. This group has four phenomic synapomorphies, all homoplastic: Reduced anterior development of the p*rocessus maxillaris* of the *planum terminale* [cs.17(0)]; presence of a suborbital white bar [cs.117(1)]; blotched flanks [cs.138(1)]; well-defined tarsal fold [cs.152(1)] (Fig. 2). For nodal support values see Fig. 2. For genomic synapomorphies see Appendix S8. Apart from the proposed phenomic synapomorphies, species of the *Dendropsophus parviceps* group have highly variable size (combined SVLs range from 15.0–31.5 mm for males and 20.0–36.6 mm for females), dorsum is usually dark brown (smooth or with bark-like markings) with orange or yellow flash colours in thighs and/or axillary membrane. Calls can present secondary notes (complex calls) or not (simple calls).

Content (20 species). *Dendropsophus bokermanni* (Goin, 1960); *D. brevifrons* (Duellman and Crump, 1974); *D. counani* Fouquet et al., 2015; *D. frosti* Motta et al., 2012; *D. garagoensis* (Kaplan, 1991); *D. giesleri* (Mertens, 1950); *D. grandisonae* (Goin, 1966); *D. kamagarini* Rivadeneira et al., 2018; *D. koechlini* (Duellman and Trueb, 1989); *D. kubricki* Rivadeneira et al., 2018; *D. luteoocellatus* (Roux, 1927); *D. microps* (Peters, 1872); *D. padreluna* (Kaplan and Ruiz-Carranza, 1997); *D. parviceps* (Boulenger, 1882); *D. pauiniensis* (Heyer, 1977); *D. praestans* (Duellman and Trueb, 1983); *D. subocularis* (Dunn, 1934); *D. timbeba* (Martins and Cardoso, 1987); *D. virolinensis* (Kaplan and Ruiz-Carranza, 1997); *D. yaracuyanus* (Mijares-Urrutia and Rivero, 2000).

Distribution. As redefined here, species of the *Dendropsophus parviceps* group have a patched distribution. Two species occur in the Atlantic Forest (*D. giesleri* and *D. microps*), two are found at Cordillera de la Costa (*D. luteoocellatus* and *D. yaracuyanus*), one at Cordillera de Mérida (*D. luteoocellatus*) three species with restricted distribution at elevations of above 2000 m on the eastern and western slope of the eastern Cordillera Oriental of Colombia (the *D. garagoensis* clade), one species on the southeastern slope of the Cordillera Central (*D. praestans*), one species on the western slope of the Cordillera Occidental and in the middle Río Magdalena Valley in Colombia up to 800 m elevation and lowlands of eastern Panama (*D. subocularis*), while the remaining species occur in lowland Amazon (all basins and the Guiana Shield), from the Atlantic shoreline to the foothills of the Andes.

Comments. The *Dendropsophus parviceps* group as recognized by Faivovich et al. (2005) has been recovered as paraphyletic in several instances (e.g. Fouquet et al., 2011; Pyron and Wiens, 2011; Motta et al., 2012). In fact, Faivovich et al. (2005) already regarded the monophyly of this group with skepticism. Considering unsampled species, we tentatively include *D. grandisonae* in this group, following Faivovich et al. (2005).

The taxonomic composition of this group has received much attention recently. Of the 15 species recognized by Faivovich et al. (2005), *Dendropsophus gaucheri* has already been recovered as part of the *D. microcephalus* group (Fouquet et al., 2011), *D. allenorum* is now considered a junior synonym of *D. timbeba* (Orrico et al., 2013), and two additional species have been described (Motta et al., 2012; Fouquet et al., 2015). *Dendropsophus ruschii* (treated above) and *D. schubarti* (found herein to be part of the *D. leucophyllatus* group) were previously considered part of this group.

The only two species of this group from the Atlantic forest, *Dendropsophus giesleri* and *D. microps*, are the sister clade of the Amazonian species *D. timbeba*. The clade composed of these three species is sister to the remaining species of the *D. parviceps* group. The monophyly of these species is expected given the similar adult morphology of *D. giesleri, D. microps*, and *D. timbeba*. Larval external morphology is also highly similar and was considered evidence of a close relationship between *D. microps* and *D. timbeba* by Wild (1992). This clade has 11 phenomic synapomorphies (Fig. 2), and in recognition of the great resemblance of these species, we propose the *D. microps* clade.

As predicted by Kaplan (1991), the *Dendropsophus garagoensis* group is not closely related to other groups found in the Andes (see below) and is nested within our *D. parviceps* group, being sister to a clade composed of *D. koechlini* and *D. pauiniensis* (Fig. 2). Thus, its phylogenetic position suggests a distinct vicariance/dispersal event involving the Andes. We recognize the *D. garagoensis* clade (containing the species previously assigned to the *D. garagoensis* group: *D. garagoensis*, *D. padreluna*, *D. praestans*, and *D. virolinensis*). Kaplan (1999) suggested that the presence of a small medial depression in the internal surface of the arytenoids to be a synapomorphy for this group. After examining material of *D. virolinensis*, we observed that this medial depression corresponds to the space between two ridges that Martin (1972) called “internal buttress” (see cc.78 and 79). Dias et al. (2019) suggested the presence of two pairs of infralabial papillae as a putative synapomorphy for this clade—with independent evolution in *D. decipiens*.

Some species of this group are reported to have terrestrial eggs. These are *Dendropsophus bokermanni*, *D. brevifrons*, *D. counani*, and *D. subocularis*. None of these species is present in our phenomic dataset but all these above-cited species of this clade, with the exception of *D. frosti* and *D.* sp._Ron whose egg clutches are unknown, have confirmed reports of terrestrial clutches (Duellman and Crump, 1974; Fouquet et al., 2015). In our optimal topologies all of these species compose a clade, sister to *D. parviceps* + *D. kamagarini*, to which the transformation of aquatic to terrestrial eggs is a synapomorphy (see “Evolution of Oviposition Site Selection” section). We recognize this clade as the *D. subocularis* clade.

We did not sample *D. grandisonae*, known only from the holotype (Cole et al., 2013), but maintain it in the *D. parviceps* group following Faivovich et al. (2005).

The Dendropsophus molitor *Group*

Sister taxon. The *Dendropsophus columbianus* group.

Characterization, diagnosis, and support. There are no phenomic synapomorphies for this group. For genomic synapomorphies see Appendix S8. For nodal support values see Fig. 2. Species of this group are highly similar and all possess blue or bluish white marking in the bellies of live specimens, rounded snouts (in both dorsal and lateral views), brown to green dorsi (with or without dorsal patterns), simple calls with 9–23 pulses, and combined SVLs range from 26.4–61.0 mm in males and 34.9–66.2 mm in females. Additionally, all species assigned to this group present traits that are not found in any other *Dendropsophus* species: blue or yellow concealed parts of the thighs (flash colours), the vomerine teeth in two round patches, a reduced axillary membrane, and enlarged nuptial pads [cs.158(1)]. We consider those traits as putative synapomorphies of this group (see comments below).

Content (4 species). *Dendropsophus molitor* (Schmidt, 1857); *D. luddeckei* Guarnizo et al., 2012; *D. meridensis* (Rivero, 1961); *D. pelidnus* (Duellman, 1989).

Distribution. On the Cordillera Oriental in Colombia and on Cordillera of Merida in Venezuela, at elevations of 2000–4100 m.

Comments. As described above, the “Andean” groups (sensu Duellman et al., 1997) do not form a monophyletic group. However, two groups (the *Dendropsophus columbianus* and *D. molitor* groups) have been consistently recovered as sister taxa (e.g. Faivovich et al., 2005; Fouquet et al., 2015)—a relationship corroborated herein. Seven character states are phenomic synapomorphies for this clade: expanded plates in the nasal cartilages [cs.51(1)]; length of the hyoid plate less than twice the tyrohyal cranial portion length [cs.70(1)]; a medially interrupted post-axillary pectoral fold [cs.124(1)]; medial ventral margins of arytenoids concave with evident frenulum [cs.74(1)]; dorsal surface of shank uniformly coloured [cs.145(0)]; tadpoles with anterior labial tooth rows [cs.173(1)]; two posterior labial tooth rows [cs.176(1)] (Fig. 2).

Our optimizations do not indicate any phenomic synapomorphy for the *Dendropsophus molitor* group because we could include only *D. molitor* in our phenomic dataset. However, four phenomic character states might be considered putative synapomorphies: the blue or yellow concealed parts of the thighs (flash colours), the vomerine teeth in two round patches, the absence of an axillary membrane, and enlarged nuptial pads [cs.158(1)].

Information about colours in life of the concealed surfaces of the thighs is rare or conflictive in the literature (see comments in Appendix S9). All four species of the group have groins and hidden surfaces of the thighs mottled with black and blue (Duellman, 1989; CBA and VGDO pers. obs.) and vomerine teeth in two round patches (see Duellman, 1989; Duellman et al., 1997). To our knowledge, these character states have not been reported in any other *Dendropsophus* species.

Faivovich et al. (2005) also cite as a putative synapomorphy of the *Dendropsophus molitor* group (as *D. labialis* group) the absence of an axillary membrane, based on Duellman (1989). Our observations show that *D. molitor* has small (or “poorly developed”) axillary membrane. The recognition of the presence and extension of the axillary membrane has problems of its own (see comments under c. 102 and 121).

Enlarged nuptial pads [cs.158(1)] are found in all species of this group (Fig. S10) and this enlargement is a putative synapomorphy for the group. Luna et al. (2018) performed histological sections on a large diversity of anurans and among which were *Dendropsophus molitor* and *D. nanus*. The glands of these two pads are significantly different; *D. nanus* is not enlarged as *D. molitor*. Nevertheless, histological analyses focusing on *Dendropsophus* diversity are necessary to better define this character state.

The Dendropsophus columbianus *Group*

Sister taxon. The *Dendropsophus molitor* group.

Characterization, diagnosis, and support. There are no phenomic synapomorphies for this group. For genomic synapomorphies see Appendix S8. For nodal support values see Fig. 2. All species of this group have brown dorsi mottled with darker spots; bellies and flanks in live specimens with dark brown spots or mottles contrasting with yellow to orange flash colours. Combined SVLs range from 21.1–33.5 mm in males and 29.2–35.8 mm in females. Advertisement calls are complex, having primary and secondary notes.

Content (5 species). *Dendropsophus battersbyi* (Rivero, 1961); *D. bogerti* (Cochran and Goin, 1970); *D. carnifex* (Duellman, 1969); *D. columbianus* (Boettger, 1892); *D. norandinus* Rivera-Correa and Gutiérrez-Cárdenas, 2012.

Distribution. On both slopes of the Cordillera Occidental in Ecuador and Colombia, and both slopes of the Cordillera Central and the Rio Cauca Valley with an isolated species in Caracas (Costal Range).

Comments. The group is well supported by molecular data but lacks phenomic evidence. All phenomic autapomorphies of *Dendropsophus columbianus* and *D. carnifex* are highly homoplastic within *Dendropsophus* and also variable within the group. A possible homoplastic synapomorphy might be the completely black testes [cs. 196(3)]—this character state also occurs in several other species not assigned to this group and other genera (e.g. *D. melanargyreus*, *D. timbeba*, *D. virolinensis*, *Pseudis minutus*, and *Lysapsus laevis*).

Dendropsophus columbianus is paraphyletic with respect to *D. bogerti*. Kaplan (1997) removed *Dendropsophus bogerti* from the synonymy of *D. carnifex* were it has been placed by Duellman (1974; see also Duellman and Trueb, 1983; Kaplan, 1997). Kaplan (1997) reported several differences between *D. bogerti* and *D. columbianus* (e.g. medial ramus of pterygoid slightly wrapping around posterior surface of pseudobasal process of palatoquadrate *vs.* not wrapping; see our c. 41 and 42). Given the small number of specimens of those species examined in the present study, we refrain from taking any taxonomic action.

Recently, Barrio-Amorós et al. (2019) assigned *Dendropsophus battersbyi* to "the *D. minutus* species group sensu Gehara et al. (2014)". Nevertheless, *D. battersbyi* lacks the putative synapomorphies for the *D. minutus* group (see below). Moreover, the male holotype of *D. battersbyi* (SVL = 33 mm) is much larger than all other species of the *D. minutus* group (male maximum SVL of species of the *D. minutus* group is 28.1 mm) but is within the range of all other species of the *D. columbianus* group. The original description of *D. battersbyi* compares it with several hylid species from Venezuela and states that this species "agrees in several characters" with *D. columbianus*. In fact, many traits of *D. battersbyi* (e.g. dorsal coloration, snout in both profiles, tights colour pattern) are similar to *D. norandinus*, especially the ventral coloration. Therefore, we tentatively assign *D. battersbyi* to this group.

The Dendropsophus marmoratus *Group*

Characterization, diagnosis, and support. This group has 13 phenomic synapomorphies; all homoplastic: Ocular foramen reaching anteriorly about halfway of parasphenoid cultriform process [cs.44(0)]; anteriorly black vocal sack [cs.113(2)]; warty skin around the margin of the lower lip [cs.114(1)]; presence of a suborbital white bar [cs.117(1)]; an uniformly black gula [cs.141(2)]; a well-defined ulnar fold [cs.150(1)]; a well-defined tarsal fold [cs.152(1)]; presence of a tibial fold [cs.153(1)]; presence of a calcar [cs.154(1)]; a nuptial pad that extends onto forearm [cs.157(2)]; tubercular dorsal skin [cs.163(2)]; tadpole oral disc with two rows of posterior marginal labial papillae [cs.170(1)]; adult pericardium without iridophores [cs.187(0)]. (Fig. 3). For nodal support values see Fig. 3. For genomic synapomorphies see Appendix S8. Apart from the proposed phenomic synapomorphies, species of the *D. marmoratus* group are medium-large sized (combined SVLs range from 27.4–44.2 mm in males and 30.0–52.0 mm in females), have bark-like coloured dorsi, simple advertisement calls with dominant frequency varying between the first and the second harmonics in the same note. Advertisement calls also have cyclic amplitude modulation (especially towards the end of the note) and many pulses (combined range 30–66 pulses per note).

Content (8 species). *Dendropsophus acreanus* (Bokermann, 1964b); *D. dutrai* (Gomes and Peixoto, 1996); *D. marmoratus* (Laurenti, 1768); *D. melanargyreus* (Cope, 1887); *D. nahdereri* (Lutz and Bokermann, 1963); *D. novaisi*

(Bokermann, 1968); *D. seniculus* (Cope, 1868); *D. soaresi* (Caramaschi and Jim, 1983).

Distribution. The group is widely distributed in cis-Andean South America and is found in the Atlantic Forest, Amazon (in the Amazon Basin and the Guiana Shield), Chaco, Cerrado, and Pantanal Biomes.

Comments. Among the proposed synapomorphies for the *Dendropsophus marmoratus* group in the literature those related to advertisement calls—see Orrico et al. (2009) and Hepp et al. (2012)—have not been included in our dataset given the difficulties found in coding behavioural characters (see Appendix S9 "Potentially informative variation not evaluated in this study"). Two of the putative synapomorphies that Faivovich et al. (2005) suggested for the group are found in all examined *Dendropsophus* species and in some outgroups. The modified pectoral *septum* identified by Tyler (1971) in *D. marmoratus* is also present in species of Dendropsophini that possess an axillary membrane (see comments in c.102). Similarly, we observed the sheath of thickened tissue at the basal portion of the tail muscle and adjacent fins (c.188; Peixoto and Gomes, 1999) in all examined larvae of Dendropsophini and it might be a synapomorphy for this tribe, pending information on *Sphaenorhynchus* (also, see comments on c.177).

The main controversy within the *Dendropsophus marmoratus* group is whether the "Northeastern Brazilian Semi-arid" (NBS) group of Gomes and Peixoto (1996) is monophyletic and if it is related to *D. seniculus*. Hepp et al. (2012) suggested that *D. seniculus* might be more closely related to *D. soaresi* because they share unique call features. This suggestion thereby contradicts the monophyly of the NBS group. Our results show that, although *D. seniculus* is related to *D. dutrai* and *D. novaisi*, *D. soaresi* is related to the Amazonian species *D. melanargyreus*. Of the NBS group, the only species whose distribution is on the Caatinga Biome is *D. soaresi* with incursions into the ecotone areas of Cerrado. Our samples of *D. dutrai* and *D. novaisi* are not reciprocally monophyletic but we refrain from taking any taxonomic action at the moment.

The Dendropsophus minutus *Group*

Characterization, diagnosis, and support. There are no phenomic synapomorphies for this group. For genomic synapomorphies see Appendix S8. For nodal support values see Fig. 3. Species of this group are small (combined SVLs range from 17–28.1 mm in males and 21–26.6 mm in females), have brown dorsi usually with a dark brown hour-glass or chevron mark. All species have long cloacal sheaths and white lines above the cloaca and heels (see below). Advertisement calls are complex with secondary and tertiary notes; notes formed by pulsed or unpulsed notes. Species of this group are the only *Dendropsophus* species known to produce unpulsed notes.

Content (7 species). *Dendropsophus amicorum* (Mijares-Urrutia, 1998), *D. aperomeus* (Duellman, 1982); *D. delarivai* (Köhler and Lötters, 2001a); *D. limai* (Bokermann, 1962a); *D. minutus* (Peters, 1872); *D. stingi* (Kaplan, 1994); *D. xapuriensis* (Martins and Cardoso, 1987).

Distribution. Cis-Andean South America in the Amazon (all basins and the Guiana Shield), Atlantic Forest, Caatinga, Cerrado, Chaco, Llanos, Pampa, and Pantanal Biomes.

Comments. Relationships among species of the *Dendropsophus minutus* group are slightly different from those retrieved by Gehara et al. (2014)—the most complete phylogenetic study of the group to date. While Gehara et al. (2014) recovered a pectinate series of species we found two clades. If these results are an effect of the different optimality criteria used—Gehara et al. (2014) used Bayesian Inference to produce their results—or the different sampling—ours is much more restricted in comparison with the over 300 samples assignable to species of this group that they used—is unknown. Nonetheless, even if we had recovered a topology identical to theirs, our discussion and conclusions would still be the same. Several of the character states that are autapomorphies of the *D. minutus* terminal associated with morphological data are likely synapomorphies of the *D. minutus* group. These include the unique rostrum shape of *D. minutus* that is associated with the posteriorly directed alary process of the premaxilla [cs.15 (2)], the long cloacal sheath [cs.145(1)], and the white line above the cloaca [cs.146(1)]—but see comments below on cloacal sheath of *D. gryllatus*. Also, all species of the *D. minutus* group have white lines above the heels [cs.147(1)]. Advertisement calls might also have synapomorphic character states. Species of the *D. minutus* group with known calls are the only *Dendropsophus* species that produce a modulated, non-pulsed harmonic note.

Dendropsophus minutus is considered a taxonomic conundrum. Gehara et al. (2014) discovered that this taxon is composed of many Amazonian lineages and many populations of related species (e.g. *D. xapuriensis*) that were previously mistaken for *D. minutus*. Whether these lineages represent one or more species is unclear. Although *D. minutus* displays highly variable advertisement calls (Cardoso and Haddad, 1984; Morais et al., 2012) and highly variable adult (e.g. Kaplan, 1994) and larval morphologies (e.g. Schulze et al., 2015) that are congruent with some of the historical lineages, the recognition as distinct species would require either that nominal *D. minutus* be split into several phenomically undiagnosable species or retained as a paraphyletic species.

Dendropsophus amicorum is known only from the holotype, collected in 1968 at Cerro Socopo, state of Falcón, Venezuela. Given the original description (Mijares-Urrutia, 1998), it is possible that it is related to *D. minutus* due to the presence of a long cloacal sheath. Photos of the holotype (USNM 216677) reveal a specimen in a poor state of preservation. Thus, the absence of lines and patterns remarked by Mijares-Urrutia (1998) might be due to discoloration. Nevertheless, a white line above the cloaca and heels are still visible. Since other characters associated with this species could not be checked (like the different hand webbing and the flecked dorsum), we recognize this species as valid. We had no sample from this species, but the presence of a long cloacal sheath and remnants of white lines above the heels are evidence that it is part of the *D. minutus* group.

Gehara et al. (2014) did not have topotypic material of *Dendropsophus amicorum* either, but their lineages 1 to 6 and 8 are from nearby localities. Lineage 8 corresponds to *D. stingi* and its original description does not provide a comparison with *D. amicorum* (see Kaplan, 1994). Lineages 1 to 6 are distributed over the Guiana Shield, and Gehara et al. (2014) suggested that they might correspond to *D. goughi*, at the time a synonym of *D. minutus* based on specimens from Trinidad—a reasonable suggestion given that many species from Trinidad are also found in the lowlands of Venezuela and Colombia (Kenny, 1969; Suarez-Mayorga and Lynch, 2001a; Suarez-Mayorga and Lynch, 2001b; Barrio-Amoros et al., 2006; Camargo et al., 2006; Smith et al., 2011). Recently, Barrio-Amorós et al., (2019) re-examined the holotype of *Dendropsophus goughi* and came to the conclusion that it should be considered a junior synonym of *D. microcephalus*. Therefore, the only available name for lineages 1–6 of Gehara et al. (2014) is *D. amicorum*.

Faivovich et al. (2005) tentatively included *Dendropsophus limai* in this group. This species is also known only from the holotype (MZUESP 73657, ex-WCAB 4, collected at São Vicente, state of São Paulo, Brazil). The specimen has a long cloacal sheath and white lines above the cloaca and heels, supporting its inclusion in the group.

The Dendropsophus leucophyllatus *Group*

Sister taxon. The *Dendropsophus microcephalus* group.

Characterization, diagnosis, and support. This group has two phenomic synapomorphies, both homoplastic: An expanded cartilaginous plate (a piece of the nasal cartilages) [cs.51(1)]; males with pectoral glands arranged in two clear distinct patches [cs.161(0)] (Fig. 3). For nodal support values, see Fig. 3. For genomic synapomorphies see Appendix S8. Apart from the proposed synapomorphies, species of this group share bright flash colours in webbings, concealed surfaces of the thighs, bellies, and flanks in orange, red, pink, or yellow (with the exception of *Dendropsophus haraldschultzi* that is morphologically unique but yet somewhat similar to species of the *D. microcephalus* group and *D. schubarti* that resembles species of the *D. parviceps* group due to the brown dorsum). Combined SVLs range from 16.0–40.0 mm in males and 20.0–50.0 mm in females. Calls are usually complex with primary and secondary notes.

Content (18 species). *Dendropsophus anceps* (Lutz, 1929); *D. arndti* Caminer et al., 2017; *D. bifurcus* (Andersson, 1945); *D. ebraccatus* (Cope, 1874); *D. elegans* (Wied-Neuwied, 1824); *D. haraldschultzi* (Bokermann, 1962a); *D. leucophyllatus* (Bereis, 1783); *D. manonegra* Rivera-Correa and Orrico, 2013; *D. mapinguari* Peloso et al., 2016; *D. miyatai* (Vigle & Goberdhan-Vigle 1990); *D. nekronastes* Dias et al., 2017; *D. reticulatus* (Jiménez de la Espada, 1870); *D. rossalleni* (Goin, 1959); *D. salli* Jungfer et al., 2010; *D. sarayacuensis* (Shreve, 1935); *D. schubarti* (Bokermann, 1963a); *D. triangulum* (Gunther, 1869); *D. vraemi* Caminer et al., 2017.

Distribution. Mexico to Colombia on both Atlantic and Pacific slopes (including the Magdalena Valley), northwestern Ecuador, and cis-Andean South America in the Amazon (all basins and the Guiana Shield), Atlantic Forest, Caatinga, Cerrado, Llanos, and Pantanal Biomes.

Comments. The inclusion of *Dendropsophus anceps* in *D. leucophyllatus* group by Faivovich et al. (2005) has been controversial (Rivera-Correa and Orrico, 2013; Peloso et al., 2016). In our results, *D. anceps* is sister to a clade that includes all other species traditionally assigned to the *D. leucophyllatus* group (Fig. 3). This clade is sister to another clade composed of *D. schubarti*, *D. miyatai*, and *D. haraldschultzi* (Fig. 3).

The phylogenetic placement of *Dendropsophus haraldschultzi* has never been tested before. Its original description states that it was not possible to relate this species to other hylid species—this position was followed by Faivovich et al. (2005). Rodriguez and Duellman (1994) suggested that this species was similar to *D. minutus*, *D. riveroi*, and *D. leali* or *Boana fasciatus* (Gunther, 1858) but their comparisons were limited to species occurring in their geographical area of interest (Iquitos Region, Amazonian Peru).

The phylogenetic relationships of *Dendropsophus schubarti* have been unstable. Bokermann (1963a) considered *D. schubarti* to be similar to *D. leucophyllatus* on the basis of the dorsal coloration pattern, but subsequent authors considered it to be part of the *D. parviceps* group (Duellman, 2001; Faivovich et al., 2005). Fouquet et al. (2011) found it to be most closely related to the *D. marmoratus* group. This species is not present in our phenomic dataset, but the presence [cs.117(1)] of two suborbital white bars [cs.118(1)] may be evidence for the inclusion of *D. schubarti* in this group—although species of the *D. parviceps* clade share these character states (with the exception of *D. frosti*).

Similarly, different phylogenetic relationships have been proposed for *Dendropsophus miyatai*. The original description (Vigle and Goberdhan-Vigle, 1990) implied that it was related to the *D. minimus* group. This was the only species of this group available to Faivovich et al (2005) that found it to be sister of *D. minutus*—the only species of the *D. minutus* group available at the time. Wiens et al. (2010) and Pyron and Wiens (2011), using Maximum Likelihood analyses, found a clade composed of *D. schubarti* and *D. miyatai* as sister to all available species assigned to *D. leucophyllatus* group, except for *D. anceps* (sister to *D. minutus* + *D. microcephalus* group) but with low levels of support. However, Wiens et al. (2010), using Maximum Parsimony analysis, retrieved *D. schubarti* + *D. miyatai* as sister to *D. anceps* and this clade sister to all available species assigned to *D. leucophyllatus* group, also with low support. Similarly, whereas Dias et al. (2017) Maximum Parsimony analysis retrieved a clade composed of *D. schubarti* + (*D. miyatai* + *D. minutus*) with low support, their Bayesian analysis did not retrieve this relationship. Peloso et al., (2016) recovered a clade composed of *D. miyatai* + *D. minutus* to be nested within their *D. leucophyllatus* group, as the sister group of a clade composed of *D. salli*, *D. ebraccatus*, and *D. elegans*.

Faivovich et al. (2005) considered the presence in both males and females of pectoral glands forming two distinct patches (see Duellman, 1970) to be the only putative synapomorphy for the *Dendropsophus leucophyllatus* group. Our results corroborate the occurrence of this character state in males (see [c.161]) as a synapomorphy for the expanded version of the group described below. Jungfer et al. (2010) excluded *D. anceps* from the *D. leucophyllatus* group due to the absence of patched pectoral glands in that species. However, although females of *D. anceps* do not possess patched pectoral glands [c.162], males do (Rivera-Correa and Orrico, 2013; Dias et al., 2017). Males of *D. miyatai* and *D. haraldschultzi* also have patched pectoral glands, but it is unknown if females of these species and of *D. schubarti* have such glands.

We redefine the *Dendropsophus leucophyllatus* group to include all species previously assigned to the *D. leucophyllatus* group, plus *D. anceps* (as done initially by Faivovich et al., 2005), *D. schubarti*, *D. miyatai*, and *D. haraldschultzi*. Within this group, we recognize the *D. haraldschultzi* clade for *D. haraldschultzi*, *D. miyatai*, and *D. schubarti* and the *D. leucophyllatus* clade for all remaining species.

The *Dendropsophus leucophyllatus* clade is supported by five phenomic synapomorphies. Four are homoplastic, including the lateral margin of the nasal bones being concave in dorsal view [cs.8(1)], a small ocular fenestra [cs.44 (0)], and the reduction of webbing on both sides of Finger IV [cs.127(3) and cs.128(3)]. The fifth synapomorphy is the occurrence of well-defined pale blotches on a dark background on the shank, [cs.145(2)], used previously as evidence for species recognition (e.g. De la Riva and Duellman, 1997; Jungfer et al., 2010).

Duellman and Trueb (1983) proposed that a violin-shaped larval body is a synapomorphy for the *Dendropsophus leucophyllatus* group. We recovered this body shape as a synapomorphy of a clade within the *D. leucophyllatus* group. Nevertheless, we do not discard the possibility that this post-ocular constriction might be, at least in some instances, an artifact caused by prolonged starvation.

We place *Dendropsophus arndti*, *D. leucophyllatus*, and *D. vraemi* in this group following the results of Caminer et al. (2017), which was published after our data sampling deadline. Given that Caminer et al. (2017) found these three species to be closely related to species included in our analysis, their absence is unlikely to have affected our results.

The Dendropsophus microcephalus *Group*

Sister taxon. *Dendropsophus leucophyllatus* group.

Characterization, diagnosis, and support. This group has nine phenomic synapomorphies, all homoplastic: Medial margins of the frontoparietals slender, not expanding medially more than the medial edge of the epiotic eminescences, leaving nearly all tectum synoticum exposed [cs.5(0)]; medial ramus of pterygoid concealing about half of the basal process length [cs.41 (1)]; posterior ramus of pterygoid not reaching squamosal ventral ramus [cs.43(1)]; cricoid esophageal margin in esophageal view straight [cs.84(1)]; tadpole oral disc without marginal labial papillae [cs.169(0)]; tadpole oral disc without posterior labial tooth rows [cs.175(0)]; tadpole tail fin uniformly brownish, mostly ground colour [cs.178(0)]; adult rectum without melanophores [cs.198(0)]; presence of pterorhodin [cs.201(1)]. (Fig. 4). For nodal support values see Fig. 4. For genomic synapomorphies see Appendix S8. Apart from the proposed phenomic synapomorphies, all species of the *Dendropsophus microcephalus* group are small (combined SVLs range from 15.0–32 mm for males and 14.5–38.7 mm for females) with a brown to yellow dorsum in life (with the exception of species of the *D. rubicundulus* clade that have green dorsi) and in preservative (with the exceptions of species of the *D. branneri* and *D. rubicundulus* clades that have pink—dark or clear—dorsi). Calls can be either simple or complex (with secondary notes). Thighs are either completely creamy white or also show yellow spots near the knees that cover the distal half of the thigh.

Content (37 species). *Dendropsophus anataliasiasi* (Bokermann, 1972); *D. araguaya* (Napoli and Caramaschi, 1998); *D. bipunctatus* (Spix, 1824); *D. branneri* (Cochran, 1948); *D. cachimbo* (Napoli and Caramaschi, 1999a); *D. cerradensis* (Napoli and Caramaschi, 1998); *D. coffea* (Köhler et al., 2005); *D. cruzi* (Pombal and Bastos, 1998); *D. elianeae* (Napoli and Caramaschi, 2000); *D. gaucheri* (Lescure and Marty, 2000); *D. jimi* (Napoli and Caramaschi, 1999b); *D. joannae* (Köhler and Lötters, 2001b); *D. juliani* Moravec et al., 2006; *D. leali* (Bokermann, 1964a); *D. mathiassoni* (Cochran and Goin, 1970); *D. meridianus* (Lutz, 1954); *D. microcephalus* (Cope, 1886); *D. minimus* (Ahl, 1933); *D. minusculus* (Rivero, 1971); *D. nanus* (Boulenger, 1889); *D. phlebodes* (Stejneger, 1906); *D. pseudomeridianus* (Cruz et al., 2000); *D. reichlei* Moravec et al., 2008; *D. rhea* (Napoli and Caramaschi, 1999b); *D. rhodopeplus* (Günther, 1858); *D. riveroi* (Cochran and Goin, 1970); *D. robertmertensi* (Taylor, 1937); *D. rozenmani* Jansen, et al., 2019; *D. rubicundulus* (Reinhardt and Lütken, 1862); *D. sanborni* (Schmidt, 1944); *D. sartori* (Smith, 1951); *D. shiwiarum* Ortega-Andrade and Ron, 2013; *D. studerae* (Carvalho-e-Silva et al., 2003); *D. tintinnabulum* (Melin, 1941); *D. tritaeniatus* (Bokermann, 1965); *D. walfordi* (Bokermann, 1962b); *D. werneri* (Cochran, 1952).

Distribution. Mexico southwards through Middle America on both Atlantic (from southern Veracruz and northern Oaxaca eastward to Belize) and Pacific slopes to Colombia (including the Pacific slopes and Magdalena and Cauca Valleys), northwestern Ecuador, Trinidad and Tobago, and cis-Andean South America (all basins and the Guiana Shield), Atlantic Forest, Caatinga, Cerrado, Chaco, Llanos, Pampa, and Pantanal Biomes; from sea level to 1700 m elevation.

Comments. Our results reject the monophyly of the *Dendropsophus microcephalus* group as recognized by Faivovich et al. (2005), with the *D. decipiens* clade here found to be distantly related and recognized as a distinct species group. Nevertheless, all other species presently assigned to the *D. microcephalus* group (Faivovich et al., 2005; Fouquet et al., 2011) are retrieved in this clade, and we corroborate Faivovich et al.'s (2005) hypothesis that the lack of marginal papillae in the oral disc [cs.169(0)] is a synapomorphy of this group.

In addition to the *Dendropsophus decipiens* clade, Faivovich et al. (2005) recognized the *D. rubicundulus* clade within the *D. microcephalus* group. Our results indicate that *D. sanborni*, which was referred to the *D. microcephalus* group but not placed in either of the recognized clades, is nested within the *D. rubicundulus* clade of Faivovich et al. (2005). The relation of *D. sanborni* with species of the *D. rubicundulus* clade of Faivovich et al. (2005) has been also retrieved by Medeiros et al. (2013) and Jansen et al. (2019).

Recently, Jansen et al. (2019) described *Dendropsophus rozenmani* for Bolivian populations previously identified as *D. tritaeniatus*. Nevertheless, although this species was sister to *D. cachimbo*, Jansen et al. (2019) refrained to assign an affiliation to any species group. Their decision was based on the paraphyly of the *D. rubicundulus* clade sensu Faivovich et al. (2005) with respect to *D. cruzi*, *D. juliani*, *D. mathiassoni*, *D. minusculus*, *D. sanborni*, and a candidate species "*D. juliani* A" in their phylogenetic results. In our results, *D. cruzi*, *D. juliani*, *D. mathiassoni*, and *D. minusculus* are part of a novel clade (discussed below), *D. sanborni* is sister to *D. anataliasiasi* + *D. elianeae*, and *D. rozenmani* is sister to *D. cachimbo*.

Faivovich et al. (2005) considered as a putative synapomorphy for the *Dendropsophus rubicundulus* clade the green dorsum in life that becomes pinkish or violet in preservative, following Napoli and Caramaschi (1998). In literature, the pink or violet hues result from the presence of Pterorhodine in the skin (Misuraca et al., 1977)—although not as conspicuous as seen in species of phyllomedusines (Iga and Bagnara, 1975; Misuraca et al., 1977). The presence of this pigment [cs.201(1)] is a synapomorphy for the *D. microcephalus* group but the green-violet reaction is only conspicuous in the *D. rubicundulus* clade, with the exception of *D. sanborni* and *D. rozenmani* that present pale pinkish hues as do other species of the *D. microcephalus* group (see comments under c. 201 for character state definitions).

Therefore, we recognize a *Dendropsophus rubicundulus* clade with the same species composition of Faivovich et al. (2005) with the addition of *D. rozenmani* and *D. sanborni*. Napoli and Caramaschi (1998, 1999a, 1999b, 2000) proposed the "*D. tritaeniatus*" complex for species with a single sacral stripe (viz. *D. araguaya*, *D. cerradensis*, *D. jimi*, *D. rhea*, and *D. tritaeniatus*) and the "*D. rubicundulus*" complex for species with double sacral stripe (viz. *D. anataliasiasi*, *D. cachimbo*, *D. elianeae*, and *D. rubicundulus*). However, in our results, the "*D. tritaeniatus*" complex is paraphyletic with respect to *D. cachimbo* and the "*D. rubicundulus*" complex is paraphyletic with respect to *D. sanborni*. Nevertheless, *D. sanborni* also has a double sacral stripe (VGDO pers. obsr). Jansen et al. (2019) did not assign *D. rozenmani* to any species group.

The *Dendropsophus rubicundulus* group is further divided into two clades, which we name as the *D. anataliasiasi* and the *D. araguaya* complexes—to avoid confusion with previous groupings. The *D. anataliasiasi* complex includes *D. anataliasiasi*, *D. elianeae*, *D. sanborni*, and *D. rubicundulus* while the *D. araguaya* complex includes *D. araguaya*, *D. cachimbo*, *D. cerradensis*, *D. jimi*, *D. rozenmani*, and (tentatively) *D. tritaeniatus*. We assign *D. rhea* to the *D. microcephalus* group and to our *D. rubicundulus* clade. Nevertheless, the position of *D. cachimbo* renders the optimization of the number of sacral stripes ambiguous. Therefore, we lack evidence to assign *D. rhea* to the *D. anataliasiasi* or the *D. araguaya* complexes.

Dendropsophus araguaya and *D. jimi* samples are paraphyletic with respect to each other and to *D. cerradensis*. All our terminals for those species are topotypes (Appendix S3) and their morphology agrees with the original descriptions. Since species-level taxonomy is not within the scope of the present contribution, this problem will be addressed elsewhere.

The paraphyly of *Dendropsophus walfordi* with respect to *D. nanus* has been recovered previously (see Fouquet et al., 2011; Medeiros et al., 2013). Nevertheless, topotypic material of *D. walfordi* is still lacking. Köhler et al. (2005) originally suggested that *D. coffea* was related to *D. meridianus* but also mentioned its resemblance to *D. nanus*, highlighting some small differences in morphology and, especially, advertisement call. Given the present topology, a comprehensive integrative assessment of phenomic traits for these species is required.

Samples of *Dendropsophus meridianus* and *D. pseudomeridianus* form a polytomy in the strict consensus (Fig. 4). Bertha Lutz (1954) described *D. meridianus* on the basis of specimens collected in the city of Rio de Janeiro, state of Rio de Janeiro, Brazil, while *D. pseudomeridianus* was described on the basis of specimens from the lowlands of the state of Rio de Janeiro, Brazil (Cruz et al., 2000). We included topotypic specimens of both species (see Appendix S3). Differences between these species are subtle and our results suggest that they might be conspecific. Nevertheless, because species-level taxonomy is not within the scope of the present contribution, this problem will be addressed elsewhere.

Five species form a novel clade that we recognize as the *Dendropsophus branneri* clade: *D. branneri*, *D. cruzi*, *D. juliani*, *D. mathiassoni*, and *D. minusculus*. Jansen et al. (2019) had sequences for four of these species (lacking *D. branneri*) and for an additional fifth putative species (*D. juliani* A) but they have not recovered this group as a monophyletic unit. In their results, *D. minusculus* and *D. mathiassoni* clustered together and the remaining species formed a clade sister to *D. rubicundulus*, by its turn, sister to the remaining of their representatives of the *D. rubicundulus* group. We believe that the different results are an effect of the different taxon sampling.

All adult specimens of species of the *Dendropsophus branneri* clade show similar coloration and patterns: dorsum pinkish to reddish brown, bluish green ventral surfaces with the exception of a white belly (both sexes), and greenish yellow vocal sacs (in males) in live specimens. This greenish coloration is that typical of the occurence of physiological chlorosis (Barrio, 1965; Taboada et a., in press) i.e. the accumulation of a biliverdin-binding protein in lymph and other tissues. Three species not included in our analyses can be tentatively referred to this clade: *D. tintinnabulum*, "*Hyla* sp.1" of Lescure and Marty (2000), and *D. juliani* A of Jansen et al. (2011, 2019). We agree with Teixeira and Giaretta (2016) that *D. tintinnabulum* belongs to the *D. microcephalus* group. Although Melin (1941) suggested a relationship with *D. nanus*, the original description states that *D. tintinnabulum* is "beneath bluish green", which agrees with our observations for the *D. branneri* clade. "*Hyla* sp.1" of Lescure and Marty (2000) shows the typical external morphology of this clade and *D. juliani* A is reported to be similar to *D. juliani* (Jansen et al., 2011) and to have "reddish tan dorsum without markings" (Jansen et al., 2019).

The last of the unsampled species is *Dendropsophus phlebodes*, which we retain in the *D. microcephalus* group following Duellman and Fouquette (1968), Duellman (1970), and Faivovich et al. (2005). All other Middle American species of the group (*D. microcephalus*, *D. robertmertensi*, and *D. sartori*) form a clade, which we recognize as the *D. microcephalus* clade. We tentatively relate *D. phlebodes* to this clade.

Species unassigned to any species group

Dendropsophus gryllatus (Duellman, 1973). This species has not been reported since its description, which states that the species lacks pectoral glands (Duellman, 1973). However, the holotype (KU 146452) and topotypic specimens (MZUSP 73742 and 73743) have these glands. The original description also reports a long cloacal sheath, a character state found in species of the *D. minutus* group, which we corroborate to be present in the holotype and two topotypic specimens. In contrast, colour pattern and advertisement call agree with those of the *D. leucophyllatus* group, but we have not included these characters in the present analysis. As such, we lack clear evidence to assign this species to either the *D. minutus* or *D. leucophyllatus* groups and prefer to leave this species unassigned to any group.

Dendropsophus minimus (Ahl, 1933). Following Duellman (1982), Faivovich et al. (2005) recognized the *D. minimus* group for *D. aperomeus*, *D. minimus*, *D. miyatai*, and *D. riveroi*. In our results, *D. riveroi* is nested within the *D. microcephalus* group, *D. aperomeus* is in the *D. minutus* group (see also Gehara et al., 2014), and *D. miyatai* is in the *D. leucophyllatus* group (see comments above).

Dendropsophus minimus is known only from the holotype (Ahl, 1933) and we were unable to secure any tissue samples for this species. Overall morphology resembles species from both the *D. decipiens* and *D. microcephalus* groups. Photos of the holotype (NHMW 19436) show that melanin deposits are present in the pelvic girdle [cs.139(1)] and that the specimen is extremely faded, nearly transparent. Given that melanin deposits are synapomorphically absent in the *D. decipiens* group, we tentatively exclude this species from that group. Nevertheless, the discoloured skin precludes the evaluation of the presence/absence of pterorhodine. Therefore, evidence is lacking to associate this species with any other group and we thus leave it as unassigned.

Evolution of oviposition site selection

Terrestrial eggs (i.e. eggs that have at least part of their development out of the water) have been reported in 19 species of *Dendropsophus* (16 of which were included in our dataset, plus *D. arndti*, *D. leucophyllatus*, and *D. vraemi*, which are not included in the matrix, but have reports of terrestriality as either *D. leucophyllatus* or *D. triangulum*—see Appendix S8). Plasticity has been reported for *D. ebraccatus* (Touchon and Warkentin, 2008) and there are isolated reports for *D. nanus*, with Lescure and Marty (2000) considering it to have terrestrial eggs and Bokermann (1963b) reporting it as “aquatic”. Moreover, we have unpublished evidence of both terrestrial and aquatic egg clutches attributable to *D. branneri* (VGDO, per. Obs.).

Egg deposition site has been widely used in the taxonomy of *Dendropsophus*. Duellman and Crump (1974) segregated *D. parviceps* from related species (e.g. *D. bokermanni* and *D. brevifrons*) because it lays eggs directly in water, whereas the other two have terrestrial egg clutches. Most species of the *D. decipiens* group lay eggs on leaves above water (Lutz, 1973a; Bastos and Pombal, 1996; Toledo et al., 2011), and this behaviour was proposed as a synapomorphy for this clade by Bastos and Pombal (1996). The exception is *D. bromeliaceus*, which is unique within *Dendropsophus* in being bromeligenous (Ferreira et al., 2015). Although its tadpoles develop in the water trapped in the bromeliad axils, the precise position of the egg clutch is not reported in the original description. Mageski et al. (2014) found eggs of *D. haddadi* in the axils of bromeliad leaves above the water.

The evolution of terrestrial egg deposition is unclear (Fig. 5), even with our phenomic dataset including almost all *Dendropsophus* species reported to have terrestrial egg deposition. To check if the species absent in our phenomic dataset that are known to have terrestrial egg deposition sites had any significant impact on the understanding of the evolution of this character state, we produced an additional matrix to maximize the data on egg deposition sites adding information for those species with known egg deposition sites, even if they were not in our phenomic dataset. This more comprehensive matrix yielded only two differences between the optimizations of the least and most complete matrices. Nevertheless, the optimization on the ancestor of *Dendropsophus* is still ambiguous, even with the addition of data from those species.

The first of those differences is one additional transformation from aquatic to terrestrial deposition in the ancestor of the *Dendropsophus subocularis* clade. The second is another additional transformation from aquatic to terrestrial deposition in the ancestor of the *D. leucophyllatus* clade—excepting *D. anceps*. This happens because the egg deposition site of *D. anceps* is unknown and because data from *D. salli* (terrestrial, see Jungfer et al., 2010) resolves the optimization of this character within this clade.

In our dataset, the ambiguity in the ancestor of *Dendropsophus* is a product of the combination of four factors: (1) lack of knowledge on the egg deposition site of *D. ozzyi* and (2) in both species of *Xenohyla*, (3) the ambiguous optimization of egg deposition site in *Sphaenorhynchus*—both because of (3a) the position of *S. pauloalvini*—with terrestrial eggs—as sister of the remaining species of the genus and (3b) the unknown state for *S. dorisae*, and (4) an internal optimization problem generated in the ancestor of all groups but the *D. ruschii* and *D. decipiens* groups which is an aquatic egg clutch placer. Thus, in this more complete scenario, the terrestrial egg clutches evolved independently from aquatic clutches at least four times during the evolutionary history of *Dendropsophus*. Touchon and Warkentin (2008) produced a supertree based on previous independent contributions and also suggested that terrestrial eggs evolved at least four times based on their topology.

We found a relationship between egg colour and deposition site. *Dendropsophus* eggs vary from unpigmented (completely yellow) as in *D. ruschii* (Weygoldt and Peixoto, 1987) and *D. subocularis* (see information on AmphibiaWeb. 2017 <https://amphibiaweb.org> University of California, Berkeley, CA, USA. Accessed 14 Dec 2017.), or lightly pigmented tan and cream, as in *D. bokermanni* and *D. brevifrons* (Duellman and Crump, 1974; Duellman, 2005), to heavily pigmented black animal pole and creamy white vegetal pole as in *D. parviceps*, *D. ebraccatus*, and *D. marmoratus* (Duellman and Crump, 1974; Duellman, 1978; Duellman, 2005; Touchon and Warkentin, 2008). Salthe and Mecham (1974) stated that “the correlation between exposed egg sites and melanin on the animal hemisphere is apparently perfect" suggesting egg pigmentation as an adaptation to exposure to sunlight (as also did Duellman and Trueb, 1986). In our results, there is a relation between egg deposition sites and melanin on the animal pole. Species with unpigmented (or lightly pigmented) eggs have terrestrial clutches, whereas species with aquatic clutches have heavily pigmented eggs (Fig. 5).

Only four species of the *Dendropsophus leucophyllatus* clade (*D. ebraccatus*, *D. elegans*, *D. reticulatus*, and *D. triangulum*), *D. nanus*, and *D. branneri* are known exceptions, having heavily-pigmented eggs and terrestrial clutches. All of these species are known to be polymorphic for clutch deposition site. Only for *D. ebraccatus* there are reports of terrestrial oviposition in nature and not in captivity.

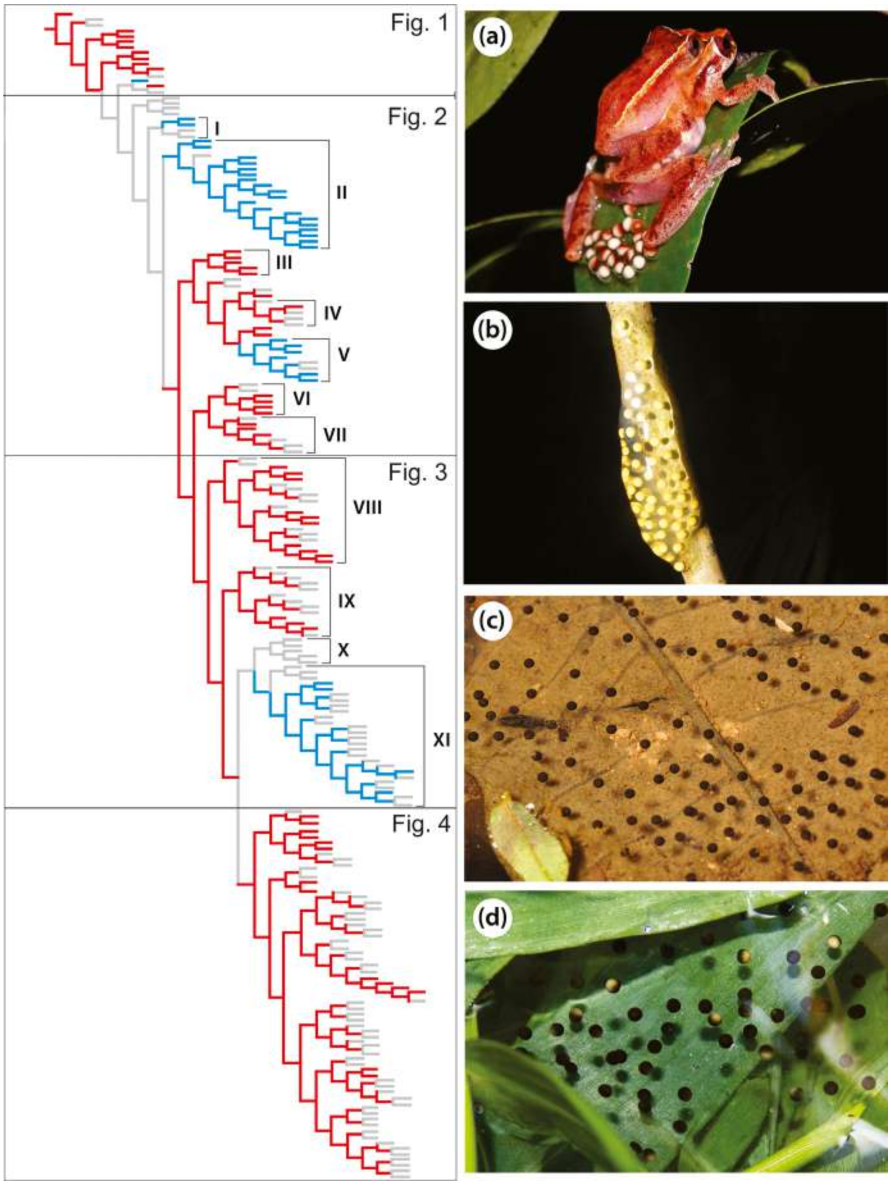

Fig. 5. Ancestral character state reconstructions of egg clutch deposition site over one of the optimal hypotheses of Dendropsophini phylogenetic relationships (on the right side). Reconstructions on the other optimal hypotheses are identical to the one depicted. Red branches stand for aquatic egg clutches, blue for terrestrial egg clutches, and grey for unknown character state or of ambiguous optimization. (a) *Dendropsophus haddadi*; (b) *D.* cf. *brevifrons* (c) *Scinax ranki*; (d) *D. branneri*. Within the inset, roman numerals stand for: (I) *D. ruschii* group; *D. decipiens* group (II); *D. microps* clade (III); *D. garagoensis* clade (IV); *D. subocularis* clade (V); *D. molitor* group (VI); *D. columbianus* group (VII); *D. marmoratus* group (VIII); *D. minutus* group (IX); *D. haraldschultzi* clade (X); *D. leucophyllatus* clade (XI). (Photos by Alexander Monico, VGDO, Renato Gaiga, DL; Images not to scale.)

Touchon and Warkentin (2008) demonstrated experimentally that *Dendropsophus ebraccatus* chooses to lay terrestrial eggs when the breeding pond has more available leaves and is therefore more shaded. Shadier environments are also moister and allow terrestrial eggs to survive in this environment. Also, shadier environments have less UV, reducing the dependence on melanin for UV protection. Different species with pigmented and unpigmented eggs inhabit the same areas —see accounts of *D. parviceps* (with pigmented eggs) and *D. bokermanni* and *D. brevifrons* (with unpigmented eggs) in Duellman and Crump (1974) and Duellman (2005)—and this could be indicative of niche segregation where species with unpigmented eggs use shadier environments.

Conclusions and future directions

We conducted the first phylogenetic analyses including a stringent test of the monophyly of all recognized formal and informal groupings in Dendropsophini, and the paraphyletic groupings were remedied with a number of taxonomic rearrangements. Species level taxonomy in *Dendropsophus* has always been complex. Our results corroborated, revealed, or made explicit multiple problems with currently recognized species, which will require extensive efforts to be clarified. Our results provide a strong foundation for future work to discuss different aspects of the taxonomy, evolutionary history, and biogeography of Dendropsophini.

Larval morphology and behaviour deserve special attention. Larval internal oral morphology and larval myology are known for few species (10 and four respectively; see Dias et al., 2017). Nevertheless, the evolution of larval morphology seems to have played an important role on the history of Dendropsophini (see above) and exploring such source of evidence is paramount.

Advertisement calls within Dendropsophini have difficult homology assessments (Orrico et al., 2009; Hepp et al., 2012) but clearly carry relevant evolutionary information. Notwithstanding, the lack of descriptions of *Xenohyla* advertisement call variables prevents a confident optimization of advertisement calls characters in our preferred topologies.

The diversification of the Neotropical vertebrate fauna has been shown to be extremely dynamic and complex and Dendropsophini is no exception. Our topology suggests multiple connections between the Atlantic Forest and the Amazon as found for other vertebrate groups (Fernandes et al., 2004; Batalha-Filho et al., 2013), including many frogs (Fouquet et al., 2012; De Sá et al., 2019). Moreover, Amazonia has smaller biogeographic subdivisions that were important in the speciation of many groups such as birds (Haffer, 1969; Ribas et al., 2011; Batalha-Filho et al., 2013), salamanders (Brcko et al., 2013), plants (Prance, 1973), reptiles (Vanzolini and Williams, 1970), and mammals (Wallace, 1852; Costa, 2003) and may had some influence in the evolution of *Dendropsophus* species that dwell there. A similar process may have taken place in the Atlantic Forest and deserves future studies (Carnaval and Moritz, 2008; Batalha-Filho et al., 2013). Phylogeographic studies with *Dendropsophus* are very limited, but are a potential source of information for elucidating some of the nuances of the evolutionary processes in the continent. The roles of major rivers and habitat change through time in Amazonia and the Atlantic Forest may hold significant explanations for the reasons of the large present-day diversity of *Dendropsophus* in Neotropical rainforests.

Our phenomic dataset included characters from multiple character systems, and, as we discussed in Appendix S9, there are many other characters that require exploration. All of these, besides their relevance as sources of phylogenetic evidence, are also interesting avenues of research on their evolution in *Dendropsophus* and the knowledge on the phylogeny of Dendropsophini now seems minimally ripe to begin studies on these issues.

Note added in proof

While this contribution was in proofing stage, Ferrão et al. (2020) described a new species of the genus (*Dendropsophus bilobatus*) and suggested the existence of one or two species more related to *D. reichlei*. Ferrão et al. (2020) highlighted the bluish-green vocal sac of *D. bilobatus* as an important diagnostic feature of the species. Although, this coloration is a putative synapomorphy of our *D. branneri* clade, their phylogenetic tree (that is similar to the one of Jansen et al. 2019) does not recover the *D. branneri* clade. We downloaded representatives of the species suggested in Ferrão et al. (2020) and performed a quick search with the same parameters of our preliminary exploratory searches. We found the unnamed species as sister to *D. reichlei* and *D. bilobatus* nested within the *D. branneri* clade confirming the bluish-green as a putative morphology of this clade. This is also an indication that previous topologies of *Dendropsophus* relationships are deeply affected by taxon and gene sampling.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Skulls, dorsal view.

Fig. S2. Lateral view of nasal cartilages.

Fig. S3. Skulls ventral, view.

Fig. S4. Lateral view of auditory regions. Numbers before the point stand for character reference number, numbers after, for character states. For character definition and character states, see SI6. (a) *Dendropsophus bipunctatus* CFBH 23081; (b) *Sphaenorhynchus prasinus* CFBH 22639; (b) *Scarthyla goinorum* CFBH 24821. Stable copy available at: 10.6084/m9.figshare.12481991

Fig. S5. Hyoid apparatus, ventral view. Numbers before the point stand for character reference number, numbers after, for character states. For character definition and character states, see SI6. (a) *Scinax littoralis* CFBH 17372; (b) *Dendropsophus rhodopeplus* CFBH 23744; (c) *Sphaenorhynchus prasinus* CFBH 22639; (d) *Lysapsus limellum* CFBH 8786; (e) *D. oliveirai* CFBH 19336; (f) *D. melanargyreus* ZUEC 10191; (g) *D. sanborni* CFBH 21200; (h) *D. virolinensis* ICN 12518; (i) *D. kamagarini* CFBH 23742. Stable copy available at: 10.6084/m9.figshare.12481997

Fig. S6. Tympanic membrane differentiation—character 120. (a) *Sphaenorhynchus pauloalvini* CFBH 22922, state 0—not clearly differentiated; (b) *Dendropsophus rhodopeplus* TG 2855, state 1—clearly differentiated. Stable copy available at: 10.6084/m9.figshare.12482015

Fig. S7. Examples of colour pattern. For character definition and character states, see SI6. (a) *Sphaenorhynchus prasinus* CFBH 22639, homogeneous; (b) *Dendropsophus melanargyreus* CFBH 900, marbled; (c) *Pseudis minutus* DL 01 blotched; (d) *Pseudis minutus* DL 01, stripped. Stable copy available at: 10.6084/m9.figshare.12482030

Fig. S8. States of characters 146 and 147 related to the cloacal area. For character definition and character states, see SI6. (a) *Dendropsophus rhodopeplus* TG 2885; (b) *D. minutus* CFBH 28981. Stable copy available at: 10.6084/m9.figshare.12482039

Fig. S9. States of characters 149 and 150, related with the ulnar fold. For character definition and character states, see SI6. (a) *Dendropsophus meridianus*, CFBH 22227; (b) *D. ruschii* MNRJ 47857; (c) *D. melanargyreus* CFBH 900; (d) *Pseudis minutus* DL 01. Stable copy available at: 10.6084/m9.figshare.12482081

Fig. S10. Nuptial pads. For character definition and character states, see SI6. (a) *Dendropsophus sarayacuensis* MNRJ 3652; (b) *D. molitor* ICN 12586; (c) *Sphaenorhynchus pauloalvini* CFBH 22922 dorsal views; (d) *D. melanargyreus* CFBH 900 ventral view of nuptial pad. Note that the nuptial pad extends onto the arm. Stable copy available at: 10.6084/m9.figshare.12482099

Fig. S11. Myocardium pigmentation—character 186. (a) *Dendropsophus seniculus* CFBH 22649, state 0—melanophores absent; (b) *D. elianeae* CFBH 21149 state 1 melanophores present (ventral views). Stable copy available at: 10.6084/m9.figshare.12482111

Fig. S12. Characters related to visceral anatomy.

Appendix S1. Possible phenomic synapomorphies (PPS) of currently recognized species groups of *Dendropsophus* suggested in literature.

Appendix S2. Historical summary of currently recognized groups.

Appendix S3. GenBank accession numbers. Bold numbers are new sequences produced for this project.

Appendix S4. Studied specimens.

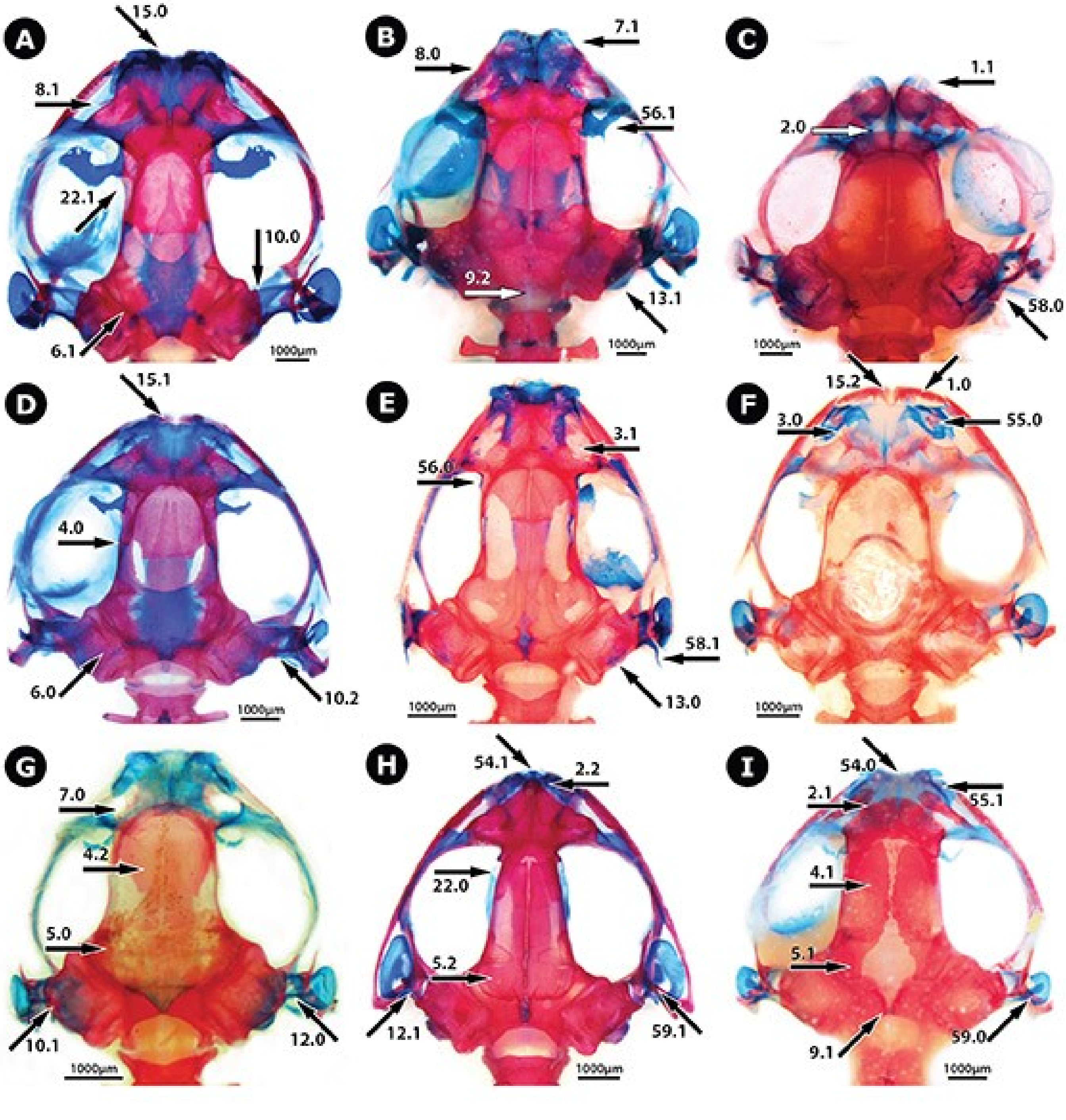
Appendix S5. Oligonucleotide primers used in this study.

Appendix S6. Phenomic characters. Stable copy available at: 10.6084/m9.figshare.12482423

Appendix S8. Data matrix. The first 201 characters are phenomic characters. The following characters are displayed in the implied alignment. The phenomic subset is available at Morphobank: http://morphobank.org/permalink/?P3755. Stable copy available at: 10.6084/m9.figshare.12478679

Appendix S8. List of morphological transformations and phenomic character optimizations over one of the most parsimonious trees.

Appendix S9. Potentially informative variation not evaluated in this study.


A
15.0
8.1
22.1
10.0
6.1
1000µm
B
7.1
8.0
56.1
9.2
13.1
1000µm
C
1.1
2.0
58.0
1000µm
D
15.1
4.0
6.0
10.2
1000µm
E
3.1
56.0
58.1
13.0
1000µm
F
15.2
1.0
3.0
55.0
1000µm
G
7.0
4.2
5.0
10.1
12.0
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H
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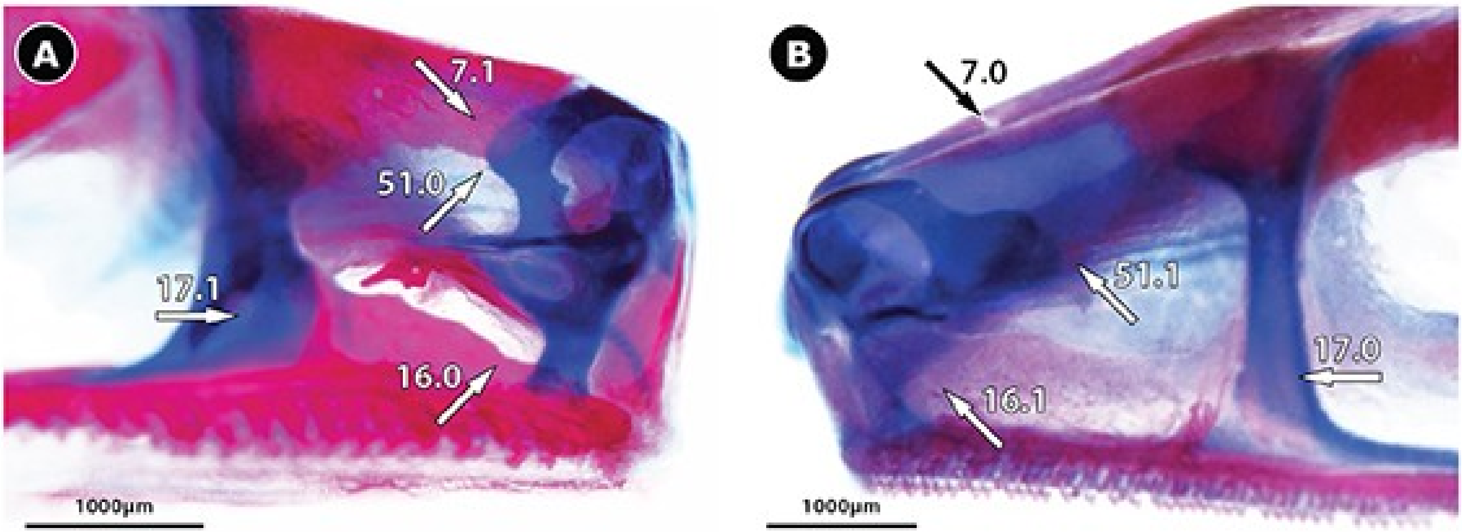
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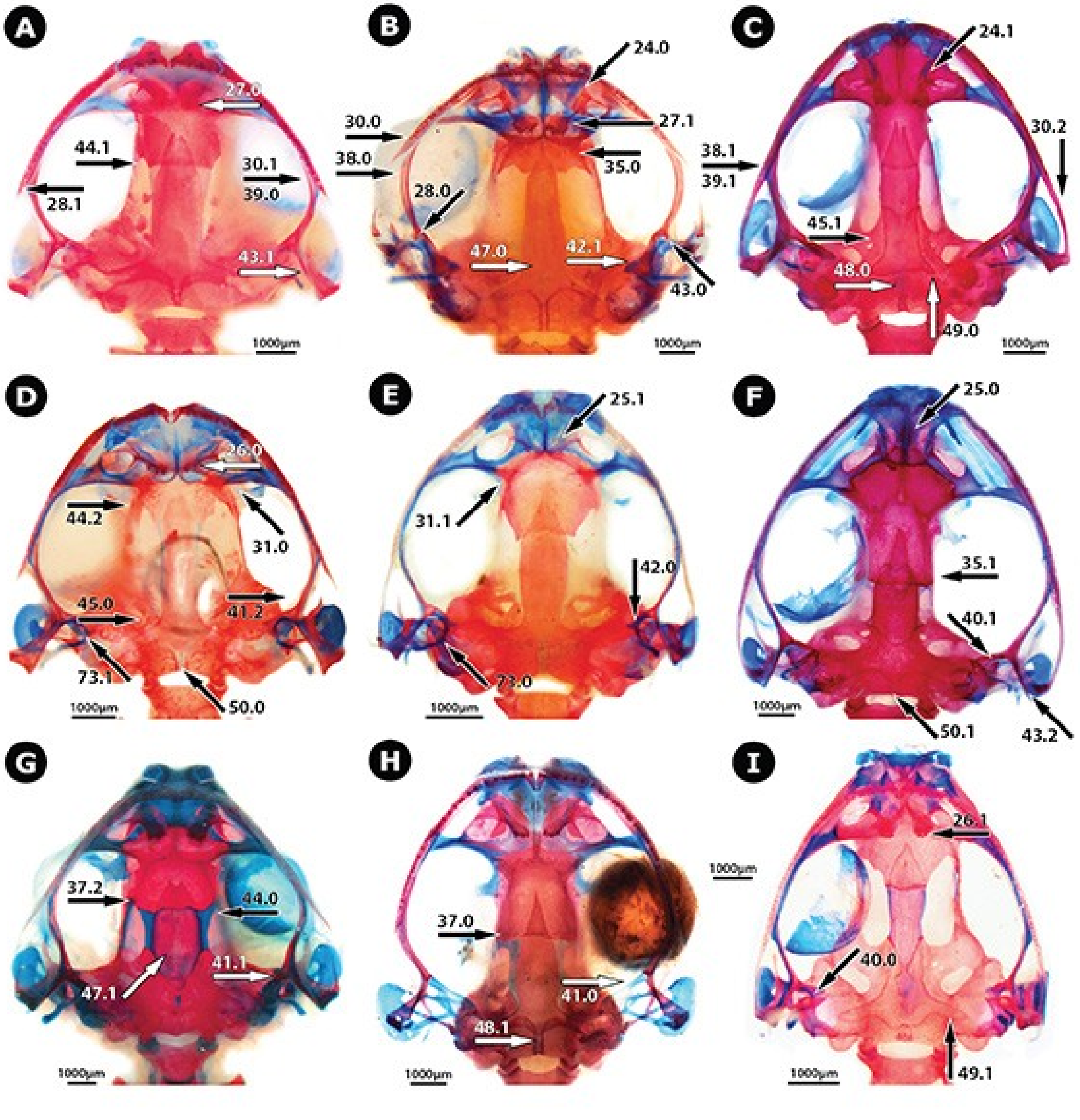
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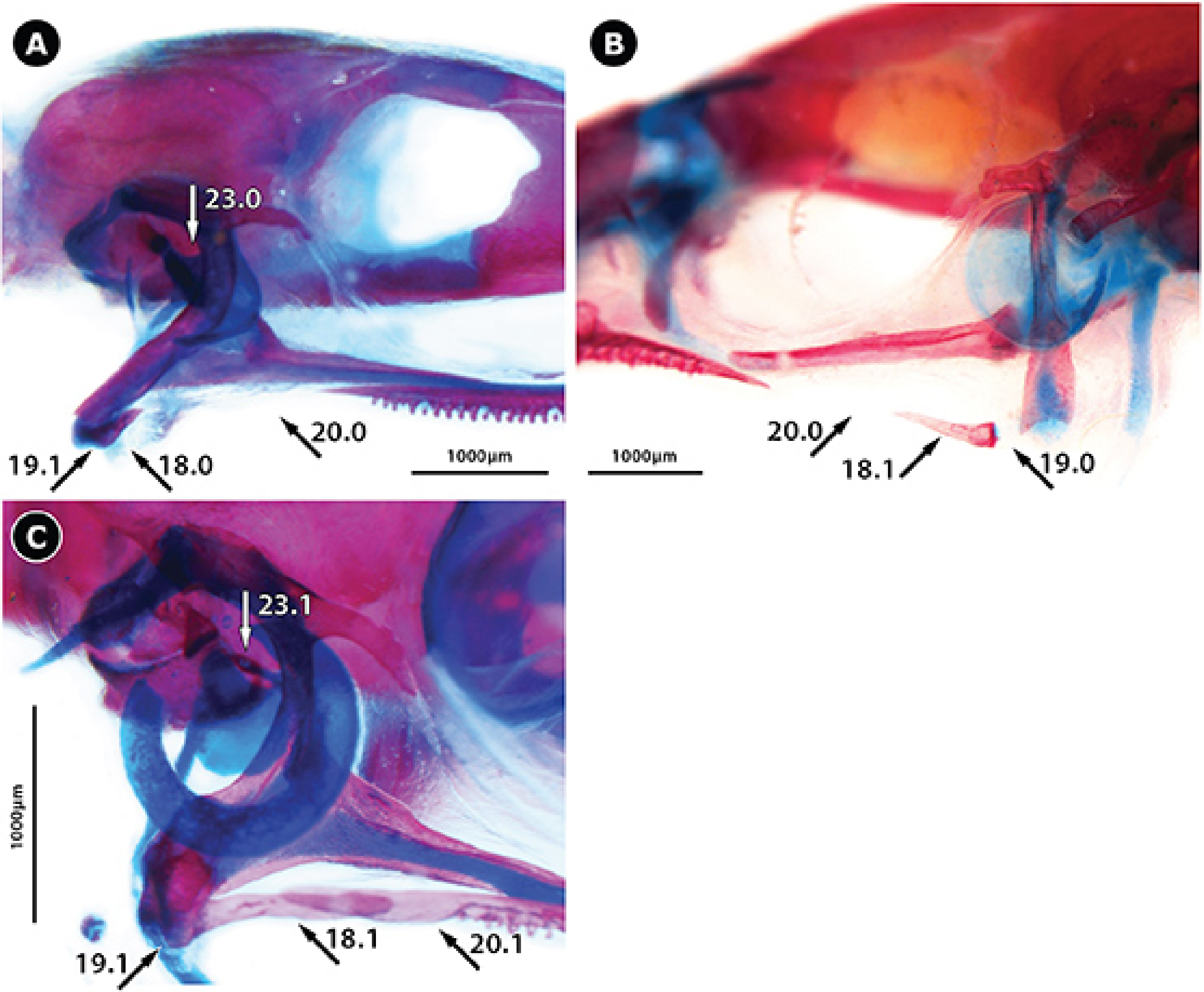
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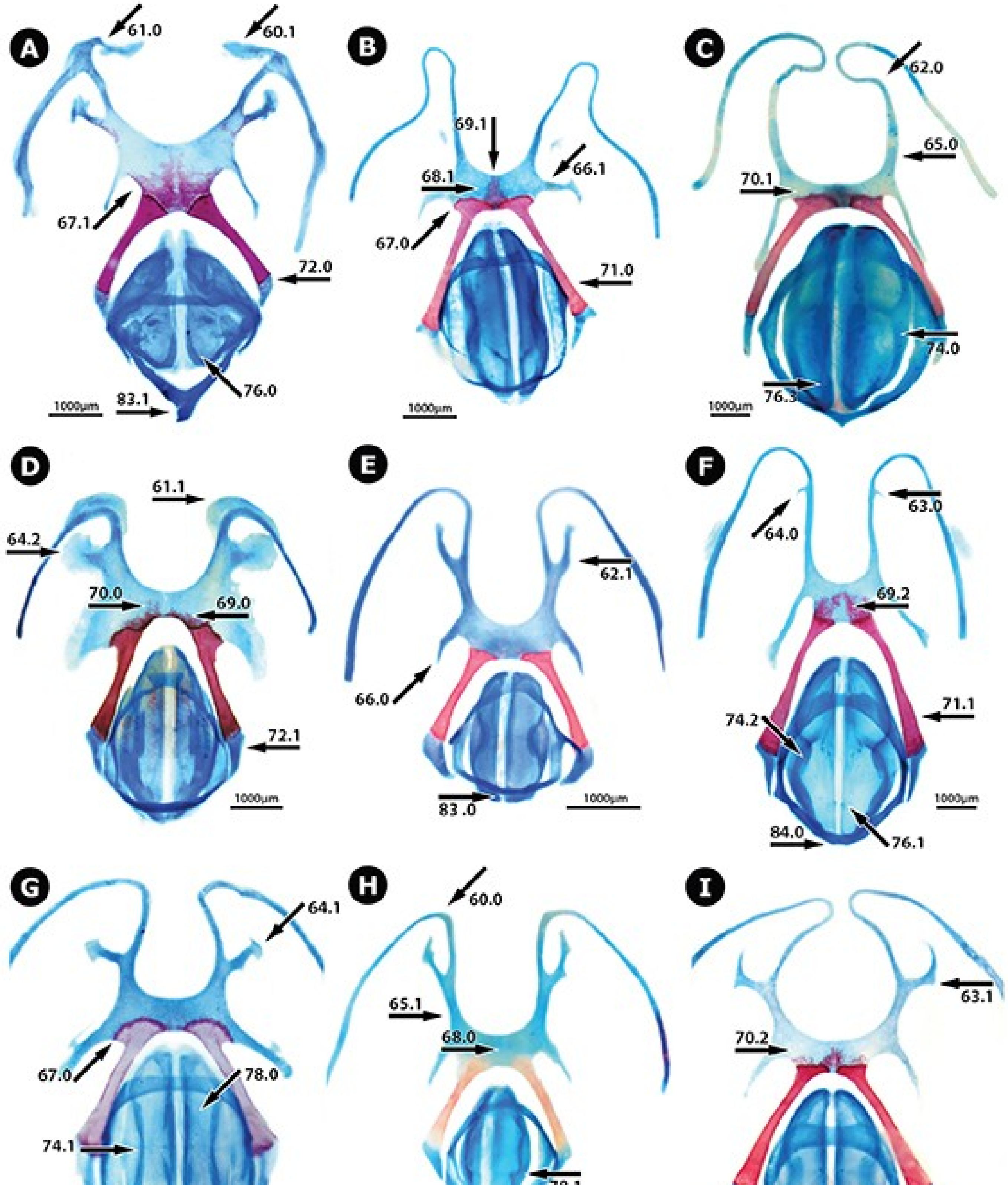
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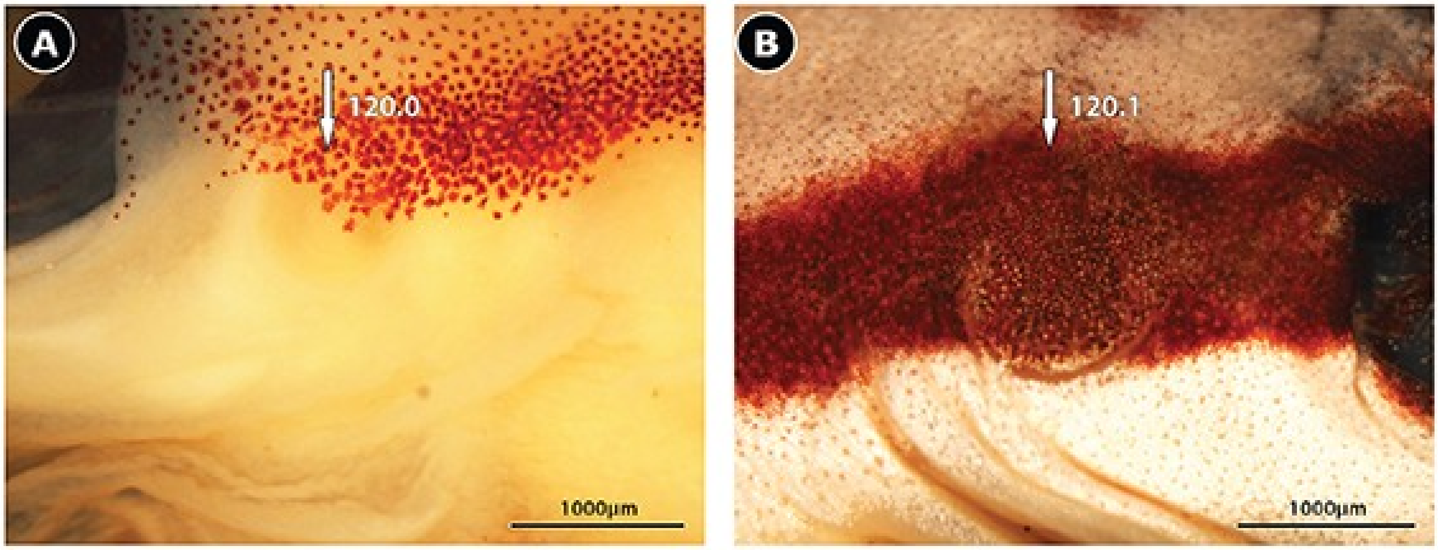
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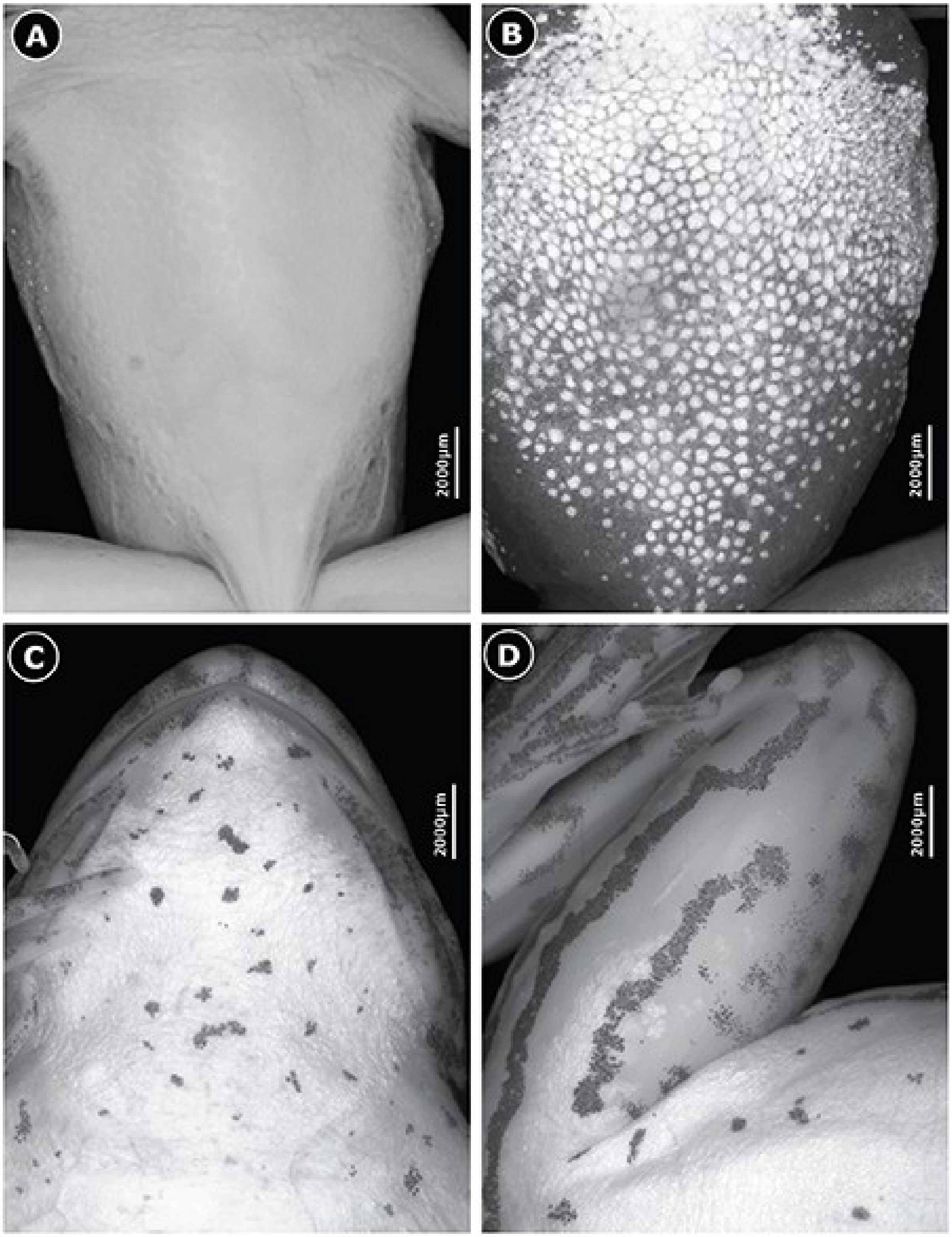
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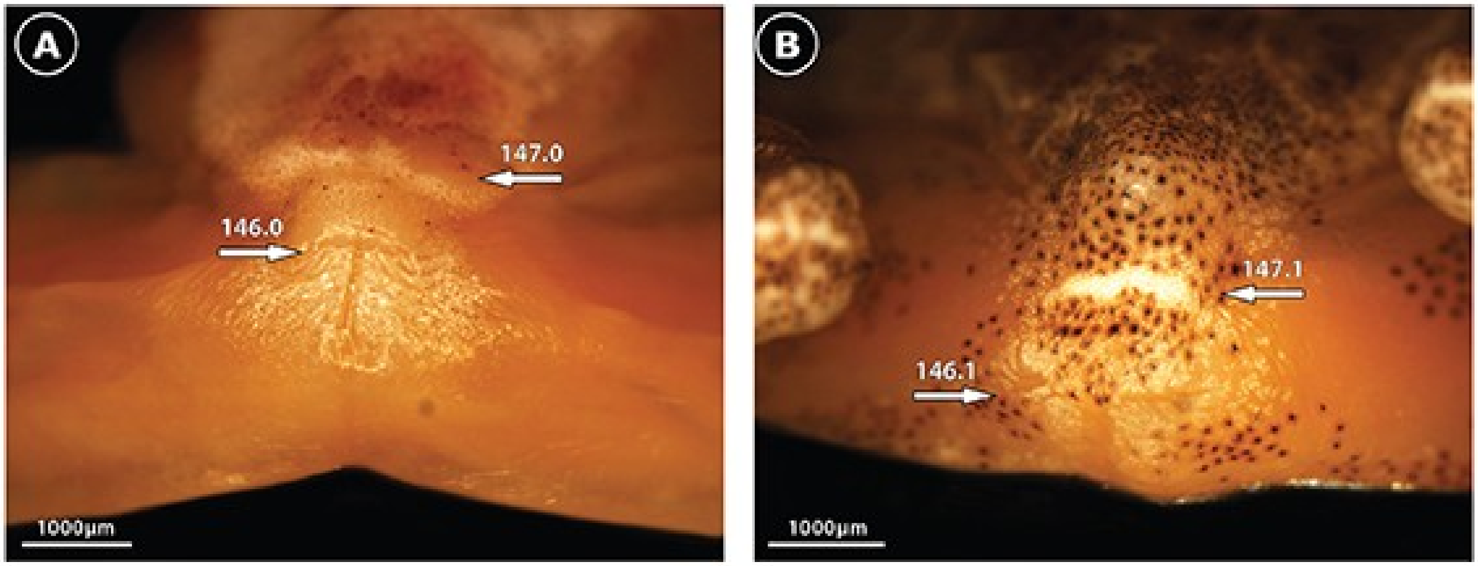
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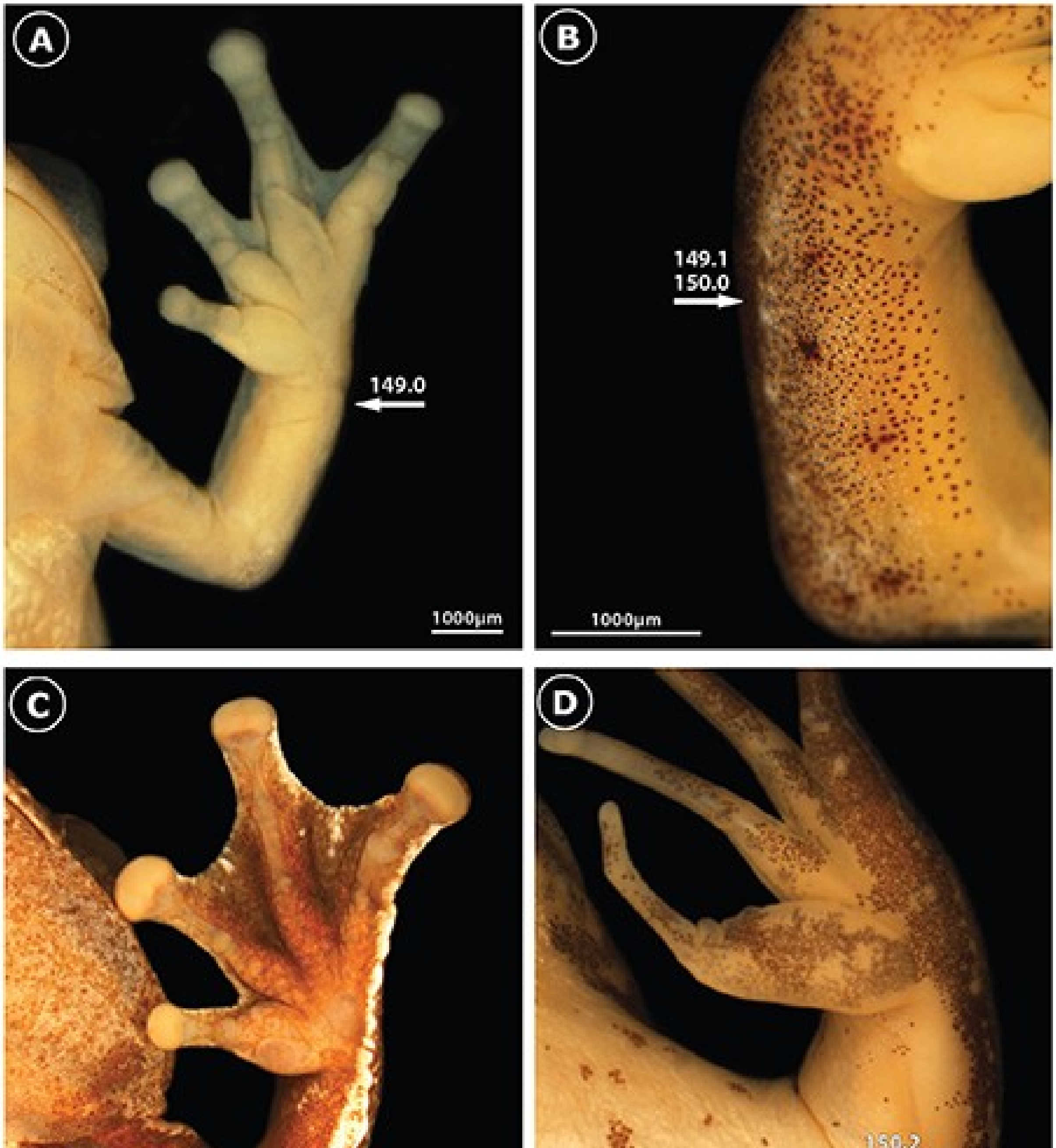
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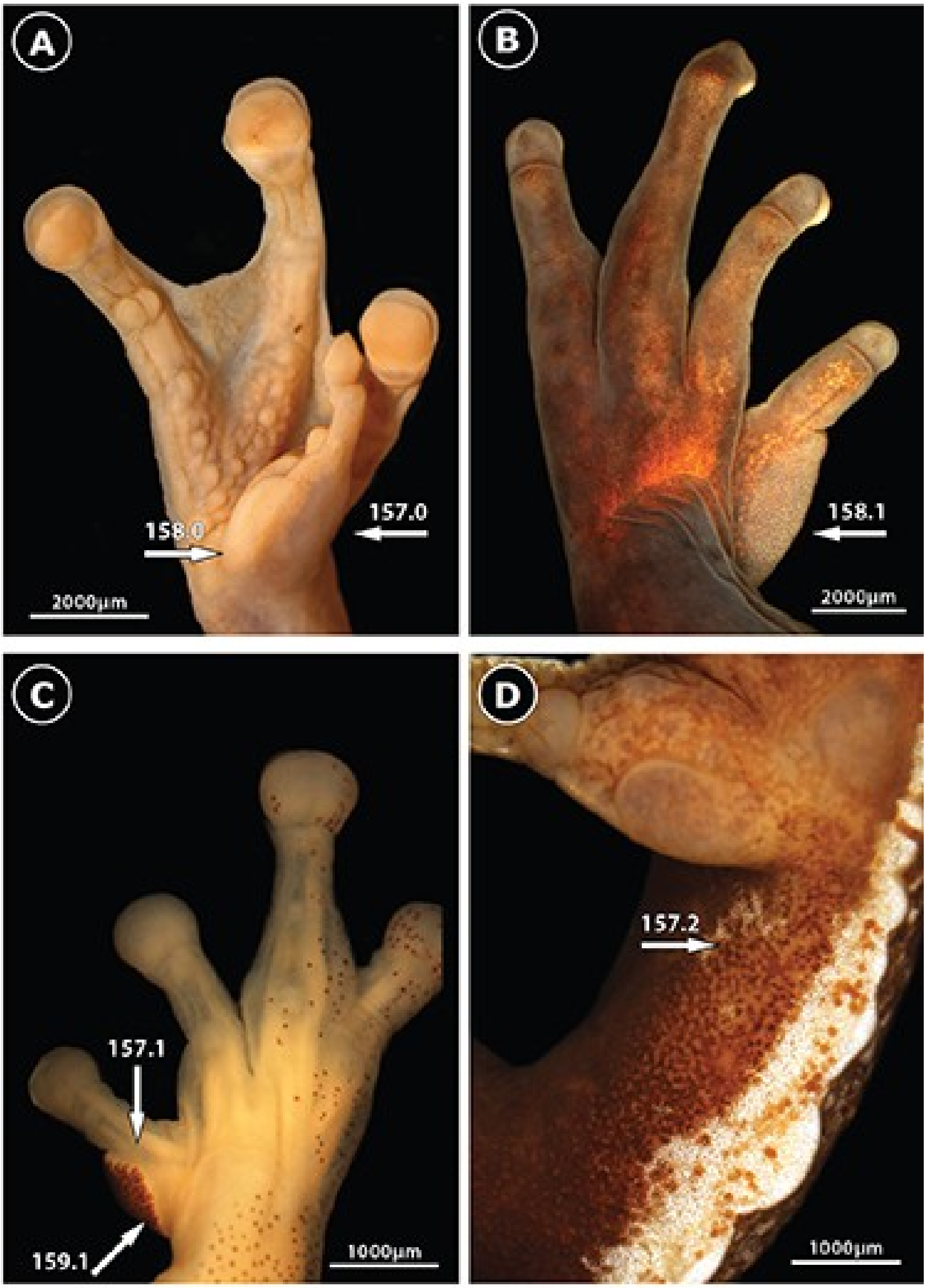
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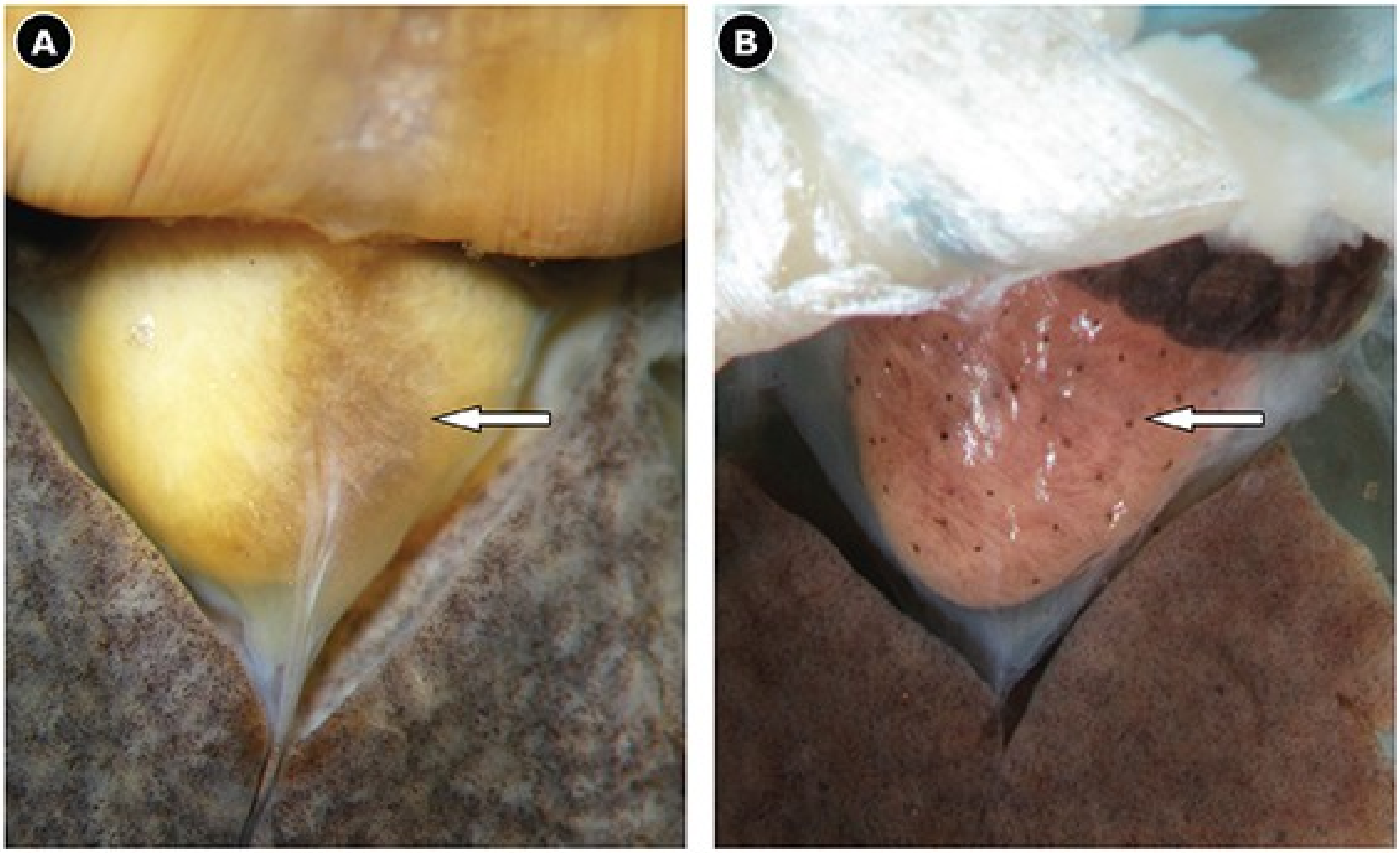
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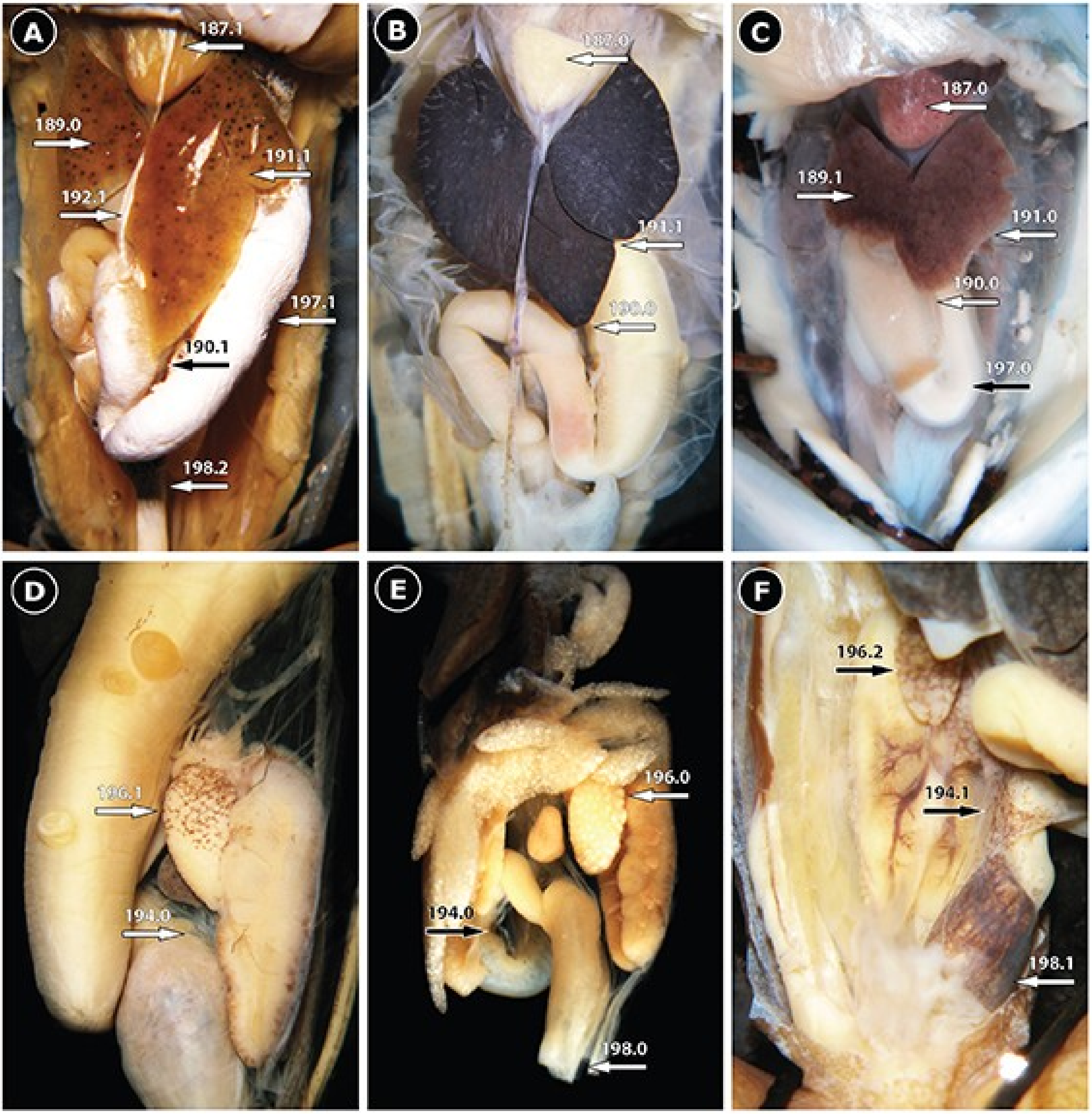
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D
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E
196.0
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F
196.2
194.1
198.1

Appendix S1.

Possible phenomic synapomorphies (PPS) of currently recognized species groups of *Dendropsophus* suggested in the literature

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Group	PPS	References of the PPS	obs
Dendropsophus			
a.	extreme reduction in the quadratojugal	Duellman and Trueb (1983)	At least one instance of homoplasy in *D. anceps* (see Wogel et al., 2000)
b.	1/2 labial tooth row formula		
c.	reduced or absent *m. contrahentis hallucis*	Burton (2004)	some other hylid species also present these character states
d.	presence of the *m. flexor teres hallucis*		
columbianus			
a.	presence of two close, triangular lateral spaces between the cricoid and arytenoids at the posterior part of the larynx	Kaplan (1999)	
garagoensis			
a.	internal surface of the arytenoids with a small medial depression	Kaplan (1999)	
leucophyllatus			
a.	presence of pectoral glands in two patches	Duellman (1970)	except for *D. anceps* (see Faivovich et al., 2005)
b.	"violin-shaped" larval body	Duellman and Trueb (1983)	
marmoratus			
a.	warty skin around the margin of the lower lip	Bokermann (1964)	
b.	crenulated margin of limbs		
c.	dorsal marbled pattern		
d.	"large vocal sacs"		
e.	pectoral lymphatic septum is modified in a way that permits the	Tyler (1971)	

	inflated sac to intrude into sub-humeral spaces		
f.	larvae share the presence of a thick sheath of tissue in the basal portion of the tail muscle and adjacent fins	Faivovich *et al.* (2005)	
g.	advertisement call with "final pulse clusters"	Orrico *et al.* (2009)	
h.	advertisement call composed of multipulsed single notes with the first two harmonics being those with most energy.	Hepp *et al.* (2012)	
microcephalus			
a.	mating call consisting of one primary note followed by a series of shorter secondary notes	Duellman and Fouquette (1968)	
b.	lack of labial tooth rows and marginal papillae*;	Duellman and Trueb (1983)	The *D. rubicundulus* clade may be diagnosed by the metachomy of the green color of live specimens to a purple tone in alcohol (see Faivovich et al., 2005)
minimus			
a.	not stated	Duellman (1982)	
minutus			
a.	a dark saddle on the back and a transverse white line above the vent and on each heel	Cochran (1955); Cochran and Goin (1970)	
b.	a long cloacal sheath	Duellman (1970)	
molitor (formerly *labialis*)			

a.	not stated	Duellman and Trueb (1983); Duellman (1989)
parviceps		
a.	a poorly developed tympanum and no distinctive axillary membrane	Duellman (1970; 1982); Duellman and Trueb (1983)
b.	pale vertical suborbital bars on the upper lip and pale spots on the thighs or shanks	

*= A reversal occurs in the *D. decipiens* clade.

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Appendix S2.

Historical summary of currently recognized groups

The Dendropsophus leucophyllatus *group.*— This group is the best understood of the currently recognized groups of *Dendropsophus*. Only *D. rossalleni* has never been included in molecular analyses (see Caminer et al., 2017; and Dias et al., 2017). Savage (2002) suggested, without evidence or justification, that the *D. microcephalus* and *D. parviceps* groups could be subgroups of a larger *D. leucophyllatus* group that would contain also a *D. leucophyllatus* subgroup. This proposal was not accepted by subsequent authors (e.g. Köhler et al., 2005) nor recovered in any phylogenetic analysis (e.g. Faivovich et al., 2005; Rivera-Correa and Orrico, 2013).

Rivera-Correa and Orrico (2013) remarked that a “core” *Dendropsophus leucophyllatus* group has been recognized as monophyletic with strong support. Nevertheless, two aspects of the group’s systematics still require special attention: the relationships of *D. elegans* and the inclusion of *D. anceps* in the group.

Duellman (1982b), based on morphological similarity, hypothesized that *Dendropsophus elegans* and *D. leucophyllatus* are sister species, but no subsequent study has found them to be closely related (e.g. Chek et al., 2001; Lougheed et al., 2006). Subsequently, Jungfer et al. (2010) recovered *D. elegans* as the sister species of a southwestern Amazonian species (*D. salli*), and most subsequent molecular phylogenetic studies also supported this clade (e.g. Dias et al., 2017). Caminer et al. (2017) described a new species based on specimens previously assigned to *D. leucophyllatus* that was recovered as sister to *D. salli* in their analysis.

The placement of *Dendropsophus anceps* in the *D. leucophyllatus* group is controversial (see comments on Rivera-Correa and Orrico, 2013). *Dendropsophus* *anceps* has been found as sister taxon to remainder species of the *D. leucophyllatus* group (e.g. Faivovich et al., 2005; Moen and Wiens, 2009; Caminer et al., 2017) or distantly related (e.g. Wiens et al., 2010). Jungfer et al. (2010) stated that *D. anceps* was related with the outgroup taxa, but the species was omitted from their consensus tree (see Jungfer et al., 2010: Fig. 7). Nevertheless, species of the *D. leucophyllatus* group resemble *D. anceps*, and the presence of pectoral glands, a putative morphological synapomorphy of the *D. leucophyllatus* group (Cochran and Goin, 1970; Duellman, 1970; Faivovich et al., 2005) also supports the relationship of *D. anceps* to this group (Rivera-Correa and Orrico, 2013).

Recently, *Dendropsophus miyatai*, a species referred to the *D. minimus* group (of Faivovich et al., 2005), has been recovered nested within the *D. leucophyllatus* group (e.g. Fouquet et al., 2011; 2015). However, these results have not been discussed.

The Dendropsophus marmoratus *group.*— This group was first recognized by Cochran (1955), and reviewed by Bokermann (1964). The group comprises eight species that share a number of diagnostic character states (see Orrico et al., 2009; Hepp et al., 2012). Several of these are now known to be homoplastic at some level, especially with members of the *D. parviceps* group. Orrico et al. (2009) proposed a combination of advertisement call characters, subsequently restricted by Hepp et al. (2012), as possibly diagnostic for the group.

Bokermann (1964) suggested on the basis of their overall morphological similarity that there is a greater affinity between *Dendropsophus melanargyreus* and *D. seniculus,* and between *D. marmoratus* and *D. acreanus.* Subsequently, Bokermann (1968) stated that "*Hyla novaisi* may be subspecifically related to *H.*

senicula". Caramaschi and Jim (1983) hypothesized that *D. soaresi* is related to *D. seniculus*, *D. melanargyreus*, and *D. novaisi.* Alternatively, (Gomes and Peixoto, 1996) hypothesized a close relationship between *D. dutrai*, *D. novaisi*, and *D. soaresi*, three species that inhabit semiarid regions in North Eastern Brazil. The most inclusive phylogenetic analyses for this group included only three species: *D. marmoratus*, *D. melanargyreus*, and *D. seniculus* (see Fouquet et al., 2015). Nevertheless, there are also sequences of *D. soaresi* and *D. novaisi* available in GenBank (see Teixeira et al., 2016). *Dendropsophus acreanus*, *D. dutrai* and *D. nahdereri* were never included in any phylogenetic analyses.

The Dendropsophus parviceps *group.—* The group was first defined by Duellman and Crump (1974) and, although it is still recognized, its monophyly is currently regarded with skepticism (see Faivovich et al., 2005 and subsequent authors). The group composition has changed extensively over the years; however, while there are still species being described and added to the group (e.g. Motta et al., 2012; Fouquet et al., 2015), recent reviews have suggested that the diversity assigned to the group might be overestimated (e.g. Fouquet et al., 2011; and Orrico et al., 2013).

Subsequent to Faivovich et al. (2005), few other studies presented trees with a reasonable number of sampled species assigned to the *Dendropsophus parviceps* group and all of them found the group to be paraphyletic. Although results from these papers are rather conflictive, most make no comment about it, with the exceptions of Fouquet et al. (2011) and Motta et al. (2012).

The most inclusive phylogenetic analyses for this group (Fouquet et al., 2015) included ten species: *Dendropsophus bokermanni*, *D. brevifrons*, *D. counani*, *D. frosti*, *D. giesleri*, *D. koechlini*, *D. microps*, *D. parviceps*, *D. schubarti*, and *D.*

timbeba. *Dendropsophus grandisonae*, *D. luteoocellatus*, *D. pauiniensis*, *D. ruschii*, and *D. subocularis* were never included in any phylogenetic analyses.

The Dendropsophus minimus *group.*— Faivovich et al. (2005) following Duellman (1982) assigned four species for this group. However, subsequently it has been shown to be polyphyletic (Moen and Wiens, 2009; Wiens et al., 2010; Pyron and Wiens, 2011). Fouquet et al. (2011) transferred *D. riveroi* to the *D. microcephalus* group, and Gehara et al. (2014) transferred *D. aperomeus* to the *D. minutus* group. The position of *D. miyatai* is unstable (see comments on the *D. leucophyllatus* group section above). *Dendropsophus minimus* has never been included in a phylogenetic analysis.

The Andean groups.— There are three species groups of the genus whose distribution is restricted to the Andes: The *Dendropsophus columbianus*, *D. garagoensis* and *D. molitor* groups—see Jungfer (2017) for the use of *molitor* instead of *labialis*. Duellman and Trueb (1983) hypothesized a close relationship between the *D. columbianus* and *D. molitor* groups as the earlier diverging groups of the "30-chromosome *Hyla*", which was followed by subsequent authors in the 1990's (Kaplan, 1991; Kaplan, 1994; Duellman et al., 1997; Kaplan, 1999). Subsequent studies based on molecular data found the *D. columbianus* and *D. molitor* groups to be sister taxa, closely related to the *D. parviceps* group (Faivovich et al., 2005). Salducci et al. (2002) found a strongly supported relationship between these groups, but their relationship to species of other groups was poorly supported.

Kaplan (1991) described *Dendropsophus garagoensis* and, based on the phylogenetic hypothesis of Duellman and Trueb(1983), placed it in a polytomy with the *D. marmoratus* group, and a clade including the *D. parviceps* + *D. leucophyllatus*

+ *D. microcephalus* groups. Kaplan and Ruiz-Carranza (1997) suggested the absence of labial tooth rows as evidence for this arrangement. As noted by Faivovich et al. (2005) there are incongruences in this character assessment and this relationship and no additional evidence is known in support of this relationship. In fact, Duellman et al. (1997) imply that this character state should be a synapomorphy for *Dendropsophus* and hypothesize that the *D. garagoensis* group would be related to the *D. marmoratus* group.

Kaplan (1999) included *Dendropsophus praestans* in the *D. garagoensis* group based on the presence of an "internal surface of the arytenoids with a small medial depression" that he considered to be a synapomorphy of this group. Thus, *D. praestans* would not be related to the *D. columbianus* group, where it was placed by Duellman and Trueb (1983). Faivovich et al. (2005) recognized the evidence advanced by Kaplan (1999) as a putative synapomorphy and retained *D. praestans* in the *D. garagoensis* group.

Among these groups, only the relationships of the *Dendropsophus molitor* group have been studied with detail (Guarnizo et al., 2009; 2012) and sequences attributed to all four valid species are available. Despite the molecular support for its monophyly, no phenotypic evidences of monophyly had been suggested.

The monophyly of the *Dendropsophus columbianus* group has not been tested in a quantitative framework. Faivovich et al. (2005) suggested the diagnostic character of Kaplan and Ruiz-Carranza (1997)—the presence of two close, triangular lateral spaces between the cricoid and arytenoids at the posterior part of the larynx}—as the only putative phenotypic synapomorphy for this group. Only *D. columbianus* has been used in phylogenetic analyses.

The Dendropsophus minutus *group.*— Cochran (1955) first created the “*Hyla minuta*” group that accommodated several species of *Dendropsophus* from southeastern Brazil. The group was diagnosed as smooth-skinned small species with “immaculate (yellow or red in life) anterior and posterior femur”. Cochran and Goin (1970) provided a different definition based exclusively on *D. minutus*. Their diagnosis (“dark saddle on the back and a transverse white line above the vent and on each heel”) was used to relate species subsequently described such as *D. delarivai* (Köhler and Lötters, 2001) and *D. xapuriensis* (Martins and Cardoso, 1987) with *D. minutus*. Kaplan (1994) discussed the relationships of *D. stingi* with *D. minutus* and although not placing them in the same group, recognized their resemblance based on the diagnosis of Cochran and Goin (1970). This diagnosis was overlooked by Duellman (1982a), as he included a species with these characteristics (*D. aperomeus*) in the *D. minimus* group (see above). Köhler (2005) noticed the resemblance and stated that *D. aperomeus* seemed related to *D. minutus*

Martins and Cardoso (1987) remarked the similarity between the advertisement calls of *Dendropsophus xapuriensis* and *D. minutus*, with both species presenting advertisement calls composed of pulsed and unpulsed notes (Cardoso and Haddad, 1984; Martins and Cardoso, 1987). Species of *Dendropsophus* usually present only pulsed advertisement call notes (VGDO pers. obs.) and the ability to produce an advertisement call that presents these two kinds of notes might be a synapomorphy for the *D. minutus* group.

Given the morphological, behavioral and molecular variation of *Dendropsophus minutus*, together with its nearly pan-continental distribution, this nominal taxon is thought to be species complex (Cardoso and Haddad, 1984; Kaplan, 1994; Hawkins et al., 2007). Gehara et al. (2014) addressed this question by sampling throughout its distribution and sequencing two mitochondrial genes (COI and 16S). Gehara et al. (2014) recovered a monophyletic *D. minutus* group with the inclusion of *D. aperomeus* and *D. stingi* (two species that were suspected to be related with *D. minutus*) and a high molecular diversity within the species *D. minutus*; it is uncertain if this molecular diversity corresponds to additional species. Of the species assigned to the group, only *D. limai* (known only from the holotype) has never been addressed in phylogenetic analyses.

The Dendropsophus microcephalus *group.*— With nearly 40% of the known diversity (40 species), this is the most species-rich group within the genus (Faivovich et al., 2005; Ortega-Andrade and Ron, 2013; Orrico et al., 2014). Historically, and mostly due to the broad distribution of species assigned to this group, papers with taxonomic objectives have limited their comments to geographical subsets of species assigned to this group (e.g. Duellman and Fouquette, 1968; Cochran and Goin, 1970; Pombal Jr. and Bastos, 1998; Cruz et al., 2000; Köhler et al., 2005; Ortega-Andrade and Ron, 2013).

Faivovich et al. (2005) recovered their single specimens of *Dendropsophus rubicundulus* and *D. berthalutzae* nested in the *D. microcephalus* group. These and their related species were pre-cladistically thought to be related to the *D. microcephalus* group but were assigned to distinct groups; the former *Hyla rubicundula* and *Hyla decipiens* groups, respectively (see Napoli and Caramaschi, 1999b; Pugliese et al., 2000). Faivovich et al. (2005) only had a single terminal assigned to each of these groups, so they could not test their monophyly, and recognized them as clades nested within the *D. microcephalus* group.

The *Dendropsophus decipiens* clade, as currently delimited (see Faivovich et al., 2005), was considered distinct from other species of the *D. microcephalus* group based on tadpole characters (Pugliese et al., 2000; Carvalho-e-Silva et al., 2003)

All species of the *Dendropsophus rubicundulus* clade have a green dorsum in life that changes to pinkish or violet when preserved (Napoli and Caramaschi, 1998). The series of contributions by Napoli and Caramaschi (1998; 1999a; 1999b; 2000), implied that species with single sacral stripes would be the "*Dendropsophus tritaeniatus*" complex (*D. araguaya*, *D. cerradensis*, *D. jimi*, *D. rhea*, and *D. tritaeniatus*) and species with double sacral lines the *D. rubicundulus* Complex (*Dendropsophus anataliasiasi*, *D. cachimbo*, *D. elianeae*, and *D. rubicundulus*).

The phylogenetic analysis of Medeiros et al. (2013) indicated that these complexes are paraphyletic with respect to each other. They have also found *Dendropsophus sanborni*, a species always assumed to be related to *D. nanus* due to morphological similarity of adults (e.g. Basso et al., 1985) and larvae (e.g. Lavilla, 1990), nested in the *D. rubicundulus* clade. However, Medeiros et al. (2013) did not make any formal rearrangement to include *D. sanborni* in their *D. rubicundulus* group (not clade), leaving it paraphyletic; we recognize the *D. rubicundulus* clade throughout the text and discuss the inclusion of *D. sanborni*.

Jansen et al. (2019) also retrieved *Dendropsophus sanborni* nested in the *D. rubicundulus* clade. Moreover, the *D. rubicundulus* clade was also paraphyletic in respect to the inclusion of the species *D. cruzi*, *D. juliani*, *D. mathiassoni*, *D. minusculus*, and a new species therein described (*D. rozenmani*) that were not previously assigned to the clade. While *D. rozenmani* was previously confused with *D. tritaeniatus*, the remaining species were highly morphologically different.

Nevertheless, Jansen et al. (2019) did not modify the clade composition because their analyses were only designed to address the specific status of *D. rozenmani*.

To date, only 20 species have been used in cladistic analyses: *D. anataliasiasi*, *D. berthalutzae*, *D. bipunctatus*, *D. cruzi*, *D. elianeae*, *D. gaucheri*, *D. jimi*, *D. juliani*, *D. leali*, *D. mathiassoni*, *D. microcephalus*, *D. minusculus*, *D. nanus*, *D. rhodopeplus*, *D. robertmertensi*, *D. rozenmani, D. sanborni*, *D. sartori*, *D. shiwiarum* (as *D. riveroi*; see results), and *D. walfordi*.

Species unassigned to a group.— Faivovich et al. (2005) left six *Dendropsophus* species unassigned to any of their groups. Those were *D. amicorum*, *D. battersbyi*, *D. haraldschultzi*, *D. stingi*, *D. tintinnabulum*, and *D. yaracuyanus*. *Dendropsophus amicorum* and *D. stingi* were later assigned to the *D. minutus* group (Gehara et al., 2014), *D. tintinnabulum* to the *D. microcephalus* group (Teixeira and Giaretta, 2016), and *D. yaracuyanus* to the *D. parviceps* group (Barrio-Amorós et al., 2019). *Dendropsophus battersbyi* is still unassigned.

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Appendix S3. Genbank accession numbers. Bold numbers are new

Nominal species	Name in tree
Dendropsophus acreanus	D acreanus M
Dendropsophus anataliasiasi	D anataliasiasi (1)
Dendropsophus anataliasiasi	D anataliasiasi (2)
Dendropsophus anceps	D anceps M
Dendropsophus anceps	D anceps (1)
Dendropsophus anceps	D anceps (2)
Dendropsophus aperomeus	D aperomeus
Dendropsophus araguaya	D araguaya I (1)
Dendropsophus araguaya	D araguaya I (2)
Dendropsophus araguaya	D araguaya II (1)
Dendropsophus araguaya	D araguaya II (2)
Dendropsophus berthalutzae	D berthalutzae (1)
Dendropsophus berthalutzae	D berthalutzae (2) M
Dendropsophus bifurcus	D bifurcus
Dendropsophus bipunctatus	D bipunctatus (1) M
Dendropsophus bipunctatus	D bipunctatus (2)
Dendropsophus bogerti	D bogerti (1)
Dendropsophus bogerti	D bogerti (2)
Dendropsophus bokermanni	D bokermanni (1)
Dendropsophus bokermanni	D bokermanni (2)
Dendropsophus branneri	D branneri (1)
Dendropsophus branneri	D branneri (2) M
Dendropsophus brevifrons	D brevifrons (1)
Dendropsophus brevifrons	D brevifrons (2)
Dendropsophus bromeliaceus	D bromeliaceus
Dendropsophus cachimbo	D cachimbo (1)
Dendropsophus cachimbo	D cachimbo (2)
Dendropsophus carnifex	D carnifex M
Dendropsophus cerradensis	D cerradensis (1)
Dendropsophus cerradensis	D cerradensis (2)
Dendropsophus goughi	D cf goughi
Dendropsophus coffea	D coffea
Dendropsophus columbianus	D columbianus (1)
Dendropsophus columbianus	D columbianus (2) M
Dendropsophus counani	D counani
Dendropsophus cruzi	D cruzi
Dendropsophus decipiens	D decipiens I M
Dendropsophus cf. decipiens	D decipiens II
Dendropsophus cf. decipiens	D decipiens III (1)
Dendropsophus cf. decipiens	D decipiens III (2)
Dendropsophus cf. decipiens	D decipiens IV (1)
Dendropsophus cf. decipiens	D decipiens IV (2)
Dendropsophus sp. (aff. decipi	D decipiens V (1)
Dendropsophus sp. (aff. decipi	D decipiens V (2)
Dendropsophus cf. decipiens	D decipiens VI (1)
Dendropsophus cf. decipiens	D decipiens VI (2)

Dendropsophus cf. decipiens	D decipiens VII
Dendropsophus cf. decipiens	D decipiens VIII
Dendropsophus delarivai	D delarivai
Dendropsophus dutrai	D dutrai M
Dendropsophus ebraccatus	D ebraccatus (1)
Dendropsophus ebraccatus	D ebraccatus (2)
Dendropsophus cf. elegans	D elegans I (1) M
Dendropsophus cf. elegans	D elegans I (2)
Dendropsophus elegans	D elegans II (1)
Dendropsophus elegans	D elegans II (2)
Dendropsophus elianeae	D elianeae (1)
Dendropsophus elianeae	D elianeae (2) M
Dendropsophus frosti	D frosti
Dendropsophus garagoensis	D garagoensis (1)
Dendropsophus garagoensis	D garagoensis (2)
Dendropsophus gaucheri	D gaucheri (1)
Dendropsophus gaucheri	D gaucheri (2)
Dendropsophus giesleri	D giesleri (1)
Dendropsophus giesleri	D giesleri (2)
Dendropsophus haddadi	D haddadi
Dendropsophus haddadi	D haddadi (2) M
Dendropsophus haddadi	D haddadi 1
Dendropsophus haraldschultzi	D haraldschultzi (1)
Dendropsophus haraldschultzi	D haraldschultzi (2) M
Dendropsophus jimi	D jimi M
Dendropsophus jimi	D jimi (1)
Dendropsophus jimi	D jimi (2)
Dendropsophus joannae	D joannae
Dendropsophus juliani	D juliani (1)
Dendropsophus juliani	D juliani (2)
Dendropsophus kamagarini	D kamagarini M
Dendropsophus koechlini	D koechlini
Dendropsophus leali	D leali (1)
Dendropsophus leali	D leali (2)
Dendropsophus luddeckei	D luddeckei (1)
Dendropsophus luddeckei	D luddeckei (2)
Dendropsophus luteoocelatus	D luteoocelatus
Dendropsophus manonegra	D manonegra (1)
Dendropsophus manonegra	D manonegra (2)
Dendropsophus mapinguari	D mapinguari (1)
Dendropsophus mapinguari	D mapinguari (2)
Dendropsophus marmoratus	D marmoratus
Dendropsophus marmoratus	D marmoratus (1) M
Dendropsophus marmoratus	D marmoratus (2)
Dendropsophus mathiassoni	D mathiassoni (1)
Dendropsophus mathiassoni	D mathiassoni (2)
Dendropsophus melanargyreu	D melanargyreus
Dendropsophus melanargyreu	D melanargyreus (1)

Dendropsophus melanargyreu	D melanargyreus (2)
Dendropsophus melanargyreu	D melanargyreus (4) M
Dendropsophus meridensis	D meridensis
Dendropsophus meridianus	D meridianus (1) M
Dendropsophus meridianus	D meridianus (2)
Dendropsophus meridianus	D “berthalutzae” GB
Dendropsophus microcephalu	D microcephalus
Dendropsophus microcephalu	D microcephalus (2)
Dendropsophus microps	D microps M
Dendropsophus minusculus	D minusculus
Dendropsophus minusculus	D minusculus (1)
Dendropsophus minusculus	D minusculus (2)
Dendropsophus sp. (aff. minut	D aff minutus
Dendropsophus minutus	D minutus I M
Dendropsophus cf. minutus	D minutus II
Dendropsophus cf. minutus	D minutus III
Dendropsophus cf. minutus	D minutus IV
Dendropsophus miyatai	D miyatai
Dendropsophus molitor	D molitor (1) M
Dendropsophus molitor	D molitor (2)
Dendropsophus nahdereri	D nahdereri (1)
Dendropsophus nahdereri	D nahdereri (2) M
Dendropsophus nanus	D nanus (1) M
Dendropsophus nanus	D nanus (2)
Dendropsophus nekronastes	D nekronastes (1)
Dendropsophus nekronastes	D nekronastes (2)
Dendropsophus norandinus	D norandinus (1)
Dendropsophus norandinus	D norandinus (2)
Dendropsophus novaisi	D novaisi
Dendropsophus novaisi	D novaisi (1) M
Dendropsophus novaisi	D novaisi (2)
Dendropsophus oliveirai	D oliveirai (1) M
Dendropsophus oliveirai	D oliveirai (2)
Dendropsophus ozzyi	D ozzyi (1)
Dendropsophus ozzyi	D ozzyi (2)
Dendropsophus padreluna	D padreluna
Dendropsophus parviceps	D parviceps
Dendropsophus pauiniensis	D pauiniensis
Dendropsophus praestans	D praestans
Dendropsophus pseudomeridia	D pseudomeridianus (1)
Dendropsophus pseudomeridia	D pseudomeridianus (2)
Dendropsophus reicheli	D reicheli (1)
Dendropsophus reicheli	D reicheli (2)
Dendropsophus reticulatus	D reticulatus Tab
Dendropsophus rhodopeplus	D rhodopeplus (1) M
Dendropsophus rhodopeplus	D rhodopeplus (2)
Dendropsophus riveroi	D riveroi M
Dendropsophus riveroi	D sp ARB 2011

Dendropsophus robertmertens	D robertmertensi
Dendropsophus rossalleni	D rossalleni (1)
Dendropsophus rossalleni	D rossalleni (2)
Dendropsophus rozenmani	D rozenmani (1)
Dendropsophus rozenmani	D rozenmani (2)
Dendropsophus rubicundulus	D rubicundulus (1)
Dendropsophus rubicundulus	D rubicundulus (2)
Dendropsophus rubicundulus	D rubicundulus GB
Dendropsophus ruschii	D ruschii (1) M
Dendropsophus ruschii	D ruschii (2)
Dendropsophus salli	D salli (1)
Dendropsophus salli	D salli (2)
Dendropsophus sanborni	D sanborni (1)
Dendropsophus sanborni	D sanborni (2) M
Dendropsophus sarayacuensis	D sarayacuensis (1)
Dendropsophus sarayacuensis	D sarayacuensis (2)
Dendropsophus sartori	D sartori (1)
Dendropsophus sartori	D sartori (2)
Dendropsophus schubarti	D schubarti (1)
Dendropsophus schubarti	D schubarti (2)
Dendropsophus seniculus	D seniculus (1)
Dendropsophus seniculus	D seniculus (2) M
Dendropsophus seniculus	D seniculus (3)
Dendropsophus shiwiarum	D shiwiarum (1)
Dendropsophus shiwiarum	D shiwiarum (2)
Dendropsophus shiwiarum	D shiwiarum (3)
Dendropsophus soaresi	D soaresi M
Dendropsophus soaresi	D soaresi (1)
Dendropsophus soaresi	D soaresi (2)
Dendropsophus stingi	D stingi (1)
Dendropsophus stingi	D stingi (2)
Dendropsophus stingi	D stingi (3)
Dendropsophus studerae	D studerae (1)
Dendropsophus studerae	D studerae (2)
Dendropsophus subocularis	D subocularis
Dendropsophus timbeba	D timbeba (1) M
Dendropsophus timbeba	D timbeba (2)
Dendropsophus triangulum	D triangulum Tab
Dendropsophus triangulum	D triangulum (1) M
Dendropsophus triangulum	D triangulum (2)
Dendropsophus virolinensis	D virolinensis M
Dendropsophus walfordi	D walfordi
Dendropsophus werneri	D werneri (1)
Dendropsophus werneri	D werneri (2)
Dendropsophus xapuriensis	D xapuriensis (1)
Dendropsophus xapuriensis	D xapuriensis (2)
Dendropsophus yaracuyanus	D yaracuyanus
Dendropsophus pelidnus	D pelidnus

Dendropsophus sp. 1	D sp SRon
Itapotihyla langsdorffi	Itapotihyla langsdorffi (1)
Itapotihyla langsdorffii	Itapotihyla langsdorffi (2)
Lysapsus laevis	Lysapus laevis (1)
Lysapus laevis	Lysapus laevis (2) M
Phyllodytes luteolus	Phyllodytes luteolous M
Pseudis minutus	Pseudis minutus M
Scarthyla goinorum	Scarthyla goinorum (1)
Scarthyla goinorum	Scarthyla goinorum (2) M
Scinax berthae	Scinax berthae M
Scinax fuscovarius	Scinax fuscovarius M
Scinax littoralis	Scinax littoralis M
Scinax perereca	Scinax perereca M
Sphaenorhynchus dorisae	Sphaenorhynchus dorisae M
Sphaenorhynchus lacteus	Sphaenorhynchus lacteus M
Sphaenorhynchus pauloalvini	Sphaenorhynchus pauloalvini M
Xenohyla eugenioi	Xenohyla eugenioi (1)
Xenohyla eugenioi	Xenohyla eugenioi (2)
Xenohyla truncata	Xenohyla truncata (1) M
Xenohyla truncata	Xenohyla truncata (2)

sequences produced in the context of this project.

Voucher	Locality
TG2792	Brazil: Acre, Cruzeiro do Sul
PHV2664	Brazil: Mato Grosso, Barra do Garcas
PHV1768	Brazil: Maranhao, Carolina
CFBH5797	Brazil: Espirito Santo, Linhares
CFBH13210 (CFBHT3755)	Brazil: Sao Paulo, Cacapava
CFBH22999 (CFBHT10908)	Brazil: Espirito Santo, Linhares
KU212083	Peru: San Martin, Rioja
PHV2558	Brazil: Mato Grosso, Araguaia
PHV2588	Brazil: Mato Grosso, Alto Taquari
CFBH14340	Brazil: Mato Grosso, Campo Verde
PHV2560	Brazil: Mato Grosso, Araguaia
CFBH15203 (CFBHT6306)	Brazil: Sao Paulo, Ilha Bela
MZUSPFIELD1337	Brazil: Sao Paulo, Santo Andre
[a]=KU257514;[b]=NoVoucher	[a]= Ecuador: Morona-Santiago, Limon; [b]= No lo
CFBH18721	Brazil: Bahia, Aurelino Leal
MRT5946	Brazil: Bahia, Jussari
MHUA4801	Colombia: Antioquia, Tamesis
MHUA3881	Colombia:Antioquia, Itagüi
MJH7101	Peru: Huanuco, Rio Llullapichis, Panguana
TG2632	Brazil: Acre, Tarauaca, FLONA Riozinho Liberdad
CFBH20829 (CFBHT09413)	Brazil: Pernambuco, Bonito
CFBH18764 (CFBHT09276)	Brazil: Bahia, Aurelino Leal
(H2708)	Brazil: Rondonia, Jirau
QCAZA48099	Ecuador: Pompeya
RFB737	Brazil: Espirito Santo, Santa Teresa
CHUNB34455	Brazil: Para, Novo Progresso
CFBH21788 (CFBHT10174)	Brazil: Mato Grosso, Chapada dos Guimaraes
NN (DFCH-USFQ899)	Ecuador: Pichincha, Tandayapa
CFBH32783	Brazil: Mato Grosso do Sul, Ribas do Rio Pardo
CFBH32780	Brazil: Mato Grosso do Sul, Ribas do Rio Pardo
mHNLS20227	Venezuela: Antonio Diaz
ZFMK82181	Bolivia: La Paz, Caranavi
MHUA5740	Colombia: Risaralda, Pereira
MAR1272	Colombia: Quindio, Filandia
MNHN20150107	French Guiana: Montagne tortue grande
CFBH27070	Brazil: Goias, Anapolis
CFBH22230 (CFBHT10937)	Brazil: Rio de Janeiro, Seropedica
MNRJ38375	Brazil: Espirito Santo, Santa Teresa
CFBH18746	Brazil: Bahia, Aurelino Leal
CFBH23688 (CFBHT11448)	Brazil: Bahia, Camacan
Novoucher (CFBT2197)	Brazil: Minas Gerais, Nanuque
CFBH18782 (CFBHT9292)	Brazil: Bahia, Aurelino Leal
Novoucher (CFBHT11322)	Brazil: Ceara, Guaramiranga
Novoucher (CFBHT11304)	Brazil: Ceara, Guaramiranga
JF2320	No locality
LBolsoni34610	Brazil: Minas Gerais, Vicosa

JZ1398 (JZ9)	Brazil: Bahia, Jequie
NoVoucher (CFBHT15736)	Brazil: Bahia, Ilheus
MHNC5961	Peru: Santo Domingo
MNRJ46746	Brazil: Sergipe, Indiaroba
MHUA4063	Colombia: Antioquia, Maceo
RdS790	Belize: Stann Creek District
LBolsoni3486	Brazil: Minas Gerais, Vicosa
[a]NoVoucher;[b]MZUSP95033 (LM3135)	No locality
CFBH14964 (CFBHT595)	Brazil: Espirito Santo, Sooretama
CFBH13294 (CFBHT4100)	Brazil: Sergipe, Itabaiana
CFBH6287 (CFBHT593)	Brazil: Sao Paulo, Rio Claro
CFBH14148 (CFBHT4762)	Brazil: Mato Grosso, Acorizal
MNCN:ADN46749	Colombia: Amazonas, Leticia
MRC728	Colombia: Boyaca, Miraflores
MRC729	Colombia: Boyaca, Miraflores
ZUEC17681	Brazil: Para, Oriximina
ZUEC17682	Brazil: Para, Oriximina
CFBH4562	Brazil: Sao Paulo, Ubatuba (Picinguaba)
MNRJ38453	No locality
FSFL1467	Brazil: Bahia, Prado
CFBH19472 (CFBHT9109;KZ2280)	Brazil: Espirito Santo, Vitoria
CFBH32043 (CFBHT15721)	Brazil: Espirito Santo, Conceicao da Barra
MNCN/ADN47562	Colombia: Amazonas, Isla de los Micos
MNCN/ADN46851	Colombia: Amazonas, Isla de los Micos
CFBH25705	Brazil: Sao Paulo, Botucatu
CFBH21936 (CFBHT10273)	Brazil: Sao Paulo, Brotas
CFBHtobeincluded	Brazil: Mato Grosso do Sul, Tres Lagoas
TG2641	Brazil: Acre, Cruzeiro do Sul
CBF:5926	Peru:Pando, Madre de Dios
NMP6V72799/3	Peru:Pando, Madre de Dios
AMNHA-139315	Brazil: Acre, Rio Branco
MNCN/ADN34662	Bolivia: La Paz
KU215258 (WED59243) (WED59244)	Peru: Madre de Dios, Cuzco Amazonica, 15 km E
KU215259	Peru: Madre de Dios, Cuzco Amazonica, 15 km E
MNCN/ADN47561	Colombia: Boyaca, Vila de Leyva
Arcabuco10	Colombia: Boyaca, Arcabuco
MHNLSnovoucher	Venezuela: Barinas: Calderas
MHUA-A7337	Colombia: Caqueta, Florencia
MHUA-A7336	Colombia: Caqueta, Florencia
MPEG28681	Brazil: Amazonas, Maues
MPEG28682	Brazil: Amazonas, Maues
MJH7116	Peru: Huanuco, Rio Llullapichis, Panguana
PS429	Brazil: Para, Juruti
USPA75:23	Brazil: Maranhao, Itapinima
MRC686	Colombia: Boyaca, Santa Maria
MRC687	Colombia: Boyaca, Santa Maria
UFMT6240	Brazil: Mato Grosso, Jauru
ZFMK72691	Bolivia: Santa Cruz: Noel Kempff National Park, F

UFMT6241	Brazil: Mato Grosso, Jauru
USPU22:55	Brazil: Mato Grosso, Vila Rica
ColCBarrio,notprovided	Colombia: Merida, Los Suarez
CFBH22236	Brazil:Rio de Janeiro, Rio de Janeiro
CFBH22239 (CFBHT10940)	Brazil: Rio de Janeiro, Seropedica
CFBH5418	Brazil: Rio de Janeiro, Duque de Caxias
MHUA5883	Colombia: Caldas, Norcasia
[a]=ENS8694 (UTAA-50632)'[b]=UTA50632	[a]= Honduras: Atlantida, Aldea Rio Viejo; [b]= H
CFBH22025/CFBHT12617	Brazil: Rio de Janeiro, Teresópolis
CFBH29140 (CFBHT14278)	Brazil: Roraima, Boa Vista
CFBH15885 (CFBHT5392)	Brazil: Ceara, Ubajara
Novoucher (CFBHT11320)	Brazil: Piaui, Ilha Grande
MPEG18956	Brazil: Para, Itaituba
CFBH24153 (CFBHT11639)	Brazil: Rio de Janeiro, Resende
MACN33799	Argentina: Misiones, San Vicente
CFBH19176 (CFBHT8295)	Brazil: Maranhao, Alcântara
CFBH14401 (CFBHT4718;KZ1969)	Brazil: Mato Grosso, Chapada dos Guimaraes
H-12939 (JPC10772g?)	Ecuador: Sucumbios
Lougheed97005 (QULC97005)	Colombia: Parque Natural Nacional Chingaza
Guadalupe01	Colombia: Santander, Guadalupe
CFBH9376 (CFBHT2095)	Brazil: Santa Catarina, Anitapolis
CFBH356 (CFBHT3242)	Brazil: Santa Catarina, Sao Bento do Sul
CFBH19993 (CFBHT7711)	Brazil: Sao Paulo, Bauru
[a]=MACN37785;[b]=USNMFieldNumber53122	[a] Argentina: Entre Rios, Dto Islas del Ibicuy; [b]
MZUESC9981	Brazil: Bahia, Almadina
MZUESC10177	Brazil: Bahia, Almadina
MAR1807	Colombia: Antioquia, Amalfi
MHUA5549	Colombia: Antioquia, Anori
NoVoucher	Brazil: Bahia, Camacan
MNRJ35380	Brazil: Bahia, Urucuca
USPA25:16	Brazil: Bahia, Jussari
CFBH18799 (CFBHT9305)	Brazil: Bahia, Maracas
CFBH26580 (CFBHT12434)	Brazil: Rio Grande do Norte, Tibau do Sul
MPEG27809	Brazil: Para, Itaituba
MPEG27810	Brazil: Para, Itaituba
MAR564	Colombia: Cundinamarca, Supata
PAG1019	Colombia: Caqueta, San Jose de la Fragua
TG2531	Brazil: Acre, Tarauaca
JD0262013	no data
CFBH22226	Brazil: Rio de Janeiro, Seropedica
CFBH22231	Brazil: Rio de Janeiro, Seropedica
MJ1803	Bolivia: Pando, Manurupi
MJ1804	Bolivia: Pando, Manurupi
MZUSP? (Tab-96042)	Brazil: Amazonas, Tabatinga
TG2780	Brazil: Acre, Cruzeiro do Sul
MHZ462	Peru: Loreto, Jenaro Herrera
MNCN/ADN47584	Colombia: Amazonas, Isla de los Micos
MNK:A:9476 (MJ1309)	Bolivia

MZFC15824	Mexico: Oaxaca, Zanatepec
MNRJ56788	Brazil: Para, Oriximina
MNCN/ADN46832	Colombia: Amazonas, Leticia
MNCN/ADN34705	Bolivia
MNCN/ADN34704	Bolivia
CFBH6740 (CFBHT787)	Brazil: Goias, Sao Joao dAlianca
CFBH24352 (CFBHT11777)	Brazil: Minas Gerais, Lagoa Santa
IT-H0653	Brazil: Sao Paulo, Buri
Novoucher (CFBT2206)	Brazil: Espirito Santo, Domingos Martins
Novoucher (CFBHT2208)	Brazil: Espirito Santo, Domingos Martins
—	No locality
MNK:A:9448 (MJ1281)	Bolivia
CFBH14300 (CFBHT5313)	Brazil: Sao Paulo, Rio Claro
BB766 (MACN38638)	Argentina: Entre Rios, Dto Islas del Ibicuy
TG2650	Brazil: Acre, Tarauaca
MJH7143	Peru: Huanuco, Rio Llullapichis, Panguana
JAC22080 (ouMZFC16014)?	no data
MZFC16014	Mexico: Guerrero
KU215300 (WED57655)	Peru: Madre de Dios, Cuzco Amazonica, 15 km E
KU215306 (WED59070)	Peru: Madre de Dios, Cuzco Amazonica, 15 km E
MNRJ44702	Brazil: Minas Gerais, Catas Altas
DZUFRJ10507	Brazil: Rio de Janeiro, Citrolândia
CFBH5761	Brazil: Rio de Janeiro, Angra dos Reis
KU217607 (LAC1968)	Ecuador: Sucumbios, Lago Agrios
KU217613 (LAC1974-GB)	Ecuador: Sucumbios, Lago Agrios
TG2819	Brazil: Acre, Cruzeiro do Sul
USPA56:65	Brazil: Goias, Minacu
CFBH15869 (CFBHT5370)	Brazil: Ceara, Ubajara
CFBH18575 (CFBHT7842)	Brazil: Alagoas, Campo Alegre
MRC737	Colombia: Boyaca, Miraflores
MAR832	Colombia: Boyaca, Santa Maria
MRC721	Colombia: Boyaca, Miraflores
URCAG767	Brazil: Alagoas, Quebrangulo
URCAG768	Brazil: Alagoas, Quebrangulo
MHUA5439	Colombia: Santander, San Vicente de Chucuri
KU215190	Peru: Madre de Dios, Cuzco Amazonica, 15 km E
KU215189 (WED58783)	Peru: Madre de Dios, Cuzco Amazonica, 15 km E
MZUSP? (Tab-96018)	Brazil: Amazonas, Tabatinga
MJH3844	Brazil: Acre, Lago Catalao
MJH7377	no data
MAR467	Colombia: Santander, Charala
MJH129	Brazil
CFBH7053	Brazil: Sao Paulo, Peruibe
CFBHT4969 (CFBH14761)	Brazil: Sao Paulo, Pariquera-Acu
JiriMoravec	no data
CFBHtobeincluded (TG2812)	Brazil: Acre, Cruzeiro do Sul
WES2031	Venezuela: Yaracuy, Sieera de Aroa
KU181108	Venezuela: Tachira, Betania

QCAZA52832	Ecuador: Canelos
CFBH29531 (CFBHT14617)	Brazil: Sao Paulo, Botucatu
[a]MACN38643;[b]USNM303287	[a] Argentina: Misiones, General Belgrano; [b] Bra
AMCC101720	Guyana: Southern Rupununi Savanah, Aishalton
CFBH29142 (CFBHT14280)	Brazil: Roraima, Boa Vista
NoVoucher	No locality
DL001	Brazil: Rio Grande do Sul, Rio Grande
TG2511	Brazil: Acre, Cruzeiro do Sul
QULC2340	Brazil: Amazonas, Igarape Nova Empresa
MLPA2137	Argentina: Buenos Aires, Atalaya
MACN38647	Argentina: Misiones, Guarani, San Vicente
CFBH12292	Brazil: Sao Paulo, Itanhaem
CFBH8055 (CFBHT1470)	Brazil: Sao Paulo, Ribeirao Branco
MJH46	Brazil: Amazonas, Manaus
[a]=USNM152136;[b]=USNM268930	[a] & [b] & [c] = Peru: Madre de Dios
MTR120985	Brazil: Espirito Santo, Linhares
JZ733	Brazil: Bahia, Boa Nova
JZ732	Brazil: Bahia, Boa Nova
CFBH23532 (CFBHT11375)	Brazil: Rio de Janeiro, Marica
CFBH7600	Brazil: Rio de Janeiro, Restinga de Marica

12S	16S	COI	CytB	POMC	RAG	RHOD
MT503913	**MT503913**	**MT483162**	**MT503792**	—	—	—
MT503873	**MT503873**	**MT483105**	**MT503744**	—	**MT504078**	**MT504120**
MT503874	**MT503874**	—	**MT503745**	**MT503989**	—	**MT504121**
AY843597	AY843597	—	AY843818	—	AY844386	AY844571
MT503901	**MT503901**	**MT483141**	**MT503780**	**MT503982**	—	**MT504150**
MT503902	**MT503902**	**MT483142**	**MT503781**	**MT503983**	—	**MT504151**
AY819450	AY819549	—	—	—	—	—
MT503883	**MT503883**	**MT483107**	**MT503752**	**MT503990**		**MT504127**
MT503882	**MT503882**	**MT483106**	**MT503751**	—	**MT504071**	**MT504123**
MT503880	**MT503880**	—	**MT503748**	—	**MT504072**	—
MT503881	**MT503881**	**MT483113**	**MT503749**		**MT504068**	**MT504128**
MT503938	**MT503938**	**MT483202**	**MT503814**			**MT504192**
MT503939	**MT503939**	**MT483203**	**MT503815**	**MT504020**		**MT504193**
DQ380350 [a]	AY362975 [b]	—	—	—	—	—
MT503893	**MT503893**	**MT483127**	**MT503773**	**MT503999**	**MT504079**	**MT504149**
AY843608	AY843608	—	AY843832	—	—	AY844585
MT503825	**MT503825**		**MT503697**		**MT504052**	**MT504167**
MT503826	**MT503826**					—
AY843611	AY843611	—	AY843836	—	AY844400	AY844589
MT503843	**MT503843**	**MT483099**	**MT503784**	**MT504018**	**MT504038**	
MT503865	**MT503865**	**MT483116**	**MT503740**		**MT504064**	**MT504154**
MT503866	**MT503866**	**MT483117**	**MT503741**	**MT504003**	**MT504076**	**MT504140**
KT721802	KT721779	—	**MT503783**	—	**MT504037**	**MT504183**
KT721826	KT721783	—	—	—	—	—
KT962842	KT962842	—	—	—	**MT504051**	—
MT503889	**MT503889**	**MT483114**	**MT503757**		**MT504073**	**MT504130**
MT503890	**MT503890**	**MT483115**	**MT503758**	**MT503995**		**MT504122**
AY843616	AY843616	—	AY843842	—	AY844404	—
MT503886	**MT503886**	**MT483110**	**MT503754**	**MT503991**		**MT504124**
MT503887	**MT503887**	**MT483111**	**MT503755**	**MT503992**		**MT504125**
—	KJ933544	KJ933631	—	—	—	—
MT503858	**MT503858**	—	**MT503725**	—	**MT504060**	—
MT503827	**MT503827**		**MT503699**	**MT503978**	**MT504053**	**MT504168**
MT503828	**MT503828**	**MT483143**	**MT503698**	**MT503979**	**MT504054**	**MT504169**
KT721794	KT721771	—	—	—	—	—
MT503867	**MT503867**	**MT483118**	**MT503737**	**MT503996**	**MT504069**	**MT504145**
MT503940	**MT503940**					—
MT503944	**MT503944**		**MT503701**			—
MT503947	**MT503947**		**MT503704**	**MT504021**		—
MT503948	**MT503948**	**MT483183**	**MT503705**	**MT504022**		**MT504172**
MT503949	**MT503949**		**MT503706**		**MT504044**	—
MT503950	**MT503950**	**MT483185**	**MT503707**		**MT504045**	**MT504177**
MT503953	**MT503953**	**MT483194**	**MT503714**	**MT504026**		**MT504181**
MT503954	**MT503954**	**MT483195**	**MT503715**	**MT504027**		**MT504182**
MT503945	**MT503945**	**MT483186**	**MT503702**			**MT504173**
MT503946	**MT503946**	**MT483187**	**MT503703**	**MT504023**		**MT504174**

MT503952	**MT503952**	**MT483188**		**MT504025**		**MT504176**
MT503951	**MT503951**	**MT483189**				—
—	KJ933557	KJ933640	—	—	—	—
MT503923	**MT503923**	**MT483171**	**MT503804**			**MT504157**
MT503957	**MT503957**	**MT483161**	**MT503809**			—
AY843624	AY843624	—	AY843853	—	AY844415	AY844604
MT503964	**MT503964**	**MT483178**		**MT503984**		**MT504131**
DQ380355 [a]	AF308103 [b]	—	AF308124 [b]	—	—	—
MT503965	**MT503965**	**MT483179**	**MT503817**			**MT504133**
MT503966	**MT503966**			**MT503985**		—
MT503875	**MT503875**		**MT503746**		**MT504066**	—
MT503876	**MT503876**	**MT483126**	**MT503759**		**MT504077**	—
JQ088283	JQ088283	—	—	—	—	—
MT503836	**MT503836**	**MT483093**	**MT503787**	**MT504016**		**MT504185**
MT503837	**MT503837**	**MT483094**	**MT503788**	**MT504017**		**MT504186**
MT503854	**MT503854**	**MT483102**	**MT503728**	—	—	—
MT503855	**MT503855**	**MT483103**		—	—	—
AY843624	AY843624		**MT503717**			
MT503832	**MT503832**		**MT503716**			—
MT503942	**MT503942**	**MT483191**	**MT503709**	**MT504028**	**MT504047**	**MT504180**
MT503941	**MT503941**	**MT483190**	**MT503708**		**MT504046**	**MT504179**
MT503943	**MT503943**	**MT483192**				—
MT503967	**MT503967**	**MT483198**				—
MT503968	**MT503968**	**MT483199**				—
MT503885	**MT503885**	**MT483109**	**MT503750**			**MT504129**
MT503884	**MT503884**	**MT483108**	**MT503753**		**MT504074**	—
MT503888	**MT503888**	**MT483112**	**MT503756**		**MT504075**	**MT504126**
MT503848	**MT503848**	**MT483135**	**MT503777**		**MT504082**	**MT504132**
MT503863	**MT503863**	—	**MT503733**		**MT504062**	—
MT503864	**MT503864**	—	**MT503734**		**MT504063**	—
AY843652	AY843652	—	AY843892	—	AY844440	AY844638
MT503834	**MT503834**	**MT483091**	**MT503695**	—	—	—
MT503847	**MT503847**	**MT483136**	**MT503732**			—
MT503846	**MT503846**	—	—	—	—	—
MT503831	**MT503831**	**MT483146**	**MT503700**			—
JF422592	JF422592	—	—	**MT503977**	—	—
MT503844	**MT503844**					—
KF009942	KF009942	**MT483148**	—	**MT503980**	**MT504057**	**MT504112**
KF009943	KF009943	**MT483149**	—	—	—	—
KX018317	KX018317	**MT483152**	**MT503807**	**MT503986**	—	**MT504117**
KX018318	KX018318	**MT483153**	**MT503808**	**MT503987**	KX018314	**MT504118**
AY843640	AY843640	—	AY843877	—	AY844428	DQ283782
MT503914	**MT503914**	**MT483163**	**MT503793**	**MT504013**		—
MT503915	**MT503915**	**MT483164**	**MT503794**		**MT504093**	—
MT503871	**MT503871**	**MT483122**	**MT503735**		**MT504085**	**MT504134**
MT503872	**MT503872**	**MT483123**	**MT503736**	**MT503997**	**MT504086**	**MT504135**
MT503918	**MT503918**	**MT483166**	**MT503797**		**MT504096**	**MT504161**
MT503916	**MT503916**		**MT503795**		**MT504094**	—

MT503917	**MT503917**	**MT483165**	**MT503796**		**MT504095**	**MT504160**
MT503919	**MT503919**	**MT483167**	**MT503798**	**MT504014**		**MT504162**
JF422585	JF422585	—	—	JF422622 [a]	—	—
MT503895	**MT503895**	**MT483130**	**MT503760**		**MT504104**	**MT504141**
MT503896	**MT503896**	**MT483131**	**MT503761**	**MT504004**	**MT504105**	**MT504142**
AY843607	AY843607	—	AY843831	—	AY844397	AY844584
MT503852	**MT503852**	**MT483137**	**MT503731**		**MT504083**	**MT504136**
AY843643	AY843643	—	AY843880	AY819121 [a]	AY844430	AY844628
MT503833	**MT503833**	**MT483147**	**MT503718**			
MT503870	**MT503870**	**MT483121**				—
MT503868	**MT503868**	**MT483119**	**MT503742**		**MT504089**	**MT504137**
MT503869	**MT503869**	**MT483120**	**MT503743**	**MT503994**		**MT504138**
MT503931	**MT503931**	**MT483159**	**MT503769**	—	—	—
MT503934	**MT503934**	KJ940047		**MT504008**	**MT504092**	**MT504156**
AY549345*	AY549345	—	AY549398	—	AY844432	DQ283758
MT503932	**MT503932**	—	**MT503768**	**MT504007**	**MT504090**	**MT504155**
MT503933	**MT503933**	—	**MT503776**	**MT504009**	**MT504091**	**MT504191**
AY843647	AY843647	—	AY843886	—	AY844435	AY844632
AY843635	AY843635	—	AY843869	**MT503975**	—	AY844618
JF422603	JF422603	—	—	**MT503976**	—	—
MT503905	**MT503905**		**MT503812**		**MT504108**	—
MT503906	**MT503906**	**MT483100**	**MT503813**		**MT504109**	**MT504194**
MT503859	**MT503859**	**MT483104**	**MT503774**	**MT503998**	**MT504061**	**MT504195**
AY549346 [a]	AY549346 [a]	—	AY843888 [a]	AY819123 [b]	AY844437 [a]	AY844634 [a]
KY552471	KY552471	—	—	—	—	—
KY552470	KY552470	—	—	—	—	—
MT503829	**MT503829**	**MT483144**			**MT504055**	**MT504170**
MT503830	**MT503830**	**MT483145**			**MT504056**	**MT504171**
MT503926	**MT503926**					—
—	**MT503924**	**MT483172**	**MT503805**		**MT504100**	**MT504159**
—	**MT503925**	**MT483193**	**MT503806**		**MT504101**	**MT504158**
MT503956	**MT503956**	**MT483197**	**MT503711**		**MT504049**	**MT504175**
MT503955	**MT503955**	**MT483196**	**MT503710**	**MT504024**	**MT504048**	**MT504178**
MT503962	**MT503962**	**MT483176**	**MT503712**			—
MT503963	**MT503963**	**MT483177**	**MT503713**	**MT504030**		**MT504196**
MT503838	**MT503838**	**MT483095**	**MT503789**		**MT504042**	**MT504187**
MT503841	**MT503841**	**MT483184**	**MT503786**		**MT504041**	**MT504189**
MT503835	**MT503835**	**MT483092**	**MT503696**	**MT504019**	**MT504040**	**MT504188**
MT503840	**MT503840**					
MT503897	**MT503897**	**MT483132**	**MT503763**		**MT504106**	**MT504143**
MT503898	**MT503898**	**MT483133**	**MT503762**			—
MT503856	**MT503856**	—	**MT503723**	—	—	—
MT503857	**MT503857**	—	**MT503724**	—	—	—
AF308078	AF308106	—	AF308125	—	—	—
MT503849	**MT503849**	**MT483138**	**MT503778**			—
AY843658	AY843658	—	—	—	AY844446	AY844647
MT503853	**MT503853**	**MT483101**	**MT503722**	—	—	—
—	JF790110					—

MT503850	**MT503850**	—	**MT503729**		—	—
MT503959	**MT503959**	**MT483150**	**MT503822**	**MT503981**		**MT504152**
MT503960	**MT503960**	**MT483151**				—
MT503891	**MT503891**	**MT483124**				—
MT503892	**MT503892**	**MT483125**				—
MT503878	**MT503878**		**MT503738**		**MT504070**	—
MT503879	**MT503879**		**MT503739**	**MT503993**	**MT504065**	**MT504139**
AY843661	AY843661	—	AY843904	—	AY844449	AY844651
MT503907	**MT503907**		**MT503719**		**MT504050**	—
MT503908	**MT503908**		**MT503720**			—
AY362976	AY362976	—	—	—	—	—
—	JF790045	—	—	—	—	—
MT503877	**MT503877**		**MT503747**		**MT504067**	—
AY843663	AY843663	—	AY843906	—	AY844450	AY844653
MT503961	**MT503961**	**MT483154**	**MT503779**	**MT503988**	**MT504059**	**MT504119**
AY843664	AY843664	—	—	—	AY844451	—
MT503851	**MT503851**		**MT503730**		**MT504084**	—
AY819453	—	—	—	AY819156	—	—
MT503903	**MT503903**	**MT483174**	**MT503810**			—
MT503904	**MT503904**	**MT483175**	**MT503811**			—
MT503927	**MT503927**		**MT503802**		**MT504102**	—
MT503928	**MT503928**	**MT483173**	**MT503803**		**MT504103**	**MT504163**
AY843666	AY843666	—	AY843910	—	AY844454	AY844657
MT503861	**MT503861**		**MT503726**			—
MT503862	**MT503862**	**MT483140**	**MT503727**			—
MT503860	**MT503860**	**MT483139**	**MT503775**	**MT504002**		**MT504146**
MT503921	**MT503921**	**MT483170**	**MT503800**	**MT504015**	**MT504098**	**MT504165**
MT503920	**MT503920**	**MT483168**	**MT503799**		**MT504097**	**MT504164**
MT503922	**MT503922**	**MT483169**	**MT503801**		**MT504099**	**MT504166**
MT503935	**MT503935**	**MT483155**	**MT503770**	**MT504010**		**MT504114**
MT503937	**MT503937**	**MT483156**	**MT503772**	**MT504011**		**MT504115**
MT503936	**MT503936**		**MT503771**	**MT504012**		**MT504116**
MT503894	**MT503894**	**MT483128**		**MT504000**	**MT504080**	**MT504147**
		MT483129		**MT504001**	**MT504081**	**MT504148**
MT503842	**MT503842**	**MT483098**	**MT503785**		**MT504039**	**MT504184**
MT503823	**MT503823**	**MT483089**	—	—	—	—
MT503824	**MT503824**	**MT483090**				—
AF308070	AF308093	—	AF308122	—	—	—
AY843680	AY843680	—	AY843926	—	AY844464	AY844673
MT503958	**MT503958**		**MT503820**		**MT504058**	**MT504153**
MT503839	**MT503839**	**MT483096**	**MT503790**			—
AY843683	AY843683	—	AY843929	—	—	AY844676
MT503899	**MT503899**		**MT503764**		**MT504107**	—
MT503900	**MT503900**	**MT483134**	**MT503765**	**MT504005**		**MT504144**
MT503930	**MT503930**		**MT503767**		**MT504088**	—
MT503929	**MT503929**	**MT483157**	**MT503766**	**MT504006**	**MT504087**	**MT504113**
MT503845	**MT503845**		**MT503721**		**MT504043**	—
AY819434	—	—	—	—	—	—

KT721827	KT721784	**MT483097**	**MT503782**	—	—	—
MT503912	**MT503912**					—
AY843706 [a]	AY843706 [a]	**MT483204**	AY843951 [a]	AY819129 [b]	AY844482 [a]	AY844697 [a]
AY843696	AY843696	**MT483205**	AY843941	—	AY844476	AY844689
MT503970	**MT503970**					—
AY843721	AY843721	**MT483206**	AY843965	**MT504031**	AY844494	AY844708
MT503971	**MT503971**	**MT483207**		**MT504033**		—
MT503972	**MT503972**		**MT503816**	**MT504034**		—
AY843752	AY843752	—	AY843997	AY819139	AY844514	AY844738
AY843754	AY843754	—	AY843999	—	—	AY844740
AY843758	AY843758	—	AY844003	—	AY844519	—
MT503973	**MT503973**	**MT483209**	**MT503821**			**MT504197**
MT503974	**MT503974**	**MT483208**	**MT503819**	**MT504035**	**MT504110**	**MT504198**
AY843766	AY843766	**MT483200**	AY844011	—	AY844526	AY844753
AY549367 [b]	AY549367 [b]	**MT483201**	AY844012 [a]	AY819144 [c]	AY844527 [a]	AY844754 [a]
MT503969	**MT503969**		**MT503818**	**MT504032**	**MT504111**	**MT504199**
MT503910	**MT503910**	**MT483181**				
MT503911	**MT503911**	**MT483182**				
MT503909	**MT503909**		**MT503791**	**MT504029**		**MT504190**
AY843775	AY843775	**MT483180**	AY844018	—	**MT504036**	—

SIA	TYR
MT504243	**MT504334**
MT504218	—
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AY844797	AY844043
—	—
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—	**MT504299**
MT504227	—
MT504223	**MT504298**
MT504232	**MT504303**
MT504262	**MT504348**
MT504263	**MT504349**
—	—
MT504211	—
AY844808	AY844053
MT504275	**MT504327**
—	—
AY844810	—
MT504260	—
MT504219	—
MT504221	**MT504309**
MT504259	—
—	—
MT504284	—
MT504233	**MT504311**
—	—
—	AY844060
—	**MT504301**
—	**MT504300**
—	—
—	—
MT504276	—
—	**MT504328**
—	—
MT504222	**MT504310**
MT504229	**MT504350**
—	**MT504351**
MT504282	—
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MT504283	**MT504354**
MT504265	—
MT504285	—
MT504286	—
MT504264	**MT504352**
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—	**MT504343**
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AY844822	AY844070
—	**MT504326**
—	—
MT504203	—
MT504204	—
MT504230	**MT504306**
MT504234	**MT504307**
—	—
MT504291	—
MT504292	—
MT504207	—
MT504208	—
MT504288	**MT504332**
MT504287	**MT504331**
MT504269	—
MT504268	—
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—	**MT504357**
—	**MT504358**
MT504224	**MT504302**
MT504228	—
MT504231	—
MT504213	**MT504316**
MT504241	—
MT504242	—
AY844856	AY844097
—	—
MT504214	—
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MT504202	—
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MT504205	—
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MT504244	**MT504335**
MT504245	**MT504336**
—	**MT504313**
MT504235	**MT504314**
—	**MT504342**
—	—

—	**MT504338**
MT504246	—
—	—
MT504236	**MT504315**
MT504237	—
AY844807	AY844052
MT504215	—
AY844846	—
—	—
—	**MT504304**
MT504240	—
—	—
—	**MT504322**
MT504256	—
—	AY844089
MT504254	**MT504318**
MT504255	—
AY844850	AY844092
AY844836	AY844080
—	—
MT504278	**MT504324**
MT504279	**MT504325**
MT504210	—
AY844852 [a]	—
—	—
—	—
MT504277	**MT504329**
—	**MT504330**
—	—
MT504250	**MT504344**
MT504251	—
MT504267	**MT504353**
MT504266	—
MT504280	—
MT504281	—
MT504293	—
—	**MT504345**
MT504272	**MT504347**
—	—
MT504238	—
MT504220	—
MT504209	—
—	**MT504297**
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—	**MT504317**
AY844864	—
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MT504216	—
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MT504225	—
MT504226	**MT504308**
—	—
—	**MT504355**
MT504270	—
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—	**MT504305**
AY844868	AY844106
MT504206	**MT504323**
AY844869	—
MT504217	—
—	—
MT504289	**MT504333**
MT504290	—
MT504248	**MT504337**
MT504249	—
AY844872	AY844109
—	—
—	**MT504312**
MT504212	—
MT504247	**MT504341**
MT504252	**MT504339**
MT504253	**MT504340**
MT504257	—
MT504258	**MT504319**
—	**MT504320**
—	—
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MT504261	—
MT504200	—
MT504201	—
—	—
—	AY844122
—	—
MT504294	—
AY844886	—
MT504239	—
—	—
MT504274	**MT504321**
MT504273	—
MT504271	**MT504346**
—	—

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—	**MT504359**
AY844903 [a]	AY844137 [a]
AY844896	AY844133
—	—
AY844913	AY844150
—	—
MT504295	—
AY844938	—
AY844940	—
—	AY844179
—	**MT504361**
MT504296	—
—	AY844187
—	AY844188 [a]
—	**MT504360**
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—	**MT504356**
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Appendix S4.

Studied specimens.

Dendropsophus acreanus. Brazil: Acre: Cruzeiro do Sul: 7º B.E.C. (ZUEC 4665), Sede do "Campus Avançado" (ZUEC 4570–4574), Vila Militar (ZUEC 4609– 4611, ZUEC 4692–4693, ZUEC 8510–8511), Vila Militar e "Campus Avançado" (ZUEC 4653); Feijó (Paratype: MZUSP 74235); Mâncio Lima: Colônia São Francisco (ZUEC 4645, ZUEC 4646–4647); Rio Branco (MZUSP 111294–111296); Tarauacá (Holotype: MZUSP 74198; Paratype: MNRJ 3971; MZUSP 73719); Xapuri (MZUSP 16353); Pauiní (MZUSP 50365), Rio Purus (USNM 201887). Mato Grosso: Chapada dos Guimarães: Serra da Mutuca (ZUEC 6111–6112). Peru: Madre de Dios: Manu: Puerto Maldonado (USNM 247117, USNM 342923, USNM 343085–343089, USNM 343200–USNM 343201, USNM 343313, USNM 344825).

***Dendropsophus* aff *acreanus*.** Brazil: Acre: Cruzeiro do Sul: Campus avançado (CFBH 36), Vila militar (CFBH 56).

Dendropsophus amicorum. Venezuela: Falcón: Cerro Socopo, 84.0 km al NO de Carora (Holotype: USNM 216677)

Dendropsophus anataliasiasi. Brazil: Goiás: Brejinho do Nazaré: rodovia Belém—Brasília, cerca de 80 km antes de Paraíso do Norte (Holotype: MZUSP 74204); São João da Aliaça (MNRJ 27772–27775).

Dendropsophus anceps. Brazil: Bahia: Porto Seguro: RPPN - Estação Vera Cruz (CFBH 3701). Espírito Santo: Aracruz (CFBH 2688–2690); Governador Lindemberg (CFBH 23067–23069), Sítio Fernando Nicole (CFBH 9681–9683); Linhares: Floresta Nacional de Goytacazes (CFBH 22999–23000, CFBH 23066, CFBH 25156, CFBH 26549), Povoação (CFBH 5795–5804). Minas Gerais: Frei Inocêncio: PCH Paiol (MCNAM 10661–10663); Resplendor (MCNAM 1328–1329, MCNAM 1358–1363). Paraná: Telêmaco Borba: Fazenda Monte Alegre (CFBH 3575). Rio de Janeiro (CFBH 23739–23740); Saquarema: Palmital (MNRJ 25444); Caçapava: Bairro daGrama (CFBH 13208–13210).

Dendropsophus aperomeus. Peru: Amazonas: 8 km NNE Balzapata (Holotype: KU 181812). Huánuco: ±30 km (airline) NE Tingo María (AMNH 91917). San Martín: Venceremos: Venceremos (KU 212084–212986).

Dendropsophus araguaya. Brazil: Mato Grosso: Alto Araguaia (MZUSP 152371–152380; Paratypes: MNRJ 17240–17241); Sapo (Holotype: MZUSP 66803; Paratypes: MZUSP 66796–66806); Alto Taquari (MZUSP 152352–152358); Santa Rita do Araguaia: Córrego Jaguatirica (Paratype: MZUSP 66719–66721).

Dendropsophus battersbyi. Venezuela: Caracas (Holotype: BMNH 53.2.4.165).

Dendropsophus berthalutzae. Brazil: Paraná: Antonina: Fazenda Gervásio - Reserva Natural Rio Cachoeira (CFBH 23194); Morretes: Estação II - IAPAR, Porto de Cima (CFBH 8112). Rio de Janeiro: Duque de Caxias: Parque Natural Municipal de Duque de Caxias (MNRJ 54699–54714); Campos dos Goytacazes (MNRJ 2288, MNRJ 11050–11052); Magé: Acampamento dos Escoteiros (CFBH 277); campo dos escoteiros (MNRJ 55238–55241); Rio de Janeiro: Av. Genemário Dantas, Jacarépaguá (MNRJ 1893, MNRJ 25554–25576). São Paulo: Biritiba Mirim (CFBH 27720); Brotas: Fazenda São José - Cerrado do Botelho (CFBH 9778–9779); Cubatão: COPEBRÁS (CFBH 11349, CFBH 11361, CFBH 11555); Ilhabela: Ilha de São Sebastião (CFBH 15194, CFBH 15210, CFBH 15212); Paranapiacaba (Holotype: MZUSP 74205); Registro (CFBH 6980); Santo André: Parque Estadual Municipal Nascentes de Paranapiacaba (CFBH 29002–29003, CFBH 29008–29009); Ubatuba: Picinguaba (CFBH 1407, CFBH 1410, CFBH 1423, CFBH 3959), Poça temporária, próxima a casa de pesquisa Picinguaba (CFBH 4314–4315).

Dendropsophus bifurcus. Equador: Morona: Santiago: Sevilla Don Bosco (MZUSP 55637). Napo: Loreto (MZUSP 116720–116724); Santa Cecilia (MZUSP 116703–116706, MZUSP 116695–116696); Pastaza: Rio Solís (MZUSP 76478), Rio Villano (MZUSP 117915).

Dendropsophus bipunctatus. Brazil: Bahia: Aurelino Leal: Fazenda Pedras Pretas (CFBH 18721–18722, CFBH 18734–18735); Caraíva (CFBH 13255). Espírito Santo: Aracruz (CFBH 2690); Cariacica: Reserva Florestal de Duas Bocas (CFBH 1361); Linhares: Fazenda São Bento, Povoação (CFBH 23081–23082).

Dendropsophus bogerti. Colômbia: Antioquia: Medellín: Bello, Estacíon Metro de Madera, La Gabriela (ICN 39758); Finca Sán José de Bella Vista (ICN 581); San Pedro: Vereda La Lana, finca La montañita (ICN 33726); Yarumal: Santa Rosa (ICN 14275), Finca Media Luna, Cto El Cedro (ICN 38278–38279)

Dendropsophus bokermanni. Brazil: Acre: Tarauaca (Holotype: MZUSP 74208). Rondônia (MZUSP 73664).

Dendropsophus branneri. Brazil: Bahia: Aurelino Leal, Fazenda Pedras Pretas: (CFBH 18777–18776, CFBH 18781, CFBH 18786). Camacan: RPPN Serra Bonita (CFBH to be deposited). Maracás: Fazenda Santo Onofre, Fazenda Cana Brava (CFBH 18801–18805; CFBH 19312; CFBH 19314–19315, CFBH 19319–19326; CFBH 19530); Una: Área próxima ao lixão da cidade, Munc. De Una (dir. Sul) (CFBH to be deposited). Espírito Santo: Linhares, Fazenda Luizitânia: Brejo, poça do lado da estrada (CFBH 18710–18713). Pernambuco: Bonito: Açude do Prata, Município de Bonito (CFBH 20825, CFBH 20829, CFBH 20833), Bonito (Holotype: USNM 48861)

Dendropsophus brevifrons. Brazil: Pará: Belém: IPEAN. Belém (KU 127846). Equador: Sucumbíos: Santa Cecilia: Santa Cecilia (Holotype: KU 126370). Sucumbíos: Santa Cecilia: Santa Cecilia (KU 111786, KU 111788, KU 127846). Sucumbíos: Santa Cecilia: Santa Cecilia (Paratype: KU 126371). Loreto: Teniente López: Teniente López (KU

221851). Madre de Dios: Puerto Maldonado: Cusco Amazónico (KU 205459), 15 km E Puerto Maldonado (KU 205460, KU 209948, KU 215197, KU 215198–215200, KU 220167)

Dendropsophus cachimbo. Brazil: Pará: Novo Progresso: Serra do Cachimbo (Holotype: MZUSP 21912; Paratypes: MZUSP 21910–21911–21918, MZUSP 21920–21926); Redenção (MZUSP 70875–70876)

Dendropsophus carnifex. Equador: Imbabura: Apuela (USNM 234925, USNM 234930, USNM 234932, USNM 234934, USNM 234939, USNM 234942, USNM 234944–234946, USNM 234948). Napo: Reventador (USNM 284313). Pichincha: Chiriboga: 4 km W Chiriboga (KU 142638), 2.2 km (by road) SW of (USNM 285834); Dos Rios: 4 km NE Dos Ríos (KU 164283–164284); Mindo: Hacienda San Vicente (USNM 284361); Los Dos Rios, 4 km NE of, Rio Orito (USNM 285833, USNM 285837–285839); Tandapi (Holotype: KU 117993; KU 124236–124237, KU 136299, KU 136200).

Dendropsophus* cf. *marmoratus. Brazil: Amazonas: Alto Tapajós (CFBH 5537–5538). Rondônia: Espigão do Oeste: Fazenda Jaburi (CFBH 5100). Maranhão: Açaílândia: Estrada do Sunil (CFBH 11457). Mato Grosso: Cáceres (CFBH 752). Pará: Altamira: Acesso ao acampamento Juruá da CNEC, Região do Rio Xingú (CFBH 900). Tocantins: Aguiarnópolis: Faz. Ituaneiras (CFBH 8151, CFBH 8152); Goianorte: Estrada Araguacema-Goitatuba (CFBH 10261); Wanderlândia (CFBH 11451).

Dendropsophus* cf. *seniculus. Brazil: Bahia: Mucuri: Adjacências do Hotel Aroços (CFBH 1998).

Dendropsophus* cf. *elegans. Brazil: Minas Gerais: Nanuque (MCNAM 7073).

Dendropsophus* cf. *leali. Brazil: Amazonas: Reservas INPA-WWF (MZUSP 77068, MZUSP 77070–77071)

Dendropsophus* cf. *melanargyreus. Brazil: Rio de Janeiro: Iguaba (MNRJ 17787).

Dendropsophus* cf. *nanus. Brazil: Mato Grosso: Pindaíba: Fazenda Brazil (MZUSP 91336–91361).

Dendropsophus* cf. *pseudomeridianus. Brazil: Rio de Janeiro: Rio de Janeiro: Brejo no gramado em frente à entrada principal da Rural (UFFRJ) (CFBH 22229).

Dendropsophus columbianus. Colômbia: Cali (Holotype: ZSM 1182/0/1-3). Cauca: Popayán (Holotype: SMF 2365). Risaralda: Mistrató: Qubrada La Palestina, San Antonio a la Fonda (ICN 30389, ICN 30393–30395); Pereira: Granja La Florida (ICN 45837); Santa Rosa: Comp. Repetidora de la Cruz (ICN 38922); Valle del Cauca (ICN 11457, ICN 11459), Calli (ICN 5478, ICN 5479, ICN 11458), La Cumbre, Vereda Chicoral, corregimiento Bitaco, cabeceras rio Bitaco, Quebrada Aguas Lindas (ICN 33334–41), Restrepo: Vereda Alegre, Campo Agua Bonita (ICN 13428–30); Dagua: Corrego Queremal (ICN 32695); Vereda La Cascada (ICN 32604).

Dendropsophus cruzi. Brazil: Goiás: Silvânia: Estação Florestal de Experimentação de Silvânia (Holotype: MNRJ 21782; Paratypes: CFBH 2939–2944).

Dendropsophus decipiens. Brazil: Bahia: Ilhéus: CEPLAC (MNRJ 31669–31675) Espírito Santo: Santa Teresa: Reserva Santa Lúcia (MNRJ 38375–38380) Minas Gerais: Carangola: Pedra Dourada (MNRJ 44606); Juiz de Fora: Sítio Ribeirão da Cachoeira (MNRJ 43652); Duque de Caxias, Parque Natural Municipal de Duque de Caxias (MNRJ 50837, MNRJ 54719–54735); Rio de Janeiro: Bosque da Barra (MNRJ 44779), Brejo no gramado em frente à entrada principal da Rural (UFFRJ) (CFBH 22230); Seropédica: FLONA Mario Xavier (CFBH 25710–25714).

Dendropsophus dutrai. Brazil: Bahia: Ilhéus: UESC (MNRJ 52406). Sergipe: Estância: Areia Branca (alótipo: MZUSP 38024; Holotype: MZUSP 38025). Sergipe: Indiaroba: Fazenda Sabão, Povoado do Retiro (MNRJ 46746); São Cristóvão: Gasoduto Catu-Camópolis (MNRJ 38910).

Dendropsophus ebraccatus. Honduras: Gracias a Dios: Kaska Tingni (USNM 559102, USNM 559105, USNM 559107, USNM 550109–550113, USNM 550115–550116).

Dendropsophus elegans. Brazil: Bahia: Gandú: Estrada para Piraí do Norte (CFBH 27974). Espírito Santo: Conceição da Barra: Itaúnas (CFBH 2402); Linhares: CRFVRD (CFBH 22663–22667), Reserva Natural da Cia. Vale do Rio Doce (CFBH 11083); Santa Tereza: Pátio do Museu Mello Leitão (CFBH 17994). Minas Gerais: Aimorés (MCNAM 9196, MCNAM 12087); Bandeira (MCNAM 3409); Barão de Cocais: Mina Dois Irmãos (MCNAM 11271); Divisa Mucurici ES - Nanuque MG: Fazenda Gemada (CFBH 23116); Genipapo de Minas (MCNAM 9878); Novo Cruzeira (MCNAM 3944); Salto da Divisa: Faz. Santa (MCNAM 4865); São Gonçalo do Rio Abaixo (MCNAM 11924). Paraná: Guaratuba: Serra do Araraquara (Fazenda Creminácio) (CFBH 23220). Rio de Janeiro: Macaé (MNRJ 53166); Rio de Janeiro: Pedra de Guaratiba (MNRJ 42960–42962). São Paulo: Apiaí e Iporanga: Parque Estadual Turístico do Alto Ribeira (PETAR) - Base Areado (CFBH 26708); Apiaí e Iporanga: Parque Estadual Turístico do Alto Ribeira (PETAR) -Núcleo Ouro Grosso (CFBH 26743); Ribeirão Grande: Fazenda Intermontes (CFBH 24541–24542); São Paulo: Núcleo Curucutu - PESM (CFBH 14744); Ubatuba: Picinguaba (CFBH 1254).

Dendropsophus elianeae. Brazil: Mato Grosso do Sul: Bela Vista (Holotype: MNRJ 17297). São Paulo: Paulínia: Rhodia (CFBH 239); Rio Claro: Sítio Zezé, Itapé (CFBH 21189–21195, CFBH 21149– 21154).

Dendropsophus garagoensis. Colômbia: Antioquia: Sonsón: Rio Verde de los montes, Vereda La Soledad (ICN 39730–39733). Boyacá: Miraflores: Finca el Vergel, 38 km (by road) NE Garagoa on road to Miraflores, Vereda el Tunjito (Holotype: ICN 17781; Paratypes: ICN 17794, ICN 17800, ICN 17803, ICN 17806, ICN 17814–17815).

Dendropsophus gaucheri. Brazil: Pará: Campos do Ariramba: Igarapé Jaramacaru (MZUSP 54051–54056); Oriximiná: Igarapé Jaramacaru, Campos do Ariramba (MZUSP 54050–54055).

***Dendropsophus giesleri*.** Brazil: Espírito Santo: Santa Teresa: Sítio do Bozza (MNRJ 28387). Minas Gerais: Nova Lima (MCNAM 7854–7855); Ouro Preto: Lagoa do Physalaemus maximus (MCNAM 7338, MNRJ 41730–41732), Lagoa próxima ao trevo de Santa Rita do Ouro Preto (MCNAM 6018–6019). Rio de Janeiro: Angra dos Reis (MNRJ 2532); Duque de Caxias: Barro Branco, Colonia de Imbarié, unwiet der Strasse von Rio nach Petropolis (Holotype: SMF 41217); Rio das Ostras: REBIO União (MNRJ 37343–37344).

Dendropsophus gryllatus. Equador: Los Ríos: Estación Biológica Río Palenque (Holotype: KU 146542); Quevedo: Estación Ecológica Rio Palenque (Paratypes: MZUSP 73742–73743), Hacienda Cerro Chico, 45 km N Quevedo rd to Sto Domingo de los Colorados (MCZ-A 94485).

Dendropsophus haddadi. Brazil: Bahia: Ilhéus (CFBH 25798–25802); São José: Fazenda Unacau (MZUSP 63516–63523). Espírito Santo: Conceição da Barra (CFBH 1538), Mata do Queixada (Holotype: MNRJ 17325; Paratypes: CFBH 1613, CFBH 1635; CFBH 1630–1631, CFBH 1634–1635, CFBH 1637); Santa Tereza: Museu de Biologia Mello-Leitão (CFBH 2595).

Dendropsophus haraldschultzi. Brazil: Amazonas: Santa Rita do Weil (Holotype: MZUSP 74192). Colômbia: Amazonas: Letícia: km 13,8 Letícia-Tarapacá (ICN 46644–46646, ICN 46650, ICN 46656, ICN 46658, ICN 46660, ICN 46664–46667, ICN 50843).

Dendropsophus jimi. Brazil: Minas Gerais: Santana do Garambéu (MCNAM 2552); Unaí (MCNAM 10679, MCNAM 10681–10690). São Paulo: Botucatu (Holotype: MNRJ 21980; Paratypes: MNRJ 21983–21990; CFBH 25705–25709)

***Dendropsophus koechlini*.** Brazil: Amazonas: Boca do Pauiní (Paratype: MZUSP 49893). Peru: Madre de Diós: Puerto Maldonado (Paratypes: ZUEC 14839–14840), Reserva Cuzco Amazonico (Holotype: KU 205692).

Dendropsophus labialis. Colômbia: Antioquia: Jericó (AL 4779–4782). Boyacá: Aquitania: Alto Rio Cuisano, Paramo de Toquillo, Km 53 via Sogamoso-Pajarito (ICN 33261); Bongui (ICN 33224); Buena Vista: Vereda Saboneta (ICN 1901); Cómbita: Finca La Concepcíon (ICN 33612, ICN 33618, ICN 33628, ICN 33631), Páramo de Sote, Finca La Concepción (ICN 33610, ICN 33620, ICN 33631); Duitama: "El Taladro", Km 57-58 Duitama-Charalá (ICN 12570, ICN 12572, ICN 12563), Páramo La Rusia (ICN 4424, ICN 12584, ICN 12586); Güican: Sn de Cocuy, Had Rita cua (ICN 5100), Vereda San Antonio de la Cueva (ICN 2077); Moniquirá: La cumbre, (ICN 33637); Santa Dofia: Vereda San Cristovao (ICN 52945). Boyacá: Santa Sofia: Vereda San Cristóbal (ICN 52944); Tunja: Las Peñitas (ICN 10347, ICN 10296). Cundinamarca: Bogotá: Ciudad

Universitária (ICN 53811); Bogotá (USNM 95874–95883); Tansa (ICN 18194). Equador: Culata, N.W. (AL 4569); Pichincha: Santo Domingo de los Colorados (ex-Orcés) (MZUSP 92547).

Dendropsophus leali. Brazil: Rondônia: Forte Príncipe da Beira (alótipo: MZUSP 74211; Holotype: MZUSP 74210; Paratype: MNRJ 3962). Amapá: Serra do Navio (MCNAM 2088). Maranhão: Estreito: Fazenda Ituaneiras (CFBH 9135), Fazenda Ouro Verde (CFBH 18038). Pará: Acará (CFBH 20322).

Dendropsophus limai. Brazil: São Paulo: São Vicente (Holotype: MZUSP 73657).

Dendropsophus marmoratus. Brazil: Amazonas: Barcelos: Posto da FUNAI (MNRJ 36241–36242); Estreitas do Equador: Rio Javari (MNRJ 3340); Humaitá, Porto Velho: km 49 Rodovia Humaitá - Porto Velho (MNRJ 17783); Limoeiro (MZUSP 50743–50775); Manaus (USNM 292660–292663); km 34, BR-319 Sr. Fernando (APL 13034–13035); Rio Negro (MNRJ 3292); Tabatinga (MZUSP 111257–111267). Mato Grosso do Sul: Aripuanã (UFMT 6182); Cotriguaçu (UFMT 6185–6186, UFMT 6190); Juina (UFMT 6183, UFMT 6192, UFMT 6194–6195, UFMT 6198, UFMT 6209). Pará: Treviso (APL 12584–12588). Rondônia: Alto Paraíso (USNM 304235); Santa Cruz da Serra (USNM 303968–303969); Ji-Paraná, Nova Brasília (USNM 304238–304240); Santa Cruz da Serra, 5 km SW of (USNM 304236–304237). Equador: Napo: Loreto (MZUSP 106636–106639). Amazonas: Galileia (USNM 568125, USNM 568128, USNM 568134, USNM 568136, USNM 568140–568141, USNM 568153, USNM 568158, USNM 568160, USNM 568161)

Dendropsophus melanargyreus. Brazil: Amazonas: Rio Solimões: Igarapé Belém (MZUSP 33564–33569, MZUSP 34708–34713, MZUSP 33264–33269). Goiás: Anápolis: Porangatu, (BR-153) (MCNAM 10000–10001); Itapirapuã (ZUEC 10220); Jataí (MZUSP 106975); Minaçu (MZUSP 130648–130650); Pires do Rio (MZUFV 6531–6535). Maranhão: Vargem Grande, Estrada São Luis a Brejo, 25 Km antes de Chapadinha (ZUEC 3861–3862), Estrada São Luis a Brejo, 28 Km após Chapadinha (ZUEC 3875). Mato Grosso do Sul: Corumbá (UFMT 2621–2623, ZUEC 7081–7082), Licenciamente Ambiental da MCR (MCNAM 7598–7599). Mato Grosso: Aparecida do Tabuado (MNRJ 17784–17785); Aripuanã (MZUSP 80611–80622); Barra do Tapirapés (MZUSP 34716–34721, MZUSP 33685–33693); Cáceres: Estrada para Barra do Bugres, about Km 30 (ZUEC 10191–10192); Cáceres (UFMT 714–715); Chapada dos Guimarães (UFMT 2945–2947, UFMT 1406–1407), 30 miles NE of Cuyabá (síntipo: ANSP 11216–11218); Jauru (UFMT 6239–6241); Nossa Senhora do Livramento (UFMT 935–937); UHE Manso (MZUSP 98756–98757); Pindaíba (MZUSP 91391–91399); Porto Esperidião (MZUSP 59702–59704); Rosário d´Oeste (MZUSP 112939); Vale de São Domingos (UFMT 1241–1242, UFMT 1823–1824). Minas Gerais: Buritis (MCNAM 3293–3296); Cabeçeira Grande: AHE Queimado (MCNAM 8902). Pará: Canaã dos Carajás: Mineração Serra do Sossego (MCNAM 2935, MCNAM 2936); Serra de Kukoinhoken (MZUSP 69302–69303, MZUSP 69970–69971); Paragominas: Rio Capim (MNRJ 23845–23846); Treviso (APL 12304); Tucuruí (MNRJ 17786). Rondônia: Igarapé Rio Marmelo (MZUSP 106629–106635). São Paulo: Magda (DZSJRP 11754–

11755). Tocantins: Darcinópolis (CFBH 19423, CFBH 19910); Guaraí (MZUSP 127094–127097); Paranã (CFBH 22052–22054); São Salvador do Tocantins (MZUSP 114470).

Dendropsophus meridensis. Venezuela: Merida: La Carbonera: Bosque San Eusébio (ICN 32424, ICN 32426–32427).

Dendropsophus meridianus. Brazil: Rio de Janeiro: Duque de Caxias: Parque Natural Municipal de Duque de Caxias (MNRJ 54687–54698); Rio de Janeiro: Brejinho do horto do MNRJ da quinta da Boa Vista (CFBH 22236–22245, CFBH 23642–23649).

Dendropsophus microps. Brazil: Minas Gerais: Antônio Carlos (MCNAM 7500–7502); Camanducaia: Hotel Cabeça de Boi- Monte Verde (CFBH 7498). Rio de Janeiro: Nova Friburgo (Holotype: ZMB 7472); Campos de Jordão (MNRJ 26349); Ribeirão Grande: Fazenda Intermontes (CFBH 24548–24549); São Luis do Paraitinga: Poça da Phrynomedusa, ca. Cachoeira do Angelim, Trilha Ipiranga (CFBH 14864).

Dendropsophus minimus. Brazil: Pará: Santarém: Taperinha (Holotype: NHMW 19436)

Dendropsophus minutus. Argentina: Missiones (dpto Guarany): San Vicente: IINTA "Cuartel Rio Victoria" (JF 640). Brazil: Mato Grosso do Sul: Bataiporã: Fazenda Primavera (MZUSP 69648, MZUSP 69650–69652, MZUSP 69657, MZUSP 69660, MZUSP 69662); Brazilândia: Fazenda Barma (MZUSP 69699). Minas Gerais: Catas Altas: Campo de Futebol, Serra do Caraça (MNRJ 44691–44699). Pará: Corumpá: Arapiranga (CFBH 24827), Lagoa da Campina (Ilha Pedras Grandes) (CFBH 24828–24829). Rio de Janeiro: Nova Friburgo (Síntipo: ZMB 7456). São Paulo: Fazenda Intervales (MZUSP 88083); Ribeirão Branco: Fazendinha São Luiz (CFBH 16602); Rio Claro: Sítio Zezé, Itapé (CFBH 21155, CFBH 21171–21186), Sítio Zezé, Itapé (CFBH 21156–21158, CFBH 21187–21188); Teodoro Sampaio: Parque Estadual Morro do Diabo (CFBH 18385). Tocantins: Paranã (CFBH 20982). Uruguai: Maldonado: San Carlos: 15 km N.E. of San Carlos (Holotype: FMNH 9581). Unknown locality (MACN 34961).

Dendropsophus miyatai. Colômbia: Amazonas: Letícia: Corrego de Tarapacá (ICN 35746–35755). Equador: Napo: Rio Napo: along a stream that flows from the Garza Cocha lake (on the property of the Hosteria La Selva just north of the Rio Napo (Holotype: MCZ-A 111570).

Dendropsophus nahdereri. Brazil: Paraná: São José dos Pinhais (CFBH 3561). Santa Catarina: Anitápolis: Indústria de Fosfatados Catarinense (IFC) (CFBH 9376, CFBH 20251–20260); Rancho Queimado (CFBH 13592); São Bento do Sul, Serra Alta: Estrada Saraiva (Topotype: MNRJ 4406–4410), Serra Alta (Lectotype: MNRJ 3295; Paralectotype: MNRJ 3509, MNRJ 3294, MNRJ 3296; WCAB 512), Estrada Rio Vermelho a Rio Natal (Topotype: CFBH 3564–3565), Rio Vermelho (MZUSP 74217, MZUSP 112938); Siderópolis: Barragem do Rio São Bento (CFBH 19223–19224).

Dendropsophus nanus. Brazil: Bahia: Serra do Ramalho (CFBH 22076–22077). Goiás: Pirenópolis (MNRJ 51202–51205); Teresópolis: Fazenda Santa Branca (CFBH 18643). Paraná: Maringá: Fazenda Cesumar (CFBH 17211). São Paulo: Pirassununga: CEPTAS - Cachoeira de Emas (CFBH 21340–21352); Rio Claro: Sítio da Zezé, Itapé (CFBH 21206–21211); Teodoro Sampaio: Parque Estadual Morro do Diabo (Represa Roda D´Água) (CFBH 22701), Parque Estadual Morro do Diabo (CFBH 18290–18291, CFBH 18688). Tocantins: Gurupi: Poças permanentes, próximo a fragmento Florestal Estacional Semidecidua (CFBH 20978).

Dendropsophus novaisi. Brazil: Bahia: Camamú (UFBA 67–68); Irajubá: mata ciliar do rio jequiriçá (UFBA 10782); Itacaré: Parque Estadual Serra do Conduru, Setor Norte (MNRJ 35380–35381); Maracás (UFBA 2437–2449, UFBA 2486–2507, UFBA 2925, UFBA 2831), Fazenda Santo Onofre (Paratypes: MNRJ 4049, MZUSP 74335–74343); APA Pratigi (UFBA 3933–3935); Reserva Veracruz Florestal (MZUSP 12673–12674); Porto Seguro: Estação Veracel (UFBA 9917); PN Bau Brazil (UFBA 9774).

Dendropsophus oliveirai. Brazil: Bahia: Maracás (Holotype: MZUSP 73659; Paratype: MNRJ 3668), Fazenda Santo Onofre, Fazenda Cana Brava (Topotypes: CFBH 19316–19318, CFBH 19327–19334, CFBH 19339), Fazendas Cana Brava e Santo Onofre (Topotype: CFBH 19336).

Dendropsophus padreluna. Colômbia: Cundinamarca: Abán: Granja Padre Luna, Vereda Las Marias (ICN 22012, ICN 22021, ICN 22027–22028, ICN 22030, ICN 22032, ICN 22035–22036, ICN 22043, ICN 22051, ICN 22053, ICN 22061, ICN 22063, ICN 22235, ICN 22254, JDL 28325), Granjas infantiles "El Gran ciudadano Padre Luna, verda Las Marias (Holotype: ICN 22065); Tena: Laguna Pedro Palo (ICN 8726–8728).

Dendropsophus parviceps. Brazil (ZUEC 11209): Acre: Cruzeiro do Sul: Mata da Infraero (TG 2887).

Dendropsophus pauiniensis. Brazil: Amazonas: Boca do Pauíni (Holotype: MZUSP 49892).

Dendropsophus pelidna. Venezuela: Táchira: Betania (KU 181108).

Dendropsophus phlebodes. Costa Rica: Alajuela Prov.: 2 mi. NE Muelle de Arenal cut over vegetation banana plantation (MNRJ 3639, MNRJ 14635).

Dendropsophus praestans. Colômbia: Huila: San Agustín: Parque Arqueológica San Agustín (KU 169574), 3 km southwest of the village of San Agustín, (Holotype: KU 169575); San Agostín: Finca Yaguará, Vereda Aranca (ICN 53818); San José de Isnos (ICN 7558–7561).

Dendropsophus pseudomeridianus. Brazil: Rio de Janeiro: Rio de Janeiro: Brejo no gramado em frente à entrada principal da Rural (UFFRJ) (CFBH 22226–22228, CFBH 22231–22235); Seropédica (Holotype: MNRJ 25502).

Dendropsophus reticulatus. Equador: Napo: Orillas del Napo (Holotype: MNCN 3474).

Dendropsophus rhea. Brazil: São Paulo: Pirassununga: Cachoeira de Emas (Holotype: MZUSP 9104; Paratypes: MZUSP 9100–9103, MZUSP 9105–9113).

Dendropsophus rhodopeplus. Brazil: Acre: Cruzeiro do Sul (TG 2860).

Dendropsophus riveroi. Brazil: Rondônia: Ji-Paraná: Nova Brasília (USNM 292375, USNM 304061–304063, USNM 304067–304072, USNM 304074, USNM 304081–304085). Colômbia: Amazonas: Letícia (USNM 152202), Km 2 via tarapacá (ICN 50616, ICN 50609–50610, ICN 50612, ICN 50614).

Dendropsophus rossaleni. Brazil: Pará: Oriximiná: Lago Acumã, Porto de Trombetas (MCNAM 8671–8672).

Dendropsophus rubicundulus. Brazil: Minas Gerais: Lagoa Santa (Síntipo: NHMW 16511).

Dendropsophus ruschii. Brazil: Espírito Santo: Pedra Azul: Parque e Nascente do Rio Juai (MNRJ 31548–31550). Minas Gerais: Pedra Dourada (MNRJ 47849–47857).

Dendropsophus salli. Brazil: Acre: Tarauacá (MZUSP 116707–116719). Rondônia: Porto Velho (MZUSP 117916–117917, MZUSP 116697–116702)

Dendropsophus sanborni. Brazil: São Paulo: Rio Claro: Sítio Zezé, Itapé (CFBH 21196–21205).

Dendropsophus sarayacuensis. Brazil: Acre: Tarauacá (MNRJ 3652). Mato Grosso: Aripuanã (MZUSP 80632–80634). Pará: Parque Rio Tapajós (MZUSP 56924). Rondônia: Porto Velho: UHE Jirau (MZUSP 148388, MZUSP 146192). Equador: Napo: Santa Cecilia (MZUSP 55604–55607).

Dendropsophus schubarti. Brazil: Acre: Tarauacá (MZUSP 92582). Amazonas: Mucuripe (MZUSP 50425). Pará: PARNA da Amazonia (Rio Tapajós) (MZUSP 58174–58186); Parque Rio Tapajós (MZUSP 56056–56058); Uruá: PARNA da Amazonia (Rio Tapajós) (MZUSP 53939). Rondônia: Ji-Paraná (MZUSP 92583; Paratypes: MZUSP 73651–73652); Nova Brasília (MZUSP 60488–60491); Rondônia (Holotype: MNRJ 3669; Paratypes: WCAB 7846–7847); Santa Cruz da Serra (MZUSP 60412).

Dendropsophus seniculus. Brazil: Bahia: Porto Seguro: PN Bau Brazil (UFBA 9775), Reserva Veracruz Florestal (MZUSP 12675), RPPN Estação Ver Cruz (MNRJ 25622–25624). Espírito Santo: Aracruz: Barra do Riacho, Eucaliptal alagado perto da fábrica de celulose (CFBH 4027); Cariacica: Reserva Biológica de Duas Bocas (MNRJ 27937–27938, MNRJ 27910–27912); Colatina: Rio Mutum (MNRJ 824); Linhares: Fazenda 3 ilhas, Povoação (CFBH 5990–5991), Fazenda Pirajú, Povoação (CFBH 5988–5989), Povoação (CFBH 4084), Reserva da Vale (MNRJ 22838–22860), Reserva Florestal Barra Seca (MNRJ 1997, MNRJ 1997b, MNRJ 1997c); Santa Tereza: Sítio Molino, Santa Lúcia (MNRJ 46721); São João de Petrópolis (MNRJ 1304); São Mateus (CFBH 1622, CFBH 1623). Minas Gerais: Almenara: Fazenda Limoeiro (MZUFV 5430–5436); Barão de Cocais (MNRJ 17788–17794); Cabeçeira Grande: AHE Queimado (MCNAM 8903); Caeté (MCNAM 786), Lagoa do Cabral (MNRJ 17795–17796); Catas Altas: Campo de Futebol, Serra do Caraça (MNRJ 47536, MNRJ 44703–44704), RPPN Serra do Caraça (MCNAM 5799); Conceição do Mato Dentro: Parque Municipal Ribeirão do Campo, Tabuleiro (MCNAM 3111–3113); Guanhães (MNRJ 17816–17836); Marliéria: Parque Estadual do Rio Doce (MZUFV 2757–2758); Peçanha (MNRJ 17797–17815); Poté: Fazenda Nossa Senhora Fátima (MZUFV 6162–6167); São Gonçalo do Rio Preto (MCNAM 11726–11727); Teófilo Otoni (MZUSP 11512–11513). Rio de Janeiro: Nova Friburgo (possibly) (ZMB 7284); Angra dos Reis (CFBH 5761), Mambucaba e Palmital (CFBH 22649–22657); Cabo Frio: Orla 500 (MNRJ 36157–36158), Restinga do Peró (MNRJ 47536); Casemiro de Abreu: Barra de São João (MZUSP 76494); Duque de Caxias: Barro Branco (MNRJ 3085–3085m); Guapiaçu: Reserva Biológica Guapiaçu (MNRJ 40442–40443, MNRJ 40447); Itaguaí: Horto Florestal de Santa Cruz (ZUEC 3496–3497); Macaé: Reserva Biológica União (MNRJ 44000–44004); Magé (DZUFRJ 3438), Acesso ao campo dos escoteiros (ZUEC 6913), campo dos escoteiros (MNRJ 55244), Sede de campo dos escoteiros (ZUEC 6306–6307); Mangaratiba: RERP - Reserva Ecológica Rio das Pedras (UNIRIO 2545); Maricá: Restinga de Maricá (MNRJ 29440); Muriqui (MNRJ 3773); Niterói: Jardim Botânico Neotropicur, Várzea da Moça, Mata Atlântica da Serra da Tiririca (MNRJ 31353–31354); Rio de Janeiro: Jacarépagua (Estrada do Cafundá) (MNRJ 1415, MNRJ 2121, MNRJ 2121b–2121g, MNRJ 7756–7763), Rua Comendador Siqueira) (MNRJ 2136, MNRJ 10808–10811), Realengo (MNRJ 3762, MNRJ 3762b–3762c); São João da Barra (MNRJ 1842, MNRJ 8133); São João do Meio (MNRJ 59370–59371); Saquarema: Palmital (MNRJ 30167, MNRJ 30287–30296). São Paulo: Iporanga: PETAR, Núcleo Caboclos (CFBH 8278–8279), Núcleo Santana (CFBH 8099–8100); Ribeirão Branco: Fazenda São Luis (CFBH 2228); Ribeirão Grande: Fazenda Intermontes (CFBH 24543–24545). Unkown locality (ZUEC 8725)

Dendropsophus soaresi. Brazil: Alagoas: Campo Alegre (MZUSP 137878–137879, CFBH 18573–18575), Fazenda Pindoba (CFBH 16362–16365); Coruripe: Fazenda Capiatão A (MNRJ 38137); São Miguel dos Campos: Fazenda Prata (MNRJ 9597–9599). Bahia: Andaraí (MZUSP 112963–112978); Bom Jesus da Lapa (UFBA 7711); Caitité (MNRJ 25032); Jandaíra (DZUFRJ 6887); Japaguá: 1-4 léguas abaixo de Japaguá (MNRJ 2445). Ceará: Caucaia: Estação Ecológica do PECEM (MNRJ 42941); Crato: Araripe (MNRJ 32062); Fortaleza: Mucuripe (MNRJ 1601, MNRJ 8330–8336); Juazeiro do Norte: FLONA do Araripe (MNRJ 42942); Tianguá: Chapada da Ibicipaba (MNRJ 42943); Ubajara: Casarão (CFBH 15864–15865), Poço 2 km (CFBH 15869–15873), Sítio Luis Gonzaga (CFBH 19304–19311); Viçosa do Ceará: Serra das Flores, Açude do Santo Mano (CFBH 19295–19303). Goiás: Estrela do Norte (MNRJ 53140); Mambaí (MNRJ 26417). Maranhão: Alcântara (CFBH 19177–19185); São Luiz (MNRJ 23841, MNRJ 23842). Minas Gerais: Araçuaí (MZUFV 4524); Bocaiúva: Terra Branca, Mineração SADA (MCNAM 1247–1251, MCNAM 1744–1749); Guarda-Mor (MCNAM 10670).

Minas Gerais: João Pinheiro: Fazenda "Fruta Danta"?, Lagoa na campina (MNRJ 50720–50729); João Pinheiro: Fazenda Veredas (MNRJ 38800–38802); Manga: Mocambinho (MNRJ 31300–31301, MNRJ 31657–31661). Paraíba: Patos: Faz Oriente (ZUEC 8725). Pernambuco: Moreno (MNRJ 58306–58310). Piauí: Picos (Parátipo: JJ 5741–5748). Sergipe: Indiaroba: Fazenda Sabão, Povoado do Retiro (MNRJ 46736–46737). Tocantins: Brejinho de Nazaré (MZUSP 106974).

***Dendropsophus* sp**. Brazil: Acre: Rio Mucu (MZUSP 116692). Pará: Corumpá: Nazaré da Mocajuba (Córrego do Zumbi) (CFBH 24826).

***Dendropsophus* sp. gr. *microcephalus*.** Brazil: Minas Gerais: Barão de Cocais: Mina Dois Irmãos (MCNAM 11244–11247).

Dendropsophus stingi. Colômbia: Boyacá: Miraflores: Finca el Vergel, 38 km (by road) NE Garagoa on road to Miraflores, Vereda el Tunjito (Holotype: ICN 15844).

Dendropsophus studearae. Brazil: Bahia: Catu (UFBA 10127–10143, UFBA 10548–10550).

Dendropsophus timbeba. Brazil (Paratypes: ZUEC 5476, ZUEC 5723; ZUEC 10641, ZUEC 11033–11034, ZUEC 11036–11038, ZUEC 11053). Acre: Xapuri: caminho para Vila Boa Vista (Holotype: MZUSP 60560). Peru: Madre de Dios: Puerto Maldonado: Cusco Amazónico (KU 207606, KU 215189), 15 km E Puerto Maldonado (KU 207607, KU 215188, KU 215190).

Dendropsophus tintinnabulum. Brazil: Amazonas: Santa Isabel do Rio Negro: Rio Uaupés (síntipo: NHMG 473(1)–473(3)).

Dendropsophus triangulum. Brazil: Acre: Cruzeiro do Sul: Vila do BEC (CFBH 4611, CFBH 4628, CFBH 4632, CFBH 4661, CFBH 4667), Vila militar (CFBH 52). Colômbia (ICN 53091).

Dendropsophus tritaeniatus. Brazil: Mato Grosso: Cuiabá: São Vicente (Holotype: MZUSP 73656; Paratype: MZUSP 73974, MZUSP 73977, MZUSP 73982).

Dendropsophus virolinensis. Colômbia: Santander: Charalá: El Reloj, El Encino (ICN 39002, ICN 39005, ICN 39010–39011, ICN 39015, ICN 39017–39019); Finca La Alianza, Virolín (ICN 11279). Santander: Charalá: Insp. De Policia de Virolin cerca a confluencia Río Guillermo y Río Cañaverales (ICN 12544–12545, ICN 12548–12549, ICN 12553, ICN 12556, ICN 12558–12559), Km 70 Duitama-Charalá (ICN 12517–12519, ICN 12526, ICN 12532).

Dendropsophus walfordi. Brazil: Rondônia: Costa Marques: Forte Príncipe da Beira (Holotype: MZUSP 73652).

Dendropsophus xapuriensis. Brazil: Acre: Xapuri: Caminho p/ Vila Boa Vista (Holotype: MZUSP 60558; Paratype: CFBH 6260).

Hyla dasynota. Brazil (Holotype: BMNH 1947.2.31.3).

Hyla goughi. Trinidad (Holotype: BMNH 1947.2.13.12).

Hyla grandisonae. Guyana: in the forest at Mazaruni (Holotype: BMNH 1938.10.3.25).

Lysapsus limellum. Brazil: Mato Grosso do Sul: Corumbá: Fazenda Nhumirim (CFBH 8781–8786).

Phyllodytes luteolus. Brazil: Espírito Santo: Guaraparí: Restinga de Setiba (CFBH 895–896); Santa Teresa (MNRJ 23298), Médio Goiapaba-Açú (MNRJ 23984).

Phyllodytes tuberculosus. Brazil: Bahia: Maracás: Fazenda Santo Onofre, Fazenda Cana Brava (Topotype: CFBH 19341)

Pseudis limellum. Brazil: Amazonas: Capim Flutuante- Rio Solimões (CFBH 4983). Mato Grosso do Sul: Corumbá: Fazenda Nhumirim, Nhecolândia (CFBH 576), Passo do Lontra (CFBH 4393). Mato Grosso: Poconé: Fazenda Ipiranga, Km 10 da Rodovia Transpantaneira (CFBH 14176).

Pseudis minutus. Unknown locality (JF 1179, JF 1237).

Scarthyla goinorum. Brazil: Acre: Cruzeiro do Sul (CFBH 24821), Comunidade Praia Grande (CFBH 24812–24820, CFBH 24824). Colômbia: Amazonas: Letícia: Quebrada de Yahuarcaca (ICN 45603–45604).

Scarthyla vigilans. Colômbia: Boyacá: Agua Negra: 10.5 km de Puerto Romero, Rio Guayaguaquí (ICN 37633); Córdoba: Covenãs: En caserio (ICN 37634–37635, ICN 37639–37641); Norte de Santander: Sardinata: 2.4 km N de Sardinata (ICN 33529–33532).

Scinax acuminatus. Argentina: Santa Fé: Vera: Estrada Las Gamas (JF 893).

Scinax angrensis. Brazil: Rio de Janeiro: Angra dos Reis (CFBH 5690).

Scinax berthae. Brazil: São Paulo: Mogi das Cruzes (CFBH 13561); Santa Bárbara: Estação Ecológica de Santa Bárbara (CFBH 22339–22342); Teodoro Sampaio: Parque Estadual Morro do Diabo (CFBH 10055, CFBH 18358). Santa Catarina: Chapecó (CFBH 3865). Unknown locality (MACN 36987).

Scinax fuscomarginatus. Brazil: Minas Gerais: Caeté (MCNAM 793–808). São Paulo: Pirassununga: CEPTAS - Cachoeira de Emas (CFBH 21331–21333).

Scinax fuscovarius. Brazil: São Paulo: Pirassununga: CEPTAS - Cachoeira de Emas (CFBH 21334–21339). Unkown locality (MACN 18861, MACN 36914).

Scinax littoralis. Brazil: São Paulo: Cubatão: COPEBRÁS (CFBH 11374); Monguaguá (CFBH 17362, CFBH 17372); Ubatuba: Itaguá (CFBH 1116), Picinguaba (CFBH 1213, CFBH 1224, CFBH 4297).

Scinax pachycrus. Brazil: Bahia: Maracás: Fazenda Santo Onofre, Fazenda Cana Brava (CFBH 19338, CFBH 19340).

Scinax perereca. Brazil: Paraná: Guaratuba (CFBH 4216). São Paulo: Apiaí e Iporanga: Parque Estadual Turístico do Alto Ribeira (PETAR) - Base Areado (CFBH 26721); Horical Minerações - próximo a Intervales (CFBH 13454); Pilar do Sul (CFBH 8930); Ribeirão Branco: Fazenda do João Zacheo Neto (CFBH 8055); Fazenda São Luis (MNRJ 25440), Fazenda São Luiz (Mathedi) (CFBH 1833). Santa Catarina: Anitápolis: Indústria de Fosfatados Catarinense - IFC (CFBH 9959). Unknown locality (MACN 36927, MACN 36926).

***Scinax* sp.** Brazil: Amazonas: Borba (APL 12523).

Sphaenorhynchus botocudo. Brazil: Bahia: Porto Seguro: RPPN Estação Vera Cruz (MCNAM 2481–2483).

Sphaenorhynchus carneus. Brazil: Acre: Cruzeiro do Sul: Comunidade Praia Grande (CFBH 24825).

Sphaenorhynchus dorisae. Brazil: Acre: Cruzeiro do Sul: Comunidade Praia Grande (CFBH 24822–24823).

Sphaenorhynchus lacteus. Brazil: Acre: Rodrigues Alves: Igarapé Croa - Alto Juruá (CFBH 15725). Amazonas: Capim Flutuante- Rio Solimões (CFBH 4993). Pará: Acará (CFBH 20321); Belém: Reserva de Utinga (CFBH 16741). Rondônia: Pimenteiros do Oeste (CFBH 20427). Unkown locality (MACN 3472)

Sphaenorhynchus pauloalvini. Brazil: Espírito Santo: Linhares: FLONA de Goytacazes (CFBH 22924, CFBH 22926–22928, CFBH 22930–22931).

Sphaenorhynchus planicola. Brazil: Espírito Santo: Linhares: CRFVRD (CFBH 22660–22662).

Sphaenorhynchus prasinus. Brazil: Espírito Santo: Linhares: Estrada para a fazenda Maria Bonita (CFBH 22639–22648). Minas Gerais: Aimorés: Área do Baixio (MCNAM 1294–1295); Bandeira (MCNAM 3414–3416); Resplendor: Faz. Boa Vista (MCNAM 1289), UEH Aimorés, Resplendor-Campo Alegre (MCNAM 1240).

Xenohyla truncata. Brazil: Rio de Janeiro: Maricá (CFBH 7600–7602; MNRJ 59340–59341), Restinga de Maricá (CFBH 20807, CFBH 23531–23534, CFBH 24625, MNRJ 33319–33331, MNRJ 57376, MNRJ 62773); Rio das Ostras: ARE Itapebussus (MNRJ 38201–38202); Rio de Janeiro: Posto Bravo 6, Ilha da Marambaia (MNRJ 20031), Restinga de Maricá (CFBH 4195–4199).

Appendix S5.

Oligonucleotide primers used in this study

Primer	Sequence	Source
sia1b	5’-TCGAGTGCCCCGTGTGYTTYGAYTA-3’	Bonacum *et al.* (2001)
sia2	5’-GAAGTGGAAGCCGAAGCAGSWYTGCATCAT-3’	Bonacum *et al.* (2001)
Rhod1A	5’-ACCATGAACGGAACAGAAGGYCC-3’	Bossuyt & Milinkovitch (2000)
Rhod1C	5’-CCAAGGGTAGCGAAGAARCCTTC-3’	Bossuyt & Milinkovitch (2000)
Rhod1Da	5’-GTAGCGAAGAARCCTTCAAMGTA-3’	Bossuyt & Milinkovitch (2000)
Tyr 1C	5’-GGCAGAGGAWCRTGCCAAGATGT-3’	Bossuyt & Milinkovitch (2000)
Tyr 1G	5’-TGCTGGGCRTCTCTCCARTCCCA-3’	Bossuyt & Milinkovitch (2000)
12sL13	5’-TTAGAAGAGGCAAGTCGTAACATGGTA-3’	Feller & Hedges (1998)
MVZ59	5’-ATAGCACTGAAAAYGCTDAGATG-3’	Graybeal (1997)
MVZ50	5’-TYTCGGTGTAAGYGARAKGCTT-3’	Graybeal (1997)
16sL2A	5’-CCAAACGAGCCTAGTGATAGCTGGTT-3’	Hedges (1994)
16sH10	5’-TGATTACGCTACCTTTGCACGGT-3’	Hedges (1994)
16sAR	5’-CGCCTGTTTATCAAAAACAT-3’	Palumbi *et al.* (1991)
16sBR	5’-CCGGTCTGAACTCAGATCACGT-3’	Palumbi *et al.* (1991)
16sWilk2	5’-GACCTGGATTACTCCGGTCTGA-3’	Wilkinson *et al.* (1996)
R1-GFF	5’-GAGAAGTCTACAAAAAVGGCAAAG-3’	Taran Grant and Julian Faivovich in Faivovich *et al.* (2005)
R1-GFR	5’-GAAGCGCCTGAACAGTTTATTAC-3’	Taran Grant and Julian Faivovich in Faivovich *et al.* (2005)
16sTitus I	5’-GGTGGCTGCTTTTAGGCC-3’	Titus & Larson (1996)
16S-frog	5'-TTACCCTRGGGATAACAGCGCAA-3'	Wiens *et al.* (2005)
tMet-frog	5' TTGGGGTATGGGCCCAAAAGCT-3'	Wiens *et al.* (2005)
POMC_DRV_F1	5'-ATATGTCATGASCCAYTTYCGCTGGAA-3'	Vieites *et al.* (2007)
POMC_DRV_R1	5'-GGCRTTYTTGAAWAGAGTCATTAGWGG-3'	Vieites *et al.* (2007)
MVZ15	5’-GAACTAATGGCCCACACWWTACGNAA-3’	Moritz *et al.* (1992)
H15149(H)	5'-AAACTGCAGCCCCTCAGAAATGATATTTGTCCTCA-3'	Kocher *et al.* (1989)

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Appendix S6

Phenomic characters.

ADULT CRANIAL OSTEOLOGY

- **1. Premaxilla, relation with nasal capsules.** (Figure SI1)
    - 0: Nasal capsules do not cover the *pars dentalis* of premaxilla in dorsal view.
    - 1: Nasal capsules cover the *pars dentalis* of premaxilla in dorsal view..
- **2. Sphenethmoid, anterior extension.** (Additive; Figure SI1)

  The septum nasi is used as an invariable landmark to describe the anterior development of the sphenethmoid. States are ordered in a postero-anterior direction (i.e., in state 0, the anterior margin of the sphenethmoid is relatively more posterior to the other states).

    - 0: Not reaching half of septum nasi.
    - 1: Reaching or surpassing half of septum nasi length but not covering all of it.
    - 2: Covering all septum nasi.
- **3. Nasals, overlap with sphenethmoid.** (Figure SI1)

  Modified from the literature. Liem (1970) character 20; Lynch (1971); Heyer (1975) character 23 (part); Cocroft (1994) character 4; Faivovich (2002) character 0; Scott (2005) character 62; Grant et al. (2006) character 135; Araújo-Vieira et al. (2019) character 3.

  Faivovich (2002) scored the relationship between nasals and sphenethmoid as overlapping or not. Previous papers describing osteological features of *Dendropsophus* species remarked the size of the nasals in relation to the sphenethmoid (e.g. Duellman and Crump, 1974). Scott (2005) codes for nasal and sphenethmoid overlap in a transverse plane. Lynch (1971) makes comments on variation among the former "Leptodactylidae".

    - 0: Nasals not overlapping with sphenethmoid.
    - 1: Nasals overlapping with sphenethmoid.
- **4. Frontoparietals, cover of frontoparietal fontanelle by the medial margins of the anterior third.** (Additive; Figure SI1)

  Modified from the literature. Duellman (1970) character DD; Liem (1970) character 19; Heyer (1975) character 24 (part); Drewes (1984) character 1; Lobo (1995) character 7; da Silva (1998) character 8; Faivovich (2002) character 3; Barg (2003) character 3; Nuin and do Val (2005) character 23; Wiens et al. (2005) character 14; Grant et al. (2006) character 136; Fabrezi (2006) character 5 (part); Araújo-Vieira et al. (2019) character 4.

  Wiens et al. (2005) character 14 is based on Duellman (1970) codification on presence and absence of a frontoparietal fontanelle. Other authors coded differently, based on different lines of thought about the degree of exposition of this fontanelle (using covered percentages or landmarks). However, since the fontanelle is always present, being covered by the medial margins of the frontoparietals or not, a coding scheme based on this bones, instead of "fontanelle variation", seem preferable.

The frontoparietals also cover a portion (or all) of the tectum synoticum and these characters seem independent given the character states taxonomic distribution found herein. The variation on the portion that covers the tectum synoticum is treated in the next character.

Scott (2005) in her character 71 and Liem (1970) in his character 19 had a different approach on the subject, treating the bone as a whole. We found independent variation on each third of the frontoparietals. However, variation on the medial third was only independent in a single terminal (*Dendropsophus triangulum*). We only had a single cleared-and-stained specimen (CFBH 22664). The whole specimen is more ossified than usually seen in other species of *Dendropsophus*. Since we have a single specimen, it is not clear if it is a different state or a development problem of this particular individual. Thus, we preferred not to code the variation of the medial third.

Wiens et al. (2005) character 12 coded for frontoparietal orientation. Here, only the orientation of the medial margin is considered. In a certain way, this coding can be comparable of the degree of sphenethmoid exposure level of Drewes (1984) character 1 because it measured how much of this bone is seen through the frontoparietals contact (or not). Drewes (1984) found more states then the ones scored herein. However, it is not clear if different (anterior or posterior) "Dorsal sphenethmoidal exposure equal to 0.6 or more of length of frontoparietals" were scored differently for example. The difficulty in coding this variation in this manner has already been stated by Faivovich (2002 pg. 377) "because a given level of exposition of the fontanelle can easily result from different morphologies of the frontoparietal anterior to the tectum synoticum." A conservative approach was taken for this character and possibly, more character states could be inside state 1 used herein.

- 0: Frontoparietals not covering the fontanelle, only as wide as the underlying sphenethmoid wall.
- 1: Frontoparietals covering the fontanelle in various degrees but leaving a nearly triangular area between the irregular margins.
- 2: Frontoparietals with smooth margins covering almost all the underlying frontoparietal fontanelle apart by a very thin rectangular space.

- **5. Fontoparietals, cover of tectum synoticum the medial margins of the posterior third .** (Additive; Figure SI1)

Modified from the literature. Duellman (1970) character DD (part); Heyer (1975) character 24 (part); da Silva (1998) character 10; Fabrezi (2006) character 6 (part).

The posterior portion is the portion of the frontoparietals that lay over tectum synoticum. This portion shows various covering degrees over the tectum. The variation found in here would—mainly, if not completely—fall under da Silva (1998) state 0 (frontoparietals not articulating over tectum synoticum).

    - 0: Medial margins of the frontoparietals slender, not expanding medially more than the medial edge of the epiotic eminescences, leaving nearly all tectum synoticum exposed.
    - 1: Medial margins of the frontoparietals expand onto tectum synoticum, passing the medial edge of the epiotic eminescences, but without contacting each other and leaving a rhomboidal space between them.
    - 2: Frontoparietals with smooth, parallel, medial margins covering almost all the underlying tectum synoticum and separated by a thin rectangular space.

- **6. Frontoparietals, posterolateral development** (Figure SI1)

  Modified from the literature. da Silva (1998), character 11; Barg (2003) character 4; Nuin and do Val (2005) character 36.

  Nuin and do Val (2005) only scored "superimposing" of the frontoparietals over the exooccipitals. da Silva (1998) and Barg (2003) coding—they used equal coding—is more similar to the variation found herein and was used.

    - 0: Posterior margin of frontoparietals not reaching epiotic eminences.
    - 1: Posterior margin of frontoparietals reaching or slightly covering epiotic eminences.

- **7. Nasal, overelapping with cartilago obliqua in dorsal view.** (Figure SI1; Figure SI2)
    - 0: Lateral portion of the nasal not covering cartilago obliqua.
    - 1: Lateral portion of the nasal covering the posterolateral portion of the cartilago obliqua.

- **8. Nasal, lateral margin in dorsal view.** (Figure SI1)
    - 0: Straight margin.
    - 1: Concave margin.

- **9. Exoccipitals, rorsal cartilaginous connection between contralateral elements.** (Additive; Figure SI1)

  Modified from the literature.

  Traditionally, the connection between exoccipitals has been scored simply as fused or not [see Grant et al. (2006) character 137 for example], never stating if this fusion is dorsal and/or ventral; possibly because in other groups, dorsal and ventral surfaces of exoccipitals varies in concert. Herein, exoccipitals are never fused although sometimes a portion of mineralized cartilage connects them. The amount of mineralization varies—when present—from slight (i.e., individual mineralization spots scattered through the area) to heavy (i.e., area is completely mineralized). Obviously, the amount of mineralization could be continuum but to the moment, there was no evidence in the analyzed material (intermediary states). In addition, the dorsal and ventral variation seems independent and is thus coded in two different characters. As evidence, at least *Scarthyla* and *Scinax* of the *S. catharinae* clade, share the same state ventrally but present different states dorsally. For ventral variation, see character 50.

    - 0: Not mineralized.

- 1: Slightly mineralized.
- 2: Heavily mineralized.

- **10. Crista parotica, ossification.** (Additive; Figure SI1)

  Modified from the literature. Faivovich (2002) character 4; Clarke (1981) character 5 (part); Scott (2005) character 67; Wiens et al. (2005) character 23 [the last based on Duellman (1970)].

  Wiens et al. (2005) coded the presence/absence of a "Bony articulation between squamosal and crista parotica", but an articulation like this can be, as stated by Faivovich (2002), "influenced by both the level of expansion of the otic plate [of squamosal] and the level of ossification of the crista parotica". Therefore, splitting those characters by each structure seemed reasonable.

  Lynch (1971) defines the crista parotica as "more a region than a structure. It is the otoccipital (fused prootic and exoccipital) lateral to the epiotic eminences" while Trueb (1970) defines it as the connection between the squamosal and prootic. Within *Dendropsophus*, variation was found in a lateral projection that does not cover any other bone than the columella, i.e., a lateral expansion of the crista parotica, that lays dorsal to the tympanic ring (henceforth, the crista parotica expansion).

  There are several degrees of ossification of the crista parotica expansion for the anterior and posterior margins. It could seem logical to apply the same rationale of splitting the character in two (one for presence/absence and other for "shape") used throughout this matrix. However, there is no evidence that the posterior margin of the crista parotica ossifies independently from the anterior margin (i.e., when the posterior margin is ossified, the anterior always is). Therefore, it seemed better to leave it as one additive character than to face the risk of creating two characters with a dependency problem.

  - 0: Without ossified expansion.
  - 1: Anteriorly ossified only (rostrally).
  - 2: Ossified anteriorly (rostrally) and posteriorly (caudally).

- **11. Squamosal, otic plate.**

  Modified from the literature. Duellman (1970) character EE; Clarke (1981) character 5 (part); Fabrezi (2006) character 10 (part); Araújo-Vieira et al. (2019) character 28.

  There are several degrees of development of the otic ramus (e.g. Lynch, 1971), ranging from the absence of an otic plate (see *Dendropsophus elianeae* specimen CFBH 21149) to a large otic plate that covers almost all length of the crista parotica extension (see *Scinax fuscovarius* specimen CFBH 21334). In fact, Clarke (1981), found at least two more states of this characters for Ranids—although his character states deal at the same time with shapes of the otic plate of squamosal and crista parotica ossification. The latter state was considered a diagnostic character of *Scinax* (sensu Duellman and Wiens, 1992 diagnostic character 13).

  Given the present variation, it seems that these could be the two extremes of a continuum. Nevertheless, for the moment, since it was possible to accommodate observed variation into two logically distinct states, it seemed a better option to evoke the variation rather than not acknowledge its existence.

  - 0: Not laying over crista parotica expansion.
  - 1: Laying over crista parotica expansion until its midpoint caudally.

- **12. Columellae, orientation to medial body axis.** (Figure SI1)

  Modified from the literature.

  This character could be interpreted as a modification of Scott (2005) character 68 (the angle of crista parotica in relation to body medial axis). Herein, it was noticed that those two characters seemed dependent and columella orientation was always nearly the same as the crista parotica orientation, but easier to assess (e.g. in *Gabohylas pauloalvini* the crista parotica orientation was not clear, but the columellae are clearly orientated at 45 degrees). Interestingly, the angled crista parotica morphology (state 1) is quite similar to what is found in species of *Acris* and *Pseudacris* (see Chantell, 1968; Gaudin, 1974; Cocroft, 1994; Maglia et al., 2007) although the columella morphology is not the same.

  - 0: Perpendicular or slightly oriented forward (up to 30 degrees of a transverse axis).
  - 1: Strongly oriented forward (about 45 degrees).

- **13. Operculum, dorsal visibility.** (Figure SI1)

  Modified from the literature. Araújo-Vieira et al. (2019) character 49.

  It was not clear if in species where the operculum was not visible in dorsal view it was due to a posterior extension of the otoccipitals that covered the opercula or if they were rotated ventrally. Araújo-Vieira et al. (2019) coded the orientation of the *pars media plectri* that reflects the variation found herein.

  - 0: Operculum not visible in dorsal view.
  - 1: Operculum visible in dorsal view.

- **14. Premaxilla, shape of alary process.**

  Modified from the literature. See Trueb (1970), Lynch (1971); Kaplan (1994) character 1; da Silva (1998) character 27; Barg (2003) characters 7 and 8.

  - 0: Base and tip subequal.
  - 1: Base much broader than tip.

- **15. Premaxilla, angle of the alary process in relation to *pars dentalis*.** (Additive; Figure SI1)

  Modified from the literature. Duellman (1970) character T; Trueb (1970); Lynch (1971); Duellman and Wiens (1992) diagnostic character 5; Barg (2003); Scott (2005) character 79; Araújo-Vieira et al. (2019) character 19.

  Barg (2003) coded in her character 6, the variation on premaxilla *pars dentalis* orientation as acute or orthogonal. Herein, however, this variation was not seen albeit in some *Scinax* it seems that the whole premaxilla rotates. Nevertheless, variation on the alary process orientation was observed and state present in *Dendropsophus minutus* is clearly different from the other two. Thus, states of Lynch (1971) are more easily applied herein.

  - o 0: Directed anteriorly.
  - o 1: Directed perpendicularly.
  - o 2: Directed posteriorly.

- **16. Maxilla, *pars facialis*.** (Figure SI2)

  Modified from the literature. Clarke (1981) character 7 (part); Scott (2005) character 74; Araújo-Vieira et al. (2019) character 11 (part).

  Usually the only variation of the *pars facialis* of the maxilla found in literature was coding for presence or absence of this bone plate as found in Wiens et al. (2005) morphological character 5. Duellman (1970) character U and W are exceptions because they the relation of the *pars facialis* of the maxilla with the nasal bone.

  Scott (2005) character 74 dealt with variation on the presence/absence and shape of the *pars facialis* of the maxilla and coded the reduction of anterior and posterior margins, assessing geometric shapes to them—see also Clarke (1981) character 7. Therefore, the *pars facialis* with reduced anterior margins were triangular. However, states found herein are logically different from the ones she found. Since Scott's states were not related to any landmarks, they are clearly assessing shape variation as said above.

  In material examined for this work, the *pars facialis* of the maxilla was always present (no terminal could be related to Scott's state 2) and although margins varied in development (i.e., height) no contact with the nasal was found. However, some had shapes that were not easy to define and both margins (anterior and posterior) could be developed while the *pars facialis* of the maxilla still presented a triangular shape. Possibly, the best example is found in *Scarthyla goinorum* (specimen CFBH 24821). In this species, the *pars facialis* of the maxilla is clearly triangular albeit it is the posterior margin that is "reduced". It is possible to see in Jürgens (1971) figures that there is a connection between the *crista subnasalis* to *solum nasi* that can be used as a landmark for the vertical expansion of the anterior margin of the *pars facialis* of the maxilla. All posterior margins were considered to be with the same height because all of them presented approximately the same vertical extension, i.e., to the mid level of *planum terminale*.

  - o 0: Not covering *crista subnasalis* laterally to the level of the *solum nasi* insertion.
  - o 1: Covering *crista subnasalis* laterally to the level of the *solum nasi* insertion.

- **17. *Processus maxillaris* of the *planum terminale,* anterior development.** (Figure SI2)

  This process was considered developed when the anterior margin of the *planum terminale* convex orientation started dorsally to the crossing point with the maxilla. Reduced when the process was completely (or nearly) covered by the maxilla itself.

  - o 0: Reduced processus.
  - o 1: Developed processus.

- **18. Quadratojugal.** (Figure SI4)

  Taken from the literature. See Trueb (1970); Duellman (1970) character JJ (part); Heyer (1975) character 21 (part); Duellman and Trueb (1983) character B; Lobo (1995), character 3 (part); Scott (2005) character 75; Wiens et al. (2005) character 17; Grant et al. (2006) character 133; Fabrezi (2006) character 21; Araújo-Vieira et al. (2019) character 22 among many others.

  The quadratojugal is commonly absent or reduced in many frogs (Lynch, 1973; Trueb, 1973; Drewes, 1984; Scott, 2005), even in some highly ossified species like *Corythomantis greeningi* Boulenger, 1896 (see Trueb, 1970). Duellman (1970) used the variation on this bone as characteristics of various groups of the, then, paraphyletic *Hyla*. He recognized three states of variation for this bone: absent; reduced, i.e., not touching the maxilla, and present. Based on the coding logic used in this study, this variation was divided into more characters.

  On the other hand, Lobo (1995) divided this bone into two components (the maxillary process and the bone *per se*) and scored the variation of these two components in one same character. It is important to notice that absent and extremely reduced quadratojugals are hard to differentiate without developmental series. Due to this difficulty, it is assumed here that all specimens presented a quadratojugal and it could be reduced or developed. A quadratojugal was considered developed when its length was at least three times its height and reduced when that relation was of 2 to 1 at the most. *Sphaenorhynchus* and other groups [see Drewes (1984) character 3] have "floating" quadratojugals, i.e., although developed, it does not touch either maxilla, neither the squamosal. This contact variation is treated separately.

  - 0: Quadratojugal absent or extremely reduced.
  - 1: Quadratojugal present.

- **19. Quadratojugal, relationship with squamosal (in males).** (Figure SI4)

  Taken from the literature. Duellman (1970) character JJ (part); Lobo (1995) character 3 (part) ; Araújo-Vieira et al. (2019) character 23.

  - 0: Not in contact.
  - 1: In contact.

- **20. Quadratojugal, relationship with maxilla (in males).** (Figure SI4)

  Taken from the literature. Drewes (1984) character 3, Lobo (1995) character 3 (part); Scott (2005) character 75; Wiens et al. (2005) character 18; Araújo-Vieira et al. (2019) character 13.

  Drewes (1984) character 3 mixes shape and contact in his state 1 ("in contact with maxilla... but greatly enlarged dorsally...) thus, authorship is given partially.

  - 0: Not in contact.
  - 1: In contact.

- **21. Maxillary process of the nasal.**

  Modified from the literature. da Silva (1998) character 6; Araújo-Vieira et al. (2019) character 2 (part).

Only sharp-edged processes, with a clear outline break were considered.

  - 0: Nasal maxillary process absent.
  - 1: Nasal maxillary process present.

- **22. Frontoparietas,l orbital flange.** (Figure SI1)

  Modified from the literature. da Silva (1998) character 13.

  Based on Trueb's (1970) comments, da Silva (1998) only considered orbital flanges to be present in casque-headed frogs. However, there is a small flange in some species observed herein. Probably not as an extensive flange as in those frogs, however, still observable. Possibly, the flanges observed herein could be interpreted as an additional state of da Silva's (1998) character

  - 0: Flange absent.
  - 1: Flange present.

- **23. *Pars externa plectri,* shape.** (Figure SI4)

  Duellman and Wiens (1992) used this structure as a diagnostic character of *Scinax*. The orientation of the *pars externa plectri* seems also a synapomorphy of *Sphaenorhynchus* (see Duellman and Wiens, 1992 diagnostic character 9 that states that the *pars externa plectri* of *Sphaenorhynchus* enters the tympanic ring posteriorly rather than dorsally) and they should not be confused. However, given that there is much more variation here than what is discussed by Duellman and Wiens (1992), it was not possible to confidently determine states for the angle of insertion of the *pars externa plectri*.

  - 0: Club-like.
  - 1: Racket-like.

- **24. Vomer, anterior process.** (Figure SI3)

  Vomers may have four processes: the anterior process anteriorly; the prechoanal and postchoanal processes medially, limiting the medial margin of the choanas, and the dentigerous process posteriorly (da Silva, 1998). Vomerine anterior processes are usually present in anurans (e.g. Clarke, 1981 assessement on Ranids). Herein, its absence could a synapomorphy of *Sphaenorhynchus* to be confirmed in a denser sampling.

  - 0: Process absent.
  - 1: Process present.

- **25. Vomer, angle of vomers medial in relation to sagital axis.** (Figure SI3)

  Taken from the literature. da Silva (1998) character 33; Faivovich (2002) character 2; Barg (2003) character 15; Nuin and do Val (2005) character 37.

  In *Phyllodytes*, the anterior margin of the vomers could be considered parallel to the sagittal axis.

  - 0: Divergent about 30 degrees of the sagittal axis.
  - 1: Divergent about 45 degrees of the sagittal axis.

- **26. Vomer, structure of dentigerous process.** (Figure SI3)

Modified from the literature. See Duellman (1970) character LL; Drewes (1984) character 4, Barg (2003) character 13; da Silva (1998) character 32; Nuin and do Val (2005) character 25; Wiens et al. (2005) character 25; Araújo-Vieira et al. (2019) character 32.

da Silva (1998) scored variation on the presence and absence of teeth along with the general orientation of the dentigerous process. Nuin and do Val (2005) scored only presence and absence. Wiens et al. (2005) scored presence and absence, and direction/variation on a second character (their character 26).

Two states could be identified in the present dataset. One, with clear, well-developed teeth arranged in one transversal series (1) and other with scattered small teeth (0) distributed over the surface of the process. Some specimens presented edentate processes. However, some specimens presented scattered teeth on one process and the other edentate. Thus, it seems that when these dentigerous processes are edentate, teeth seemed to have been broken.

  - 0: With scattered, unaligned teeth.
  - 1: With clearly aligned teeth.

- **27. Vomer, relationship between dentigerous process and the main body.** (Figure SI3)

  Modified from the literature. Araújo-Vieira et al. (2019) character 33. Species of *Sphaenorhynchus* present unusual morphological relationships of the dentigerous and the remaining processes of the vomers. Although certainly state 1 represents two states, for the time being, we rather highlight the uniqueness of these morphologies and focus on *Dendropsophus* instead of having multiple states for *Sphaenorhynchus*.

  - 0: Dentigerous process is continuous to the main body of vomer.
  - 1: Dentigerous process is separated of the main body of vomer or connected by a medial constricted portion.

- **28. Maxillary teeth.** (Figure SI3)

  Modified from the literature. da Silva (1998), character 23; Barg (2003) character 9; Araújo-Vieira et al. (2019) character 14 (part).

  da Silva (1998) and Barg (2003) coded variation related to reaching degrees of maxillary teeth to the pterygoid fossa. Araújo-Vieira et al. (2019) coded the presence and absence of the maxillary and premaxillary teeth together what suggests that these teeth vary in concert.

  - 0: Maxillary teeth not reaching the end of maxilla.
  - 1: Maxillary teeth reaching the end of maxilla.

- **29. Mandibular odontoids.**

  Modified from the literature.

  These odontoids are the classical diagnostic character of the genus *Phyllodytes*. Literature describe it only as "mandibular odontoids (e.g. Duellman, 1970 character OO; Caramaschi et al., 1992; Peixoto et al., 2003; Caramaschi et al., 2004) without further comment. The only reference to the osteological origin of these structures is a personal communication of Dr. L.

Trueb in Fabrezi and Emerson (2003) that "...apparently, [these odointoids are] derived entirely from the Mentomeckelian". Fabrezi (2006) character 23 codes the presence/absence of "Fangs in lower jaw" what could be confused with the present character. However, her state 2 clearly codes for "a spur-like projection formed by dentary and mentomeckelian bones" where, as stated above, would be different from the odontoids of *Phyllodytes* with Mentomeckelian only origin.

Since herein their presence is an autapomorphy for *Phyllodytes*, it does not affect our results. However, we follow the classical terminology, remarking that we are not advocating any given homology hypothesis for these odontoids.

- 0: Odontoids absent.
- 1: Odontoids present.

- **30. Maxilla, length.** (Additive; Figure SI3)

  Modified from the literature. Duellman and Wiens (1992); Araújo-Vieira et al. (2019) character 10.

  - 0: Small; ending about 1/3 of orbit.
  - 1: Medium; reaching about 1/2 the orbit length, ending between posterior margin of sphenethmoid and pterygoid central point.
  - 2: Long; ending at about 2/3 of orbit length, at pterygoid central point level.

- **31. Palatines, medial margin shape.** (Figure SI3)

  Modified from the literature. Laurent (1973) character 9.

  Trueb (1970) recognized variation in the shape of casque-headed hylid frogs (some current species of Hylini and most Lophiohylini). The character states relate to massive structures, quite different from the ones found in *Dendropsophus* however.

  - 0: Lateral edge club-like; blunt.
  - 1: Lateral edge needle-like; pointed.

- **32. Palatines, lateral development.** (Additive)

  Taken from the literature. Duellman (1970) character Y (part); Laurent (1973) character 9; Lobo (1995) character 5; Barg (2003) character 17; Araújo-Vieira et al. (2019) character 40.

  Duellman (1970) character Y mixes character states of both lateral and medial margins of the palatines. We split this variation into two characters. Laurent (1973) character 9 and Lobo (1995) character 5 found state (Lobo, 1995 implicitly) that there were no intermediate states i.e., the palatines reach or not the maxilla. Lobo (1995) found a much more explicit variation (given by its figure 3). On the other hand, even though Laurent (1973) character 9 presents only two states, some pages later, while explaining the symbols used in his dendrogram, he acknowledges a variation similar to the one found herein.

  - 0: Reduced; palatines lateral edges are not covered by the maxilla.
  - 1: Lateral edges of the palatines covered by maxilla, nearly reaching maxilla.

- 2: Lateral edges of palatines in contact with maxilla.

- **33. Palatines, medial development.** (Additive)

  Taken from the literature. Duellman (1970) character Y (part); da Silva (1998) character 36; Nuin and do Val (2005) character 45.

  - 0: Not reaching choanae medial wall.
  - 1: Palatines reach the level of choanae medial wall.
  - 2: Palatines passes choanae medial wall but do not reach the level of vomerine dentigerous process.
  - 3: Palatines reach the level of vomer dentigerous process.

- **34. Sphenethmoid, anterior degree of ventral ossification.** (Additive)

  Modified from the literature. Cocroft (1994) character 5; Laurent (1973) character 4 (part); da Silva (1998) character 46; Araújo-Vieira et al. (2019) character 9.

  - 0: Anterior ossification not reaching the palatines.
  - 1: Passing the palatines but not passing the level of the planum antorbitale.
  - 2: Extending to midlevel of the choanae.
  - 3: Including entire septum nasi.

- **35. Sphenethmoid, posterior degree of ventral ossification.** (Figure SI3)

  Modified from the literature. Liem (1970) character 21 (part); da Silva (1998) character 48 (part).

  - 0: Not reaching orbit midpoint.
  - 1: Reaching orbit midpoint.

- **36. Sphenethmoid, lateral degree of ossification.** (Additive)

  Modified from the literature. da Silva (1998) character 47. It is possible that the state 0 encompasses more states. The condition of *Sphaenorhynchus prasinus* (CFBH 22639) seems slightly different from the one present in *Dendropsophus* specimens.

  - 0: Planum antorbitale entirely cartilaginous.
  - 1: Ossification of the planum antorbitale extending to the level of, but not including the anterior process of the postnasal wall.
  - 2: Ossification extending to the level of anterior process of postnasal wall.

- **37. Sphenethmoid, degree of ossification of lateral margins.** (Additive; Figure SI3)

  Modified from the literature. da Silva (1998) character 48 (part).

  da Silva (1998) found four states for the degree of ossification of the sphenethmoid posteriorly.

  - 0: Not reaching ocular fenestra.
  - 1: Reaching anterior (cranial) wall of ocular fenestra, but only ventrally.

  - 2: Reaching anterior (cranial) wall of ocular fenestra both ventrally and dorsally (in lateral view, the left posterior wall of sphenethmoid has a "C"-shape.

- **38. Pterygoid, relationship between anterior ramus and maxilla.** (Figure SI3)

  Modified from the literature. da Silva (1998) character 34; Fabrezi (2006) character 17.

  Lynch (1971) provided a large review of the variation of this character within his "Leptodactyloids".

  - 0: Not reaching.
  - 1: Reaching.

- **39. Pterygoid, nature of contact between anterior ramus and maxilla.** (Figure SI3)

  Trueb (1970) recorded variation in the shape and relative rami size in casque-headed hylid frogs and possibly the present character is similar to Duellman (1970) character HH. However, both contributions described the variation on the position of the articulation of the anterior ramus os the pterygoid with "maxillary" in terms of "Anterior" and "Posterior" without a reference landmark.

  - 0: Reduced; >40% of anterior ramus length or less.
  - 1: Extensive; <50% anterior ramus length.

- **40. Pterygoid, medial flange.** (Figure SI3)

  - 0: Flange absent.
  - 1: Flange present.

- **41. Pterygoyd, length of the medial ramus.** (Additive; Figure SI3)

  Modified from the literature. See Trueb (1970);Duellman (1970) character GG; da Silva (1998) character 31; Barg (2003) character 12; Scott (2005) character 57 (part).

  Several authors noticed different levels of variation for this character (e.g. Duellman and Wiens, 1992). All papers that proposed a cladistic approach for the morphological variation of this ramus found much more variation than the variation of the ramus found herein. Previous characters states sum the variation found herein as described in the state 0 of da Silva (1998) and—simultaneously—in Scott (2005) state 1. Herein, states are defined in relation to the amount of the anterior wall of the basal process covered by ossification of the medial ramus.

  - 0: Reduced, reaching the basal process, not concealing it.
  - 1: Concealing about half of the basal process length.
  - 2: Covering all (or almost) of the basal process.

- **42. Pterygoid, margin of the basal process covered by the medial ramus.** (Figure SI3)

  - 0: Anterior margin.
  - 1: Ventral margin.

- **43. Pterygoid, length of the posterior ramus.** (Additive; Figure SI3)

  Modified from the literature. Different states of this character were diagnostic characters of *Scarthyla* (Duellman and De Sá, 1988) and *Scinax* (Duellman and Wiens, 1992).

  - 0: Extremely short; length and width are similar.
  - 1: Evident but not reaching squamosal ventral ramus; length is more than 3x the width.
  - 2: Reaching squamosal ventral ramus.

- **44. Ocular foramen, size.** (Additive; Figure SI3)

  Scored in a posterior–anterior direction. There are possibly more states within state 1. Although there is some variation in the size of the parasphenoid cultrifom process within Anura (see Lynch, 1971), the processes analyzed here are of similar length (all reaching the orbitonasal foramen; see the "Potentially informative variation not included in this study section"). We recognize that this scoring based on relations between two independent structures is problematic but the similar length of the cultrifom process in our dataset ameliorates the problem.

  - 0: Reaching anteriorly about halfway of parasphenoid cultriform process.
  - 1: Reaching anteriorly about three-fourths through parasphenoid cultriform process.
  - 2: Reaching or passing the anterior tip of parasphenoid cultriform process.

- **45. Oculomotor foramen, ossification of medial margin.** (Figure SI3)

  - 0: Not ossified.
  - 1: Ossified.

- **46. Relationship between prootic and exooccipital ventrally.**

  Modified from the literature. Lynch (1971). Lynch (1971) makes comments on variation among his "Leptodactylidae". Since different specimens of *Sphaenorhynchus lacteus* presented different states, it is a possibility that there is ontogenetic change in this character.

  - 0: Not fused.
  - 1: Fused.

- **47. Parasphenoid, cultriform process margins.** (Figure SI3)

  Modified from the literature. Clarke (1981) character 12; da Silva (1998) character 42; Scott (2005) character 55; Araújo-Vieira et al. (2019) character 42.

  Clarke (1981) character 12 and Scott's (2005) character 55 score more acute differences then the ones found herein. Both their characters states 0—that have a similar definition—deal with a more slender cultriform process than the *Dendropsophus* assigned with this state.

  - 0: Subparallel margins.
  - 1: Convex margins.

- **48. Parasphenoid, posterior margin.** (Figure SI3)

Modified from the literature. da Silva (1998) character 44; Barg (2003) character 22.

  - 0: Convexly rounded.
  - 1: Presenting a posteromedial process shaped as a triangular tip.

- **49. Parasphenoid, lateral extension of alae.** (Figure SI3)

  Modified from the literature. Trueb (1970); Lynch (1971); Clarke (1981) character 14; Barg (2003) character 21 and 24; Scott (2005) character 60; Araújo-Vieira et al. (2019) character 44.

  Possibly there are more states within state 1. Barg (2003) coded the relative length of the parasphenoid alae in her character 21 and their shape in her character 24. However, in the present study, both characters varied together and therefore, considered non-independent.

  - 0: Reaching the otic capsules.
  - 1: Extending onto ventral face of the otic capsule.

- **50. Exoccipitals, ventral cartilaginous contact.** (Figure SI3)

  Taken from the literature. Faivovich (2002) character 1.

  Only the ventral portions of these bones are considered. See comments in character 9 for the dorsal views and for explanation on independence between both characters.

  - 0: Slightly mineralized.
  - 1: Heavily mineralized.

NASAL CARTILAGES

- **51. Cartilaginous plate.** (Figure SI2)

  This cartilaginous plate is the caudal continuation of the *planum terminale* (Jurgens, 1971).

  - 0: Regular.
  - 1: Expanded.

- **52. *Crista subnasalis*, ventral edge.**

  - 0: Single, straight.
  - 1: Bicapitate.

- **53. Confluence between *processus lingularis* and *lamina orbitonasalis*.**

  Some species of *Sphaenorhynchus* present a confluence between the processus lingularis and the lamina orbitonasalis. Jurgens (1971) found a similar morphology for other species (e.g. *Spea intermontana*—as *Scaphiopus intermontanus*). While in the present dataset, the confluent condition has been found solely for an internal clade of *Sphaenorhynchus*, it surely deserves consideration in future studies.

  - 0: *Processus lingularis* and *lamina orbitonasalis* not confluent.

  - 1: *Processus lingularis* and *lamina orbitonasalis* confluent.

- **54. *Processus prenasalis medius*.** (Figure SI1)

  Taken from the literature. da Silva (1998) character 45; Faivovich (2002) character 7.

  The observed variation exceeded the definition of da Silva (1998) and thus, our state 1 is slightly different. *Processus prenasalis medius* has a large variation on length and some in shape. While some are cylindrical rods (*Dendropsophus sanborni*), others are flattened. However, it was not possible to produce clear definitions for the differences observed.

  - 0: *Processus prenasalis medius* absent.
  - 1: *Processus prenasalis medius* present.

- **55. *Cartilago obliqua*, lateral margin curvature in relation to medial axis.** (Figure SI1)

  - 0: *Cartilago obliqua* concave.
  - 1: *Cartilago obliqua* convex or almost straight.

- **56. *Crista supraorbitalis*.** (Figure SI1)

  Modified from the literature. da Silva (1998) character 49; Wiens et al. (2005) character 33; Araújo-Vieira et al. (2019) character 10 (part).

  da Silva (1998) scored the *crista supraorbitalis* presence and shape variation together while Wiens et al. (2005) discussed the presence or absence of an "Orbital cartilage" in their character 33. Herein, presence and shape variation were scored separately.

  Species scored as not presenting a *crista supraorbitalis* often present a cartilage piece that "swells" into the orbit at the same location where the *crista supraorbitalis* has its origin. This small isolated body of cartilage is surrounded by bone. It is not clear if it is homologous to the *crista supraorbitalis* in other species, which is an extension of the *planum antorbitale*. The relative size of the *crista* to the orbit also seems to vary (compare *Dendropsophus columbianus* [small] with *D. acreanus* [large]). Nevertheless, it was not possible to define clearly distinct states or to find a landmark that would make comparisons objective.

  - 0: A small piece of cartilage that does not invade the orbita transversally.
  - 1: A cartilaginous structure that invades the orbita transversally.

- **57. Crista supraorbitalis, shape.**

  - 0: Without distal expansion; straight.
  - 1: Anterolaterally expanded; angled.

TYMPANIC RING AND CRISTA PAROTICA

- **58. Retrolateral process of *crista parotica*.** (Figure SI1)

Modified from the literature. da Silva (1998) character 51; Scott (2005) character 66; Wiens et al. (2005) character 35; Araújo-Vieira et al. (2019) character 45.

Only the presence of the retrolateral process was scored here since all processes observed had the same general shape despite variation in size. Kaplan (1994) found its length to vary intraspecifically in various populations of *Dendropsophus minutus*.

- 0: Retrolateral process absent.
- 1: Retrolateral process present.

- **59. Relationship between the *annulus tympanicus* and *crista parotica*.** (Figure SI1)

Modified from the literature. da Silva (1997) character 2; da Silva (1998) character 52; Wiens et al. (2005) characters 35 and 36.

Fewer states are used here than those used by da Silva (1998). According to him, the fusion of the *annulus tympanicus* with the *crista parotica* presumably is a synapomorphy of *Pseudis* + *Lysapsus*. *Phyllodytes* also presents this character state and it could be a synapomorphy for this genus as well. Wiens et al. (2005) characters 35 and 36 dealt with variation in the *annulus tympanicus* and can be understood as a different interpretation of da Silva's (1998) character 52 definition.

- 0: *Annulus tympanicus* free from *crista parotica*.
- 1: *Anterior portion of annulus* fused to *crista parotica*.

HYOID

- **60. Anterior process of hyoid.** (Figure SI5)

Modified from the literature. Liem (1970) character 13; Heyer (1975) character 30; Drewes (1984) character 11, da Silva (1998) character 60; Faivovich (2002) character 8; Barg (2003) character 38; Nuin and do Val (2005) character 29; Scott (2005) character 83; Wiens et al. (2005) character 42; Grant et al. (2006) character 117. All based on Lynch (1971) and/or Myers (1986) contributions.

Trewavas (1933) already noted presences and absences of anterior processes of the hyal. Duellman and Wiens (1992) used this character in their diagnosis of *Scinax*, but it is present in other groups (as in *Sphaenorhynchus*).

- 0: Anterior process of hyoid absent.
- 1: Anterior process of hyoid present.

- **61. Anterior process of hyoid, shape.** (Figure SI5)

Modified from the literature. Liem (1970) character 14.

Liem (1970) found more variation and remarks the presence of additional processes and plates. *Scarthyla* (and other genera as *Xenohyla*) seem to have a real cartilaginous plate. This plate is depicted in Duellman and de Sá (1988) although there is no mention to it in subsequent papers dealing with Hylid phylogeny.

  - 0: Process transverse to hyal "axis"; subcilindric.
  - 1: Plate along the hyal "axis"; laminar.

- **62. Hyoid anterolateral—or alary—process.** (Figure SI5)

  Taken from the literature. Liem (1970) character 11; Heyer (1975) character 31 (part); da Silva (1998) character 61; Nuin and do Val (2005) character 30; Wiens et al. (2005) character 43 [based on Lynch (1971)]; Fabrezi (2006) character 27 (part); Araújo-Vieira et al. (2019) character 64.

  Duellman and Wiens (1992) used this character in their diagnosis of *Scinax*, but it is present in other groups.

  - 0: Anterolateral process absent.
  - 1: Anterolateral process present.

- **63. Hyoid anterolateral—or alary—process, shape.** (Figure SI5)

  Modified from the literature. Liem (1970) character 11 (part); Heyer (1975) character 31 (part); Scott (2005) character 84; Fabrezi (2006) character 27 (part); Araújo-Vieira et al. (2019) character 65 (part). For character state images, see Liem (1970) Figures 16—18 (present state 1) versus 19 (present state 0).

  - 0: Strongly reduced to a laminar blade parallel to hyal axis.
  - 1: Anterolateral process developed as a transversal rod.

- **64. Anterolateral process of hyoid, shape of the tip.** (Additive; Figure SI5)

  Modified from the literature. Liem (1970) character 12; Scott (2005) character 85 and 86; Wiens et al. (2005) character 44; Araújo-Vieira et al. (2019) character 66 (part).

  Scott (2005) found much more variation than the variation observed in our sample. Nevertheless, her characters (85 and 86) deal with different aspects of shape variation of the anterolateral process of the hyoid. Scott (2005) character 85 [as do Wiens et al. (2005) character 44] deals with the width of the stalk base and 86, tip width. In our sample, only variation in the tip was found. We define a tip as slightly expanded when stalk length is similar to tip width.

  Liem (1970) character 12 divided the alary process in distal end and stalk but the character states mix variation of both structures. Duellman and Wiens (1992) used this character in their diagnosis of *Scinax*, but it is present in other groups as well.

  - 0: Acute.
  - 1: Subrectangular.
  - 2: Racket-like or expanded.

- **65. Hyal basal portion.** (Figure SI5)

  - 0: Thin.
  - 1: Broad.

- **66. Hyoid posterolateral process, orientation.** (Figure SI5)

Although present in all species analyzed herein, in some groups it can be absent (Drewes, 1984; Scott, 2005; Fabrezi, 2006). A difference in orientation was found and is coded in this character.

  - 0: Directed 45 degrees posteriorly in relation to hyoid plate.
  - 1: Directed laterally (90 degrees in relation to hyoid plate).
  - 2: Completely directed posteriorly (pointing caudally).

- **67. Hyoid posterolateral process, origin.** (Figure SI5)

  The variation of the origin of the posterolateral process of the hyoid could possibly be divided into more character states (splitting the present state 0). However, for the moment, given the lack of a proper character state diagnosis, we opted to score these morphologies in a single character state.

  - 0: At, or just above, thyrohyal level.
  - 1: Separated by more than one posterolateral process width from the thyrohyal.

- **68. Hyoid plate, medial mineralization.** (Figure SI5)

  Modified from the literature. da Silva (1998) character 64; Fabrezi (2006) character 33. Duellman and Wiens (1992) used this character in their diagnosis of *Scinax*, but it is present in other groups as well.

  - 0: Mineralization absent.
  - 1: Mineralization present.

- **69. Hyoid plate, medial mineralization shape.** (Additive; Figure SI5)

  This character was scored as additive because state 0 is included in state 1 and both in state 2. When state 2 happens, the mineralization area overlay the areas relative to the other character.

  - 0: Without a discernible regular shape, and only between the tyrohyals not reaching the anterior margin of the hyoid plate.
  - 1: Nearly triangular, extending through the hyoid plate but covering only the anterior medial portion in a cranio-caudal direction.
  - 2: Nearly retangular, covering all (or almost all) hyoid plate between the posterolateral processes.

- **70. Hyoid plate, area.** (Additive; Figure SI5)

  Modified from the literature. da Silva (1998) character 65; Scott (2005) character 88; Wiens et al. (2005) character 45; Araújo-Vieira et al. (2019) character 68).

  da Silva (1998, Scott (2005), and Araújo-Vieira et al. (2019) treated this variation in terms hyoglossal sinus depth possibly following the terminology of Trewavas (1933). Roughly, the deepness of the sinus was measured according to its relation with the anterolateral or posterolateral processes. However, Wiens et al. (2005) used an approximation closer to the one used here that scores whether the hyoid plate was (0) wider than long or (1) longer than wide. Most of the variation found herein would fall under da Silva (1998) state 1 and Scott (2005) sate 0 (deep sinus). However, *Pseudis minuta* has an even deeper hyoglossal sinus that we consider to be different from the deep hyoglossal sinus of other taxa.

  - 0: Thin (total length is nearly the same of the retrolateral processes cranial portion).
  - 1: Medium (total length is approximately less than two times the tyrohyal cranial portion or less).
  - 2: Wide (total length is approximately more than two times the retrolateral processes cranial portion).

- **71. Thyrohyals, caudal portion.** (Figure SI5)

  Modified from the literature. Scott (2005) character 97.

  Scott's (2005) character 97 only mention unexpanded versus expanded caudal portions of the thyrohyals. Herein we provide a more objective character state description.

  - 0: Not expanded; with approximately the same width of the rest (with exception of the caudal cartilaginous portion of the thyrohyals).
  - 1: Expanded; wider, at least 1.5x, than the rest (approximately the width of the thyrohyals caudal cartilaginous portion).

- **72. Thyrohyals, shape of the posterior (caudal) cartilaginous portion.** (Additive; Figure SI5)

  Modified from the literature. da Silva (1998) character 63.

  - 0: An uneven rectangle, with nearly straight margins.
  - 1: With two unequal apexes, posterior margin curved.
  - 2: Fairly triangular (almost a right triangle).

- **73. Point of attachment of hyale to the skull.** (Figure SI3)

  Taken from the literature. da Silva (1998) character 67; Araújo-Vieira et al. (2019) character 71.

  - 0: Hyale attaching to the basal process.
  - 1: Hyale attaching to the prootic.

LARYNX

- **74. Arytenoids, medial ventral margins.** (Additive; Figure SI5)

  Modified from the literature. Trewavas (1933).

  - 0: Frenulum inconspicuous with medial margin convex.
  - 1: Evident frenulum, with medial margin concave.
  - 2: Evident frenulum, with medial margin with secondary constriction.

- **75. Arytenoids, medioventral fibrous masses.**

  Modified from the literature. Araújo-Vieira et al. (2019) character 79.

In *Scinax berthae*, and in the drawings of vocal cartilages of *Scinax littoralis* in Faivovich (2002) fig 6b, there is a clear ventral process emerging from the midpoint of the arytenoid lateral margins.

- 0: Not extending ventrally of arytenoid margin.
- 1: Extending ventrally of arytenoid margin.

- **76. Arytenoids, inner longitudinal ridges.** (Figure SI5)

  These ridges are not cited in any previous literature dealing with anuran larynx morphology. Trewavas (1933) performed the most comprehensive review so far and also does not describe these ridges in her influential contribution. These ridges are located in the internal surfaces of the medial margins of the arytenoids. There are usually two, separate, esophageal and pharyngeal ridges that extend in direction to the medial point of the respective arytenoid and are connected to the pharyngeal external margins of the arytenoids. This point of connection between the internal and external margins is the same point of insertion of the fibrous vocal pulvinaria. There is no evidence that esophageal and pharyngeal ridges vary independently. Shapes of the ridges vary, but we chose to have a conservative approach for the moment due to the lack of functional studies of these structures and to the difficulty of defining clear character states from the variation found.

  - 0: Absent.
  - 1: Present.

- **77. Vocal chords, ventromedial ligaments.** (Additive)

  Modified from the literature. Araújo-Vieira et al. (2019) character 77.

  Martin (1972) states that in hylids, vocal chords attach both on cricoid and arytenoid posterior portion. However, none of the specimens examined here presented this character state. Herein, vocal chords always attached to the arytenoid only.

  Specimens of the *Scinax* of the *S. ruber* clade were examined and all presented a chondrified structures in the distal portions of the vocal chords (in each vocal chord there is a pair; one at each distal portion). While in other taxa the vocal chords attached to the arytenoid by a fibrous ligament (the vocal pulvinaria), in the species of the *Scinax*, between the fibrous ligament and the fibrous vocal chords, there is a rod of cartilage before this fibrous ligament.

  Histological sections are still lacking, thus, it is not clear if these rods are chondrified portions of the vocal chords or something else. Trewavas (1933) in her description of "*Hyla rubra*" from "Therezopolis, Brazil" (Teresópolis municipality, Rio de Janeiro state Brazil. Possibly a specimen of *Scinax hayii*) refer to "a short rod of cartilage supporting each end of the vocal chord" (Trewavas, 1933, pg. 439). Lambiris (1994) found "cartilaginous support rods" in the larynxes of the South African bufonids he examined. However, material of these species was not available and it is not clear what his "supporting rods" are.

  - 0: Fibrous.
  - 1: Distal portions slightly chondrified.
  - 2: Distal portions deeply chondrified.

- **78. Arytenoids, internal buttresses.** (Figure SI5)

  Modified from the literature. Kaplan (1999) character 1; Faivovich (2002) character 17; Araújo-Vieira et al. (2019) character 75. Based on Martin (1972) terminology.

  Kaplan (1999) character 1 scored for a small medial depression at the internal surface of the arytenoids delimited by two ridges that flank this depression and proposed this small depression as a synapomorphy of the *Dendropsophus garagoensis* species group. Comparing the arytenoids of *D. virolinensis* with the arytenoids of other *Dendropsophus* species it became clear that the depression is only the area delimited by the two internal buttresses of the arytenoids. Since there was a variation of the number of buttresses, we score that rather than the less clearly defined depression.

  - 0: Buttresses absent.
  - 1: Buttresses present.

- **79. Arytenoids, central buttresses.**

  Modified from the literature. Araújo-Vieira et al. (2019) character 77.

  When present, it is possible to observe one to three internal arytenoid buttresses in different species. These can be subdivided as the central buttress and the paramedial buttresses. The central buttress divides the internal surface of the arytenoid in half (albeit not touching both margins) and the paramedial buttresses, in three sections.

  - 0: Absent.
  - 1: Present.

- **80. Arytenoids, paramedial buttresses.**

  - 0: Absent.
  - 1: Present.

- **81. Arytenoids, dorsomedial prominence.**

  Modified from the literature. Faivovich (2002) character 16.

  Faivovich (2002) states that there is more variation than what the current character states represent. Although herein four states are represented, Faivovich's (2002) opinion that this character may be better described as a continuum is corroborated. Nevertheless, register these differences can help future researchers solve the case. Faivovich's (2002) character states were reordered to follow the general organization of the other characters and to demonstrate (although not used) a possible additive series. Possibly, the different states relate to different morphologies of the *m. dilator laryngis* that inserts therein (see Martin, 1972).

  - 0: Poorly developed; major axis parallel to arytenoids.
  - 1: Well developed; right triangle shaped, with major axis parallel to arytenoids.
  - 2: Well developed; isosceles triangle shaped, with anterior margin slightly convex.

    - 3: Well developed; right triangle shaped, with major axis perpendicular to arytenoids.

- **82. Cricoid, bronchial process, point of origin.** (Additive)
    - 0: Anterior to the cricoid ring midpoint.
    - 1: At or posterior to cricoid ring midpoint.

- **83. Cricoid, esophageal process in males.** (Additive; Figure SI5)

  Modified from the literature. Faivovich (2002) character 11; Araújo-Vieira et al. (2019) character 72..

    - 0: Process absent.
    - 1: Process present; oriented esophageally (perpendicular to the medio-sagittal plane of the cricoid ring).
    - 2: Process present; oriented caudally (following the main axis of cricoid ring).

- **84. Cricoid, esophageal margin in esophageal view.** (Figure SI5)

  Modified from the literature. Kaplan (1999) character 2.

  Kaplan (1999) suggested the presence of two close, triangular lateral spaces between the cricoid and arytenoids at the posterior part of the larynx as a synapomorphy supporting *Dendropsophus bogerti*, *D. carnifex*, and *D. columbianus* as a group. This preposition excluded *D. praestans* from the *D. columbianus* group in opposition to the proposal of Duellman and Trueb (1983) which included those four species in the *D. columbianus* group (without explicit proposals for synapomorphies). These "spaces" are found if the posterior margin of the cricoid ring is "straight", i.e., if it is not a circular ring and the whole cricoid ring is "shorter" than the arytenoids. Note that these two conditions are independent; the esophageal margin of the cricoid ring variation is scored in the following character. Since the appearance of these spaces is influenced by more than one trait, it seemed more reasonable to code this variation in two characters (See *D. molitor* specimen ICN 13631 that has these "spaces" perfectly clear).

    - 0: Curved margin.
    - 1: Straight margin.

- **85. Arytenoids, posterior margins in lateral view.**

  For *Sphaenorhynchus prasinus*, *Dendropsophus acreanus* and *D. soaresi* it is scored that the posterior borders of arytenoids do not pass the cricoid ring. There is some difference in morphology between *S. prasinus* and these other species, however it was not possible to describe exactly what is different. Thus, a conservative approach was taken and the same character state was assigned to these terminals.

    - 0: Not or slightly passing cricoid ring.
    - 1: Clearly passing cricoid ring.

ADULT APPENDICULAR SKELETON

- **86. Xiphisternum, distalmost shape.**

  Modified from the literature. Heyer (1975) character 32 (part); Drewes (1984) character 17; da Silva (1998) character 80; Nuin and do Val (2005) character 31; 48 and 49; Scott (2005) character 32; Fabrezi (2006) character 47 (part).

  Nuin and do Val (2005) character 31 deals with variation of the "posterior sternum". The variation they found is very similar to the one found herein. However, Nuin and do Val (2005) character 31 sorts the variation scored herein in additional different character states whereas Heyer (1975) found much more variation of this character in leptodactylids than the staes we coded herein.

  - 0: Triangular; unnotched, round.
  - 1: Notched; bilobated.

- **87. Coracoid, crest.**

  Taken from the literature. da Silva (1998) character 79; Faivovich (2002) character 19.

  - 0: Crest absent.
  - 1: Crest present.

- **88. Suprascapula, Anterior process.**

  Taken from the literature. da Silva (1998) character 75; Faivovich (2002) character 20; Araújo-Vieira et al. (2019) character 85.

  - 0: Process absent.
  - 1: Process present.

- **89. Distal prepolical elements, number.**

  Modified from the literature. Lobo (1995) character 11; da Silva (1998) character 69; Fabrezi (2006) character 66 (part); Araújo-Vieira et al. (2019) character 97.

  - 0: One.
  - 1: Two.
  - 2: Three.

- **90. Intercalary elements between ultimate and penultimate phalanges, mineralization.** (Additive)

  Modified from the literature. See Duellman and de Sá (1988); da Silva (1998) character 73; Faivovich (2002) character 22; Duellman and Wiens (1992) character 22; Araújo-Vieira et al. (2019) character 101.

  Information on intercalary element (IC) has been long used to infer evolutionary relationships among anuran lineages (e.g. Duellman and De Sá, 1988; Paukstis and Brown, 1991). In fact, all states of the present character where already retrieved by Duellman and de Sá (1988). The IC's ossification may vary ontogenetically because in species where more than one individual was cleared-and-stained, the degree of ossification was individually variable.

  Drewes (1984) coded this variation in Hyperoliids (character 24) and it was reviewed by Vences et al. (2003). The latter found a result similar from hylines, i.e., high levels of individual variation between exemplars, without, however hypothesizing the developmental causes of it. Duellman and Wiens (1992) discussed mineralization of IC without distinction between fingers and toes what is followed herein. Only the finger IC's were coded, they were congruent with states found in toe ICs.

  - 0: Not mineralized.
  - 1: Partially mineralized.
  - 2: Completely mineralized.

- **91. Intercalary elements between ultimate and penultimate phalanges, shape.**

  Taken from the literature. Lynch (1973) character 16; Cocroft (1994) character 40; da Silva (1998) character 73 and 74; Haas (2003) character 151; Araújo-Vieira et al. (2019) character 100.

  Historically, the presence of an IC has been understood as an indicative of an arboreal life in Anura [see comments in Paukstis and Brown (1991 pg. 1291) and Haas (2003 pg. 48)]. The IC presence has been reported in many species of Neobatrachia [more specifically marsupial frogs, hylids, centrolenids, hyperollids, arthroleptids, rhacophorids, mantellids and the microhylid *Phrynomantis bifasciatus* Smith, 1847 (e.g. Drewes, 1984; Haas, 2003; Manzano et al., 2007; Guayasamin et al., 2008; Guayasamin et al., 2009 and references therein).

  Paukstis and Brown (1991) and Manzano et al. (2007) divided the intercalary element morphology into a series of putative independent characters—even though Paukstis and Brown (1991) have not made a cladistic analysis. While Paukstis and Brown (1991) used this information directly to infer relationships without a qualitative context, Manzano et al. (2007) mapped into a consensus tree based on several molecular studies, cross-referencing its presence with arboreality. Manzano et al. (2007) analysis revealed that while IC have appeared 5–7 times with 2–4 losses. Arboreality (as defined by them) appeared 3–6 times and has been lost 1–2 times. Therefore, it does not seem obvious that the presence of an intercalary element is related to arboreality (as understood by them).

  Classically, the presence of long, linearly aligned, intercalary elements has been proposed as diagnostic character for *Lysapsus* and *Pseudis* (Savage and Carvalho, 1953; Paukstis and Brown, 1991; Garda and Cannatella, 2007). As other authors before [see a review in Manzano et al. (2007)], da Silva (1998) coded only the presence and absence of the intercalary element (IC) and the ossification of the fingers intercalary element in two characters (73 and 74). Herein, the coding of the shape of IC's comprises both fingers and toes because the characters would be redundant and dependent; finger IC shape varies taxonomically in concert with toe IC shape.

  - 0: Short; cuboidal, transverse to other phalanges.
  - 1: Elongated; linearly aligned with other phalanges.

- **92. Presacral Vertebra VI, posterior margin of neural arch.**

  In fact, both the posterior margin of the neural arch of PV VI and the anterior margin of the neural arch of PV VII share the same morphology. The curved structure of both consecutive neural arches produces, in dorsal view, a wide rounded space between them. If the margins are straight, the space is narrow rather than round and more closed in comparison with the case of curved margins.

- 0: Straight; neural arch wider than long (>1.2x).
- 1: Curved; neural arch as wide as long (<1.1x).

- **93. Sacral diapophysis, shape.**

  Taken from the literature. Heyer (1975) character 34; Duellman and Wiens (1992) character 19; Cocroft (1994) character 8; Faivovich (2002) character 21; Fabrezi (2006) character 42; Araújo-Vieira et al. (2019) character 95.

  The same coding of Faivovich (2002) was used here.

  - 0: Expanded diapophysis (index maximum/minimum length of diapophysis> 6).
  - 1: Rounded diapophysis (index maximum/minimum length of diapophysis < 3.5).

- **94. Transverse process of Presacral Vertebra IV.**

  Modified from the literature. da Silva (1998) character 95; Araújo-Vieira et al. (2019) character 92.

  An additional state (lateral process of Presacral Vertebra IV strongly angled posteriorly) was found in some species.

  - 0: Transverse process of PV IV transverse or slightly angled posteriorly ($<15^{o}$).
  - 1: Transverse process of PV IV strongly angled posteriorly ($>30^{o}$).
  - 2: Transverse process of PV IV L-shaped.

- **95. Sacral sesamoid.**

  Taken from the literature. da Silva (1998) character 85.

  - 0: Sesamoid absent.
  - 1: Sesamoid present.

- **96. Sacral sesamoid tissue.**

  - 0: Cartilaginous.
  - 1: Ossified.

- **97. Metatarsal I sesamoid presence.**

  Modified from the literature. Fabrezi (2006) character 63.

  The metacarpal and metatarsal sesamoids are called "glide sesamoids" and can be found ventral, medial, lateral or dorsal to the hand and feet bones—carpus, metacarpus, phalangi, etc. (see Ponssa et al., 2010). Herein, the selected taxa presented only glide sesamoids dorsal to the metacarpi. Ponssa et al. (2010 Table 1) shows that glide sesamoids would be evenly—meaning absently—distributed among Hylids. Ponssa et al. (2010) analyzed one *Dendropsophus* species (*D. nanus*) based on data present in Fabrezi (2006). However, specimens of *D.*

nanus analyzed herein presented glide sesamoids. Also, our own data shows that their presence in association to different bones is independent [Ponssa et al. (2010) treat same surface glide sesamoids as dependent].

  - 0: Sesamoid absent.
  - 1: Sesamoid present.

- **98. Metatarsal II sesamoid.**
  - 0: Sesamoid absent.
  - 1: Sesamoid present.
- **99. Metatarsal II sesamoid shape.**
  - 0: As a tiny crest.
  - 1: Spherical.
- **100. Metatarsal III sesamoid .**

  Taken from the literature. da Silva (1998) character 82.
  - 0: Sesamoid absent.
  - 1: Sesamoid present.
- **101. Metatarsal III sesamoid shape.**
  - 0: Cartilaginous (or slightly ossified) crest.
  - 1: Spherical.

MYOLOGY

102. *M. pectoralis portio axillary* presence.

Taken from the literature. da Silva (1998) character 105.

da Silva (1998) proposed that the presence of this muscle could be related to the origin of the axillary fold as defined by Duellman (1970). Nevertheless, Duellman (1970) only reported a pectoral fold and an axillary membrane. Dissections for the present study showed that the pectoral fold's presence could be related to variations of the pectoral lymph septum and not to the presence of *m. pectoralis portio abdominalis*. Dissections also showed that in species with a *m. pectoralis portio axillary*, this muscle pierces the pectoral lymph septum that is fixed in the middle of the axillary membrane (i.e., the point of the axillary membrane that is equally distant from the axillary membranes insertion points).

Historically, the presence of the axillary membrane was usually related to the presence of the *m. pectoralis portio axillary* (see comments on character 121). Differences in how extensive the axillary membrane is, obviously exists. Through literature, some species of *Dendropsophus* such as *D. carnifex* (Duellman, 1969), *D. allenorum* and *D. koechlini* (Duellman and Trueb, 1989) were described as not possessing an axillary membrane. Specimens of *D. columbianus* and *D. koechlini* were available to us and they presented an *m. pectoralis portio axillary* piercing the pectoral lymphatic septum, albeit not an axillary membrane (see character 121).

Although there seems to be a real difference between extents of the axillary membrane in different taxa. In some cases, differences in the fixation angle between the arm and trunk substantially affect the observer's capacity to determinate the extent of the axillary portion of the pectoral septum because it could bend or twist. In addition, lymphatic septa are elastic structures and fixation artifacts can drastically modify such structures thus affecting the distance to which the axillary membrane can reach from the axilla. The points of detachment of the *m. pectoralis portio axillary* from the *m. pectoralis portio abdominalis* and from the arm also vary. There seems to be some influence of fixation position and procedure in these traits as well.

- 0: Absent.
- 1: Present.

- **103.** ***M. pectoralis*** **origin.**

Taken from the literature. da Silva (1998) character 103; Faivovich (2002) character 38; Araújo-Vieira et al. (2019) character 189.

The origin of the fibers on the pelvis with a inconspicuous tendon is a synapomorphy of Scinaxini.

- 0: Fibers originate at midbody.
- 1: Fibers originate on pelvis; tendon inconspicuous.

- **104. Pectoral lymph septum.**

Modified from the literature. Tyler (1971a; 1971b).

This character was scored for females and in dissected individuals when possible. Tyler (1971b) noted a large vocal sac in *Dendropsophus marmoratus* and called the attention that the pectoral septum is modified so that the inflated vocal sac can intrude into sub-humeral spaces. This condition also seems to occur in some Hyperoliids (Drewes, 1984). Tyler (1971b), however, did not describe the pectoral septum condition of *D. marmoratus* in detail. Based on data gathered herein, in all *Dendropsophus* and *Sphaenorhynchus* specimens examined, the pectoral lymph septum runs over the pectoral girdle and "inserts" in the axillary membrane.

Bokermann (1964) used "a large vocal sac" as diagnostic character of his "*Hyla marmorata* group". However, all *Dendropsophus* and *Sphaenorhynchus* species have proportionally large vocal sacs. Tyler (1971b) did not mention this "modified" condition of the pectoral lymph septum for *S. lacteus*, however, specimens of *Sphaenorhynchus* analyzed herein presented this same condition.

A "large vocal sac" was always associated with this "different" condition, and "a small vocal sac", with the regular condition, in which the lateral edges of the pectoral lymph septum were inserted above the shoulder. Thus, it was understood that both characters were not independent. A definition of a large or small vocal sac is based on a subjective notion of size relation and is altered by fixation artifacts [see Faivovich (2002)]. Thus, it seemed preferable to score this variation based on a more objective criteria with more clearly defined states, i.e., the pectoral lymph septum insertion point.

  - 0: Pectoral lymph septum not extending into arm; lateral fixation points in the *m. deltoideus*.
  - 1: Pectoral lymph septum extending into arm; lateral fixation point in the axillary membrane.

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- **105. Frontal lines.**

  In frontal view, some species present a line or a pair of lines that run vertically (sagittaly), from the nostril to the lip. Usually, they are connected with the dorsolateral lines through a canthal stripe (Rivero, 1971; Weygoldt and Peixoto, 1987; Cruz et al., 2000).

  - 0: Lines absent.
  - 1: Lines present.
- **106. Frontal lines, number.**
  - 0: One, vertical, dividing rostrum in two halves.
  - 1: Two, forming a "V" in frontal view.
- **107. Frontal lines, thickness.**
  - 0: Thin line(s).
  - 1: Thick line(s).
- **108. Canthal stripe.**

  A stripe that passes in the canthus rostralis. It sometimes can be connected with dorsolateral stripes.

  - 0: Stripe absent.
  - 1: Stripe present.
- **109. Canthal stripe, color.**
  - 0: White.
  - 1: Black.
- **110. Frontal and canthal lines connection.**
  - 0: Connecting dorsally to the nares.
  - 1: Connecting laterally to the nares.
- **111. Inferior margin of the orbit position in relation to the nostrils.**
  - 0: Inferior margin of the orbit lower than nostrils.
  - 1: Inferior margin of the orbit higher than nostrils.
- **112. Vocal sac morphology.**

  Taken from the literature. Duellman (1970) character G; Grant et al. (2006) character 76; Araújo-Vieira et al. (2019) character 106.

The vocal sac morphology has been long recognized as a differential diagnostic character in many levels among anurans and exhibits large variation (Liu, 1935). This character has been suggested as evidence of relationship between *Pseudis minuta* and *Pseudis cardosoi* vs. *Lysapsus* vs. other *Pseudis* species and was summarized by Garda et al. (2010).

Gunther (1869 "1868") and Boulenger (1882) described a pair of vocal sacs in the type of *Hyla dasynotus*. This species was later considered as synonym of *Dendropsophus seniculus* by Cochran (1955). Yet, no specimen examined in our study had this kind of vocal sac. All of them presented a sac composed of a single structure. On the other hand, all photos of calling *Dendropsophus* assigned to the *D. marmoratus* group with fully expanded vocal sacs, present slightly bilobated vocal sacs. Although all *Dendropsophus* specimens presented a transverse lymphatic septum that connects the *m. interhyoideus* with the gular skin, it is not obvious that this structure could be related to this bilobated morphology. Other species that present this structure do not present the same vocal sac morphology. In addition, photographic information that could help score this character was scarce and, thus, it was not possible to score the exact state with confidence. Clearly, the state 0 seems to group different structures. Species assigned for this character state should be revisited in the future.

- 0: Single, subgular.
- 1: Double.

- **113. Color of the vocal sac inflatable portion in preservative.**

Character states were scored in preserved specimens. This character scores only the color pattern of the inflatable portion of the vocal sac. The variation on the non-inflatable portion coloration is scored in character 141. As a convention, the non-inflatable portion of the vocal sac refers to the skin above the *m. intermandibularis* and the inflatable portion to the skin covering the *m. interhyoideus* or its modifications.

Visual cues play important role in anuran communication (e.g. Haddad and Giaretta, 1999; Lüddecke, 1999) and the vocal sac is one of the primary sources of such cues (Wells, 2007). It has been experimentally demonstrated that advertisement call playbacks without synchronized visual reference of an inflating vocal sac have little attractiveness for females (e.g. Rosenthal et al., 2004). At least two species [*Phrynobatrachus krefftii* Boulenger 1909 and *Mannophryne trinitatis* (Garman, 1888 “1887”)] use soundless inflations of the vocal sacs to communicate (Wells, 1980; Hirschmann and Hödl, 2006). The usual hypothesis is that bright, colorful inflated vocal sacs have enhanced contrast with the surroundings would provide "a readily detectable source of information in addition to the call" (Rosenthal et al., 2004).

In life, many vocal sacs are colorful with bright colors (see Wells, 2007) and so are many of the species scored herein with state 0 have bright colored inflated vocals sacs. Some are yellow (e.g. *Dendropsophus elianeae*), what usually relate to the presence of carotenoid pigments that are highly costly immune function enhancing molecules (see Richardson et al., 2009). Four species (*D. anceps*, *D. molitor*—few specimens, *Pseudis minuta* and *Lysapsus limellum*) present black vocal sacs. How these last could function to enhance the visual signaling is still undetermined.

  - 0: Clear cream or white.
  - 1: Blotched.
  - 2: Anteriorly black.
  - 3: Completely black.

- **114. Skin around the margin of the lower lip.**

  Taken from the literature. Cochran (1955); Bokermann (1964).

  Cochran (1955) and Bokermann (1964) used this character as diagnostic of their *Hyla marmorata* groups, which also included also species now placed in the *Dendropsophus parviceps* species group.

  - 0: Smooth.
  - 1: Warty.

- **115. Nostril position.**

  Taken from the literature. Izecksohn (1996) diagnostic character 1 (part); Araújo-Vieira et al. (2019) character 107 (part).

  Izecksohn (1996) diagnostic character 1 dealt with head variation as a whole. The nostril position in relation to the snout was only a part of his diagnostic character. *Scarthyla*, *Sphaenorhynchus* and *Xenohyla* present lateral nostrils, an uncommon character in Hylids. Izecksohn (1996) used this character to infer a relationship between them.

  - 0: At the top of snout, dorsolateral.
  - 1: Lateral to the snout, frontally or laterally directed.

- **116. Subnarial spot.**

  A white vertical mark in the lip. In lateral view, under the nostril.

  - 0: Spot absent.
  - 1: Spot present.

- **117. Suborbital white bar presence.**

  Modified from the literature. Araújo-Vieira et al. (2019) character 112.

  The presence, amount and extension of this bar were used as taxonomic character and to diagnose groups in *Dendropsophus* (Cochran, 1948; Lutz and Bokermann, 1963; Duellman and Fouquette, 1968; Duellman, 1970; Duellman and Crump, 1974). However, especially in smaller species, a silvery area below the eye can be seen. Its color is due to the bone and/or the fibrous connective tissue that surrounds the eye and that is visible through the transparent skin. Some may confuse it with the "real" suborbital bar formed by pigment. In addition, individuals of species that typically possess—or are diagnosed by—bars or spots may present them only in one side of the head or are absent at all.

  Bertha Lutz (1973) noticed that the presence of white bars was more frequent in populations of *Dendropsophus branneri* from Southeastern Brazil and gradually decreased in a South to North cline until the Northeastern Brazil populations where the bar presence frequency was much lower. Bertha Lutz and Bokermann (1963) used the presence of this bar to recognize *D. nahdereri* as distinct from other species of the *D. marmoratus* group. However, other species of this group do present a similar bar.

  - 0: Bar absent,
  - 1: Bar present.

- **118. Number of suborbital white bars.** (Additive)

  The number of suborbital white bars has been used for species diagnoses within the *Dendropsophus parviceps* group (Duellman and Crump, 1974).

  - 0: One.
  - 1: Two.
  - 2: Many small spots.

- **119. Suborbital white bar - extension.**

  Although "under the eye" clearly assembles some different states (a small spot vs. a bar that covers all infraorbital area) it could be simply a continuum. Since available specimens per species were numerically distinct, assessing this variation could be biased by highly polymorphic species. Thus, we took a more conservative approach for this character.

  - 0: Under the eye only.
  - 1: Extending onto the body.
  - 2: Extending from rostrum to posterior edge of the eye.

- **120. Tympanic membrane differentiation.** (Figure SI6)

  Modified from the literature. Duellman (1970); Heyer (1975) character 2; Wiens et al. (2005) character 108; Araújo-Vieira et al. (2019) character 113 (among many others).

  In *Dendropsophus*, the presence of concealed and exposed tympani has been referred to as a diagnostic character for many groups (e.g. Duellman, 1970; Duellman and Crump, 1974; Duellman, 1982; Duellman and Trueb, 1983). However, there has been some confusion in the literature relating to the external amphibian ear. Lynch and Duellman (1997) performed a review and defined "four character combinations of the ear" based on Eleutherodactylinae frogs in Ecuador (most species are today assigned to the genus *Pristimantis* Jiménez de la Espada, 1870). The variation observed herein is slightly different, although it follows the same basic scheme described by Lynch and Duellman (1997). Because their descriptors mix character states on a single character, these were used as a guideline for the external visibility of the tympanic membrane and tympanic annulus independently [e.g. Duellman, 1970; Wiens et al., 2005 character 108].

  Even though there seems to be independent variation between the visibility of the anterior and posterior margins of the tympanic annulus, it was not possible to confidently assign an evident/concealed state for either margin; fixation seemed to play some role in the distinctiveness of this character. Until a more reliable way to assign character states for tympanic ring visibility is proposed, we leave this variation as potentially informative.

The tympanic membrane was considered as "evident" when it was transparent enough to see inside the middle ear or distinct enough in general coloration (usually much clearer than the rest of surrounding skin). If not, it was considered not clearly differentiated. Although this character deals with the tympanic membrane, the "tympanum visibility" character previously studied by other authors may refer also (or not) to the tympanic ring visibility. However, tympanic ring visibility is a more difficult issue. A number of authors used this character to demonstrate variation among various groups. When it comes to *Dendropsophus*, previous authors noted that species of different groups had different tympanum and tympanic ring conditions. Nevertheless, confusion is widespread when it comes to definitions. For comments on tympanic annulus visibility, see the Potentially Informative Variation section.

  - 0: Tympanic membrane not clearly differentiated.
  - 1: Evident tympanic membrane.

- **121. Axillary membrane.**

As commented above on character 102 the presence of an axillary membrane has been used as diagnostic characters of various *Dendropsophus* groups (e.g. Duellman and Fouquette, 1968; Duellman, 1970; Duellman and Crump, 1974; Duellman and Trueb, 1983; Kaplan, 1991; Kaplan and Ruiz-Carranza, 1997). Axillary membranes were scored with arms positioned at a 90 degrees angle to the body. Also stated above (character 102), there is much influence on fixation artifacts on the relative size of the axillary membrane. However, its presence or absence is consistently scored, in a large measure, for different individuals of the same species being the distinct individuals usually the ones in the worst state of conservation.

  - 0: Membrane absent.
  - 1: Membrane present.

- **122. Preaxillary pectoral fold.**

Modified from the literature. Faivovich (2002) character 26 and 27.

As did Faivovich (2002), Tyler (1971a) terminology was used and variation in the two axillary pectoral folds was scored only in females or in males with the vocal sac poorly distended. Faivovich's (2002) coding is slightly different from the one applied here. His character 26 dealt with pectoral fold presence and absence as a single structure and his character 27 coded variation on simple and compound folds. Folds seem to vary independently since some species have only one of them [see Tyler (1971a)'s figure 1 and *Scarthyla goinorum* herein]. Therefore, pre- and postaxillary folds were coded independently. The preaxillary fold can be easily confused with fixation artifacts. If the head is slightly adpressed over the body, the resulting fold can be confused with a preaxillary fold. Herein, the preaxillary fold was considered present only if head movements did not affect it; this mostly coincides with species that possess deep compound folds [see Faivovich (2002) figure 11B]. Tyler (1971a) states that both folds are the external appearance of lymphatic *septae*. However, most species revealed under dissection, a preaxillary lymphatic septum that usually connects the *m. interhyoideus* with the gular skin, although not all of those presented an external fold.

  - 0: Fold absent.
  - 1: Fold present.

- **123. Postaxillar pectoral fold presence.**

  Modified from the literature. Faivovich (2002) character 26 and 27.

  - 0: Fold absent.
  - 1: Fold present.

- **124. Shape of the postaxillar pectoral fold.**

  Modified from the literature. Faivovich (2002) character 27.

  Some variation in the pectoral fold extension is due to the presence (or absence) and shape of the pectoral gland. In many *Dendropsophus* (such as *D. carnifex*), the postaxillary fold is interrupted medially. Because of that variation and the different anatomical position, we use a different character description from Faivovich (2002).

  - 0: Continuous.
  - 1: Interrupted medially.

- **125. Webbing between fingers II and III (scored on II).** (Additive)

  Modified from the literature.

  The amount of webbing on hands and feet has been used in hylid systematics for a longtime [as in Anura as well, e.g. Heyer (1975) character 9]. Hylids present an enormous variation in the extent of fingers and toes webbing and these structures have been used throughout literature as a descriptive character and for some cases, diagnostic characters of groups or genera (Lutz, 1950; Cochran, 1955; Duellman, 1970; Lutz, 1973).

  Grant et al. (2006) made an extensive discussion on variation of Dendrobatoidea finger fringes and toe webbing. Although Dendrobatoidea do not present webbing on the fingers, the same reasoning used for scoring their toe webbing is applicable to the webbing of toes and fingers of Hylids. Grant et al. (2006) state that there is ample evidence that the extent of webbing along each edge of each digit varies independently although not providing references. In addition, insertions on both sides (medial and lateral) of finger IV are independent given that in Centrolenids they are distinctively different (e.g. Guayasamin et al., 2009 fig. 15). The same can be said about the webbing insertions on toes I and II. Those insertions can be reduced without correlated with webbing reduction on other fingers (e.g. Scinaxini vs. Centrolenids). Other insertions are not that clearly independent.

  We agree that "functional independence is at most secondary to historical independence" (Grant et al., 2006 pg. 72), and correlated variation between different webbings is not straightforward—as neither it is for individuals as a whole (Grant et al., 2006). Nevertheless, correlated variation should be "*tested* a posteriori *by the independently resultant topology, or they can be suggested by the character states distribution documented by the cladogram*" (Desutter-Grandcolas et al., 2003) and the coding scheme of Grant et al. (2006) seems the best to do it.

Observations on the variation in the hylid webbing (VGDO pers. obs.) showed that there is individual variation in the exact extent to which a given webbing is inserted on its respective digit. However, this variation is small, equivalent to the length of about one subarticular tubercle in a given species. Thus, character states were designed regarding this variation. After scoring medial and lateral insertions separately, the only insertions that presented correlated variation were those of insertions connecting finger II to finger III. Since we are not aware of any instance from which we could infer that they are indeed independent and that our results are an artifact of group sampling, we treated these insertions as one single character. All other insertions presented independent variation.

  - 0: Webbing absent.
  - 1: Reduced to a narrow fringe.
  - 2: Reaching subarticular tubercle II.

- **126. Webbing insertion between fingers III and IV (scored on III).** (Additive)
  - 0: Webbing absent.
  - 1: Reduced to a narrow fringe.
  - 2: Reaching subarticular tubercle II.
  - 3: Reaching subarticular tubercle I.
- **127. Webbing insertion between fingers III and IV (scored on IV).** (Additive)

  Modified from the literature. Araújo-Vieira et al. (2019) character 127.
  - 0: Webbing absent.
  - 1: Reduced to a narrow fringe.
  - 2: Reaching subarticular tubercle III.
  - 3: Reaching subarticular tubercle II.
- **128. Webbing insertion between fingers IV and V (scored on IV).** (Additive)

  Modified from the literature. Araújo-Vieira et al. (2019) character 128.
  - 0: Webbing absent.
  - 1: Reduced to a narrow fringe.
  - 2: Reaching subarticular tubercle III.
  - 3: Reaching subarticular tubercle II.
- **129. Webbing insertion between fingers IV and V (scored on V).** (Additive)
  - 0: Webbing absent.
  - 1: Reduced to a narrow fringe.
  - 2: Reaching subarticular tubercle III.
  - 3: Reaching subarticular tubercle II.
  - 4: Reaching the subarticular tubercle I or digital disc.
- **130. Webbing insertion between toes I and II (scored on I).**

  Modified from the literature. Araújo-Vieira et al. (2019) character 129.

    - 0: Absent or reduced to a narrow fringe.
    - 1: Reaching the subarticular tubercle I or digital disc.
- **131. Webbing insertion between toes I and II (scored on II).** (Additive)
    - 0: Lower than subarticular tubercle II or webbing absent.
    - 1: Reaching subarticular tubercle II level.
    - 2: Reaching the subarticular tubercle I or digital disc.
- **132. Webbing insertion between toes II and III (scored on II).** (Additive)
    - 0: Absent or reduced to a narrow fringe.
    - 1: Reaching subarticular tubercle II.
    - 2: Reaching the subarticular tubercle I or digital disc.
- **133. Webbing insertion between toes II and III (scored on III).** (Additive)
    - 0: Webbing absent.
    - 1: Reaching subarticular tubercle III.
    - 2: Reaching subarticular tubercle II.
    - 3: Reaching the subarticular tubercle I or digital disc.
- **134. Webbing insertion between toes III and IV (scored on III).** (Additive)
    - 0: Webbing absent.
    - 1: Reaching subarticular tubercle III.
    - 2: Reaching subarticular tubercle II.
    - 3: Reaching the subarticular tubercle I or digital disc.
- **135. Webbing insertion between toes III and IV (scored on IV).** (Additive)
  Modified from the literature. Araújo-Vieira et al. (2019) character 130.
    - 0: Absent or reduced to a narrow fringe.
    - 1: Reaching subarticular tubercle III.
    - 2: Reaching subarticular tubercle II.
    - 3: Reaching the subarticular tubercle I or digital disc.
- **136. Webbing insertion between toes IV and V (scored on IV).** (Additive)
  Modified from the literature. Araújo-Vieira et al. (2019) character 131.
    - 0: Absent or reduced to a narrow fringe.
    - 1: Reaching subarticular tubercle III.
    - 2: Reaching subarticular tubercle II.
    - 3: Reaching the subarticular tubercle I or digital disc.
- **137. Webbing insertion between toes IV and V (scored on V).** (Additive)
    - 0: Absent or reduced to a narrow fringe.
    - 1: Reaching subarticular tubercle II.

  - 2: Reaching the subarticular tubercle I or digital disc.

- **138. Flanks ornamentation pattern.**

  Only the area covered by the thighs near to the groin was considered as flank. Here and throughout the text, marbled is considered when over a black base, the belly granules are white. Blotched, when there are black areas over a white background, not associated with a specific pattern. For this and for other characters dealing with ornamentation pattern, see Figure SI7 for a reference.

  - 0: Uniformly colored.
  - 1: Blotched.
  - 2: Stripped.
  - 3: Marbled.

- **139. Pelvic girdle melanin deposits.**

  The "visible subdermal black lymphatic septae" (Cochran and Goin, 1970) were used as diagnostic character of *Dendropsophus mathiassoni* (Cochran and Goin, 1970). Dissections showed that these melanin deposits seem to be on lymphatic hearts. We make no hypotheses on the reasons of why this melanin deposits there.

  - 0: Deposits absent.
  - 1: Deposits present.

- **140. Ventral pattern.**

  - 0: Uniformly clear.
  - 1: Blotched.
  - 2: Marbled.
  - 3: Uniformly black.

- **141. Gular pattern.**

  This character only scores variation on non-inflatable portion of the vocal sac coloration. For inflatable portion coloration, see character 113.

  - 0: Uniformly clear.
  - 1: Blotched.
  - 2: Marbled.
  - 3: Uniformly black.

- **142. Thigh posterior and dorsal areas color patter comparison.**

  Some species possess a dorsal stripe on the thighs that presents the same coloration of the dorsum and of the dorsal surfaces of the shanks. Others have completely uniform thighs. Therefore, the character refers to differences in this stripe, nevertheless, it was simpler (and more self-explanatory) to describe it through the similarity of distinctiveness of these thigh areas.

  - 0: Dorsal and posterior areas of the thighs uniform, not blotched nor differentiable through color pattern.

    - 1: Dorsal area different from posterior area. Dorsal following the general dorsal pattern that is different from the posterior area pattern.
    - 2: Dorsal and posterior areas of the thighs both uniformly blotched.
- **143. Thigh posterior area pattern.**
    - 0: Uniformly colored.
    - 1: Well defined blotched or marbled.
    - 2: Longitudinally stripped.
    - 3: Loosely blotched or marbled.
- **144. Thigh ventral area pattern.**
    - 0: Uniformly colored.
    - 1: Blotched.
    - 2: Longitudinally stripped.
- **145. Shanks dorsal coloration pattern.**
    - 0: Uniform; i.e., not differentiable from other areas of the shanks.
    - 1: With dark transversal stripes.
    - 2: With well-defined clear blotches over a darker base, regardless of the number and similar to dorsal coloration
    - 3: With loosely defined dark blotches over a lighter base, regardless of the number and similar to dorsal coloration
- **146. Cloacal sheath.** (Figure SI8)

  Modified from the literature. Duellman (1970; 2001a; 2001b); Araújo-Vieira et al. (2019) character 119.

  All specimens analyzed presented some kind of skin covering over the cloacal opening, and some variation in length was observed. Given the caveats made by Grant et al. (2006), that the presence and shape of the cloacal sheath may be due to preservations artifacts, sheaths were scored only in well-preserved individuals, in comparable anatomical positions.

  In the present dataset, only *Dendropsophus minutus* and species of *Sphaenorhynchus* presented a long cloacal sheath. Additionally examined specimens of *D. stingi* and *D. xapuriensis* also presented a long sheath, covering the entire cloaca in a posterior view. This sheath has been used as evidence of close relationships between the species assigned (or related) to the *D. minutus* species group (Mijares-Urrutia, 1998; Köhler and Lötters, 2001).

    - 0: Short; not covering the entire cloaca in posterior view.
    - 1: Long; covering the entire cloaca in posterior view.
- **147. White line above cloaca.** (Figure SI8)

  Modified from the literature.

  Cochran and Goin (1970) restricted the definition proposed by Cochran (1955) to the *Hyla minuta* group and defined it as "Small, pale to yellowish frogs with a dark saddle on the back and a transverse white line above the vent and on each heel." Herein, this definition is broken into its independent variables (see next character). The white line above the cloaca was especially used to relate species to *Dendropsophus minutus* and could possibly be a synapomorphy for the *D. minutus* group (Kaplan, 1994). Nevertheless, it is not always visible in all living individuals, although the line may appear after fixation of the specimen (Kenny, 1969).

Sphaenorhynchus species have a white line (or granules) below the cloaca. Donnelly and Myers (1991) report that some individuals do not have either lines. However, is seems a fixation artifact. *Dendropsophus anceps* also have this line, although differently. While the lines of species of the *D. minutus* group are short and located exclusively above the cloaca, the line of *D. anceps* in fact borders a large dark spot that covers all the cloacal region and invades the thighs. Duellman and Trueb (1989) state that *D. timbeba* (as *Hyla allenorum*), has a yellowish cream anal stripe. Specimens examined by us did not have any stripe.

  - 0: Line absent.
  - 1: Line present.

- **148. White lines above heels.**

  Many papers that described *Dendropsophus* species pointed out the presence of a white line (over a dark background) located at the rump, dorsal to the cloaca and above each heel (see previous character discussion). Herein, we scored the presence and absence of the lines above the heels. When present, it was always in both heels.

  - 0: Lines absent.
  - 1: Lines present.

- **149. Ulnar fold.** (Figure SI9)

  Modified from the literature. Duellman (1970) character Q (part).

  Duellman (1970) character Q scored variation for all limbs together. However, based on the character state distribution in *Sphaenorhynchus lacteus* and *Dendropsophus elegans*, fringes on distinct limbs and segments seemed independent. According to Grant et al. (2006)—see comments of their characters 11 to 18—only the brachial region was considered for scoring this character. Many hylid species present some kind of fringe in the outer surface of the arm and in other regions of the body. In the examined specimens of *Pseudis*, instead of a sheath of skin, a series of small spiculae was found. These structures were coded as brachial fringes because some authors (Duellman, 1970; Lynch and Duellman, 1973; Cisneros-Heredia and McDiarmid, 2007) considered them to be dermal appendages comparable to warts and flaps. Although clearly a dermal modification also, these spiculae were not considered homolog to the warts and flaps usually found because they are not limited to the same geographical area. Instead they (once again, usually) are distributed all over the dorsal surfaces of the specimens. In the examined material no "keel" (sensu Grant et al. 2006) was recognized. All material presenting linear dermal modifications, that were not spiculae, were considered fringes.

  - 0: Ulnar fold absent.
  - 1: Ulnar fold present.

- **150. Ulnar fold structure.** (Figure SI9)

  The delimitation of different states of dermal modifications is often arbitrary (Lynch and Duellman, 1997). All dermal modifications seem to be based on differences of a glandular tissue. Here, three states of fimbriae are recognizable (except for *Pseudis* and *Lysapsus* specimens because their spiculae were not considered as homologs). Of course, as for the Dendrobatoidea "keels" and fringes (see Grant. et al., 2006), the limits between these states could be arbitrary. We recognize a well-defined fringe, i.e., a clear transversally directed fold of skin (the transversal length is larger than the orthogonal width), a "tubercular fringe", i.e., a line of tubercles independent from each other although arranged serially and a "delicate" fringe (the transversal length is smaller than the orthogonal width). As a convention, a—usually—white line of "swollen" skin where the transversal expansion was not as protruded as its width was considered a "delicate" fringe.

  - 0: Delicate.
  - 1: Well-defined fold.
  - 2: Tubercular fringe.
- **151. Tarsal fold presence.**

  Modified from the literature. Heyer (1975) character 6 (part); Araújo-Vieira et al. (2019) character 123 (part). This character describes skin structures located laterally (on the outer surfaces of the tarsus). Specimens of *Pseudis* and *Lysapsus* present a medial fold, not comparable to the ones treated herein.

  - 0: Tarsal fold absent.
  - 1: Tarsal fold present.
- **152. Tarsal fold nature.**

  Modified from the literature. Araújo-Vieira et al. (2019) character 123 (part).

  - 0: Delicate.
  - 1: Well-defined fold.
  - 2: Tubercular fringe.
- **153. Tibial ventral fold.**
  - 0: Tibial ventral fold absent.
  - 1: Tibial ventral fold present.
- **154. Calcar presence.**

  Taken from the literature. Duellman (1970) character P; Araújo-Vieira et al. (2019) character 124 (part).

  - 0: Calcar absent.
  - 1: Calcar present.
- **155. Calcar shape.**
  - 0: Tubercular.
  - 1: Rounded fringe.

- **156. Toe I disc shape.**

  Modified from the literature. Liem (1970) character 33 (part); Duellman and Wiens (1992) diagnostic character 2; Faivovich (2002) character 24 Araújo-Vieira et al. (2019) character 126.

  Duellman and Wiens (1992) and Faivovich (2002) took into account all hand fingers when scoring their data. However, there is some variation among fingers and toes. There also seems to be a sexual dimorphism in *Dendropsophus* species. With the exception of finger II and toe I, females have rounded discs while males have transversally elliptic discs. It is important to remark that many toe discs of *Dendropsophus* species are described in literature as "rounded", are indeed transversally elliptical; albeit not in the same levels seen on *Phyllodytes*, *Itapotihyla*, and *Scinax*. Nevertheless, Toe I is not sexually dimorphic and is consistently rounded in all examined *Dendropsophus* species. The exception is *D. shiwiarum* that has pointed toe discs (Ortega-Andrade and Ron, 2013). This is a unique feature and this species was not considered in our analyses. Possibly a meristic approach could be more informative and recover more states then the ones herein.

  The *Pseudis* and *Lysapsus* species used here deserve comment. Garda et al. (2010) reviewed, described and analyzed extensive variation in the digital discs of *Pseudis*. In some species discs are usually absent, yet conspicuous discs are observable in large individuals. Nevertheless, in all specimens analyzed herein (a much smaller sample than that of Garda et al., 2010) discs were longer than wide, i.e., longitudinally elliptic.

  - 0: Rounded.
  - 1: Transversely elliptical.
  - 2: Longitudinally elliptical.

- **157. Nuptial pad, extension.** (Additive; Figure SI10)

  Modified from the literature. Liem (1970) character 35 (part); Heyer (1975) character 3 (part).

  All studied species have nuptial pads. Nuptial pad presence in Dendropsophini could be seasonal as in other groups (see Noble, 1931; Luna et al., 2018). Due to possible seasonal changes, if any specimen presented the pad, the terminal was scored as present. There are possibly more character states within our state 1 (the extension of the pad on fingers). Nevertheless, it is very easy to miss small isolated acini and we chose to be conservative for the moment.

  - 0: Pad only in lateral areas of prepollex, not reaching dorsal areas.
  - 1: Pad covering dorsal areas of prepollex and fingers.
  - 2: Pad extending onto forearm.

- **158. Nuptial pad, shape.** (Figure SI10)

  Modified from the literature. Heyer (1975) character 3 (part). In species related to *Dendropsophus molitor* (see examined material), the nuptial pad is hypertrophied when compared to other species of *Dendropsophus*. Non-histological sections revealed that the glands composing this macrogland are alongated, different from the glands of other examined species that were of a more common presentation (small spheres). No other species presented a similar elongated condition. In fact, *D. molitor* nuptial pads have many unique histological features (see Luna et a., 2018).

  - 0: Overall appearance as a non-hypertrophied pad.
  - 1: Overall appearance as a largely hypertrophied pad.

- **159. Nuptial pad, structure.** (Additive; Figure SI10)

  Modified from the literature. Liem (1970) character 35 (part); Duellman (1970) character N; Heyer (1975) character 3 (part); Grant et al. (2006) character 23; Araújo-Vieira et al. (2019) character (114) and (115).

  Nuptial pads are composed of dermal and epidermal components. These include the sexualy dimorphic skin glands in the dermis (always present; most frequently specialized mucous glands) and the epidermal projections (EPs), that are papillary (with dermal and epidermal components) or non-papillary _(only involving epidermis; see Luna et al., 2018 for a recent review).. Sometimes the stratum corneum is dark colored, what has usually been referred to as nuptial excrescences. Araújo-Vieira et al. (2019: ch. 116) scored the relative sizes of the epidermal projections of the nuptial pad (using as a proxy the density of EPs). We have not evaluated this variation and these characters should not be confused.

  Although colored epidermal projections are common among hylids, most species of *Dendropsophus* lack them (Duellman, 1970). In addition, their presence could be seasonal (see character 157). We followed the same reasoning used for. 157–158 and inferred their presence for the species even if only one examined individual presented them.

  - 0: Without macroscopically evident papillae.
  - 1: With light colored epidermal projections.
  - 2: With dark colored epidermal projections.

- **160. Pectoral glands, occurrence in males.**

  Modified from the literature. Duellman (1970; 2001a) "*Hyla leucophyllata*" species group diagnostic character.

  Faivovich et al. (2005) recovered *Dendropsophus anceps* as sister species of all other members of the *D. leucophyllatus* group and placed it within it noticing that 'with the exception of [*D. anceps*], all other members of the group share the presence of pectoral glands in males and females'. Although *D. anceps* females do not have pectoral glands divided into two patches, males do have them. Therefore, we studied variation on the presence and presentation of pectoral glands for males and females separately.

  Although Duellman and Trueb (1983) used the absence of pectoral glands as diagnostic character of the "*Hyla columbiana*" group. Examined specimens of *Dendropsophus carnifex* had pectoral glands. In this species these are thin instead of clearly differentiated patches as found in *D. elegans* (for instance). It then possible that Duellman and Trueb (1983) considered glands to be present only when thick patches were observed.

The available number of males was significantly higher than the number of females, so it was possible to check for variation in the pectoral glands of males. The morphology of pectoral glands of females are not always the same as in males. This is the case of *Dendropsophus anceps* (since females do not have glandular patches) but also in other species (e.g. *D. carnifex*; *D. virolinensis*) where males and females present different glandular types of glands (thick patch vs. scattered acini respectively in both cases). Although these three states were scored in the following character, this character was coded only with gross dissection.

Histological sections could reveal different character states. As said for the nuptial pad, some glands seem to present seasonal variation and their conspicuousness is often affected by individual variation of fixation artifacts (secretion-loaded acini are easily detected wile empty ones not). Thus, presence was scored even if a single individual presented the gland.

  - 0: Glands absent.
  - 1: Glands present.

- **161. Pectoral glands,, arrangement in males.**

  This character was coded only with gross dissection. It is possibly that histological sections reveal different states of the ones herein. Some species present a thickened skin in the pectoral region that can be divided in two distinct patches. Other (as *Dendropsophus oliveirai*) only present some scattered acini in non-thickened skin.

  - 0: Two clear distinct patches.
  - 1: A single structure, not divided.
  - 2: As scattered acini.

- **162. Pectoral glands, occurrence in females.**
  - 0: Glands absent.
  - 1: Glands present.

- **163. Dorsal skin, ornamentation.**

  Modified from the literature. Wiens et al (2005) character 110.

  Trueb and Duellman (1970) called the attention to the long history of taxonomic usage of variation on dorsal skin ornamentation of *Osteocephalus* species. It is important to notice that *Dendropsophus haraldschultzi* and *D. pauiniensis* possess dorsal ornamentation (although a histological study is still lacking). In *Dendropsophus haraldschultzi* warts and spiculae are concentrated on the top of the head, dorsal surfaces of arms and on the anterior half of the dorsum. Spicules are absent in some individuals and may be temporary structures during mating season. In *D. pauiniensis*, spiculae are distributed more or less uniformely over the dorsum.

  - 0: Smooth.
  - 1: With spiculae.
  - 2: With tubercles.

CHROMOSOMES

- **164. Chromosome number.**

  Taken from the literature. Duellman and Trueb (1983) character A.

  The 30–chromosome number has long been used as a "diagnostic character for *Dendropsophus*" within Hylidae (Duellman, 1967; Duellman, 1970; Duellman and Trueb, 1983; Kaplan, 1991 among many others). Other authors, like Heyer (1975 see character 37), also coded the number of chromosomes, but given the restricted taxonomic occurrence of this diploid number (only known for *Dendropsophus* and *Litoria*), they have not a correspondent character state. A recent broad-spectrum karyological survey of Dendropsophini (Suarez et al., 2013) discovered significant diversity of diploid chromosome numbers Dendropsophini ranging from 2N = 22 in *Scarthyla goinorum* to 2N = 28 in *Pseudis cardosoi* (Busin et al., 2001; Suarez et al., 2013), the optimization of the chromosome numbers within the tribe (based on Faivovich et al., 2005 tree) confirmed that the only Dendropsophini species with 2N = 30 were *Dendropsophus*. However, the present analysis is the first to actually test this character state in a cladistic analysis.

  - 0: 22.
  - 1: 24.
  - 2: 30.

LARVAL EXTERNAL MORPHOLOGY

Dendropsophus larvae are quite similar morphologically. In fact, larval morphology is largely conservative within our dataset. Exceptions are the two species of *Scarthyla* that have radically different larvae (see Lynch and Suarez-Mayorga, 2011) and *Scinax ariadne* (Bokermann, 1967) whose larva has an unusually large oral disc in comparison to other species of *Scinax* of the *S. catharinae* clade (see Conte et al., 2007). Many synapomorphies of Dendropsophini clades are based on larval characters (e.g. Faivovich et al., 2005; Conte et al., 2007).

Although the larvae of many species have been described, there has been a long confusion on the literature regarding the larvae of *Dendropsophus nanus* and *D. sanborni*. Bokermann (1963) described the larva of *D. nanus* from Campo Grande, São Paulo, Brazil. Langone and Basso (1987) examined adults of the material studied by Bokermann (1963) and identified it as *D. sanborni*. Lavilla (1990) described the larva of *D. nanus* from Roque Saenz Peña, Chaco, Argentina (where there is only *D. nanus*; B. Blotto person. comm.) and list some differences between both larvae. Rossa-Feres et al. (2004) state that both *D. nanus* and *D. sanborni* occurred in the pond they studied but their larvae were indistinguishable. Rossa-Feres and Nomura (2006) also revisited the lot described by Bokermann (1963) and state that they are identical to the ones they collected in Nova Itapirema, São Paulo, Brazil where, as noted by Medeiros et al. (2003), both species occur. It is not clear if both species also occur at Campo Grande, São Paulo. Thus, it is not clear if the larva of *D. sanborni* is accurately described or not. For the present moment, we assume the description of Bokermann (1963) as *D. sanborni* based on Langone and Basso (1987) observations.

Lynch and Suarez-Mayorga (2011) included in their illustrated key for lowland Colombian tadpole specimens that were identified as larvae of *Dendropsophus riveroi*. Based on the large difference between this larva and the other larvae of *Dendropsophus*, Lynch and Suarez-Mayorga (2011) suggested that the generic placement of this species was incorrect. It seems odd that the larva of *D. riveroi* resembled so much a *Scinax* larva according to Lynch and Suarez-Mayorga (2011). These authors made an effort to collect developmental series in order to correctly correlate adults and larvae. Nevertheless, it is not clear if they were able to do so for all species they collected. In the light of the larval morphology within the tribe, we suspect that the tadpole of *D. riveroi* may have been misidentified in Lynch and Suarez-Mayorga (2011) and a reinvestigation is needed. All other evidence available for *D. riveroi* indicates similarities with members of the *D. microcephalus* species group. For the present moment, we will treat the larva of *D. riveroi* as unknown.

- **165. Larval body shape, dorsal view.**

  Taken from the literature. Duellman and Trueb (1983) character D.

  A violin-shaped larval body in dorsal view has been considered a synapomorphy of the *Dendropsophus leucophyllatus* species group (Duellman and Trueb, 1983). Other species of *Dendropsophus* (as *D. nanus*) also possess violin-shaped bodies (see Lavilla, 1990). However, none was available to Duellman and Trueb (1983) at the time.

  - 0: Rounded; ovoid.
  - 1: Violin-shaped.
- **166. Larval body shape, lateral view.** (Additive)

  Taken from the literature. Duellman and Trueb (1983) character E.

  Although scored here as "rounded", *Phyllodytes* tadpoles bodies are dorsoventrally depressed (see Kenny, 1969). This is a common trait among bromeliad or other confined space dwellers (Altig and Johnston, 1989; Altig and McDiarmid, 1999). Duellman (1970) character QQ scored variation on larval body shape without stating in which view. His character states imply they were derived from lateral views. However, it is not clear what meant states "Deep" and "Robust". For our character states, we aggregated the terminology used to describe the larval shape in various instances of the literature. “Cuneiform” gather acutely triangular (~30^{o} angle) lateral profiles while “not cuneiform” gather less acute triangular profiles (>40^{o})

  - 0: Anteriorly abruptly ending; rounded; oval.
  - 1: Triangular but not cuneiform.
  - 2: Triangular; cuneiform; depressed.
- **167. Tail, shape.**

  Taken from the literature. Duellman and Trueb (1983) character E based on Duellman (1978).

  - 0: Acute.
  - 1: Xiphicercal (Y-shaped).

- **168. Oral disc, position.**

  Modified from the literature. Duellman (1970) character VV; Duellman and Trueb (1983) character F; Faivovich (2002) character 74; Araújo-Vieira et al. (2019) character 134.

  All oral discs of examined species are indeed positioned anteroventrally, some being anteriorly directed. Therefore, if descriptions stated "anterior" mouth, it was considered anteriorly directed. Two important remarks should be made here: one on *Dendropsophus nanus* and *D. sanborni* larvae and another on the larva of the *Scinax acuminatus* and larvae of the *S. rostratus* species group.

  Bokermann (1963) described the larva of *Dendropsophus sanborni* (see comments above) as possessing an oral disc modified into a sucker. Lavilla (1990) reported that the larva of *D. nanus* had the oral disc modified as a protrusible tube. Examined larval specimens of *D. nanus* (CFBH 22701) did not present a morphology distinct form other species of *Dendropsophus* or *Xenohyla* with respect to a protusible oral structure. Although Bokermann (1963) and Lavilla (1990) described the oral apparatus of the larvae they were studying as 'suctorial' and 'U-shaped', they present the same general morphology found in other species of *Dendropsophus*. In fact, the main differences between all those oral apparati seem to be the papillation around the oral disc. Living tadpoles of *X. truncata* and *Dendropsophus* spp. presented the same buccal movements.

  Larvae of *Scinax acuminatus* (and its sister taxon; the *S. rostratus* species group) have terminal oral discs and dorsolateral anteriorly directed nostrils. For the nostrils, it is another indication that their position and orientation are independent (see characters 182 and 183).

  - 0: Anterior; terminal; directed anteriorly oral disc.
  - 1: Anteroventral oral disc; directed more ventrally then anteriorly.
  - 2: Ventral oral disc.

- **169. Oral disc, marginal labial papillae.**

  Modified from the literature. Duellman (1970) character XX (part); Duellman and Trueb (1983) character G; Araújo-Vieira et al. (2019) character 136.

  Duellman (1970) character XX coded the presence and interruption of labial papillae together; we split it into two characters. The absence of oral disc labial papillae has been hypothesized as a synapomorphy of the *Dendropsophus microcephalus* group, with a reversal in the *D. decipiens* clade (Faivovich et al., 2005).

  - 0: Papillae absent.
  - 1: Papillae present.

- **170. Marginal labial papillae, posterolateral gap.**

  Modified from the literature. Duellman (1970) character XX (part); Araújo-Vieira et al. (2019) character 137.

  Duellman (1970) character XX is not clear to define in which species "incomplete" labial papillae are lacking.

  - 0: Continuous.

  - 1: Gaped.
- **171. Posterior marginal labial papillae, number of rows** (Additive)
  - 0: One.
  - 1: Two.
  - 2: Multiple.
- **172. Lateral marginal labial papillae, number of rows** (Additive)
  - 0: One.
  - 1: Two.
  - 2: Multiple.
- **173. Anterior labial tooth rows.**

  Modified from the literature. Duellman and Crump (1974) diagnostic character of the *Hyla parviceps* species group 23 (part); Wild (1992) tadpole key, step 1; Grant et al. (2006) characters 93; Fabrezi (2006) character 77 (part); Araújo-Vieira et al. (2019) character 138.

  There are differences in the number of larval tooth rows present on various taxa, not only *Dendropsophus*. Homology between rows is not clear. While some authors code their presence and absence as a whole (e.g. Fabrezi, 2006), Grant et al. (2006) assumed that rows are independent in each side (anterior and posterior) and that are summed in addition. Therefore, we coded this variation in two additive characters (174 and 176). The findings of Thibaudeau and Altig (1988) seem to support this idea. Other contributions also presented some evidence that rows are added sequentially (see Kenny, 1969; Cei, 1980; Orrico et al., 2007; Kolenc et al., 2008). As did Grant et al. (2006), we too score the highest number of rows known for a given species. Since rows appear and then are atrophied (Thibaudeau and Altig, 1988), it seemed just logical to score the maximum number of rows.

  - 0: Rows absent.
  - 1: Rows present.
- **174. Anterior labial tooth rows, number** (Additive)

  Modified from the literature. Araújo-Vieira et al. (2019) character 139.

  - 0: One.
  - 1: Two.
  - 2: Three.
- **175. Posterior labial tooth rows.**

  Modified from the literature. Duellman and Crump (1974) diagnostic character of the *Hyla parviceps* group 23 (part); Wild (1992) tadpole key, step 1; Grant et al. (2006) character 94; Araújo-Vieira et al. (2019) character 140.

  Larvae of *Dendropsophus decipiens* and *D. oliveirai* do not possess larval teeth (keratodonts). Pugliese et al. (2000), however, called the attention to ridges between the lower beak and oral disc papillae. Santos et al. (1998) also found these same ridges in *D. microps*. They also state that in the specimens of *D.*

microps that had keratodont rows, these were located on these rides. Thibaudeau and Altig (1988) demonstrated that keratodont rows form on top and along these ridges. Thibaudeau and Altig (1988) described that in larvae of *D. sarayacuensis* there are ridges in the positions of AR-1 and PR-2 in the reference species *Hyla chrysoscelis*. These authors noticed that there were no keratodont rows in the final oral configuration of *D. sarayacuensi* larva. Nevertheless, they also stated that the apparent ridge for P-2 of *D. sarayacuensis* persisted as a strongly pigmented ridge throughout ontogeny. Keratodonts may decolorize (or fall out) for many different reasons whereas ridges persist (see Knapp and Morgan, 2006; Orrico et al., 2007 and references therein). Thus, it is possible that the larvae studied by Santos et al. (1998) and Pugliese et al. (2000) had no keratodonts or if these decolorized or fell out.

  - 0: Rows absent.
  - 1: Rows present.

- **176. Posterior labial tooth rows, number.** (Additive)

  Modified from the literature. Araújo-Vieira et al. (2019) character 141.

  - 0: One.
  - 1: Two.
  - 2: Three.

- **177. Sheath of thickened tissue in the basal portion of the tail muscle and adjacent fins.**

  Modified from the literature.

  Faivovich et al. (2005) hypothesized the presence of this sheath as a possible synapomorphy for the *Dendropsophus marmoratus* species group based on Peixoto and Gomes (1999) drawings of *D. nahdereri* larva and by O. L. Peixoto confirmation in a personal communication cited in Altig and McDiarmid (1999). However, Kaplan (1994) draws a similar sheath in *D. stingi* larva too (his fig. 5A).

  The studied specimens showed individual variation within this character. Since many terminals were scored based on data from the literature, it was not possible to assure that the layer was truly absent, if the source just did not explicitly mention it. We were able to examine collection lots of *Dendropsophus minutus* larvae that either had or lacked the sheath. We agree with Altig and McDiarmid (1999) that fixation artifacts could affect this layer. To the naked eye, a similar sheath is observed in *Kassina senegalensis* (Hyperoliid), *Hemisus marmoratus* (Hemisiotidae), *Lithobates sphenocephalus* (Ranidae) and various microhylids like *Gastrophryne carolinensis* (see Altig and McDiarmid, 1999), *Stereocyclops incrassatus* (see Altig and McDiarmid, 1999), *Dermatonotus muelleri* (see Lavilla, 1992) and *Elachistocleis* spp. (VGDO pers. observ.).

  Haas (2003), made histological sections of some of these species and found a double-layered dermis [see Haas 2003: ch. 13; figure 7]. In fact, Haas (2003), recovers the presence of a double-layered dermis as a synapomorphy of Microhylidae with reversals or independent origins on the other taxa. Haas (2003) also comments that other taxa presented a dermal thickness that was not coupled with the presence of double layers because frog larvae from some groups (e.g. phyllomedusines) have developed relatively thick dermal connective tissue but possess only a single layer. Haas (2003) had one *Dendropsophus* (*D. ebraccatus*) and scored this taxon as single-layered dermis.

  - 0: Sheath absent.
  - 1: Sheath present.

- **178. Tail fin, coloration.**

  Modified from the literature. Grant et al (2006) character 87.

  - 0: Uniformly brownish, mostly ground color.
  - 1: Zebra like, with black or dark brown bars separated by semitransparent ones.
  - 2: Blotched or marbled.
  - 3: Completely semitransparent; unpigmented.

- **179. Tail fin, relative heights.**

  Taken from the literature. Duellman (1970) character TT.

  Different tail fin heights have been associated with different ecomorphological guilds (see Altig and Johnston, 1989). Almost all terminals examined herein have larvae that dwell in standing, large water bodies; exceptions are *Phyllodytes* spp. (phytotelmata) and some species of *Scinax* of the *S. catharinae* clade (either rheophilous or phytotelmata). Although the ecomorphological guilds are not congruent with phylogenetic groupings, at a smaller scale, they can reflect the historical relations between some taxa or suggest characters that can be used to retrieve such information. Some of the species examined had symmetrical and others had asymmetrical tail fin heights but dorsal and ventral fins seem to vary independently. Therefore, score them in relation to one another does not seem at a first moment indicated (due to character interdependence). Possibly, the ideal scoring would be to create two characters about the development of each fin. However, it was impossible to determine with exactitude different states of "developed" and "non-developed" tail fins.

  - 0: Dorsal clearly shallower.
  - 1: Equal or subequal.
  - 2: Ventral clearly shallower.

- **180. Dorsal coloration.**

  Santos et al. (1998) noticed a pair of paramedian yellow or cream stripes in the larvae of *Dendropsophus microps* and *D. giesleri*. The larva of *D. rubicundulus* also presents these stripes (Pugliese et al., 2001).

  - 0: Without a pair of paramedian yellow or cream stripes.
  - 1: With a pair of paramedian yellow or cream stripes.

- **181. Tail fin, initial lateral profile.**

  Laterally, tails can start at acute angles of about 30 degrees or less, or less acute angles (about 45 degrees). Usually, the first portion of low profile dorsal tail fin is even slightly concave.

- 0: Dorsal tail fin initial lateral profile ≤ 30°.
- 1: Dorsal tail fin initial lateral profile ≥ 45°.

- **182. Larval nostril, position.**

  Nostrils of *Dendropsophus* larvae are directed frontally (margins of the nostril are parallel to the frontal plane. In more advanced *D. molitor* larvae (>Gosner's stage 40), the nostrils become dorsolateral albeit still directing forward. We conclude that nostrils position and orientation are independent. This character was scored for less advanced individuals. Examined tadpoles of *Scinax acuminatus* also presented dorsolateral, anteriorly directed nostril openings.

  - 0: Dorsolateral.
  - 1: Frontal.

- **183. Larval nostril, orientation.**

  - 0: Upwards (margins of the nostrils are parallel to the medial plane).
  - 1: Forward (margins of the nostrils are parallel to the frontal plane).

- **184. Larval nostril, shape.**

  Modified from the literature. Araújo-Vieira et al. (2019) character 133.

  Kenny (1969) noticed that the larvae of *Sphaenorhynchus* had a peculiar morphology with a prominent mesial flap that Cruz (1973) called "valved-shaped" nostrils in oposition to the more usual "kidney-shaped" nostrils of tadpoles. Faivovich et al. (2005) lists this character as a possible synapomorphy for the genus. Araújo-Vieira et al. (2019) scored this character as the presence of fleshy flanges on internal margins of the nostrils and suggested the presence as a synapomorphy for *Sphaenorhynchus*.

  - 0: Kidney-shaped.
  - 1: Valved-shaped.

- **185. Vent tube, position with respect to the ventral caudal fin.**

  Taken from the literature. Faivovich (2002) character 75.

  - 0: Dorsal to the margin of the lower fin.
  - 1: At the margin of the lower fin.

ADULT VISCERAL MORPHOLOGY

- **186. Myocardium, pigmentation.** (Figure SI11)

  There is extensive variation on visceral melanophore pigmentation and intraspecific distribution on many anurans (e.g. Cei, 1980; Grant, 2004; Franco-Belussi et al., 2009). Although some species seem to present variation on the degree of pigmentation associated to the reproductive cycle (Moresco and Oliveira, 2009), others present ontogenetic variation (Grant, 2004). It seems that pigmentation of different organs is independent (see data of Franco-Belussi et al., 2011). Also, the variation found by Franco-Belussi et al. (2011) is somehow in contrast with the one found by Grant (2004). While Grant (2004) found that pigmentation polymorphism is rare (in Dendrobatid testes), Franco-Belussi et al.

(2011) could find up to three of their categories in the same organs of different individuals. Nevertheless, testicular pigmentation was consistent between *Dendropsophus* individuals.

Franco-Belussi et al. (2009) also presented a protocol that assign states based on the differences in the intensity of pigmentation with four categories ranging from 0 (no pigmentation) to 3 (completely black). The difference between their categories 1 and 2 is somewhat subjective and non-mutually exclusive since these two are described as overlapping fractions of blackish intensities of (>0% to <50% and >50% to <100%) in the subject organ. Literature scoring melanophore intensity variation was usually in three states as did by Grant et al. (2006). Scoring here was based on the material at hand, avoiding the use of literature data due to the subjectivity involved in scoring some of these categories. In addition, due to the possibility that these pigmentations are seasonal (Franco-Belussi et al., 2009), maximum intensity found is scored; the same rationale used for glandular structures.

  - 0: Melanophores absent.
  - 1: Melanophores present.

- **187. Pericardium, pigmentation.**
  - 0: Iridophores absent.
  - 1: Iridophores present.
- **188. Lung, pigmentation.**

There were some differences in pigmentation levels of the lungs among different species of *Dendropsophus*. Franco-Belussi et al. (2011, figure 1) provides a good example of the maximum differences seen. However, because melanophores were distributed sparsely, the lungs are mainly transparent. Differences between the states were not as clear as the ones seen in other organs. Thus, we took a conservative approach and scored only presence and absence of melanophores.

  - 0: Melanophores absent.
  - 1: Melanophores present.

- **189. Liver, coloration.** (Figure SI12)

States were assigned with preserved individuals. Possibly, there are more states within state 1.

  - 0: Sandy yellow, with sparse melanophores.
  - 1: Dark.

- **190. Liver, size.** (Figure SI12)

The liver portion that reaches the pylorus is the posterior portion of the left dorsal lobe. In some species, the liver is so large and caudally extended that its caudal most portion reaches the level of the pylorus.

  - 0: Covering only a small part of the stomach.
  - 1: Reaching the pylorus.

- **191. Liver, visible liver lobes in ventral view.** (Figure SI12)

The liver presented four lobes in all specimens examined. However, the cranial lobes (left and right) are disposed differently. Thus, when looking in ventral view, in species of the *Dendropsophus microcephalus* group, *D. riveroi* and in the analyzed specimens of *Lysapsus limellum* both dorsal lobes are hidden by the ventral ones. In other species, the left dorsal lobe is visible.

  - 0: Two.
  - 1: Three.

- **192. Liver, relative size of lobes.** (Figure SI12)

  Modified from the literature.

  Hedges (1990 "1989"-b; 1990 "1989"-a) and Hedges et al. (2008) propose that species from the subgenera *Diasporus, Euhyas* and *Syrrhophus* present the left lobe of the liver long and pointed whereas the right lobe is smaller and rounded for the remaining species of Brachycephaloidea (Padial et al., 2014). However, "Liver shape has yet to be surveyed extensively outside of Eleutherodactylidae" (sensu Hedges et al., 2008).

  Hedges et al. (2008) state: "Distinct characteristics of liver shape have been proposed as synapomorphic for each of the subgenera". However, the optimization of this character is still restricted to few of their clades and many of their proposed groups lack information about their character states (e.g. all their outgroups). For this character, both lobes of the sides of the liver are considered together. While right lobes were similar in size, left lobes presented more variation. Usually, in livers where the left size is larger, its dorsal and ventral lobes are subequal. The exception if *Sphaenorhynchus prasinus* whose ventral lobe is smaller than the dorsal one.

  - 0: Subequal.
  - 1: Left clearly larger.

- **193. Kidneys posterior cardinal sinus.**
  - 0: Melanophores absent.
  - 1: Melanophores present.

- **194. Mesenterium.** (Figure SI12)
  - 0: Melanophores absent.
  - 1: Melanophores present.

- **195. Testes, size.**
  - 0: Small testes; not larger than half kidney length.
  - 1: Large testes; about the same length of the kidney.

- **196. Testes, pigmentation.** (Additive; Figure SI12)

  Modified from the literature. Faivovich (2002) character 37; Grant et al (2006) character 67.

  Taylor ("1939"[1940]) proposed the presence of a black mesorchia as a diagnostic character for his genus *Microbatrachylus* (= *Craugastor*). Later, Hedges et al. (2008) proposed the presence of a black mesorchia as a possible synapomorphy for the *Craugastor* (*Craugastor*) *mexicanus* Species Series (where the species of *Microbatrachylus* are currently), given the results of Hedges (1990 "1989"-b; 1990 "1989"-a) and Lynch (2000). See Grant's et al (2006) discussion on evidence of additivism for this character.

  - 0: White; without melanophores.
  - 1: Cranially marbled.
  - 2: With sparse melanophores; completely marbled.
  - 3: Completely black.

- **197. Intestinal visceral peritoneum, pigmentation.** (Figure SI12)
  - 0: Clear; transparent.
  - 1: Iridophores present.
- **198. Rectum, pigmentation.** (Additive; Figure SI12)

  Taken from the literature. Grant et al. (2006) character 66.

  See Grant's et al (2006) discussion on evidence of additivity for this character. In state 2, different from Grant's et al (2006) figure 51, is not possible to recognize individual melanophores (as black dots) on the edges of the melanic area. Histological studies of the melanic viscera of *Dendropsophus minutus* and species that share this character state are still lacking. Thus, it is not completely clear if these recta are black due to pigmentation or by the deposit of black, non-pigmentary, metabolites, such as iron (C. Taboada pers. com.).

  - 0: Without melanophores.
  - 1: With sparse melanophores; marbled.
  - 2: Completely black.
- **199. Urinary bladder, pigmentation.**
  - 0: Clear, transparent.
  - 1: Iridophores present.

Natural history

- **200. Site of clutch deposition.**

  Taken from the literature. Lynch (1971); da Silva (1998) character 116; Faivovich (2002) character 85; Grant et al. (2006) character 107.

  Although information about the reproductive mode for *Dendropsophus* species has been recorded for a long time (e.g., Lutz, 1947), data for nearly half of the species assigned to the genus is lacking (Touchon and Warkentin, 2008). Some species are known to lay eggs directly on water or above it, perched on branches or leaves and this ability to lay terrestrial clutches was proposed by Bastos and Pombal Jr. (1996) to be a diagnostic character of the *D. decipiens* group.

  There are only two known cases of phytotelmata breeding in Dendropsophini. Mageski et al. (2014) suggested that *Dendropsophus haddadi* can use bromeliads as a site for egg clutch deposition in the absence of more permanent lentic water bodies and that it could demonstrate the reproductive mode 6 of Haddad and Prado (2005); i.e., eggs and exotrophic bromeligenous (sensu Peixoto, 1995) tadpoles. In this case, the clutch is still terrestrial for the purposes of the present character. Ferreira et al. (2015) described a new species (*Dendropsophus bromeliaceus*) whose exotrophic tadpoles were found in the rainwater accumulated inside bromeliads. However, they explicitly state that they have not found amplectant pairs or eggs and it is therefore not possible to assign a state of the present character for this species. Alternatively, *Phyllodytes* species actively place its clutches in the water of the phytotelmata environments where tadpoles develop. Therefore, *P. luteolous* has been considered as an "aquatic" placer.

- 0: Aquatic.
- 1: Terrestrial (perched on branches or leaves).

BIOCHEMISTRY

- **201. Pterorhodin, occurrence.**

Modified from the literature.

A green dorsum in life that changes to violet in alcohol has been proposed as diagnostic character and synapomorphy for the *Dendropsophus rubicundulus* clade (Faivovich et al., 2005). There are other groups where a similar change occurs (*Rhacophorus*: Rhacophoridae; Bordoloi et al., 2007; *Boophis*: Mantellidae; Wollenberg et al., 2008). It is not known whether or not the pigments involved are the same.

Some specimens of other species such as *Dendropsophus bipunctatus* (see Carvalho-e-Silva et al., 2003), *D. branneri*, *D. decipiens* (pers. obs.) and *D. minusculus* (Rivero, 1971) present a pinkish brown tint in preservative. This tint is similar to the violet found in poorly preserved specimens of the *Dendropsophus rubicundulus* clade species. These were treated as distinct character states because the exact tint was not the same. The present character state reflects the green-to-violet metachromatic transformation that is different from the brown/yellow-to-pink one in the species mentioned. KOH solutions at 1% determined that the pink pigment of some *Dendropsophus* species likely is pterorhodin (a formal test is still lacking). It is different from what is observed in Phyllomedusinaes where the pigment exudes from the skin sample (Bagnara and Obika, 1965; Misuraca et al., 1977). In *Dendropsophus* species where it is present, it only turns pink without exudation.

- 0: Pterorhodin absent.
- 1: Pterorhodin present.

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Appendix S9.

Potentially informative variation not evaluated in this study.

Due to time and resources constrains it was not possible to access all sources of evidence for the analysis. Myology (for instance) has been a source of important synapomorphies for a number of anuran clades (e.g., Drewes, 1984; Faivovich, 2002; Araújo-Vieira et al., 2019) but has been used quite lightly in our study, in part for the reported absence of variation within *Dendropsophus* (e.g Burton, 2004). Nevertheless, we strongly advocate that all sources of evidence must be checked and are potentially informative. In this section, we discuss some instances of observed phenomic variation where we had difficulties to propose reliable homology hypotheses.

Adult coloration in life

Much attention has been given, in a taxonomic context, to colors of living specimens (e.g., Duellman, 1970). With the exception of the *Dendropsophus minimus* group, all groups (and clades) recognized so far had at least one diagnostic trait referring to the colors of living specimens. The colors (specially the flash colors in the hidden surfaces of the thighs, shanks, and webbings) range from bright red (e.g., *D. anceps*) to black (e.g., *D. manonegra*). Many species present these same areas with aposematic color combinations (e.g., the yellow and black webbings of *D. marmoratus*).

At the same time, many species present have coloration. It seems quite straightforward to infer relationships between *Dendropsophus* species based on its colors; however, the underlying homology assessments are quite difficult. To avoid a subjective identification of colors, one could score the underlying pigment variation (as we have done for Pterorhodine). However, this requires chemical, cytohistochemical, or spectroscopical techniques (e.g., Bagnara et al., 1973; Misuraca et al., 1997), which would require additional knowledge, time and resources, not available during the development of this manuscript. Also, different regions of the body present different colors in different species.

Males of some species of *Scinax* become completely yellow when in reproductive activity (e.g., Pombal Jr. and Gordo, 1991; Faivovich, 2005). Breeding mode color change seems widespread in frogs (Bourke et al., 2011) and also happens in some species of *Dendropsophus* like *D. microps* (e.g., Maffei et al., 2009). Yellow colors are usually a result of carotenoid based pigments and have been shown to be present in reproductive males of some species of Hylini (see Richardson et al., 2009). The homology assessment of metachromy is also difficult because it depends on the observation of a specific moment of the species life history and the physiological mechanism behind it—not the change itself. There are many physiological pathways for color change (e.g., Bagnara, 1963; Bagnara et al., 1973; Bagnara, 1974; Iga and Bagnara, 1975); none known for any Dendropsophini.

Adult coloration pattern

Coloration patterns are independent of the exact colors they are constituted. Instead, the relations between different colors define them; i.e. both clear blotches over a dark base or vice-versa define a blotched pattern. General color is somewhat constant through individuals of a same species. Coloration pattern however, may be not.

Cochran (1955) was the first to use a coloration pattern (presence of dorsolateral stripes) to group *Dendropsophus* species. Later, other patterns were described and used as diagnostic characters for a number of *Dendropsophus* Groups or to relate species (e.g., Bokermann, 1964; Duellman, 1982; Kaplan and Ruiz-Carranza, 1997; Goin, "1959"[1960]).

Different specimens of some *Dendropsophus* species may present many, highly distinct, coloration patterns. In fact, Cochran (1955) classified the amount of individual variation as “astonishing”. Possibly, the extreme case is the “*Hyla favosa*” pattern in species of the *D. leucophyllatus* group. Titus et al. (1989) demonstrated that the "giraffe" pattern of "*H. favosa*" was a variant pattern of *D. leucophyllatus*. Individuals of other species from the *D. leucophyllatus* group may also present this pattern or a similar one (Gomes and Peixoto, 1991; Rodriguez and Duellman, 1994; Jungfer et al., 2010).

Some species of the *Dendropsophus microcephalus* group also present high levels of variation in their dorsal pattern. As examples, individuals of *D. juliani* depicted in Figures 1 and 3 of Moravec et al. (2006) represent two of the most common patterns (homogeneous vs. blotched dorsum).

Although hitherto not reported in species of *Dendropsophus*, ontogenetic variation could occur. Izecksohn (1996) and Izecksohn and Carvalho-e-Silva (2001) pointed out that *Xenohyla truncata* juveniles present a distinct frame that largely resembles the one found in some species of *Dendropsophus* that disappears in adults. In fact, the diagnostic character for *X. eugenioi* (Caramaschi, 1998), the second species of the genus, is that adults maintain those stripes (Caramaschi, 1998).

Duellman and Thomas (1996) state that their *Dendropsophus acreanus* specimens had an “anterior X-shaped mark on the dorsum separate from the chevron [mark]”; *D. marmoratus* specimens had “a brown Y-shaped mark in the occipital region”. Cochran (1955) used as diagnostic character for the *Dendropsophus marmoratus* Group a marbled color pattern in the back. Bokermann (1964) referred to this pattern as “lichenous”. It is unclear what the relation between lichenous and those marks described by Duellman and Thomas (1996) could be.

Dendropsophus elegans has been described as having a dorsal pattern that resembles a “frame” (e.g., Izecksohn and Carvalho-e-Silva, 2001) surrounding a darker square. Gomes and Peixoto (1991) demonstrated that the shape and extension of the “framed” blotch could vary in a given population through a large, but gradual, variation.

Dendropsophus minutus has many synonyms (at least six according to Frost, 2020). Peters (1872) original description states that the dorsal pattern of this species is an hourglass (*sanduhrförmige* in the original). *Hyla bivittata* (Boulenger, 1888) was considered a synonym of *D. minutus* by Cochran (1955). Boulenger’s (1888) specimens had “two parallel darker bands along the back... widening anteriorly and sometimes uniting on the interorbital region...” (see Fig. 18). Cardoso and Haddad (1984) corroborated the co-specific status of these populations demonstrating that advertisement calls were not significantly different. At a first glance, the relation between the chevron marks and dorsolateral lines is not obvious. However, a hypothetical additive series, a transformation from the frame with two dorsolateral stripes—found in species like *D. bokermanni*—needs one topological change that leads to a “frame” pattern—like the one in *D. elegans*. A second one, leads to an “hourglass” pattern—as in *D. minutus*—and the last, to the “chevron” pattern found in many species of the *D. microcephalus* group. Within that logic, it becomes possible to find these lines in other kind of dorsal patterns (ike lichenous). Therefore, different dorsal markings could be understood as shape variations of the lines that compose them, even in lichenous species. It seems clear that these different patterns may house valid transformation series; the delimitation of states remains unsolved.

Shape variation is usually treated with the use of landmark-based analyses (Monteiro and Reis, 1999). A method that allows the optimization of landmark has been developed (Catalano et al., 2010; Goloboff and Catalano, 2011).

The examples used in this section are quite simple; the whole set of dorsal pattern variation is not. While comparisons between patterns within a landmark optimization scenario seem straightforward, it is so only in the case of patterns constituted of continuous lines. Apart from completely homogeneous dorsal patterns, other patterns (as the "*Hyla favosa*" pattern) can be understood as anastomotic connections of the dorsolateral lines with numerous connections what would generate a multiplicity of landmarks.

Morphometry

Species of the *Dendropsophus rubicundulus* clade seems to have a longer head (from the midpoint of a line that connects dorsally the posterior borders of tympanum to the tip of the snout). In addition, the relative width of the toes discs seems different, especially when only the disc of the fourth toe is considered. While *D. acreanus* and *D. marmoratus* have large digital discs (even when compared to closely related species like *D. seniculus*), species of the *D. rubicundulus* clade have small digital discs.

Some osteological features also could potentially be informative under the reasoning of morphometric characters. Most of this kind of variation that is already found could be translated into discrete characters, even if tentatively (e.g., relative widths of the sacral diapophysis; c. 93).

Pugliese et al. (2000) and Carvalho-e-Silva et al. (2003) suggested some diagnostic characters of the *Dendropsophus decipiens* group. Two were of morphometric nature: the eye position in relation to body in larvae (eyes almost in the middle of the body length in the *D. microcephalus* group vs. in the anterior third in *D. decipiens* group) and the point of origin of the dorsal fin (starting at the posterior third of the body in the *D. microcephalus* group vs. starting at the end of the body third in *D. decipiens* group). However, confidence limits between the states of these characters are not obvious and an approach treating them as continuous seems more appropriate.

Chromosome morphology

All species assigned to *Dendropsophus* today that have known karyotypes, have a diploid number of 30 chromosomes (Duellman and Cole, 1965; Skuk and Langone, 1992; Kaiser et al., 1996; Medeiros et al., 2013; Suarez et al., 2013) and that number is a synapomorphy for the genus. The most closely related species that presents such number is *Litoria angiana* (Duellman, 1967). However, the case of *Litoria angiana* seems an exception in Pelodryadinae caryological context. Other specimens of this species as all other Pelodryadines with known karyotypes present a diploid number of 26 with the exception of *L. infrafrenata* with 24 (see Menzies and Tippett, 1976). The presence of B-chromosomes has been reported in species of *Dendropsophus* (Medeiros et al., 2006) and is also a potential evidence source.

Unfortunately, it is quite hard to assess homeology with species with different diploid number. Although some variation in centrometric indexes between *Dendropsophus* species has been described (e.g., Skuk and Langone, 1992; Gruber et al., 2005) there is no reliable way to compare this variation with variation found for other species (Medeiros et al., 2013; Suarez et al., 2013). As discussed by Medeiros et al. (2013) small differences in numeration decisions can deeply influence the final karyotype descriptions of *Dendropsophus* species. There is also a large variation on the number of NOR sites, but the difficult homeology also hinders its interpretation (Suarez et al., 2013).

Adult osteology

Although the bulk of morphological characters is derived from the morphology of bones and cartilages of adult specimens, there are certainly many more characters to be assessed there. Since character assessment is biased to ingroup variation many characters that are informative (or autapomorphic) only for few outgroups were not considered (e.g., it would be possible to include many characters more that would be synapomorphies for Pseudini).

In addition, we were not able to find a proper coding scheme for some of the variation found. Although not included in the final matrix, we list them below as a reference for future work.

A) *Degree of prootic dorsomedial ossification*.

The prootic advances dorsomedialy over the *tectum synoticum* and different levels of development were seen. However, it was not possible to assign states that would be unequivocally distinct.

B) *Number of foramina piercing the prootic.*

There are four foramina related to the prootic: optic, prootic, trochlear and oculomotor (Trueb, 1970; Duellman and De Sá, 1988). Relative position, number nerve-foramen independence—in some, nerves can exit together by a single foramen—vary in hylids (Trueb, 1970; da Silva1998). *Scarthyla* was described as having four foramina, but different specimens presented different states. In addition, a specimen of *Xenohyla truncata* (MNRJ 63113) has a distinct state in each prootic. Until more individuals per species are clear-and-stained, we refrain to insert this information in the matrix.

C) *Squamosal zygomatic ramus length.*

Various authors coded variation in the length of the zygomatic ramus of the squamosal. However, Lynch (1971), da Silva (1998), Nuin and do Val (2005), Grant et al. (2006), and Araújo-Viera et al. (2019) found much more variation than the one found herein. Barg (2003) coded a relation between the otic and the zygomatic rami. The obvious problem of this coding is if two species can present the same state with different configurations (large *vs*. large and small *vs*. small).

Although there were species with knob-like squamosals (e.g., *Sphaenorhynchus lacteus*) and others with squamosals that reached the eyeball (e.g., *Scinax littoralis*) and other that would fall in a category in between (e.g., *Dendropsophus bipunctatus*), it was not possible to find a landmark that wouldn't suffer from the same problem of Barg's coding. Possibly, given the variation involved in the structures that provide the landmarks, a meristic or landmark approach would be better.

D) *Shape of tympanic* annulus *margins.*

There seems to be a variation in the shape and width of the tympanic *annulus* margins, both anterior and posterior. Some species have tympanic *annuli* with vertical posterior margins (e.g., *Dendropsophus oliveirai*), others have deeply curved posterior margins (e.g., *Sphaenorhynchus prasinus*), and others have intermediary curvatures (e.g., *D. melanargyreus*). Both margins widths vary from thin (e.g., *D. oliveirai*) to wide (e.g., *D. melanargyreus*). Therefore, it was not possible to assign states that would allow unequivocal specimen assignments—see also comments on tympanic ring external visibility above.

E) *Pars ascendens plectri.*

The *pars ascendens plectri* of the columella is described as a small and thin cartilage connection between the *pars externa plectri* and the *crista parotica* (Wever, 1985). In many specimens however, it was not stained with alcian blue. It is not clear if this is an effect of a poor general staining (as is the case for *Dendropsophus seniculus*). Many times, only a projection of the *pars externa plectri* was stained while the rest of the *pars ascendens plectri* was not, the remaining portion was visible only through refraction. The only case where it was surely absent was in *Phyllodytes luteolous* because the specimen was well stained and the *pars externa plectri* did not present any projection. The delicate nature of the structure and the relative difficulty of staining prevented us to confidently score its presence for the time being.

F) *Relative length of parasphenoid cultriform process anterior margin.*

There is some variation in the size of the parasphenoid cultrifom process within Anura (see Lynch, 1971). da Silva (1998) coded variation based on the relation of anterior end of parasphenoid cultrifom process and *foramen* orbitonasal. Scott (2005) coded the variation on this bone also, using a distinct landmark where different states of parashenoid cultirfom processes lengths were scored in relation to the orbit. Herein, although all parashenoid cultirfom processes seemed of different lengths (although somewhat similar) all reached the foramen orbitonasal and da Silva (1998) does not apply. In addition, parashenoid cultrifom processes lengths of *Sphaenorhynchus* spp. and of *Dendropsophus soaresi* and *D. triangulum* seem the extremes of a *continuum*.

G) *Parasphenoid cultriform process width at midpoint.*

It was clear that in some species, the parapshenoid cultrifom process does not covers all chondrocranium dorsal to it (e.g., *Scinax berthae*; specimen CFBH 17372, while in others it does (e.g., *Scinax fuscovarius*; specimen CFBH 21334). However, it was not possible to determine if a given morphology was a product of a wide parapshenoid cultrifom process or a narrow—or poorly stained—chondrocranium.

H) *Vertebra VII transverse process.*

Some outgroups (*Xenohyla, Pseudis*, see matrix) presented elongated Presacral VII transverse processes. Elongated processes are longer than the vertebral length; short, are shorter (measured between the pre and post zygapophysis). However, both *Dendropsophus elegans* and *D. triangulum* were instances were these measurements were equal. Of course, one could simply assign an extra state; we see this as an evidence of a *continuum* and believe that this character, although potentially informative, deserves a different approach.

I) *Urostyle transverse processes.*

The presence of transverse processes in the urostyle may be considered a signal of different ontogenetic pathways for the formation of the sacrum+ urostyle joint (see Pugener and Maglia, 2009). However, if specimens of the Dendropsophini tribe follow the pattern proposed for *Acris crepitans* Baird, 1854 (as a model for Hylidae) the urostyle should not bear transverse processes (according to the scheme of Pugener and Maglia, 2009) and its presence should be interpreted as a teratology. One evidence favoring the latter hypothesis is that one examined specimen of *Dendropsophus melanargyreus* (ZUEC 10191) has only one process (the left). Also, the shape of the referred processes is different between distinct taxa that present it within *Dendropsophus*. While in *D. nahdereri* the processes are large and obvious while in others (like *Sphaenorhynchus prasinus*; CFBH 22639) it is quite small. We rather not score this character until developmental series are available.

Lymphatic **septae** *and sacs*

Although there are a few characters in the matrix dealing with lymphatic system variation, there still much variation that was not scored because once the skin is separated from the body it is often impossible to recover information from lymphatic *septae* and sacs. In the species of *Pseudis* and *Lysapsus* analyzed here, it seems that there are more lymphatic *septae* between the muscles and the skin. Variation on fixating points and extension should be found.

Adult external morphology

Adult external morphology has been widely used as a taxonomic and systematic tool (e.g., Duellman, 2001a; Duellman, 2001b). Although we explored this source of evidence in the matrix, more characters could arise from it. Below, we call attention to some characters that were important in *Dendropsophus* literature but we were unable to arrange variation into clear, distinct character states.

A) *Overall head shape in dorsal view.*

Dendropsophus species have rounded heads but this morphology seems a composite of various characters as the shape of the nasals and the shape of the maxillary arc (itself composed by up to three bones). However, it was not possible to determine exactly an osteological basis leading to this morphology. Species from the *D. rubicundulus* clade have a longer head in comparison to other *Dendropsophus*, which could be described as triangular; but not as triangular as in *Xenohyla* for instance. Producing a fine limit for this variation thus seemed arbitrary. Possibly a landmark optimization (as described in Catalano et al., 2010; Goloboff and Catalano, 2011) would be more appropriate.

B) *Dorsum overall color in preservative.*

The dorsal color has been widely used in the taxonomy and systematics of *Dendropsophus* species (e.g., Motta et al., 2012; Orrico et al., 2013; Rivera-Correa and Orrico, 2013). Many species were phenetically grouped by its color pattern (see how Lutz, 1973 arranged Brazilian species of hylids) and those phenetic groups were the ground where Faivovich et al. (2005) erected relationship hypotheses for species not included in their analysis. Also, this is possibly the one information that is always present in species descriptions, accounts, etc. Therefore, it seemed important to use this information on the present analysis. We surveyed literature for dorsal color and pattern data and compared the results with our observations on the specimens. Cochran (1955) noticed that *Dendropsophus* color patterns presented high levels of individual variation; an approach based on overall dorsum ground color could circumvent this variation allowing the creation of distinct unique character states.

The survey revealed a very complex scenario. While some differences seemed clear (gray or and yellow/brown dorsi), many alternative states appeared within the individual variation (e.g., most specimens of *Dendropsophus molitor* and *D. meridensis* are green while the remaining are brown). In some cases, the definition of a ground color was not always easy. As an example, many specimens of *D. oliveirai* are yellow with bright yellowish-white interocular and dorsolateral stripes (i.e. a "frame" pattern see Cochran, 1955), many were brownish-yellow and some directly brown (see specimens CFBH 19316–19317; 19327–19334; 19336); usually, the larger the lot, the easier to find intermediate states of coloration.

Nevertheless, at least gray and yellow/brown dorsi seemed candidates for reliable character states but a close inspection revealed a more complex scenario. "Gray" species in fact present a dorsum composed by areas of many hues of black and brown, making it difficult to differentiate it from a brown character state. ”Gray” species are usually described in the literature as “Lichenous” (e.g., Lutz, 1973) due to the marbled pattern of their dorsi. Although this marbled pattern seems a variation of the frame pattern delimitate clear independent states for the many frame patters was not possible.

Although there is a clearl relationship between phylogenetic proximity and overall dorsal coloration (groups retrieved in the present contribution usually include species with similar dorsal colors), the amount of variation many times seemed continuous. We remark that if future studies can develop a way to confidently score the variation found in discrete states, dorsum color will certainly prove itself a valuable source of evidence.

C) *Tympanic annulus visibility.*

A number of authors used tympanic annulus to demonstrate variation among various groups. When it comes to *Dendropsophus*, previous authors noted that species of different groups had different tympanum and tympanic ring conditions. Nevertheless, like tympanic membrane, confusion is widespread when it comes to definitions.

Duellman and Crump (1974) stated that frogs of the "*Hyla parviceps*" group have a visible tympanum but tympanic annulus indistinct or absent. However, studied specimens of *Dendropsophus microps* and *D. parviceps*, presented distinct tympanic rings while specimens of *D. timbeba* had not. Likely, Kaplan (1991) stated that *D. garagoensis* does not have an externally visible tympanic annulus although from his text it is possible to infer that a tympanic membrane, at least, should be visible externally in this taxon. Although Duellman (1969) described *D. carnifex* as having an "indistinct or concealed" tympanum, Duellman and Trueb (1983) stated that *D. carnifex* had a visible tympanum but the tympanic annulus was indistinct.

Evident tympanic rings were considered to happen when the structure limits (inner and outer margins of tympanic ring) were clear. However, it was not possible to confidently assign an evident/concealed state; fixation seemed to play some role in the distinctiveness of this character. Until a more reliable way to assign character states for tympanic ring visibility is proposed, we leave this variation as potentially informative.

Glandular morphology

Glandular characters were coded based on external observation and occasionally with gross dissection only. Clearly, the use of histological techniques can provide interesting insights.

Some glandular areas were not addressed in the present study. Two of them deserve consideration: A sheath of glandular tissue around the toes, especially toe IV and acini found in the ventral surfaces of the shanks of *Dendropsophus oliveirai*.

The sheath of glandular tissue around the toes is found in several species, especially around toe IV. In *Dendropsophus* it is a clear patch, visible to the naked eye in some individuals. In other taxa, it is usually not as thick and many times is hindered by the dark coloration of the skin of the feet. In these cases, the sheath is still recognizable as a hard patch of tissue surrounding the toe. It was not possible however, to assign clear independent states, especially for the outgroup taxa.

The acini found in the ventral surfaces of the shanks of *Dendropsophus oliveirai* were not found in other species. These secretion-full acini were clearly visible in fresh specimens and it is possible that fixation artifacts could hinder their presence in other specimens and species.

Fat bodies

There are different areas were *Dendropsophus* species store fat bodies. The two most usual are the one caudal to the tympanic ring and the fat bodies of the reproductive system. Fat bodies can be found in other areas (in *D. molitor* and *Pseudis minuta*, there is a unidentified tissue body surrounding the trunk, linked to the fat stored behind the tympanic ring that could also be fat). There seems to be variation in the shape of the fat bodies of the reproductive system.

The amount of stored fat also varied, specially the ones associated with male mesotestes. It is reasonable to assume that since fat bodies are en energy reserve, males collected in different moments of the breeding cycle could present different amounts of stored fat in these bodies.

General internal anatomy

Most of the characters that relate to the anatomy of internal organs are based on basic morphological observations. Details on fine morphology of systems (urinary; respiratory; circulatory; etc.) are almost completely absent for Hylinae and should include many more characters. As an example, there are different pathways of the *m. pectoralis portio axilaris*. In some species (*e.g., Dendropsophus molitor*), the *m. pectoralis portio axilaris* is entangled by (at least) the *arteria brachialis*. Other species, like *D. rhodopeplus*, present a free *m. pectoralis portio axilaris* i.e. not entangled by the *arteria brachialis*. Species that were coded with the free condition were usually smaller and clearer species. It is therefore possible that all species of *Dendropsophus* present a *m. pectoralis portio axillaris* entangled by the *arteria brachialis* and the difference would be the pigmentation of the artery. It was not possible to be sure if we have accidentally sectioned arteries of some terminals scored as “free”.

Larval morphology

Most of the character states regarding larval morphology were retrieved from literature descriptions because for most species, there are few known larval individuals. The number of species with larval material available for partially destructive procedures such as clear-and-staining and for myology studies is even smaller. Nevertheless, based on literature, some comments are in order.

A) *External morphology.*

Altig and McDiarmid (1999) credit Duellman (1978) for the original labeling of larvae with tails that narrow abruptly to a distinct *flagellum* as xiphicercal. The flagellum is the terminal part of the tail muscle and its associated reduced fins and this set may undulate independently from the rest of the tail (Altig and McDiarmid, 1999).

Kenny (1969) observed that living *Sphaenorhynchus lacteus* tadpoles could beat the tip “independently of the rest of the tail and the animal is capable of maintaining itself in mid-water" although the tail is not xiphicercal. This is similar to what is observed in larvae of some species of *Scinax* (VGDO pers. obs.).

Larvae of *Pseudis*, *Xenohyla* and most *Dendropsophus* have xiphicercal tails (see Kenny, 1969; and Izecksohn, 1996). While *Scarthyla goinorum* has a deeply modified larva (Duellman and De Sá, 1988), *Sca. vigilans* has a *Pseudis*-like larva (Suarez-Mayorga and Lynch, 2001; Lynch, 2006; Lynch and Suarez-Mayorga, 2011).

Other hylid larvae have different tail movements and comments on this are scarce. Phyllomedusidae, *Kassina* and *Xenopus* larvae also have a flagellum (Altig and McDiarmid, 1999) although the tail is not xiphicercal and fins depths are largely different.

Another character not evaluated was the presence of dark longitudinal stripes on the larval hind limbs that Kaplan and Ruiz-Carranza (1997) proposed as a synapomorphy for the *Dendropsophus garagoensis* group. However, the original description of the character is not clear. Kaplan and Ruiz-Carranza (1997) described this character solely as “hind limb of larvae with alternate pigmented and unpigmented longitudinal stripes” (p. 243). It is clear that when describing the trait, Kaplan and Ruiz-Carranza (1997) used many larvae of different developmental states (see their pages 236 and 241); the exact developmental state which they based their figure 7 is not do not stated. It is clear that they used “old” larvae (their figure 7 clearly shows hind limbs with developed toe discs) but the view represented is neither obvious nor stated. In their figure 5, the longitudinal stripes are seen in larvae they classified at stages 35–38 (Gosner, 1960) but the staging does not seem correct. The depicted larva of *D. padreluna* has small hind limbs and is assigned to stage 38 while the depicted larva of *D. virolinensis* is assigned to stage 35 or 37 (the caption is not clear) and presents long hind limbs.

Anyway, it should be enough that larvae of stages above 35 (at least) presented the character state. The anatomical view required to access the character is also not provided. This is important because Kaplan and Ruiz-Carranza (1997)’s figure 7 depict the hind limbs of *Dendropsophus padreluna* and *D. virolinensis*. While the hind limb of *D. padreluna* is clearly depicted in dorsal view (their figure 7A), the view used to depict the hind limb of *D. virolinensis* is ventrolateral. While the hind limb of *D. padreluna* present longitudinal stripes in the shank and tarsus, the hind limb of *D. virolinensis* present one stripe in the thigh and clear shank and tarsus. Thus, it is not clear in which section(s) the character should be scored. Examination of *D. padreluna* larvae (lot JDL 28325) revealed a condition similar to the one found in all examined species where the hind limbs present different dorsal and ventral colors (and patterns). Therefore, we chose to avoid scoring this particular character until a better definition of its states is provided.

B) *Internal oral morphology.*

There are few[1] descriptions of internal oral morphology of larvae of *Dendropsophus* (Wassersug, 1980; Echeverria, 1997; Kaplan and Ruiz-Carranza, 1997; Vera Candioti et al., 2004; Dias et al., 2019). As noted by Faivovich et al. (2005), internal oral structures of *Dendropsophus* display an extreme reduction in all of them. This includes reduction of most internal papillation, of branchial baskets, of secretory ridges and secretory pits (or their absence) and also in the density of the filter mesh of the branchial baskets in comparison with other hylid larvae (Wassersug, 1980). Other genera, such as *Scinax*, do not present such levels of reduction (e.g., Alcalde et al., 2011). Nevertheless, studies on the internal oral morphology of *Xenohyla* and *Sphaenorhynchus* are missing.

One possible explanation for these differences could be the ecological feeding habits of the species (Vera Candioti et al., 2004). While *Dendropsophus minutus* is known to have predatory habits (Peixoto and Gomes, 1997); *Scarthyla goinorum* probably feed on plant and algae (Duellman and De Sá, 1988) although it is not known which is the habit of *S. vigilans* that has a more “traditional” larva, in fact, resembling some species of *Pseudis* (Suarez-Mayorga and Lynch, 2001; Lynch, 2006; Lynch and Suarez-Mayorga, 2011). Nevertheless, *D. minutus* is also reported to feed on vegetal and algal matter (Echeverria, 1997).

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[1] Although *D. garagoensis* and *D. stingi* are mentioned in the captions of Kaplan and Ruiz-Carranza (1997) figures 8 and 10, it seems a mistake since they are not mentioned anywhere else in their paper in the context of larval oral morphology.

Faivovich et al. (2005), Vera Candioti (2007), and Dias et al. (2019) have already remarked that descriptions of internal oral features are still pending for various taxa and among them, various species of *Dendropsophus*. Based on the above comments, such data seems fruitful for characters. Also, it is abundantly clear that the thorough study of larval characters of *Xenohyla* will help assess the polarities of several characters (Dias et al., 2019).

C) Chondrocranium.

As seen above for internal oral morphology, few papers deal or describe chondrocrania of *Dendropsophus* species. In addition, descriptions are still lacking for *Sphaenorhynchus*, *Scarthyla* and *Xenohyla*.

The few available descriptions (Fabrezi and Lavilla, 1992; Vera Candioti et al., 2004; Dias et al., 2019) deal only with three species. Two (*Dendropsophus microcephalus* and *D. nanus*) are extremely similar both as adults and as larvae. Both have tall and large muscular processes; small trabecular horns and the width at mid-body (at the level of the suborbital bar) is smaller than the width at the level of the otic capsule among other distinctive characteristics. Possibly, this mid-body constriction could be related the violin-shaped body described by Duellman and Trueb (1983) for larvae of the *D. leucophyllatus* group. The third (*D. decipiens*) however, is remarkably different from the other two (Dias et al., 2019) and does not present the mid-body constriction. Given the phylogenetic placement of *D. decipiens* and that other genera do not present many of these features (Vera Candioti, 2007), it seems that once more descriptions are available, the study of the phylogeny of *Dendropsophus* will greatly benefit greatly from the study of chondrocrania.

D) *Larval myology.*

If larval internal oral morphology and chondrocrania of *Dendropsophus* are poorly known, larval myology is nearly unknown. There are only four species with larval myology information being one (*D. ebraccatus*) scattered in Haas's (2003) matrix, two (*D. microcephalus* and *D. nanus*) closely related, both summarized in Vera Candioti (2007), and the last is *D. decipiens* (Dias et al., 2019).

Dendropsophus larval muscles are as unique as their chondrocrania and many modifications seem related. An immense *m. orbitohyoideus* is attached to the also immense muscular process (Haas, 2001; Vera Candioti et al., 2004; Vera Candioti, 2007; Dias et al., 2019). Additionally, other muscles have distinct shapes and insertions or can be absent at all in distinction to other hylids (Vera Candioti et al., 2004; Vera Candioti, 2007).

In fact, larval myology can have a wider impact in Hylidae phylogeny. Vera Candioti et al. (2004) mentions that the *m. levator mandibulae lateralis* in *Dendropsophus* and *Pseudis* larvae have the same configuration, extending from the extreme of the suprarostral cartilage to the anterolateral dorsal region of the *pars articularis quadrati* while *Scinax* has not such arrangement. Actually, *Scinax* poses the hardest question Hylidae relationships and a study on the variation of tadpole muscles could add interesting characters. In the other hand, since there are only four species with known larval myology, information for supporting relationships inside *Dendropsophus* is compromised.

E) *Larval feeding habits.*

As corollaries of the above larval morphological data, larval feeding behavior could house interesting variation. Within our dataset, *Scarthyla goinorum* is considered to be herbivorous after Duellman and de Sá (1988) statement that "the gut contain greenish yellow plant material that is coarse and fragmentary and appears to have been cut apart. Probably these are the remains of the leaves of the duckweed". It is of course not a definitive assessment since the duckweed present in *S. goinorum* guts could be ingested together with other material that was already digested at the time of Duellman de Sá (1988) observation.

Dendropsophus larvae have been considered macrophagous due to the presence of hyobranchial skeletons with robust, rostrocaudally long ceratohyals and reduced branchial baskets with short ceratobranchials devoid of lateral projections and spicules (Vera Candioti, 2007). Other oral features of *Dendropsophus* larvae as reduced oral papillation and keratinized structures, and scarce filtering structures in the buccal roof and floor are, as well, indicatives of a macrophagous diet (Wassersug, 1980; Vera Candioti, 2007; Dias et al. 2019).

Analyses of larval diets are scarce in the literature (Alford, 1999; Hoff et al., 1999). Wassersug (1980), based on internal oral morphology, hypothesized that *Dendropsophus* larvae would show a particular type of macrophagy dealing with coarse plant matter and detritus rather than large, live prey. However, Peixoto and Gomes (1997) reported an active predatory behavior for *Dendropsophus minutus* and Vera Candioti (2007) found whole and fragmented oligochaetes in the gut content of *D. microcephalus* and *D. nanus*. *Dendropsophus ruschii* larvae were considered active predators that could also feed on vegetable matter, but not accepting dead items of prey and carrion (Weygoldt and Peixoto, 1987). *Dendropsophus minutus* also seems to feed both on vegetal and animal matter (Echeverria, 1997; Peixoto and Gomes, 1997). It seems very likely that most *Dendropsophus* larvae are active predators. Hence, it could be possible that behavior associated to feeding and hunting (as predatory techniques) harbors interesting variation as well.

The chondrocranium of *Xenohyla* is undescribed. Larvae of *Xenohyla truncata* in captivity fed on meat, rejecting vegetal matter and cannibalized one individual in about eight hours although it is not known if it was a predatory attack or only opportunistic necrophagy (VGDO pers. obs.).

F) *Interruption of larval labial tooth rows.*

Both anterior and posterior larval labial tooth rows can be interrupted. Many taxa within Hylidae present species in which interruptions are present and others where they are not (e.g., Conte et al., 2007). Thus, it seems *a priori* a potential source of evidence. However, to code interruptions between species with different row numbers is not straightforward because homology between rows is not straightforward.

Behavior

Species of *Dendropsophus* are usually very common, but papers dealing with *Dendropsophus* behavior usually are restrained to describe advertisement calls. Exceptions (e.g., Amezquita and Hödl, 2004) presented remarkable behaviors fulfilled with interesting variation and implications. Although *Xenohyla truncata* is known to be frugivorus, this quite sums up the behavioral information known for *Xenonyla* as a genus. The call of *X. truncata* is described only as "somewhat similar to the call of *Dendropsophus seniculus*" (Izecksohn and Carvalho-e-Silva, 2001); the call of *X. eugenioi* is unknown. This lack of knowledge prevents a confident optimization of advertisement calls characters in our preferred topologies.

Various *Dendropsophus* groups had traits of their advertisement calls proposed as diagnostic (e.g., Duellman and Fouquette, 1968; Duellman, 1970; Duellman and Crump, 1974; Duellman and Trueb, 1983; Orrico et al., 2009; Hepp et al., 2012). Oviposition behavior (terrestrial egg clutches perched on leaves above water) was one of the reasons that led Bastos and Pombal Jr. (1996) to consider small 30-chromosome yellow *Hyla* presenting this behavior to be distinct from the *Hyla microcephala* group to whom they were then thought to be related.

Grant et al. (2006) could extract much information on such source of evidence (18 characters) possibly because Dendrobatoidea [*sensu* Grant et al. (2006)] have been subject to many studies of the kind; anecdotal information in literature based on field or captivity data is extensive.

One case on Grant et al.'s (2006) characters calls attention: all variation on advertisement calls is under a single character—according to their call types (trills, buzz, etc.). Grant et al. (2006) noticed this situation and explained as follows: "It is clear that call types are composites of temporal and spectral transformation series that should be decomposed into independent characters for phylogenetic analysis"; i.e. the coding of behavioral characters has problems of its own due to difficult homology assessments (Robillard et al., 2006a).

Different coding schemes of behavioral data can deeply impact the results of cladistic analyses (Robillard et al., 2006b; Goicochea et al., 2010). The use of dynamic homology is reported to ameliorate these difficulties (Robillard et al., 2006b; Japyassu and Machado, 2010); implementation and coding for these cases however, are not straightforward (e.g., Japyassu and Machado, 2010). Additionally, some particular behaviors are context dependent and many present large levels of inter and intra specific variation to which explanations still unknown (Grant et al., 2006).

It is clear that much information can be extracted from *Dendropsophus* behavior apart from the one presented in this analysis (a single character). Below, we call attention to two cases:

A) *Advertisement calls*.

Anuran advertisement calls are important pre-mating isolation systems (Blair, 1955; Giacoma and Castellano, 2001; Wells, 2007) but much variation has been found and was related to various factors (e.g., Schwartz and Wells, 1985; Bee et al., 2000; Martins and Jim, 2003; Amezquita et al., 2006; Padial et al., 2008). There are no qualitative descriptions of *Xenohyla* advertisement calls. Within *Dendropsophus*, there is only scattered information, and for a few species, on how males behave while in chorus (e.g., Cardoso and Haddad, 1984; Haddad, 1990; Martins and Jim, 2003; Amezquita and Hödl, 2004; Wogel and Pombal Jr., 2007) and how environment affects communication (e.g., Wollerman, 1999).

Most *Dendropsophus* advertisement calls are defined in literature as groups of smaller units (the terminology of which varying according to the author) described as "simple" or "complex" calls having "secondary" notes or not (e.g., Duellman, 1970). Lutz (1954) onomatopoeic advertisement call descriptions of *D. anceps*, *D. bipunctatus*, *D. decipiens*, *D. elegans*, *D. meridianus*, *D. minutus* and *D. seniculus* are clear to illustrate this.

While some are described with two or more distinct sounds, some are trills or buzzes (B. Lutz uses "little saw" for *Dendropsophus decipiens*). Observations on advertisement call structures revealed a scenario where "secondary" notes (sensu Duellman, 1970) could be achieved by suffixation; i.e. addition of distinct sound structures in the end of a given call.

Marquez et al. (1993) reported that *Dendropsophus rhodopeplus* advertisement call was "composed by a succession of several [simple] notes that occasionally evolved into a more complex call, render impossible categorizing the notes into a definite number of types". Orrico et al. (2009) found a similar effect on *D. nahdereri*. They noticed that sometimes "the final portion of [advertisement calls] can be composed of one to three spaced blocks of three to seven pulses", which are produced along with the other pulses of the "main note" i.e. the advertisement call (quotation marks in the original) that Orrico et al. (2009) called "final pulse clusters". They also noticed that the advertisement call of *D. acreanus* reported by Marquez et al. (1993) could present a similar structure.

Orrico et al. (2009) suggested that a combination of multipulsed single notes, presence of two-harmonics, low-frequency dominant harmonics and presence of final pulse clusters could be diagnostic for the *D. marmoratus* Group. Hepp et al. (2012) suggested that "the absence of pulse clusters and the presence of more than two harmonics in *D. seniculus* preclude this diagnosis". Both diagnoses deal with many individually variable traits and potentially informative. If each individual trait is understood as a character state, even the absence of those traits in some species of a given group does not preclude it to be a synapomorphy for this same group.

Many species have multipulsed notes (Toledo et al., 2007; Pugliese et al., 2009; Bastos et al., 2011). A survey on dominant frequency ranges within the tribe using a continuous character approach may provide interesting insights in the correlate evolution of advertisement call frequencies and body size and mass.

Hepp et al. (2012) argues that *D. seniculus* and *D. soaresi* present "a longer pulse with cyclic amplitude modulation and frequency modulation at the end of the call" instead of the pulse clusters. Decomposing this trait in its independent variable characters leave us with duration of the final pulse, cyclic amplitude modulation and frequency modulation. Individual ZUFRJ 11745 (Hepp et al., 2012 figure 2) does not present frequency modulation highlighting the independence of these characters.

Given this apparent uniformity, it seems that relating differences from the high-pitched; short; single-note call of *Dendropsophus branneri* (see Nunes et al.,

2007) to the low-pitched; long; complex calls of *D. anceps* (see Gomes and Martins, 2006) would be easy. However, homology assessments are not straightforward.

Escalated aggression levels lead to different responses in different *Dendropsophus* species. While some modify their advertisement call rates on various traits (e.g., Bastos and Haddad, 1996; Köhler and Böhme, 1996) others produce distinct calls and visual displays (e.g., Cardoso and Haddad, 1984; Amezquita and Hödl, 2004). *Dendropsophus minutus* has an advertisement call with three distinct notes (e.g., Cardoso and Haddad, 1984) whose emission seems to be related with different levels of aggression levels. In fact, some individuals produced calls composed only by aggressive notes (Cardoso and Haddad, 1984 notes "B" and "C") randomly combined—apparently.

Gathering call data from literature has an additional hurdle. Apart from the plethora of distinct unit definitions, many advertisement call descriptions are based on low-quality recordings, leading to artifact-full audiospectrograms and/or poorly defined oscillograms. Orrico et al. (2009) noticed artifacts in previous descriptions of advertisement call descriptions of species of the *Dendropsophus marmoratus* Group. (*D. marmoratus* and *D. seniculus*). Márquez et al. (1993) noticed that the dominant frequency they found for *D. rhodopeplus* was extremely low (154 Hz). Duellman's (1972) data on the same species yield a dominant frequency of 3925 Hz. Márquez et al. (1993) also found energy concentrations on higher harmonics (3119 and 6326 Hz) that are similar to the dominant frequency Duellman (1972) reported (3925 and 7850 Hz). To the ear, *D. rhodopeplus* advertisement call surely seems to have a high-pitch dominant frequency—yet, nothing compared to the nearly ultrasonic call of *D. ozzyi* (see Orrico et al., 2014).

Many of the above cited problems could be ameliorated by the use of a mechanistic approach on call descriptions (Robillard et al., 2006a). To produce these descriptions however is not an easy task (McLister et al., 1995). We agree with Grant et al. (2006) that “Clearly there are legitimate transformation series hidden in these observations, but more information is needed before characters can be delimited”.

B) *Male feet position during the amplexus.*

Amplectic position has been used in the literature as an important character. However, as done by Lynch (1971), discussions are usually on pelvic vs. axillary amplexus only and minor variation is ignored. Luna et al. (2018) presented a throughout review on amplexus data suggesting a relation with sexually dimorphic glands, especially the nuptial pad.

We found, a subtle, but recognizable, variation in the placement of legs within the species examined for this study. In all *Dendropsophus* species where the amplexus was observed (in photographs or in field), males seem to grasp the female with feet as well, pressing them over female abdomen. Only a species of *Scinax* (*S. nebulosus*) presented a similar position, however, male feet are only laying over female legs and not on female trunk. In this species, this position is probably due to the large difference in size (VGDO pers. obs.). The same leg position is found on Phyllomedusidae and species of both clades (Pyllomedusidae and *Dendropsophus*) are known to lay their egg clutches terrestrially (Noble, 1927; Duellman, 1970; Faivovich et al., 2010). For *Sphaenorhynchus*, only a picture of *Sphaenorhynchus caramaschii* was available; male feet position however, was inconclusive. A picture of *S. prasinus* clearly shows a loose position of the male feet, not lying over the female’s body. However, the amplexus itself is a dynamic moment subject to much variation. Thus, we preferred to call attention for this subject instead of including it in the matrix.

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