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Research paper

A new genus of lime treefrogs (Anura: Hylidae: Sphaenorhynchini)

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ABSTRACT

The hylid tribe Sphaenorhynchini is composed of the single genus *Sphaenorhynchus*. A recent total evidence phylogenetic analysis of all the 15 currently described species of *Sphaenorhynchus* recovered *S. pauloalvini* as the earliest diverging taxon of this genus. *Sphaenorhynchus pauloalvini* is diagnosed by molecular evidence and several phenotypic characters that differentiate it from the remaining species of *Sphaenorhynchus*. On the basis of molecular evidence and an extensive list of phenotypic characters, we erect a new monotypic genus for *S. pauloalvini* and redefine the former *Sphaenorhynchus* to include the remaining species of this genus.

1. Introduction

The hylid tribe Sphaenorhynchini was defined by Faivovich et al. (2018) to comprise the single genus *Sphaenorhynchus* Tschudi, 1838. The relationship between Sphaenorhynchini and related tribes is poorly supported and remain controversial within Hylidae. This tribe was poorly supported as sister taxon of Dendropsophini (*Dendropsophus* Fitzinger 1843 + *Xenohyla* Izecksohn 1998), closely related to Pseudini (*Lysapsus* Cope 1862, *Pseudis* Wagler 1830, and *Scarthyla* Duellman & de Sá 1988) and Scinaxini (*Scinax* Wagler 1830) (Faivovich et al., 2005), or was obtained as sister taxon of Scinaxini (always poorly supported) closely or distantly related to Dendropsophini and Pseudini (Wiens et al., 2006 2010; Pyron & Wiens 2011; Pyron 2014; Duellman et al., 2016; Jetz & Pyron 2018).

Sphaenorhynchus is currently composed of 15 green-colored small species widespread in South America in the Amazon and Orinoco basins, Trinidad, northeastern Brazil, and in the Atlantic Forest of southeastern and northeastern Brazil (Araujo-Vieira et al., 2019; Frost 2020). These species generally inhabit ponds in open areas and forest edges, where males call perched on the aquatic vegetation or partially submerged in the water with their notably distended vocal sac (e.g., Bokermann 1966; Caramaschi et al., 2009; Roberto et al., 2017). For those species whose oviposition is known, it occurs on the submerged vegetation (Rodriguez & Duellman 1994; Toledo et al., 2007), except for *S. pauloalvini* Bokermann, 1973 that deposits eggs on leaves overhanging water (Bokermann 1973). *Sphaenorhynchus carneus* (Cope 1868) lays eggs on leaves out of the water (Bokermann 1973) or in the water (Crump 1974; W. Hödl pers. comm. in Araujo-Vieira et al., 2019).

The larvae of all species of *Sphaenorhynchus* have been described except those of *S. botocudo* Caramaschi et al., 2009, *S. cammaeus* Roberto et al., 2017, and *S. mirim* Caramaschi et al., 2009 (Caramaschi et al., 2009; Roberto et al., 2017). These larvae are characterized by having elliptical and anteriorly directed nostrils with fleshy flanges on the internal margins, notably large marginal papillae on the oral disc (in some species), and spiracles with different degrees of posterior elongation (e.g., Bokermann 1973; Cruz 1973; Suárez-Mayorga & Lynch 2001; Caramaschi 2010; Araujo-Vieira et al., 2015a,b).

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The monophyly of *Sphaenorhynchus* was supported in previous phylogenetic analyses with a limited taxonomic sampling [*S. dorisae* (Goin 1957), *S. lacteus* (Daudin 1800), and *S. platycephalus* (Werner 1894); e.g., Faivovich et al., 2005; Wiens et al., 2006; Duellman et al., 2016; Jetz & Pyron 2018] and many morphological putative synapomorphies were proposed for the genus (Duellman & Wiens 1992; Faivovich et al., 2005; Araujo-Vieira et al., 2015a). The relationships between the species and the taxonomic distribution of character-states in *Sphaenorhynchus* remained largely unknown over the years. A recent total evidence phylogenetic analysis including all currently described species of *Sphaenorhynchus* based on a comprehensive molecular and phenotypic dataset corroborated the monophyly of *Sphaenorhynchus* and provided several molecular and phenotypic synapomorphies for the genus and its internal clades (Araujo-Vieira et al., 2019). *Sphaenorhynchus pauloalvini* was recovered as the earliest diverging taxon of *Sphaenorhynchus*, followed by *S. carneus* as the sister taxon of all remaining species of the genus. Furthermore, three well-supported species groups were recognized: the *S. lacteus* (*S. dorisae* and *S. lacteus*), *S. planicola* [*S. mirim* and *S. planicola* (Lutz & Lutz 1938)], and *S. platycephalus* groups [*S. botocudo*, *S. bromelicola* Bokermann, 1966, *S. cammaeus*, *S. canga* Araujo-Vieira et al., 2015b, *S. caramaschii* Toledo et al., 2007, *S. palustris* Bokermann, 1966, *S. platycephalus*, and *S. surdus* (Cochran 1953)]; only *S. carneus*, *S. pauloalvini*, and *S. prasinus* Bokermann, 1973 remained unassigned to species group (Araujo-Vieira et al., 2019).

Sphaenorhynchus is currently well-supported (100% jackknife support; 90 Goodman-Bremer support) by molecular evidence and 25 phenotypic synapomorphies, including the presence of a white parietal peritoneum (Araujo-Vieira et al., 2019). *Sphaenorhynchus pauloalvini*, the earliest divergent taxon of the genus, is a unique species within *Sphaenorhynchus*. This species is diagnosed by molecular evidence and 12 phenotypic autapomorphic character-states. Some of them are unique within *Sphaenorhynchus*, such as the presence of a cloacal sheath and a white lateral line bordered above by a black lateral line in adults (Araujo-Vieira et al., 2019). The sister taxon of *S. pauloalvini*, which includes the remaining *Sphaenorhynchus* is a well-supported clade (100% jackknife support and 48 Goodman-Bremer support) by molecular evidence and 27 phenotypic synapomorphies, among them the elongate transverse process of presacral vertebra IV and the m. *petrohyoideus anterior* with an additional layer of fibers over the hyoid plate, which are known only in this genus among hylines (Araujo-Vieira et al., 2019).

In light of the phylogenetic hypothesis proposed to *Sphaenorhynchus* and, on the basis of molecular evidence and several phenotypic characters (adult and larval external morphology, osteology, myology, and reproductive biology), we erect and diagnose a new genus for *S. pauloalvini*, and redefine and diagnose the former *Sphaenorhynchus* to include the remaining species of this genus.

2. Material and methods

Specimens of *Sphaenorhynchus* analyzed in this study are those in the list of examined material of Araujo-Vieira et al. (2019: appendices S1 and S2; see also Appendix A), supplemented with one cleared and double-stained adult male of *S. pauloalvini* (CFBH 22920) from Floresta Nacional de Goytacazes, Municipality of Linhares, State of Espírito Santo, Brazil. We studied all voucher specimens of *Sphaenorhynchus* used in the total evidence analysis (combined morphological and molecular dataset) of Araujo-Vieira et al. (2019) to corroborate its specific identity. This dataset includes type material of several species of *Sphaenorhynchus* and the specimens listed in the tree (Fig. 1). Institutional abbreviations follow Sabaj (2016). Dorsal and profile outline standards of snout shape of adult specimens and the measurement of the snout-vent length (SVL) are those employed by Duellman (1970). Webbing formula follows Savage & Heyer (1967) as modified by Myers & Duellman (1982). Fingers were numbered II to V following Fabrezi & Alberch (1996). Sex was determined by visual inspection of external secondary sexual characters (nuptial pads, vocal slits, and expansion of the vocal sac) or by direct inspection of the gonads.

Osteological characters were taken from specimens that were cleared and double-stained with alcian blue and alizarin red following Taylor & Van Dyke (1985). The terminology employed for the skull and postcranial morphology follows Jurgens (1971) and Trueb (1973 1993), and Faivovich (2002) for laryngeal morphology. The terminology for larval morphology follows Altig & McDiarmid (1999). Methylene blue was employed to enhance the visualization of oral disc structures.

The terminology employed for nuptial pad morphology follows Luna et al. (2018). The nuptial pads of four species (*Sphaenorhynchus botocudo*, *S. dorisae*, *S. pauloalvini*, and *S. prasinus*; see Appendix B) were removed for scanning electronic microscopy. Then, they were dehydrated through an ascending series of ethanol up to 100%, dried using a critical point dryer (EMS 850 and Baltec CPD 030), coated with gold: palladium (40:60; SC 7620 Mini Sputter Coater Termo VG Scientific and Cressington Sputter Coater 108A), and studied using SEM with a Philips XL30 TMP New Look microscope.

Phenotypic character-states (Chs.) referred in the text are those proposed by Araujo-Vieira et al. (2019: appendices S5 and S6 and figs. S3–S15). Synapomorphies and character-states optimizations were obtained using TNT v1.5 (Goloboff et al., 2008; Goloboff & Catalano 2016) based on the total evidence dataset (molecular and phenotypic data) of Araujo-Vieira et al. (2019). List of molecular and phenotypic synapomorphies common to all dichotomic trees was generated using TNT's command "apo [" (Appendix C). Phenotypic synapomorphies in Fig. 1 were generated with YBYRÁ (Machado 2015) using TNT. See Araujo-Vieira et al. (2019: appendix S1) for the list of voucher specimens and GenBank accession numbers of mitochondrial and nuclear genes sequences employed in their study.

3. Results

Sphaenorhynchus pauloalvini is the earliest diverging taxon of *Sphaenorhynchus* (Araujo-Vieira et al., 2019). This species is diagnosed by molecular evidence and several phenotypic characters (adult external morphology, osteology, myology, and reproductive biology), which included 12 phenotypic autapomorphies that differentiate it from the remaining species of *Sphaenorhynchus* (Araujo-Vieira et al., 2019; this study). These phenotypic autapomorphies comprise remarkable character-states, such as the presence of cloacal sheath, the white lateral line bordered above by a black lateral line in adults [Fig. 2; also present in *Scarthyla goinorum* (Bokermann 1962) from the species included in this study], and the oviposition site on leaves out of the water [*S. carneus* lays eggs on leaves overhanging the water or in the water (polymorphic)]. Moreover, adult males of *S. pauloalvini* have dark-colored nuptial pads on Finger II with rounded, large papillary epidermal projections (PEPs), which seems to be an exclusive characteristic within *Sphaenorhynchus* (PEPs ~38 μm in diameter in *S. pauloalvini* vs. ~27 μm in *S. prasinus*). Given the amount of molecular and phenotypic evidence that diagnoses and differentiates *S. pauloalvini*, we considered that this taxon should better be allocated to a new genus.

Therefore, *Sphaenorhynchus* is redefined to include the remaining 14 known species of the genus. It is diagnosed by molecular and 25 phenotypic synapomorphies, instead of 27, as reported by Araujo-Vieira et al. (2019). The list of phenotypic

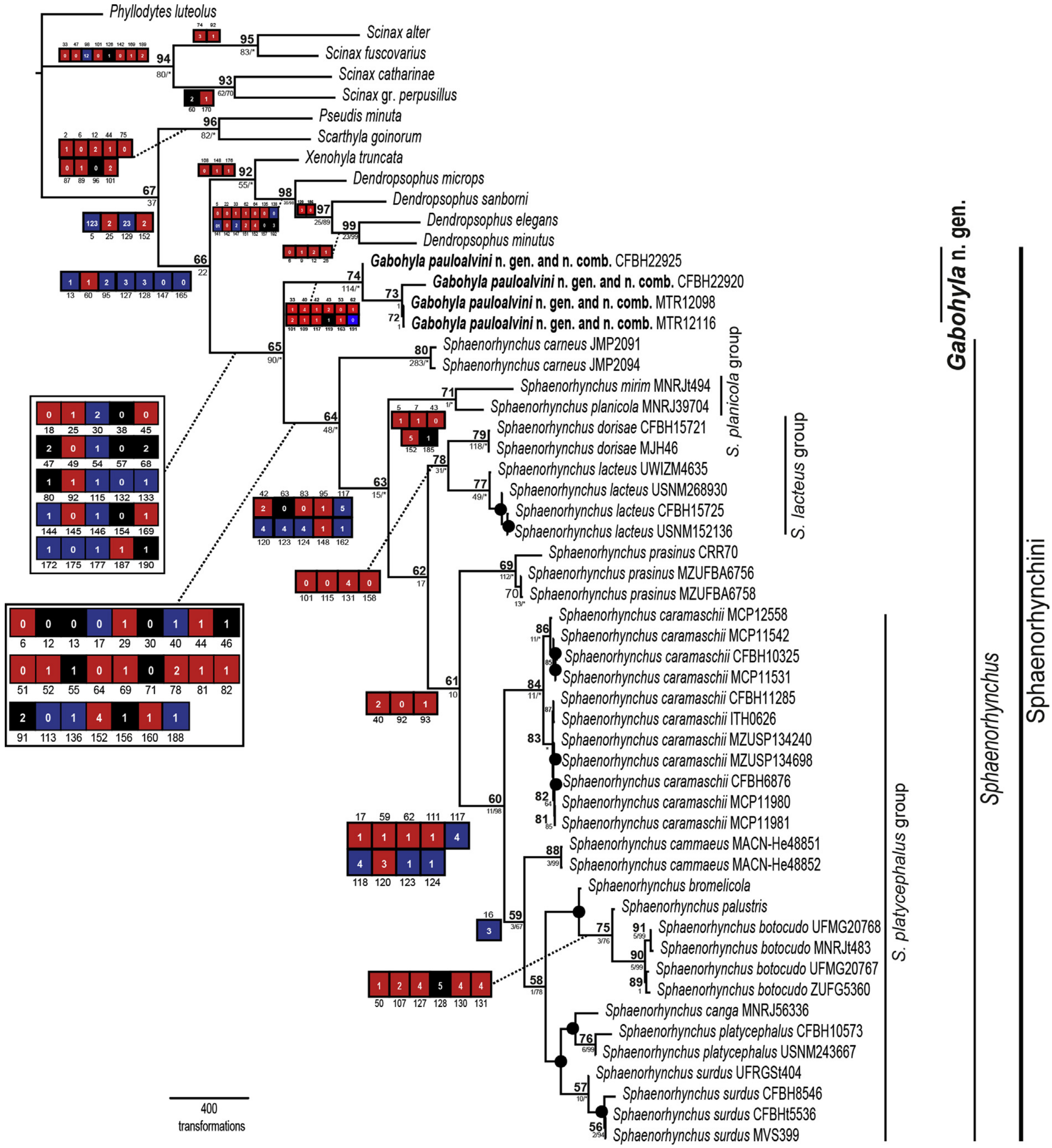

Fig. 1. Phylogenetic relationships of Sphaenorhynchini as recovered in the analysis of total evidence of Araujo-Vieira et al. (2019). Black circles indicate nodes that collapse in the strict consensus. Numbers above nodes correspond to the nodes in the list of synapomorphies provided in Appendix C. Values below nodes are parsimony jackknife support and Goodman-Bremer support, respectively. An asterisk (*) indicates groups with 100% for parsimony jackknife frequencies. Nodes lacking values have <50% jackknife support. Nodes are labeled with unambiguously optimized phenotypic synapomorphies (black square = unique, nonhomoplastic; red square = unique, homoplastic; blue square = nonunique, homoplastic; character number below or above squares; derived character-states inside squares). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

synapomorphies includes osteological structures (e.g., the posterior reduction of the maxilla, the extreme reduction of the posterior ramus of the pterygoid, palatines reduced to rudimentary bumps, and the elongated transverse process of presacral vertebra IV); musculature (e.g., the m. *petrohyoideus anterior* with one additional layer of fibers over the hyoid plate); and adult and larval morphology (the absence of tympanic membrane in adults and the presence of few enlarged marginal papillae of the oral disc in larvae).

Below we provide a complete diagnosis and characterization of the new genus and the redefined *Sphaenorhynchus*, and briefly comment on the diversity of nuptial pads in Sphaenorhynchini, as well as the optimization of some character-states based on previous phylogenetic hypotheses (Faivovich et al., 2005; Wiens et al., 2006

2010; Pyron & Wiens 2011; Pyron 2014; Duellman et al., 2016; Jetz & Pyron 2018; Araujo-Vieira et al., 2019).

3.1. *Taxonomic accounts*

Gabohyla, new genus
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3.1.1. *Type species*

Sphaenorhynchus pauloalvini Bokermann, 1973.

3.1.2. *Diagnosis*

The new genus is assigned to the tribe Sphaenorhynchini based on molecular evidence and 25 phenotypic synapomorphies (Araujo-Vieira et al., 2019). *Gabohyla* n. gen. is well-supported by molecular evidence and 12 phenotypic autapomorphies (Araujo-Vieira et al., 2019; see also Fig. 1 and Appendix C). These include (1) vomers with a dentigerous process located medially to the postchoanal process, approximately at the level of postnasal wall (Ch. 33.1; with instances of homoplasy in the *Dendropsophus* clade and *Pseudis minuta* Günther 1858); (2) palatines elongated, reaching the neurocranial portion of the sphenethmoid [Ch. 40.4; with instances of homoplasy in *Dendropsophus elegans* (Wied-Neuwied 1824), *D. microps* (Peters 1872), and *D. minutus* (Peters 1872)]; (3) cultriform process of the parasphenoid with a rounded anterior portion [Ch. 42.1; with instances of homoplasy in *Scarthyla goinorum*, *Sphaenorhynchus canga*, and *S. mirim*]; (4) posteromedial process of the parasphenoid reaching half of the distance between the posterior margin of alary process and *foramen magnum* (Ch. 43.2; with many instances of homoplasy in *D. elegans*, *S. goinorum*, and some species of *Scinax* and *Sphaenorhynchus*); (5) *pars interna plectri* mineralized [Ch. 53.0; with one instance of homoplasy in *Xenohyla truncata* (Izecksohn 1959)]; (6) presence of cartilaginous lamina that extends from the cartilaginous branch to the inferior margin of the oblique cartilage (Ch. 62.1; with instances of homoplasy in the *Dendropsophus* clade, *Sphaenorhynchus lacteus*, and the *S. platycephalus* group); (7) intercalary elements between ultimate and penultimate phalanges completely mineralized (Ch. 101.2; with some instances of homoplasy in the *Pseudis* + *Scarthyla* clade, some species of *Dendropsophus* and *Sphaenorhynchus*); (8) presence of a white lateral line bordered above by a black lateral line (Ch. 109.1; with one instance of homoplasy in *S. goinorum*); (9) presence of small, rounded tubercles on the subcloacal region [Ch. 117.1; with instances of homoplasy in *D. microps*, *Scinax fuscovarius* (Lutz 1925), and *S. perpusillus* (Lutz & Lutz 1939)]; (10) presence of cloacal sheath (Ch. 119.1); (11) m. *hyoglossus* originates from the posterior end of the posteromedial process of the hyoid [Ch. 163.1; with one instance of homoplasy in *Scinax catharinae* (Boulenger 1888)]; and (12) eggs laid out of the water, on leaves overhanging water [Ch. 191.0; *Sphaenorhynchus carneus* lays eggs on leaves overhanging the water or in the water (polymorphic)].

In addition, the single species of the new genus can be differentiated from all species of *Sphaenorhynchus* by the following combination of characters: (1) tympanic membrane present; (2) dark-colored nuptial pads on Finger II in males with rounded, large in diameter papillary epidermal projections (PEPs ~38 μm; Fig. 3A, E); (3) *tectum synoticum* ossified; (4) *pars facialis* of the maxilla about two times higher than the *pars dentalis* height; (5) posterior extreme of maxilla reaching approximately 2/3 of the distance from the anterior extreme of the maxilla to the articulation between the ventral ramus of squamosal and quadratojugal; (6) mediodistal portion of the medial ramus of the pterygoid directed posteromedially; (7) posterior ramus of pterygoid reaching more than the 3/4 of the distance between the point of origin of the posterior ramus and the distal portion of quadrate; (8) tympanic annulus shallow; (9) medial end of *pars media plectri* dilated, very narrow gap between basal plate and operculum; (10) angulosplenial and dentary in contact or adjacent, the Meckel's cartilage is covered by the angulosplenial; (11) anterior process of hyale present; (12) hyale straight, not curved medially; (13) hyale attached to the limit between basal process and otic capsule; (14) coracoids short, length 0.10–0.14 times the SVL; (15) clavicles short, length 0.08–0.10 times the SVL; (16) transverse process of the presacral vertebra IV moderately long, distal end at the level of the anterior margin of the base of the transverse process of presacral vertebra V; and (17) m. *petrohyoideus anterior* inserted on the lateral margin of the hyoid plate, subjacent to the alary process of the hyoid.

3.1.3. *Characterization*

Small treefrogs (SVL 18.0–20.0 mm in males, $n = 22$; 22.0–24.0 mm in females, $n = 8$; Bokermann 1973) with truncate snout in lateral view (Fig. 2); vocal sac without lateral longitudinal folds, and ventrally not reaching the pectoral region; males with dark-colored nuptial pads on Finger II, with large papillary epidermal projections (PEPs ~38 μm of diameter; Fig. 3A, E), which have pointy cytoplasmatic projections on the top of each PEP (Fig. 3I); tympanic membrane present; folds on forearm, tarsus, elbow, heel (e.g., calcar appendages absent), and subcloacal region absent (only tubercles present); eggs laid out of the water, on leaves overhanging water; tadpoles with small and homogeneously sized marginal papillae on the oral disc, two anterior labial tooth rows, A2 interrupted medially, short spiracle (3–11% of the body length) positioned closer to the eyes, and presence of oblique, canthal, and ventrolateral black stripes on the body, and a single dark stripe on the inferior border of the tail musculature (see also Bokermann 1973; Araujo-Vieira et al., 2015a); pedicellate premaxillary and maxillary teeth continuously present along the entire extension of the *pars dentalis*; quadratojugal short with the length corresponding to approximately 1/6 of the distance from the articulation of the ventral ramus of squamosal with quadratojugal to the anterior extreme of the maxilla; quadratojugal articulating posteriorly with the anterior process of palatoquadrate cartilage or with the squamosal; zygomatic ramus of the squamosal short, 2.2–2.4 times longer than the minimum width of the ventral ramus; and sacral diapophyses strongly expanded, at least 4.5 times wider at the tip than at the base.

3.1.4. *Etymology*

The new genus is named in honor to the late Dr. Gabriel Omar Skuk Sugliano (1962–2011), a Uruguayan Herpetologist that made his remarkable career in Brazil, who was kindly known as "Gabo" by his friends and colleagues. His passion and enthusiasm by the natural world inspired several young students, among them the first author of this paper. The name derives from the combination of Gabo + the classical genus of treefrogs *Hyla* (see Myers & Stothers 2006). The gender is feminine.

3.1.5. *Content*

Monotypic. *Gabohyla pauloalvini* (Bokermann 1973), new combination.

3.1.6. *Comments*

The lateral white line is bordered above by a black lateral line and begins at the tip of snout, slightly after the tip or below the eye. Posteriorly, it extends to a point immediately anterior to the sacrum or reaches the groin region. The black lateral line extends posteriorly from the tip of snout to the groin. It could be conspicuously or slightly pigmented on the region between the posterior corner of the eye and the groin. The posterior extension of this line varies

Fig. 2. Coloration in life of *Gabohyla pauloalvini* n. gen. and n. comb.. (A) and (B) Two solitary males. (C) A pair in axillary amplexus; the oocytes are visible by transparency in the abdomen of the female. Specimens collected at the Universidade Estadual de Santa Cruz, Municipality of Ilhéus, State of Bahia, Brazil. Photos are courtesy of M. Sena.

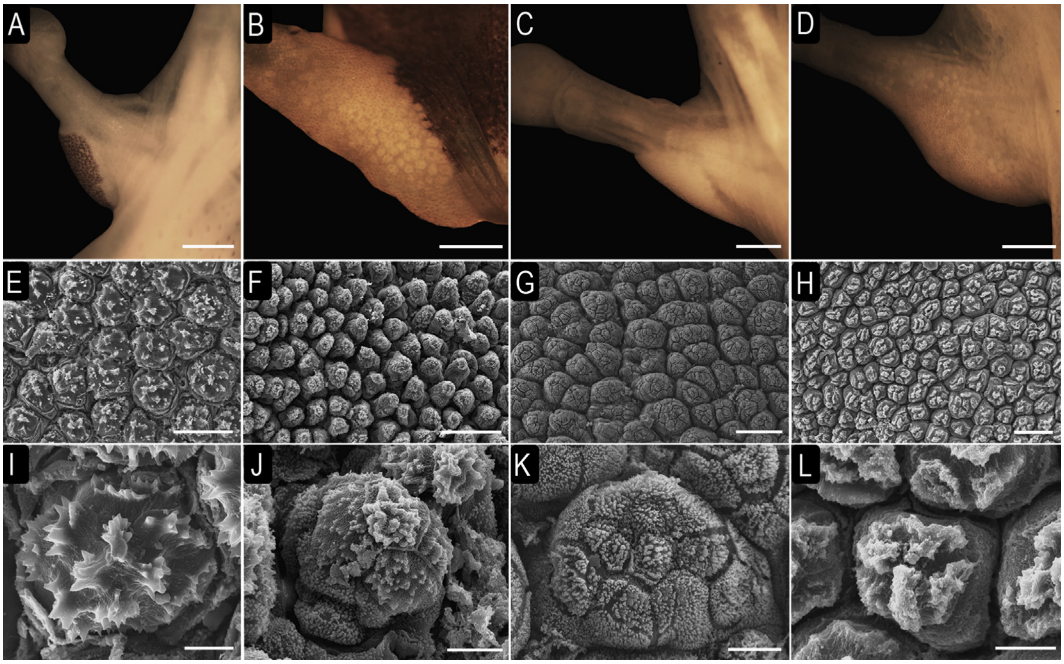

Fig. 3. Nuptial pad diversity in Sphaenorhynchini. (A–D). External morphology showing light (C) and dark-colored nuptial pads (A, B, D). Scale bar: 500 μm. (E–H). Nuptial pad area under scanning electron microscopy. Note the difference in densities of papillary epidermal projections in E versus F, G, H. Scale bar: 50 μm. (I–L). Detail of a single papillary epidermal projection. Notice the pointy ornamentations (I), versus the blunter/rounder ornamentations (J, K, L). Scale bar: 10 μm. A, E, I. *Gabohyla pauloalvini* n. gen. and n. comb. (A: MTR 12256. E, I: MNRJ 4312). B, F, J. *Sphaenorhynchus botocudo* (MACN-He 46459). C, G, K. *Sphaenorhynchus dorisae* (MCP 10595). D, H, L. *Sphaenorhynchus prasinus* (MZUESC 6862).

intraspecifically along the flanks. Females (SVL 22.0–24.0 mm, $n = 8$) are slightly larger than males (SVL 18.0–20.0 mm in males, $n = 22$), and lacking nuptial pads on Finger II. Temporal and spectral parameters are similar between calls recorded at the municipalities of Ilhéus (Bokermann 1973) and Una (Toledo et al., 2014), both in the Brazilian State of Bahia. Larvae were first described by Bokermann (1973). Araujo-Vieira et al. (2015a) reported additional external morphological information on larvae, as the length of the spiracle and size of the marginal papillae on the oral disc. Stripes on the body and tail of larvae could vary in the intensity of pigmentation and extension. Bokermann (1973: 594) reported adults reproducing in a pond (CEPEC, Ilhéus) where males were vocalizing while perched on leaves (between 50 and 100 cm high) of the aquatic vegetation “aguapé” (*Eichhornia crassipes*, Pontederiaceae); green-colored eggs (between 60 and 70) were laid out of the water, on leaves overhanging water (ca. 50 cm high). No relevant information about its biology has been published since then.

We listed 12 autapomorphies for *Gabohyla pauloalvini* n. gen. and n. comb. (see Diagnosis section of *Gabohyla*, new genus). Most of these character-states remain as autapomorphies of the new genus independently of the different sister relationships of Sphaenorhynchini within Hylidae: sister taxon of Dendropsophini, closely related to Pseudini and Scinaxini (Faivovich et al., 2005), or sister taxon of Scinaxini closely or distantly related to Dendropsophini and Pseudini (Wiens et al., 2006 2010; Pyron & Wiens 2011; Pyron 2014; Duellman et al., 2016; Jetz & Pyron 2018). These autapomorphies include the nine character-states 33.1, 40.4, 42.1, 53.0, 62.1, 101.2, 109.1, 119.1, and 191.0.

In the phylogenetic hypotheses with Sphaenorhynchini as sister taxon of Scinaxini (Wiens et al., 2006 2010; Pyron & Wiens 2011; Pyron 2014; Duellman et al., 2016; Jetz & Pyron 2018), the three remaining character-states 43.2, 117.1, and 163.1 could be plesiomorphies for the new genus given they have known instances of homoplasy in *Scinax* (see the Diagnosis section of *Gabohyla*, new genus).

The taxonomic distribution of these autapomorphies in several species of the other related tribes (Dendropsophini, Pseudini, and Scinaxini) is still poorly known. For instance, seven osteological and myological character-states (Chs. 33, 40, 42, 43, 53, 62, and 163) are unknown for other species of *Dendropsophus* and *Scinax* besides those used in the phylogenetic analyses of Araujo-Vieira et al. (2019)—they included *Dendropsophus elegans*, *D. microps*, *D. minutus*, *D. sanborni* (Schmidt 1944), *Scinax alter* (Lutz 1973), *S. catharinae*, *S. fuscovarius*, and *S. perpusillus*—and two other vary intra- and interspecifically in *Scinax* (Chs. 101 and 117; see Faivovich 2002: ch. 22; K. Araujo-Vieira pers. obs.). Future studies improving knowledge about the taxonomic distribution of these character-states in species of Dendropsophini, Pseudini, and Scinaxini, as well as phylogenetic studies that could solve the phylogenetic position of the tribe Sphaenorhynchini within Hylidae will test the optimizations of the character-states considered autapomorphies of *Gabohyla* n. gen.. In the meantime, we consider these 12 character-states as autapomorphies of the new genus according to the results of the total evidence analysis of Araujo-Vieira et al. (2019).

3.1.7. Geographic distribution

Municipalities of Ilhéus (type locality of *Sphaenorhynchus pauloalvini*) and Una in the State of Bahia, and in the Municipality of Linhares in the State of Espírito Santo, Brazil (Bokermann 1973; Peixoto & Pimenta 2004; Freitas et al., 2009; Araujo-Vieira et al., 2019).

Sphaenorhynchus Tschudi, 1838.

3.1.8. Diagnosis

Sphaenorhynchus is redefined here to include all known species of *Sphaenorhynchus* but the former *S. pauloalvini*. *Sphaenorhynchus* is well-supported (100% jackknife support; 48 Goodman-Bremer support) by molecular evidence and 25 phenotypic synapomorphies (Araujo-Vieira et al., 2019; see also Fig. 1 and Appendix C). These include (1) *tectum synoticum* cartilaginous (Ch. 6.0, with instances of homoplasy in the *Pseudis* + *Scarthyla* and the *Dendropsophus elegans* + *D. minutus* clades); (2) *pars facialis* of the maxilla 1–1.2 times higher than the *pars dentalis* height (Ch. 12.0); (3) posterior extreme of maxilla reaching approximately 1/2 of distance from the anterior extreme of the maxilla to the articulation between the ventral ramus of squamosal and quadratojugal (Ch. 13.0); (4) maxilla and premaxilla separate, not overlapping (Ch. 17.0, with reversals in *S. lacteus* and the *S. platycephalus* group); (5) mediodistal portion of the medial ramus of the pterygoid directed posterolaterally (Ch. 29.1, with one instance of homoplasy in *D. elegans*); (6) posterior ramus of the pterygoid extremely short, reduced to rudimentary bumps (Ch. 30.0); (7) palatines overlapping only 3/4 of planum antorbitale (Ch. 40.1, with some instances of homoplasy in *S. bromelicola*, *S. palustris*, and *S. platycephalus*); (8) alary process of the parasphenoid short, at level of condyloid fossa (Ch. 44.1, with instances of homoplasy in *D. microps* and the *Pseudis* + *Scarthyla* clade); (9) tympanic annulus deep and expanded internally, with the medial surface unusually concave (Ch. 46.1); (10) medial end of *pars media plectri* reduced, large gap between basal plate and operculum (Ch. 51.0, with one instance of homoplasy in *Xenohyla truncata*); (11) *pars interna plectri* reduced, occupying a small space in the fenestra ovalis (Ch. 52.1, with one instance of homoplasy in *X. truncata*); (12) angulosplenial and dentary without contact, ample space is visible between these bones, exposing the Meckel’s cartilage (Ch. 55.1); (13) anterior process of the hyale absent (Ch. 64.0, with one instance of homoplasy in the *Dendropsophus* clade); (14) hyale curved medially [Ch. 69.1, with instances of homoplasy in *D. elegans* and *Phyllodytes luteolus* (Wied-Neuwied 1821)]; (15) hyale attached to the basal process (Ch. 71.0); (16) fibrous masses of the larynx chondrified (Ch. 78.2, with one instance of homoplasy in *D. elegans*); (17) coracoids elongate, length at least 0.17 times the SVL (Ch. 81.1, with one instance of homoplasy in *P. luteolus*); (18) clavicles elongate, length at least 0.15 times the SVL (Ch. 82.1, with one instance of homoplasy in *P. luteolus*); (19) transverse process of presacral vertebra IV elongate, distal end aligns behind of the posterior margin of the base of the transverse process of presacral vertebra V (Ch. 91.2); (20) tympanic membrane absent (Ch. 113.0, with one reversal in *S. lacteus*); (21) presence of few enlarged marginal papillae of the oral disc in larvae, about two times larger than the small papillae (Ch. 136.1, with reversals in *S. bromelicola*, *S. dorisae*, *S. platycephalus*, and *S. surdus*); (22) m. *interhyoideus* reaching the posterior margin of the m. *pectoralis esternalis* (Ch. 152.4, with one instance of homoplasy in *D. microps*); (23) m. *petrohyoideus* anterior with one additional layer of fibers over the hyoid plate (Ch. 156.1); (24) ventral and dorsal strips of the m. *sternohyoideus* with distinct insertions (Ch. 160.1, with one instance of homoplasy in *Scarthyla goinorum*); and (25) fibers of the m. *extensor brevis distalis digiti V*, lateral slip reaching the distal margin of the second phalange (Ch. 188.1).

3.1.9. Characterization

Small to medium-sized treefrogs (combined SVL in males 15.1–41.0 mm, females 36.0–46.0 mm; Araujo-Vieira et al., 2019) with pointed, rounded or protruding snout in lateral view; vocal sac without (in *Sphaenorhynchus dorisae*, *S. prasinus*) or with lateral longitudinal folds (in the remaining species of the genus), and ventrally not reaching the pectoral region (in *S. prasinus*) or enlarged reaching the pectoral fold (in the remaining species of the genus); males with light (in *S. canga*, *S. dorisae*, *S. lacteus*; Fig. 3C) or dark-colored nuptial pads on Finger II (in the remaining species of the genus; Fig. 3B, D), with rounded papillary epidermal projections (PEPs smaller in diameter: e.g., ~27 μm in *S. prasinus*; Fig. 3B–D, F–H) which have rounded or blunted cytoplasmatic projections on the top of each PEP (Fig. 3B–D, F–H, J–L); presence (in *S. lacteus*) or absence of tympanic membrane (in the remaining species of the genus); presence (in *S. dorisae*, *S. lacteus*, *S. mirim*, *S. planicola*, *S. prasinus*) or absence of dermal ornamentation (folds and/or calcar appendages) on forearm, tarsus, elbow, heel, and subcloacal region in adult males and females (in the remaining species of the genus); eggs laid in water, attached to submerged vegetation (*S. carneus* laid eggs in water or on leaves overhanging water [polymorphic]); absence (in *S. carneus*, *S. dorisae*, *S. mirim*, *S. planicola*) or presence of premaxillary, maxillary, and vomerine teeth (in the remaining species of the genus; vomerine teeth also present in *S. dorisae* [polymorphic]); tadpoles with uniform (in *S. bromelicola*, *S. dorisae*, *S. platycephalus*, *S. surdus*) or irregular size marginal papillae (in *S. canga*, *S. caramaschii*, *S. carneus*, *S. lacteus*, *S. palustris*, *S. planicola*, *S. prasinus*); one (in *S. carneus*) or two anterior labial tooth rows (in the remaining species of the genus; A2 uninterrupted medially in *S. lacteus*); and short (in *S. caramaschii*, *S. carneus*, *S. dorisae*, *S. lacteus*, *S. planicola*, *S. prasinus*), medium-sized (in *S. bromelicola*, *S. canga*, *S. platycephalus*, *S. surdus*) or extreme long spiracle (in *S. palustris*); pedicellate and non-pedicellate premaxillary and maxillary teeth present; maxilla with a *pars dentalis* edentate in 35–40% (in *S. caramaschii*, *S. lacteus*, *S. prasinus*, *S. surdus*), 55–80% (in *S. palustris*, *S. platycephalus*), and 95% of its length (in *S. canga*); premaxilla with teeth continuously present along the entire extension of *pars dentalis* (in *S. prasinus*) or distinctly separated by diastemata, parts of the *pars dentalis* are edentate (in the remaining species of the genus); quadratojugal extremely short (knob-shaped quadratojugal in *S. carneus*) or elongate with the length corresponding to 1/5–1/3 of the distance from the articulation of the ventral ramus of squamosal with quadratojugal to the anterior extreme of the maxilla (in the remaining species of the genus); quadratojugal articulating posteriorly with the anterior process of palatoquadrate cartilage; zygomatic ramus of the squamosal extremely short, 1.0–1.5 times longer than the minimum width of the ventral ramus [zygomatic ramus extremely short or short (2.2–2.4 times) in *S. prasinus* (polymorphic)]; and sacral diapophyses unexpanded (in *S. mirim*) or moderately expanded, 1.5–3 times wider at the tip than at the base (in the remaining species of the genus).

3.1.10. Content

This genus contains 14 species, 12 of which are placed in three species groups (the *S. lacteus*, *S. planicola*, and *S. platycephalus* groups), and two are unassigned to groups (*S. carneus* and *S. prasinus*).

3.1.11. Geographic distribution

Widely distributed in Amazon and Orinoco basins of Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela; Trinidad, Guyana, Surinam, French Guyana. Atlantic Forest of Brazil, from Pernambuco in the northeastern to Rio Grande do Sul in the south (Araujo-Vieira et al., 2019; Frost et al., 2020).

3.1.12. Comments

We revised the list of synapomorphies resulting from the phylogenetic analyses of Araujo-Vieira et al. (2019: Fig. 1) and found few inconsistencies in the optimizations of some characters-states. Two characters do not optimize as synapomorphies of the redefined *Sphaenorhynchus*: the anterolateral process of the hyale laminar (Ch. 66.2) and cardiac process of the cricoid ring laminar, width similar to or slightly thinner than adjacent parts of the ring (Ch. 74.2). They optimize ambiguously in the total evidence phylogenetic hypothesis of Araujo-Vieira et al. (2019). The former could be a synapomorphy of Sphaenorhynchini (with a reversal to a slender, not expanded distally anterolateral process in *Gabohyla pauloalvini* n. gen. and n. comb.), or it could be a synapomorphy of *Sphaenorhynchus*. The latter transformation optimizes ambiguously in different internal nodes of *Sphaenorhynchus* (*S. caramaschii*, *S. dorisae*, *S. mirim*, *S. platycephalus*, and *S. surdus* share this character-state).

We also noted that three synapomorphies were omitted in the list provided by Araujo-Vieira et al. (2019: Fig. 1 and appendix A). They should include two synapomorphies for the sister taxon of *S. carneus*: anterior portion of the cultriform process of the parasphenoid indented (Ch. 42.2, with instances of homoplasy in *Dendropsophus sanborni*, *Phyllodytes luteolus*, *Scinax alter*, and *Xenohyla truncata*) and presence of well-developed and smooth dermal folds on the forearms (Ch. 120.4, with reversals in *S. mirim* and the *S. platycephalus* group). And another one for the *S. platycephalus* group: presence of poorly developed and weakly crenulated dermal folds on forearms of adults (Ch. 120.3, with most species in this group being polymorphic for the character-states 120.1 and 120.3). Other equivocal optimizations are restricted to some outgroup nodes (compare nodes 66, 92, 94, 96–98 in our Fig. 1 with the corresponding nodes in Araujo-Vieira et al. 2019: Fig. 1). However, these mistakes did not affect the discussion of the character-states in Araujo-Vieira et al. (2019). We provide a complete list of synapomorphies for *Sphaenorhynchus* and its internal clades in Appendix C. Some character-states are shown in Fig. 1.

Sphaenorhynchini Faivovich et al., 2018.

The tribe Sphaenorhynchini includes two genera *Gabohyla* n. gen. and *Sphaenorhynchus*. The monophyly of this tribe is supported by molecular evidence and 25 phenotypic synapomorphies (jackknife support = 100%; GB = 90; Araujo Vieira et al., 2019; see also Fig. 1 and Appendix C). Diagnosis, synapomorphies, characterization, and species distribution for Sphaenorhynchini are those described for *Sphaenorhynchus* in Araujo-Vieira et al. (2019: Fig. 1 and appendix A).

3.1.13. Comments

All species of Sphaenorhynchini have nuptial pads formed by a single element covering the base of Finger II. The coloration of the nuptial pads varies among species, being light colored in *Sphaenorhynchus canga*, *S. dorisae*, and *S. lacteus* and dark-colored in the remaining species of *Sphaenorhynchus* and *Gabohyla pauloalvini* n. gen. and n. comb (Fig. 3). They also have variation in the ornamentations over the surface of each papillary epidermal projection (PEP). *Gabohyla pauloalvini* has pointy cytoplasmatic projections on top of each PEP, whereas *S. botocudo*, *S. dorisae*, and *S. prasinus* have blunted or rounded-shaped PEPs. However, the main difference in the PEPs between *G. pauloalvini* and these species of *Sphaenorhynchus* is in size and therefore, in the density of PEPs in the nuptial pad area. *Gabohyla pauloalvini* has less PEPs, which are larger in diameter when compared to the rest of the species (~38 µm of diameter in *G. pauloalvini* vs. ~27 µm in *S. prasinus*). It corroborated observations by Araujo-Vieira et al. (2019: appendix S6, ch. 116) on the relative density of PEPs in Sphaenorhynchini. They reported that *G. pauloalvini* (as *S. pauloalvini*) has 5–7 PEPs by quadrant of 0.01 mm^2 taken from photos using a camera attached to a Nikon stereomicroscope (SMZ-800), whereas species of *Sphaenorhynchus* have between 10 and 12 PEPs by quadrant.

4. Discussion

The recognition of *Gabohyla* n. gen. as a monotypic genus is not required for preserving the monophyly of the former *Sphaenorhynchus* (sensu Araujo-Vieira et al., 2019). However, our major criterion to divide a taxonomic unit that is already monophyletic is based on the several phenotypic synapomorphies that diagnosed the new genus and differentiated it from *Sphaenorhynchus*. Vences et al. (2013: table 4) defined their phenotypic diagnosability criterion where a taxon to which a Linnaean rank is assigned should be diagnosable and identifiable phenotypically, preferably through externally-visible, diagnostic characters, including synapomorphies, that are present in both sexes and as many life-history stages as possible.

While it may not seem necessary to carry out the generic partition of the former *Sphaenorhynchus*, this taxonomic change does not affect the clade stability and support of the redefined *Sphaenorhynchus* as well as the new genus, since both *Gabohyla* and *Sphaenorhynchus* are well-supported by molecular and phenotypic synapomorphies in the parsimony phylogenetic analyses of Araujo-Vieira et al. (2019; see the clade stability criterion of Vences et al., 2013). Moreover, we provide an adequate diagnosis and list of phenotypic synapomorphies for these genera. These were inferred in a quantitative total evidence phylogenetic analysis that stems from a consideration of all the biological information regarding both genera that could be described as homology hypotheses.

We agree that deliberately creating monotypic taxa should be avoided (Farris 1976; Wiley 1979; Vences et al., 2013). However, in some cases these lineages can be very distinct morphologically and reflect a particular distribution of variation, and should be recognized as such in the Linnaean classification (Vences et al., 2013). *Sphaenorhynchus pauloalvini* was undoubtedly the most morphologically-divergent taxon of the former *Sphaenorhynchus* (see Bokermann 1973; Araujo-Vieira et al., 2019). The combination of 12 morphological autapomorphies and several phenotypic diagnostic characters makes *G. pauloalvini* n. gen. and n. comb. morphologically unique among the Hylinae (see the Diagnosis section and also Araujo-Vieira et al., 2019). For example, external morphological characteristics such as the presence of cloacal sheath, a white lateral line bordered above by a black lateral line, and dark-colored nuptial pads on Finger II in males with rounded, large papillary epidermal projections differentiate *G. pauloalvini* from all species of *Sphaenorhynchus*. Given the high morphological differences of this taxon, the phenotypic diagnosability criterion of Vences et al. (2013), as mentioned above, can be used as an argument for the recognition of this monotypic genus. Furthermore, as more species are discovered and described, we could associate them to the particular phenotype of either *Gabohyla* or *Sphaenorhynchus*, and newly-discovered species can be allocated to any of these genera without conflict.

5. Conclusions

Our observations showed that *Sphaenorhynchus pauloalvini* is a morphologically unique species in *Sphaenorhynchus*, and for these reason we erected the new monotypic genus *Gabohyla* for this species, and then redefined *Sphaenorhynchus* to include the remaining 14 species in the genus. *Gabohyla* and *Sphaenorhynchus* were properly diagnosed and characterized, including several phenotypic synapomorphies. The recognition of this new genus is built upon the increased knowledge of the diversity and phylogenetic relationships of Sphaenorhynchini and as such the proposed taxonomy reflects this progress.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcz.2020.04.002.

References

Altig, R., McDiarmid, R.W., 1999. Body plan. Development and morphology. In: McDiarmid, R.W., Altig, R. (Eds.), Tadpoles: the Biology of Anuran Larvae. University of Chicago Press, Chicago, USA, pp. 24–51.

Araujo-Vieira, K., Tacioli, A., Faivovich, J., Orrico, V.G.D., Grant, T., 2015a. The tadpole of *Sphaenorhynchus caramaschii*, with comments on larval morphology of *Sphaenorhynchus* (Anura: Hylidae). Zootaxa 3904, 270–282. https://doi.org/10.11646/zootaxa.3904.2.6.

Araujo-Vieira, K., Lacerda, J.V.A., Pezzuti, T.L., Leite, F.S., Assis, C.L., Cruz, C.A.G., 2015b. A new species of hatchet-faced treefrog *Sphaenorhynchus* Tschudi (Anura: Hylidae) from quadrilátero ferrífero, minas gerais, southeastern Brazil. Zootaxa 4059, 96–114. https://doi.org/10.11646/zootaxa.4059.1.5.

Araujo-Vieira, K., Blotto, B.L., Caramaschi, U., Haddad, C.F.B., Faivovich, J., Grant, T., 2019. A total evidence analysis of the phylogeny of hatchet-faced treefrogs (Anura: Hylidae: *Sphaenorhynchus*). Cladistics 35, 469–486.

Bokermann, W.C.A., 1962. Cuatro nuevos hylidos del Brasil. Neotropica. La Plata 8, 81–92.

Bokermann, W.C.A., 1966. Duas novas espécies de “*Sphaenorhynchus*” (Amphibia, Hylidae). Rev. Bras. Biol. 26, 15–21.

Bokermann, W.C.A., 1973. Duas novas espécies de “*Sphaenorhynchus*” da Bahia (Anura, Hylidae). Rev. Bras. Biol. 33, 589–594.

Boulenger, G.A., 1888. A list of batrachians from the province Santa Catharina, Brazil. Ann. Mag. Nat. Hist., Series 6, 415–417.

Caramaschi, U., 2010. Descrição do girino de *Sphaenorhynchus surdus* (Cochran, 1953) (Anura, Hylidae). Bol. M. Biol. Prof. Mello Leitão, Nova Série 27, 67–74.

Caramaschi, U., Almeida, A.P., Gasparini, J.L., 2009. Description of two new species of *Sphaenorhynchus* (Anura, Hylidae). Zootaxa 2115, 34–46.

Cochran, D.M., 1953. Three new Brazilian frogs. Herpetologica 8, 111–115.

Cope, E.D., 1862. On some new and little known American Anura. Proc. Acad. Nat. Sci. Phila. 4, 151–159.

Cope, E.D., 1868. An examination of the reptilia and Batrachia obtained by the orton expedition to equador and the upper Amazon, with notes on other species. Proc. Acad. Nat. Sci. Phila. 20, 96–140.

Crump, M.L., 1974. Reproductive strategies in a tropical anuran community. Misc. Publ. Univ. Kans. Mus. Nat. Hist. 61, 1–65.

Cruz, C.A.G., 1973. Observações sobre o girino de *Sphaenorhynchus planicola* (Lutz & Lutz, 1938) (Amphibia, Anura, Hylidae). Arch. Mus. Nac. Rio de J. 3, 83–86.

Daudin, F.M., 1800. Histoire naturelle des quadrupedes ovipares, vol. 2. Livraison, Marchant et Cie, Paris.

Duellman, W.E., 1970. The hylid frogs of Middle America. Monogr. Mus. Nat. Hist. Univ. Kans. 1, 1–753.

Duellman, W.E., Wiens, J.J., 1992. The status of the hylid frog genus *Ololygon* and the recognition of *Scinax* Wagler, 1830. Misc. Publ. Univ. Kans. Mus. Nat. Hist. 15, 1–23.

Duellman, W.E., de Sá, R.O., 1988. A new genus and species of South American hylid frog with a highly modified tadpole. Trop. Zool. 1, 117–136.

Duellman, W.E., Marion, A.M., Hedges, S.B., 2016. Phylogenetics, classification, and biogeography of the treefrogs (Amphibia: Anura: Arboranae). Zootaxa 4104, 1–109. https://doi.org/10.11646/zootaxa.4104.1.1.

Fabrezi, M., Alberch, P., 1996. The carpal elements of anurans. Herpetologica 52, 188–204.

Faivovich, J., 2002. A cladistic analysis of *Scinax* (Anura: Hylidae). Cladistics 18, 367–393. https://doi.org/10.1111/j.1096-0031.2002.tb00157.x.

Faivovich, F., Haddad, C.F.B., Garcia, P.C.A., Frost, D.R., Campbell, J.A., Wheeler, W.C., 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. Bull. Am. Mus. Nat. Hist. 294, 240. http://hdl.handle.net/2246/462.

Faivovich, J., Pereyra, M.O., Luna, M.C., Hertz, A., Blotto, B.L., Vásquez-Almazán, C.R., Mccranie Jr., Sanchez-Ramirez, D., Baêta, D., Araujo-Vieira, K., Köhler, G., Kubicki, B., Campbell, J.A., Frost, D.R., Haddad, C.F.B., 2018. On the monophyly and relationships of several genera of Hylini (Anura: Hylidae: Hylinae). S. Am. J. Herpetol. 13, 1–32. https://doi.org/10.2994/SAJH-D-17-00115.1.

Farris, J.S., 1976. Phylogenetic classification of fossils with recent species. Syst. Zool. 25, 271–282. https://doi.org/10.2307/2412495.

Fitzinger, L.J.F.J., 1843. Systema Reptilium. Fasciculus Primus. Braumüller und Seidel, Wien.

Freitas, M.A. De, Silva, T.F.S., Loebmann, D., 2009. Amphibia, Hylidae, *Sphaenorhynchus pauloalvini* Bokermann, 1973: distribution extension and rediscovery in nature. Check List. 5, 200–201.

Frost, D.R., 2020. Amphibian Species of the World: an Online Reference. Version 6.0. 23 Jan 2020. American Museum of Natural History, New York, USA. Available from: http://research.amnh.org/herpetology/amphibia/index.html.

Günther, A.C.L.G., 1858. Neue Batrachier in der Sammlung des britischen Museums. Arch. Naturgesch. 24, 319–328.

Goloboff, P.A., Catalano, S.A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32, 221–238. https://doi.org/10.1111/cla.12160.

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24, 774–786. https://doi.org/10.1111/j.1096-0031.2008.00217.x.

Goin, C.J., 1957. Status of the frog genus *Sphoenohyla* with a synopsis of the species. Caldasia 8, 11–31.

Izecksohn, E., 1959. Uma nova espécie de "Hylidae" da Baixada Fluminense, Estado do Rio de Janeiro, Brasil. Rev. Bras. Biol. 19, 259–264.

Izecksohn, E., 1998. [1996]. Novo gênero de Hylidae brasileiro (Amphibia, Anura). Rev. Univ. Rural, Cienc. Vida 18, 47–52.

Jetz, W., Pyron, R.A., 2018. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. Nat. Ecol. Evol. 2, 850–858. https://doi.org/10.1038/s41559-018-0515-5.

Jurgens, J.D., 1971. The morphology of the nasal region of Amphibia and its bearing on the phylogeny of the group. Ann. - Univ. Stellenbosch 46, 1–146.

Luna, M.C., Mcdiarmid, R.W., Faivovich, J., 2018. From erotic excrescences to pheromone shots: structure and diversity of nuptial pads in anurans. Biol. J. Linn. Soc. 124, 403–446. https://doi.org/10.1093/biolinnean/bly048.

Lutz, A., 1925. Batraciens du Brésil. C. r. séances Soc. biol. ses. fil. 93, 211–214.

Lutz, B., 1973. Brazilian Species of *Hyla*. University of Texas Press, Austin.

Lutz, A., Lutz, B., 1938. I. On *Hyla aurantiaca* Daudin and *Sphoenorhynchus* Tschudi and on two allied hylae from southeastern Brasil. An. Acad. Bras. Ciênc. 10, 175–194.

Lutz, A., Lutz, B., 1939. New Hylidae from Brazil/hylideos novos do Brasil. An. Acad. Bras. Ciênc. 11, 67–89.

Machado, D.J., 2015. YBYRÁ facilitates comparison of large phylogenetic trees. BMC Bioinf. 16, 204. https://doi.org/10.1186/s12859-015-0642-9.

Myers, C.W., Duellman, W.E., 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from Western Panama. Am. Mus. Novit. 2752, 1–32.

Myers, C.W., Stothers, R.B., 2006. The myth of Hylas revisited: the frog name *Hyla* and other commentary on *Specimen medicum* (1768) of J. N. Laurenti, the "father of Herpetology". Arch. Nat. Hist. 33, 241–266. https://doi.org/10.3366/anh.2006.33.2.241.

Peixoto, O.L., Pimenta, B., 2004. *Sphaenorhynchus pauloalvini*. The IUCN Red List of Threatened Species 2004: e.T56018A11409979. https://doi.org/10.2305/IUCN.UK.2004.RLTS.T56018A11409979.en. (Accessed 22 February 2019).

Peters, W.C.H., 1872. Über eine Sammlung von Batrachiern aus Neu-Freiburg in Brasilien. Ber. Akad. Wiss. Berlin 1872, 680–684.

Pyron, R.A., 2014. Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. Syst. Biol. 63, 779–797. https://doi.org/10.1093/sysbio/syu042.

Pyron, R.A., Wiens, J.J., 2011. A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. Mol. Phylogenet. Evol. 61, 543–583. https://doi.org/10.1016/j.ympev.2011.06.012.

Roberto, I.J., Araujo-Vieira, K., Carvalho-e-Silva, S.P., Ávila, R.W., 2017. A new species of *Sphaenorhynchus* (Anura: Hylidae) from northeastern Brazil. Herpetologica 73, 148–161. https://doi.org/10.1655/HERPETOLOGICA-D-16-00021.

Rodriguez, L.O., Duellman, W.E., 1994. Guide to the frogs of the iquitos region, Amazonian Peru. Sci. Pap. Univ. Kans. Mus. Nat. Hist. 22, 1–80.

Sabaj, M.H., 2016. Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology: an Online Reference (v6.5. American Society of Ichthyologists and Herpetologists, USA. Available at: http://www.asih.org. (Accessed 16 August 2016) http://www.webcitation.org/query.php.

Savage, J.M., Heyer, R.W., 1967. Variation and distribution of the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. Beitr. Neotrop. Fauna 5, 111–131. https://doi.org/10.1080/01650526709360400.

Schmidt, K.P., 1944. New frogs from misiones and Uruguay. Field Columbian Mus. Publ. Zool. Ser. 29, 153–160.

Suárez-Mayorga, A.M., Lynch, J.D., 2001. Los renacuajos colombianos de *Sphaenorhynchus* (Hylidae), descripciones, anotaciones sistemáticas y ecológicas. Rev. Acad. Colomb. Cienc. Exactas Fis. Nat. 25, 411–420.

Taylor, W.R., Van Dyke, G.C., 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9, 107–119.

Toledo, L.F., Garcia, P.C.A., Lingnau, R., Haddad, C.F.B., 2007. A new species of *Sphaenorhynchus* (Anura; Hylidae) from Brazil. Zootaxa 1658, 57–68. https://doi.org/10.11646/zootaxa.1658.1.4.

Toledo, L.F., Llusia, D., Vieira, C.A., Corbo, M., Márquez, M., 2014. Neither convergence nor divergence in the advertisement call of sympatric congeneric Neotropical frogs. Bioacoustics 2014, 1–17. https://doi.org/10.1080/09524622.2014.926831.

Trueb, L., 1973. Bones, frogs, and evolution. In: Vial, J.L. (Ed.), Evolutionary Biology of the Anurans: Contemporary Research on Major Problems. University of Missouri Press, USA, pp. 65–132.

Trueb, L., 1993. Patterns of cranial diversification among the Lissamphibia. In: Hanken, J., Hall, B.K. (Eds.), The Skull. University of Chicago Press, Chicago, USA, pp. 255–343.

Tschudi, J.J. Von, 1838. Classification der Batrachier mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. Neuchâtel: Petitpierre 1838, 1–111.

Vences, M., Guyasamin, J.M., Miralles, A., de la Riva, Ignacio, 2013. To name or not to name: criteria to promote economy of change in Linnaean classification schemes. Zootaxa 3636, 201–244. https://doi.org/10.11646/zootaxa.3636.2.1.

Wagler, J., 1830. Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel. Ein Beitrag zur vergleichenden Zoologie. München, Stuttgart and Tübingen. J. G. Cotta.

Werner, F., 1894. Über einige Novitäten der herpetologischen Sammlung des Wiener zoolog. Vergl. Anatom Instituts. Zool. Anz. 17, 155–157.

Wied-Neuwied, M.A.P., zu, Prinz, 1821. Reise nach Brasilien in den Jahren 1815 bis 1817, vol. 1. Franfurt a. M.: Henrich Ludwig Brönner.

Wied-Neuwied, M.A.P., Prinz, zu, 1824. Verzeichnis der Amphibien welche in zweiten Bande der Naturgeschichte Brasiliens von Prinz max von Neuwied werden beschreiben Werden. Isis von Oken 14, 661–673.

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A., Reeder, T.W., 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. Am. Nat. 168, 579–596. https://doi.org/10.1086/507882.

Wiens, J.J., Kuczynski, C.A., Hua, X., Moen, D.S., 2010. An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. Mol. Phylogenet. Evol. 55, 871–882. https://doi.org/10.1016/j.ympev.2010.03.013.

Wiley, E.O., 1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. Syst. Zool. 28, 308–337. https://doi.org/10.2307/2412585.