Zoological Journal of the Linnean Society, 2021, **XX**, 1–27. With 7 figures.

Prepollex diversity and evolution in Cophomantini (Anura: Hylidae: Hylinae)

PAULO D. P. PINHEIRO[1,*], BORIS L. BLOTTO[1,2], SANTIAGO R. RON[3], EDWARD L. STANLEY[4], PAULO C. A. GARCIA[5], CÉLIO F. B. HADDAD[2], TARAN GRANT[1] and JULIÁN FAIVOVICH[6,7,*]

[1]*Laboratório de Anfíbios, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, São Paulo, Brazil*
[2]*Laboratório de Herpetologia e Centro de Aquicultura (CAUNESP), Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil*
[3]*Museo de Zoología, Escuela de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador*
[4]*Department of Natural History, Florida Museum of Natural History, Gainesville, Florida, USA*
[5]*Laboratório de Herpetologia, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil*
[6]*División Herpetología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' – CONICET, Angel Gallardo 470, C1405DJR, Buenos Aires, Argentina*
[7]*Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina*

Received 20 June 2021; revised 10 August 2021; accepted for publication 24 August 2021

Several species of Cophomantini are known to have an enlarged prepollex, commonly modified as an osseous spine. We surveyed the osteology and myology of the prepollex and associated elements of 94 of the 190 species of Cophomantini, sampling all genera, except *Nesorohyla*. Two distinct prepollex morphologies were found: a blade-shaped and a spine-shaped morphology. We described the observed variation in 17 discrete characters to study their evolution in the most inclusive phylogenetic hypothesis for Cophomantini. Both morphologies evolved multiple times during the evolutionary history of this clade, but the origin of the spine-shaped distal prepollex in *Boana* and *Bokermannohyla* is ambiguous. The articulation of metacarpal II with the prepollex through a medial expansion of the metacarpal proximal epiphysis is a synapomorphy for *Boana*. The shape of the curve of the spine, and a large post-articular process of the distal prepollex, are synapomorphies for the *Boana pulchella* group, the latter being homoplastic in the *Bokermannohyla martinsi* group. Muscle character states associated with the spine-shaped prepollex are plesiomorphic for Cophomantini. We discuss evolution, function, behaviour and sexual dimorphism related to the prepollical elements. A bony spine is associated with fights between males, but forearm hypertrophy could be more related with habitat than with territorial combat.

ADDITIONAL KEYWORDS: carpus – comparative morphology – gladiator frogs – myology – osteology.

INTRODUCTION

> *"The fighting males encircle each other's heads and necks with the arms and place their hands into positions that permit them to drive the sharp, curved pollex rudiments into the enemy."*
>
> (B. Lutz, 1960a)

The prepollex of anurans is a mesopodial structure positioned proximally with respect to digit II (first finger), in the preaxial region, being the last carpal element to differentiate during hand development (between larval stage 36 and metamorphosis; Gosner, 1960; Fabrezi, 1992, 2001; Fabrezi & Alberch, 1996). The radius gives origin, by segmentation, to the radiale, the element Y and the prepollex (in this sequence; Shubin & Alberch, 1986). In anurans, the prepollex is usually formed by two elements (one proximal, the

---

*Corresponding authors. E-mail: pdp.pinheiro@gmail.com; julian@macn.gov.ar

other distal), but can also be formed by three or more elements or even be absent (Fabrezi, 2001).

Fabrezi (2001) surveyed the diversity of the prepollex in anurans. She also discussed the hypothesis of its homology with the first digit of other Tetrapoda, concluding that these two structures are not homologous, and briefly discussed its evolution, involving specialization in both morphology and function. However, developmental and gene-expression evidence (Hayashi *et al.*, 2015), and identification of elements found in some mammals as a prepollex (e.g. Le Minor, 1994; Kley & Kearney, 2007; Echeverría *et al.*, 2019), suggest that the issue of homology between the prepollex and first digit of other Tetrapoda is still controversial.

One specialization of the prepollex is a distal element modified as an enlarged spine that protrudes through the medial outline of digit II and sometimes even through the skin. Males of many species use this prepollical spine during intraspecific combats for limited resources, such as vocalization or oviposition sites (e.g. Shine, 1979; Kluge, 1981; Martins & Haddad, 1988) or as a defensive structure against predators (Toledo *et al.*, 2011). The prepollical spine occurs in some phylogenetically distant groups of anurans: ranids [*Babina holsti* (Boulenger, 1892) and *Babina subaspera* (Barbour, 1908); Boulenger, 1892; Barbour, 1908; Van Denburgh, 1912; see Table 1 for taxonomic authorities of taxa mentioned throughout the text], centrolenids (e.g. *Centrolene lynchi*, *Cochranella duidaeana*, *Teratohyla spinosa* and *Vitreorana gorzulae*; Taylor, 1949; Flores, 1985; Señaris & Ayarzagüena, 2005), mantellids (the *Boophis albilabris* group; Vences *et al.*, 2010a), microhylids (e.g. *Anodonthyla*, *Hoplophryne rogersi* and *Metaphrynella pollicaris*; Boulenger, 1890; Noble, 1931, Vences *et al.*, 2010b) and hylids. Within this last family, the prepollical spine occurs in the tribe Hylini (in several *Plectrohyla* and in *Ecnomiohyla miliaria*; Duellman, 1961, 1968, 1970; Duellman & Campbell, 1992) and in several species of Cophomantini (most species of *Boana*, all species of *Bokermannohyla* and some species of *Hyloscirtus*; Kizirian *et al.*, 2003; Faivovich *et al.*, 2005; Almendáriz *et al.*, 2014; Rivera-Correa *et al.*, 2016; Ron *et al.*, 2018). Cophomantini is a clade that has been characterized as having an enlarged prepollex, differentiated as a spine or not (Faivovich *et al.*, 2005).

Cophomantini includes 190 species in six genera (Frost, 2021). The clade is widely distributed from Argentina to Nicaragua, occurring also in some Caribbean islands. Its species reproduce in streams (e.g. *Bokermannohyla*, *Hyloscirtus* and several species of *Boana*; Lutz & Orton, 1946; Bokermann, 1964; Duellman, 1972), ponds (e.g. several species of *Boana*; Lutz, 1973; Heyer *et al.* 1990), bromeliads (one species of *Bokermannohyla*; Malagoli *et al.*, 2021), mud or vegetation basins constructed by the male (the *Boana faber* group, some species of the *Boana semilineata* group and some *Bokermannohyla*; e.g. Goeldi, 1895; Lutz, 1960a, 1973; Martins & Haddad, 1988; Martins & Moreira, 1991; Haddad & Prado 2005; Montesinos *et al.*, 2021) and subterranean nests constructed by the male (*Aplastodiscus*; Haddad & Sawaya, 2000) or in natural cavities (one species of *Boana*; Landestoy, 2013). Cophomantini has a complex biogeographic history [see a brief discussion in Faivovich *et al.* (2005)], and the evolution of several character systems has been explored recently in a phylogenetic context (e.g. Faivovich *et al.*, 2013; Brunetti *et al.*, 2015; Ferro *et al.*, 2018; Pinheiro *et al.*, 2019; Lyra *et al.*, 2020).

Spine variation among the 130 species in several genera of Cophomantini having a prepollical spine has already been described (e.g. Bokermann, 1964; Garcia & Haddad, 2008; Faivovich *et al.*, 2009). Further, a reasonably stable hypothesis of phylogenetic relationships for the tribe (e.g. Faivovich *et al*., 2005, 2013; Pinheiro *et al.*, 2019; Lyra *et al.*, 2020) make this clade appropriate to study prepollical diversity and evolution. As such, on the basis of a survey of the diversity and taxonomic distribution of prepollical elements and associated metacarpal and carpal elements (element Y, distal carpal 2 and metacarpal II) in Cophomantini, we describe the musculature related to those elements and their taxonomic variation, propose hypotheses of homology to account for the observed variation and analyse the evolutionary history of the character system through ancestral character-state reconstruction on the most recent and densely sampled phylogenetic hypothesis of the tribe (Lyra *et al.*, 2020). Finally, we discuss the evolutionary aspects and anatomy of the prepollex and related structures in Cophomantini.

MATERIAL AND METHODS

We studied the osteology and myology of the prepollex and associated carpal elements (i.e. distal prepollex, proximal prepollex, element Y, distal carpal 2 and metacarpal II) of species pertaining to all taxonomic groups of Cophomantini, except the monotypic *Hyloscirtus jahni* group and *Nesorohyla*. Studied specimens are listed in the Supporting Information, File S1. The abbreviations of collections follow Sabaj (2020).

Most studied specimens were cleared and double-stained males and females prepared following the method of Taylor & Van Dyke (1985). They were studied with stereomicroscopes coupled to digital cameras. *Bokermannohyla juiju* and *Bokermannohyla langei* were studied through X-ray images obtained with Faxitron X-ray equipment. Several other species of *Boana* and *Hyloscirtus* were also assessed through

Table 1. List of taxa included in the main text with the respective taxonomic authorities

Bufonidae Gray, 1825
Bufo japonicus Temminck & Schlegel, 1838
Centrolenidae Taylor, 1951

Centrolene lynchi (Duellman, 1980)
Cochranella duidaeana (Ayarzagüena, 1992)
Cochranella riveroi (Ayarzagüena, 1992)

Teratohyla spinosa (Taylor, 1949)
Vitreorana castroviejoi (Ayarzagüena & Señaris, 1997)
Vitreorana gorzulae (Ayarzagüena, 1992)
Vitreorana helenae (Ayarzagüena, 1992)
Vitreorana ritae (Lutz, 1952)
Hylidae Rafinesque, 1815
Acris crepitans Baird, 1854
***Aplastodiscus* Lutz, 1950**
Aplastodiscus albosignatus (Lutz & Lutz, 1938)
Aplastodiscus arildae (Cruz & Peixoto, 1987)
Aplastodiscus cavicola (Cruz & Peixoto, 1985)
Aplastodiscus cochranae (Mertens, 1952)

Aplastodiscus ehrhardti (Müller, 1924)
Aplastodiscus perviridis (Lutz, 1950)
Aplastodiscus sibilatus (Cruz *et al.*, 2003)
***Boana* Gray, 1825**
Boana albomarginata (Spix, 1824)
Boana albopunctata (Spix, 1824)
Boana appendiculata (Boulenger, 1882)
Boana benitezi (Rivero, 1961)
Boana boans (Linnaeus, 1758)
Boana cinerascens (Spix, 1824)
Boana claresignata (Lutz & Lutz, 1939)

Boana clepsydra (Lutz, 1925)
Boana diabolica (Fouquet *et al.*, 2016)
Boana ericae (Caramaschi & Cruz, 2000)
Boana faber (Wied, 1821)
Boana geographica (Spix, 1824)
Boana heilprini (Noble, 1923)
Boana hutchinsi (Pyburn & Hall, 1984)
Boana polytaenia (Cope, 1870)
Boana pombali (Caramaschi *et al.*, 2004)
Boana pulchella (Duméril & Bibron, 1841)
Boana punctata (Schneider, 1799)
Boana riojana (Koslowsky, 1895)
Boana roraima (Duellman & Hoogmoed, 1992)
Boana rosenbergi (Boulenger, 1898)

Boana semilineata (Spix, 1824)
Boana tepuiana (Barrio-Amorós & Brewer-Carias, 2008)
Boana ventrimaculata Caminer & Ron, 2020
Bokermannohyla Faivovich *et al.*, 2005
Bokermannohyla alvarengai (Bokermann, 1956)
Bokermannohyla hylax (Heyer, 1985)
Bokermannohyla ibitiguara (Cardoso, 1983)
Bokermannohyla juiju Faivovich *et al.*, 2009
Bokermannohyla langei (Bokermann, 1965)
Bokermannohyla martinsi (Bokermann, 1964)
Bokermannohyla oxente Lugli & Haddad, 2006
Bokermannohyla pseudopseudis (Miranda-Ribeiro, 1937)

Bokermannohyla saxicola (Bokermann, 1964)
Dendropsophus labialis (Peters, 1863)
Dendropsophus luddeckei Guarnizo *et al.*, 2012
Dendropsophus nanus (Boulenger, 1889)
Ecnomiohyla Faivovich *et al.*, 2005
Economiohyla miliaria (Cope, 1886)
Hyla cinerea (Schneider, 1799)
***Hyloscirtus* Peters, 1882**
Hyloscirtus lindae (Duellman & Altig, 1978)
Hyloscirtus alytolylax (Duellman, 1972)
Hyloscirtus antioquia Rivera-Correa & Faivovich, 2013

Hyloscirtus armatus (Boulenger, 1902)
Hyloscirtus bogotensis (Peters, 1882)
Hyloscirtus callipeza (Duellman, 1989)
Hyloscirtus colymba (Dunn, 1931)
Hyloscirtus condor Almendáriz *et al.*, 2014
Hyloscirtus criptico Coloma *et al.*, 2012
Hyloscirtus diabolus Rivera-Correa *et al.*, 2016
Hyloscirtus princecharlesi Coloma *et al.*, 2012
Hyloscirtus psarolaimus (Duellman & Hillis, 1990)
Hyloscirtus ptychodactylus (Duellman & Hillis, 1990)
Hyloscirtus simmonsi (Duellman, 1989)
Hyloscirtus staufferorum (Duellman & Coloma, 1993)
Hyloscirtus tapichalaca (Kizirian *et al.*, 2003)
Hyloscirtus tigrinus Mueses-Cisneros & Anganoy-Criollo, 2008

Hyloscirtus torrenticola (Duellman & Altig, 1978)
Myersiohyla Faivovich *et al.*, 2005
Myersiohyla chamaeleo Faivovich *et al.*, 2013
Myersiohyla neblinaria Faivovich *et al.*, 2013
***Nesorohyla* Pinheiro *et al.*, 2018**
Phrynomedusa appendiculata (Lutz, 1925)
Phrynomedusa dryade Baêta *et al.*, 2016
Phyllodytes luteolus (Wied, 1821)
Pseudis minuta Günther, 1858
***Plectrohyla* Brocchi, 1877**
Scinax cruentomma (Duellman, 1972)
Scinax staufferi (Cope, 1865)

Trachycephalus typhonius (Linnaeus, 1758)
Leptodactylidae Werner, 1896
***Leptodactylus* Fitzinger, 1826**
Leptodactylus latrans (Steffen, 1815)
Leptodactylus melanonotus (Hallowell, 1861)
Leptodactylus pentadactylus (Laurenti, 1768)
Mantellidae Laurent, 1946
Boophis albilabris (Boulenger, 1888)
Boophis occidentalis Glaw & Vences, 1994
Microhylidae Günther, 1858
Anodonthyla Müller, 1892

Anodonthyla boulengeri Müller, 1892
Hoplophryne rogersi Barbour & Loveridge, 1928
Metaphrynella Parker, 1934
Metaphrynella pollicaris (Boulenger, 1890)
Petropedetidae Noble, 1931
Arthroleptides martiensseni Nieden, 1911
***Petropedetes* Reichenow, 1874**

Table 1. Continued

Boana joaquini (Lutz, 1968)	*Hyloscirtus hillisi* Ron *et al.*, 2018	*Petropedetes cameronensis* Reichenow, 1874
Boana latistriata (Caramaschi & Cruz, 2004)	*Hyloscirtus jahni* (Rivero, 1961)	**Ranidae Batsch, 1796**
Boana lundii (Burmeister, 1856)	*Hyloscirtus larinopygion* (Duellman, 1973)	***Babina* Thompson, 1912**
Boana microderma (Pyburn, 1977)	*Hyloscirtus lynchi* (Ruiz-Carranza & Ardila-Robayo, 1991)	*Babina holsti* (Boulenger, 1892)
Boana nigra Caminer & Ron, 2020	*Hyloscirtus pacha* (Duellman & Hillis, 1990)	*Babina subaspera* (Barbour, 1908)
Boana nympha (Faivovich *et al.*, 2006)	*Hyloscirtus palmeri* (Boulenger, 1908)	***Pelophylax* Fitzinger, 1843**
Boana pellucens (Werner, 1901)	*Hyloscirtus pantostictus* (Duellman & Berger, 1982)	*Rana esculenta* Linnaeus, 1758
Boana picturata (Boulenger, 1899)	*Hyloscirtus platydactylus* (Boulenger, 1905)	

X-ray images (see Supporting Information, File S1) available at the website Anfíbios del Ecuador (https://bioweb.bio/faunaweb/amphibiaweb; Ron *et al.*, 2019). *Hyloscirtus armatus*, *Myersiohyla chamaeleo* and *M. neblinaria* were studied through micro-CT scanning microtomography images. The holotypes of *M. chamaeleo* and *M. neblinaria* were imaged using a GE phoenix v|tome|x s CT system with a micro-focus 240 kV X-ray tube at the Microscopy and Imaging Facility Lab of the American Museum of Natural History, New York, USA (see Supporting Information, File S2 for details of the scannings). The resulting radiographs were converted to tomograms using GE phoenix datos|x v.2.3 software. The *Hyloscirtus armatus* specimen was scanned using a SkyScan 1176 X-ray Microtomograph (Antwerp, Belgium) equipment from the Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil, and images were processed by the SkyScan NRecon software. 3D rendering and segmentation for the three specimens were performed with VGStudio MAX v.3.4 (Volume Graphics GmbH).

We measured the length of metacarpal II as the distance between distal and proximal margins of its epiphyses and the length of the distal prepollex as the distance from the tip of the distal element to a point in the midlength of the articulation with the proximal prepollex (Supporting Information, File S2). Measurements were taken with tpsDIG2 (v.2.31) free software. Because females have a partially or completely cartilaginous prepollex and the X-ray does not detect cartilaginous structures, we did not measure the prepollex of females in several species examined through X-ray images. Terminology of autopodial bones follows Shubin & Alberch (1986) and Fabrezi & Alberch (1996), and for phalanges and hand muscles follows Blotto *et al.* (2020).

Ancestral character-state reconstruction was performed on the most inclusive phylogenetic hypothesis available for Cophomantini (Lyra *et al.*, 2020) using additive (ordered; Farris, 1970) and non-additive (unordered; Fitch, 1971) optimization in TNT v.1.5 (Goloboff & Catalano, 2016). Among the studied species, only those analysed by Lyra *et al.* (2020) were included for ancestral character-state reconstruction. Because *Boana latistriata* was synonymized with *Boana polytaenia* (Faivovich *et al.*, 2021), we pruned *Boana latistriata* from the tree. Some taxa from the phylogenetic hypothesis of Lyra *et al.* (2020) representing key groups were unavailable for this study and were replaced by closely related species, as follows: *Boana clepsydra* instead of *Boana claresignata*, *Phrynomedusa appendiculata* instead of *P. dryade* and *Scinax cruentomma* instead of *S. staufferi*.

For the present study, we assessed the external and internal morphology of several species of

Cophomantini. All specimens with an integumentary projection on digit II also have a spine-shaped distal prepollex, with the integumentary projection enveloping the tip of the spine. All other studied specimens lack an integumentary projection on digit II, but have an expanded inner metacarpal tubercle that is internally supported by a blade-shaped distal prepollex. These external characteristics allowed us to infer the general morphology of the prepollex for the 96 species of Cophomantini not examined in this study by consulting the pertinent literature (see Supporting Information, File S3). For these taxa, we only inferred the overall shape of the prepollex, as more detailed information cannot be obtained from external morphology. For comments on the sexual dimorphism on forearm width, we compiled data from the literature complementing it with available photographs (i.e. if there is clear difference in proportions of forearm width between sexes, the forearm was considered dimorphic).

The sequences of the candidate species of the *Boana semilineata* group employed by Lyra *et al.* (2020) were named following Peloso *et al.* (2018), as updated by Caminer & Ron (2020). In the same way, sequences of some candidate species of the *Boana albopunctata* group employed by Lyra *et al.* (2020) were named as updated by Fouquet *et al.* (2021).

RESULTS

OSTEOLOGY

We studied the carpal osteology of 94 species of Cophomantini and seven undescribed taxa, totaling 101 taxonomic units (Supporting Information, Files S1, S3). The carpal morphology of all studied species of Cophomantini, and the outgroups, corresponds to Morphology C of Fabrezi (1992), consisting of six carpal elements: distal carpal 3-4-5, distal carpal 2, ulnare, radiale, element Y and the prepollex (which has two elements, proximal prepollex and distal prepollex).

Proximal prepollex: This is a cubic element that does not exhibit significant variation among the studied taxa. It articulates with the element Y proximally, metacarpal II distally and post-axially, and with the distal prepollex distally (Figs 1A, 2A).

Distal prepollex: In all studied taxa, the distal prepollex articulates with the proximal prepollex proximally and metacarpal II laterally. In Cophomantini it presents two distinct morphologies: blade-shaped (Fig. 1) and spine-shaped (Fig. 2).

The blade-shaped distal prepollex is an enlarged element, longer than wide, with its overall shape similar to a knife blade (although it is not a sharp-edged structure; Fig. 1). It is depressed and its length is 0.41–0.88 the length of metacarpal II (Table 2). Its medial margin is convex, unossified (cartilaginous) in many species and lacks a dorsal crest. The lateral margin is straight or concave. Its tip generally points at metacarpal II and may include one or two small, additional, mineralized or entirely cartilaginous distal elements (Fig. 1A–C, G, I). The proximal and distal elements of the prepollex are fused in one specimen of *Hyloscirtus armatus* (USNM 206715).

The blade-shaped distal prepollex is present in *Myersiohyla*, *Hyloscirtus* (except the clade including *H. condor*, *H. hillisi* and *H. tapichalaca*), *Aplastodiscus* and a clade of the *Boana semilineata* group that includes *B. appendiculata*, *B. diabolica*, *B. geographica*, *B. semilineata*, *B. ventrimaculata* and *B.* candidate SP1 and SP3 (referred to as the *Boana semilineata* complex). In the *Hyloscirtus armatus* group, the prepollex has a medial ossified surface expanded dorsoventrally. This dorsoventral expansion supports a flat and elliptical sesamoid medially (Fig. 1K).

Small, additional elements, distal to the blade-shaped distal prepollex, occur in several species (Fig. 1). In *M. chamaeleo* and in *B. semilineata*, one additional ossified element varies between being present or absent. One small, unossified element occurs in *Hyloscirtus alytolylax*, *H.* aff. *alytolylax*, *H. bogotensis* and *H. colymba* (*H. bogotensis* group) and *H. staufferorum* (*H. larinopygion* group). This small element may be present or absent in *H.* aff. *piceigularis* and *H.* aff. *simmonsi* 1. In *H. callipeza*, *H. lynchi* and *H. platydactylus* (*H. bogotensis* group) there are two small distal elements, pointing at metacarpal II – the proximal additional element is partially mineralized (Fig. 1B) in *H. platydactylus*. One specimen of *H. torrenticola* lacks additional elements, while the other has two additional cartilaginous elements.

The spine-shaped distal prepollex is an enlarged element that is wide proximally, ending distally in an acute tip, forming a spine (Figs 2, 3). This spine is curved mediad (Figs 2A, B, D–K, 3) or straight (Fig. 2C). The length of the spine-shaped distal prepollex is 0.63–1.35 the length of metacarpal II (Table 2). Its position varies from medial to ventral to metacarpal II. While the articulations between the proximal and distal elements, and between them and metacarpal II, do not vary across Cophomantini, the shape of the curve of the spine does vary. The spine is curved mediad in most species and straight in a few (Fig. 2A–I). In some species the curvature of the spine, starting from its proximal portion, first turns laterad, passing ventral to metacarpal II, and then turns mediad, ending in an acute tip (Fig. 2J, K). Generally, the spine-shaped distal prepollex has a dorsal crest on its medial margin. In a few species there is a

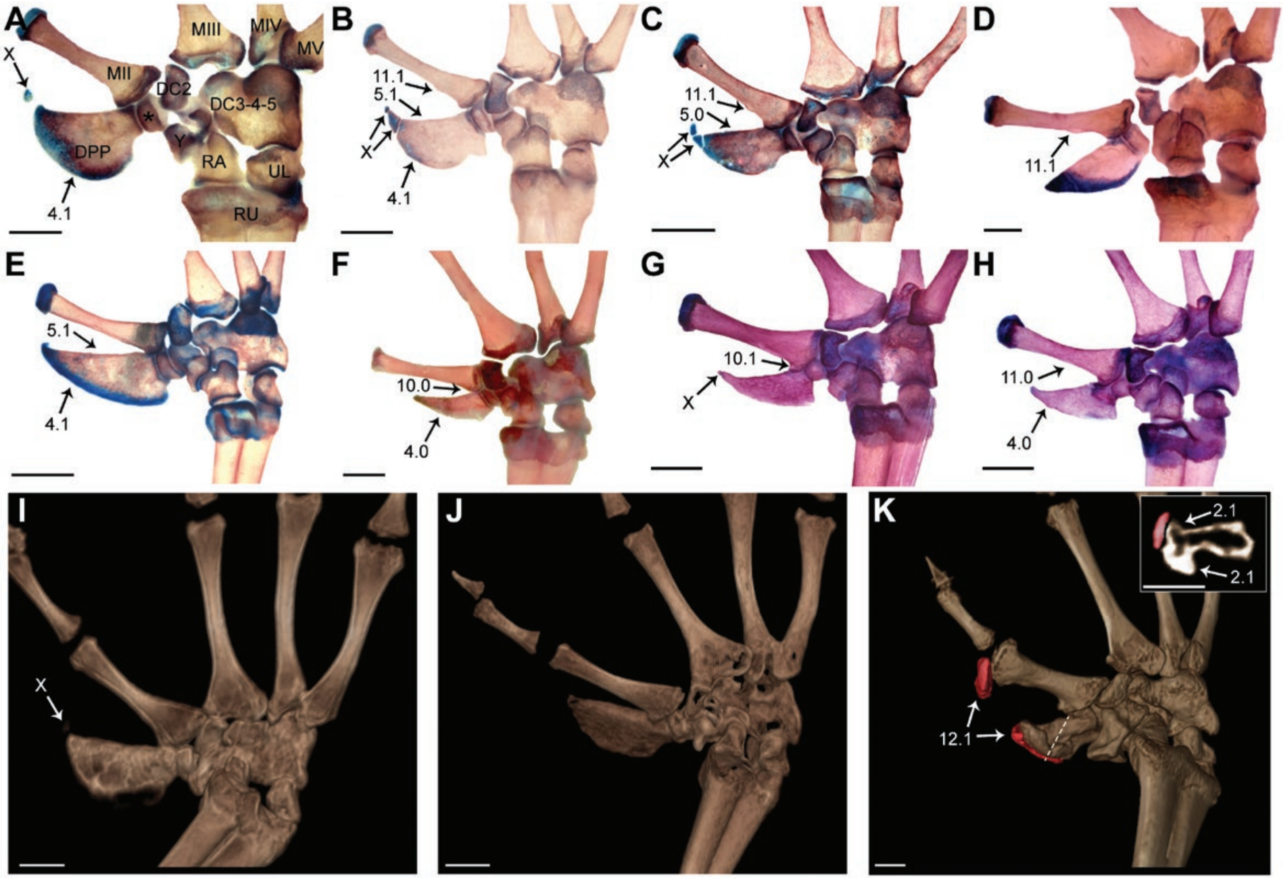


Figure 1. Dorsal view of clear and double-stained (A–H) and micro-CT reconstructions (I–K) of hands of adult males of species with blade-shaped distal prepollex. Numbers are 'character.character-state' (see Hypotheses of homology for details). A, *Hyloscirtus bogotensis* ICN 4420; B, *H. platydactylus* ICN 10471; C, *H. callipeza* VR 5150; D, *H. antioquia* ICN 9392; E, *Aplastodiscus ehrhardti* CFBH 3183; F, *A. albosignatus* CFBH 4944; G, H, *Boana semilineata* CFBH 10524 and 10530, respectively; I, *Myersiohyla neblinaria* USNM 562071; J, *M. chamaeleo* AMNH-A 131173; K, *Hyloscirtus armatus* USNM 206715. Inset in (K) is a transversal slice view corresponding to the white dashed line on the distal prepollex. The distal prepollex has a medial dorsoventral expansion (Ch. 2.1) in (K), absent in the others. A medial cartilaginous margin (Ch. 4.1) occurs in (A), (C), (D) and (E), and is barely distinct in (B); ossified (Ch. 4.0) in the others. The lateral margin of the distal prepollex is straight (Ch. 5.1) in (C, D); concave (Ch. 5.0) in the others. The metacarpal II articulates with the prepollex through a medial expansion of the proximal epiphysis (Ch. 10.1) in (G, H); without a medial expansion (Ch. 10.0) in the others. The metacarpal II has a dorsomedial process on the point of insertion of the m. abductor pollicis longus (Ch. 11.1) in (B–D); the process is absent in the others (Ch. 11.0). Sesamoid (in red) occuring medially to distal epiphysis of metacarpal II and medially to the distal prepollex (Ch. 12.1) in (K); absent in the others. DC2 = distal carpal 2; DC3-4-5 = distal carpal 3-4-5; DPP = distal prepollex; MII–V = metacarpals II to V respectively; RA = radiale; UL = ulnare; Y = element Y (fractured in A); * = proximal prepollex; X = additional distal elements. For figure clarity, different character states are indicated only in part of the images. Scale bars 1 mm.

smaller, additional spine, positioned medially, that seems to be a distal extension of this crest (Fig. 2B, K). In many species, the distal prepollex also has a variable-sized post-articular process proximally (Fig. 2B, E, F, H–K).

The spine-shaped distal prepollex occurs in most species of *Boana* (except *B. semilineata* and *B. geographica*; for other species not included in our study see Supporting Information, File S3), *Bokermannohyla* and within the *H. larinopygion* group, in the clade including *Hyloscirtus condor*, *H. hillisi* and *H. tapichalaca*. The spine-shaped distal prepollex is entirely osseous in adult males and entirely or partially cartilaginous in adult females (Fig. 3). Given that we were able to study females of several species using only X-ray images (see Supporting Information, File S1), there is a large amount of missing information on the prepollex of females.

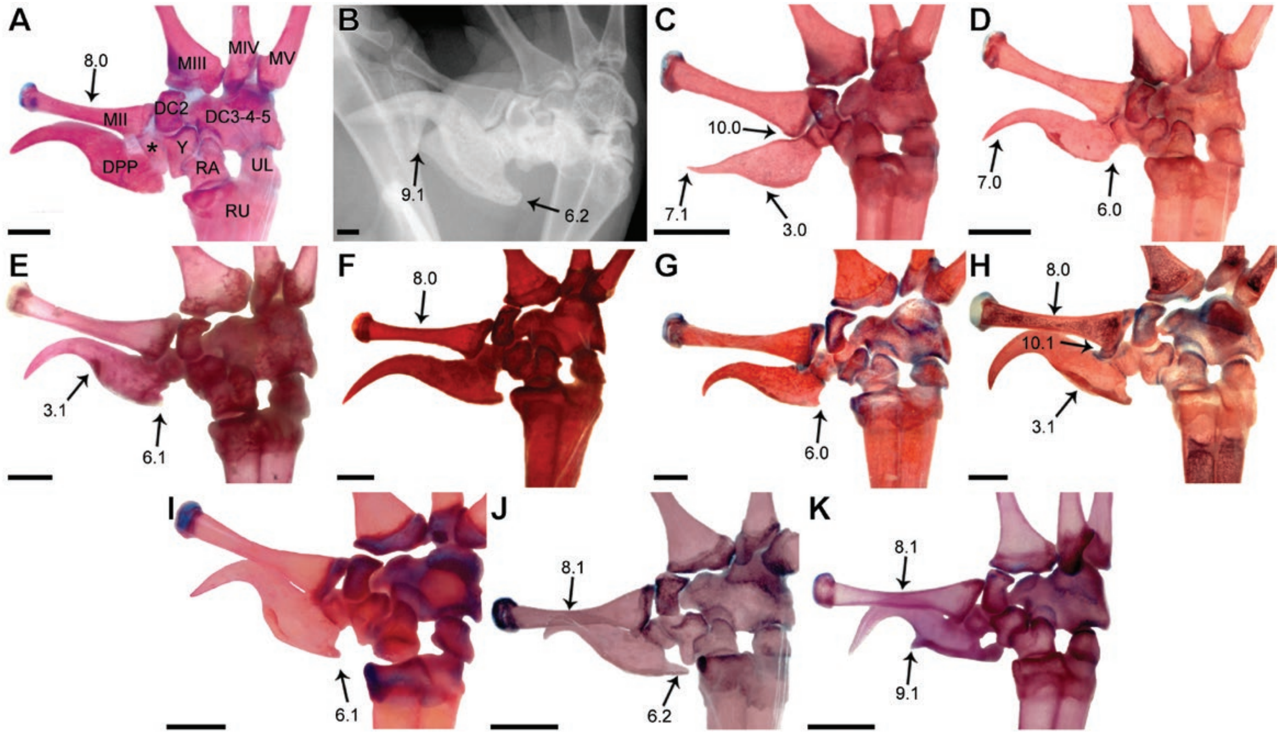


Figure 2. Cleared and double stained (A, C–K) and X-ray image (B) of the right hand of adult males with spine-shaped distal prepollex in dorsal view. Numbers are 'character.character-state' (see Hypotheses of homology for details). A, *Bokermannohyla ibitiguara* CFBH 17323; B, *Bokermannohyla langei* MZUSP 74275; C, *Boana microderma* MZUSP 159194; D, *Boana tepuiana* MZUSP 159179; E, *Boana pombali* CFBH 14917; F, *Boana heilprini* UFMG 8641; G, *Boana raniceps* UFMG 1547; H, *Boana crepitans* UFMG 6937; I, *Boana clepsydra* MNRJ 112612; J, *Boana pulchella* MACN 54563; K, *Boana ericae* CFBH 3604. Dorsal crest on the medial margin of the distal prepollex absent (Ch. 3.0) in (C); present (Ch. 3.1) in the others. Post-articular process absent or as a rudimentary tip (Ch. 6.0) in (A, C, D, G); present, intermediate sized (Ch. 6.1) in (E, F, H, I); present and long (Ch. 6.2) in (B, J, K). Spine straight (Ch. 7.1) in (C); curved (Ch. 7.0) in the others. For the curved spines, the curve of the spine passes ventral to metacarpal II before turning mediad (Ch. 8.1) in (J, K); the curve of the spine is directed mediad, without passing ventral to metacarpal II (Ch. 8.0) in the others. Distal projection forming an additional spine present (Ch. 9.1) in (B, K); absent in the others. Metacarpal II articulates with the prepollex through a medial expansion of the proximal epiphysis (Ch. 10.1) in (D, E, G–K); without a medial expansion (Ch. 10.0) in (A–C, F). For abbreviations see Figure 1 legend. For figure clarity, different character states are indicated only in part of the images. Scale bars 1 mm.

The distal prepollex is entirely cartilaginous in females of *Boana albopunctata*, *Boana punctata*, *Boana rufitela*, *Bokermannohyla hylax* and *Bokermannohyla oxente*, or cartilaginous with an ossified distal tip in *Boana albomarginata*, *Boana boans*, *Boana ericae*, *Boana faber*, *Boana joaquini*, *Boana microderma*, *Boana tepuiana* and *Bokermannohyla martinsi*. In females of *Bokermannohyla alvarengai* the proximal portion and distal tip are mineralized, with the middle portion cartilaginous, whereas the opposite occurs in females of *Bokermannohyla saxicola* (i.e. an osseous middle-portion and cartilaginous proximal and distal portions). In the X-ray images studied, only females of *Hyloscirtus tapichalca* (N = 3) have a completely ossified distal prepollex (Fig. 3E, F). X-ray images of females of *Boana boans*, *Boana cinerascens*, *Boana nympha* and *Boana punctata* reveal no prepollical element, indicating that it is completely cartilaginous in those specimens. In females of *Boana rosenbergi*, the distal prepollex is osseous proximally and presumably possesses a cartilaginous tip (our observations are not conclusive). In females of *Boana pellucens* and *Boana picturata*, the distal prepollex is like that of *Bokermannohyla alvarengai*.

Metacarpal II: This element articulates with the prepollex via the medial surface of its proximal epiphysis. In most studied species of *Boana* (except *Boana heilprini*, *Boana microderma*, *Boana pellucens* and *Boana rufitela*), and a few *Bokermannohyla* and *Hyloscirtus*, the proximal epiphysis is expanded mediad at the articulation with the prepollex. In *Aplastodiscus*, *Myersiohyla* and the remaining

Table 2. Variation in the ratio distal prepollex/metacarpal II lengths in males and females of the species groups of Cophomantini

Blade-shaped distal prepollex			Spine-shaped distal prepollex		
Species group	Males	Females	Species group	Males	Females
Aplastodiscus albofrenatus gr.	0.70–0.88 (N = 4)	0.79 (N = 1)	*Boana albopunctata* gr.	0.63–1.14 (N = 18)	0.68 (N = 1)
A. albosignatus gr.	0.62–0.66 (N = 3)	0.61 (N = 1)	*Boana benitezi* gr.	0.64–0.85 (N = 8)	0.76–0.77 (N = 2)
A. perviridis gr.	0.50–0.66 (N = 3)	0.49 (N = 1)	*Boana claresignata* gr.	0.81–0.86 (N = 2)	–
A. sibilatus gr.	0.7 (N = 1)	–	*Boana faber* gr.	0.69–0.92 (N = 14)	0.65–0.78 (N = 2)
Boana semilineata gr.	0.41–0.74 (N = 14)	0.37–0.69 (N = 4)	*Boana pellucens* gr.	0.85–1.04 (N = 4)	0.67 (N = 1)
Hyloscirtus armatus gr.	0.60–0.62 (N = 2)	–	*Boana pulchella* gr.	0.70–1.06 (N = 25)	0.69–0.94 (N = 2)
H. bogotensis gr.	0.44–0.77 (N = 26)	0.58–0.59 (N = 2)	*Boana punctata* gr.	0.68–0.80 (N = 10)	0.67 (N = 1)
H. larinopygion gr.	0.42–0.74 (N = 20)	–	*Boana semilineata* gr.	0.68–0.86 (N = 4)	0.70 (N =1)
Myersiohyla	0.70–0.86 (N = 3)	–	*Bokermannohyla circumdata* gr.	0.95–1.14 (N = 5)	0.69–0.79 (N = 2)
			Bokermannohyla martinsi gr.	1–1.31 (N = 5)	0.78 (N =1)
			Bokermannohyla pseudopseudis gr.	0.84–1.35 (N = 8)	0.87–0.92 (N = 2)
			Hyloscirtus larinopygion gr.	1.01–1.31 (N = 12)	1.08–1.1 (N = 3)

species of *Boana*, *Bokermannohyla* and *Hyloscirtus*, the proximal epiphysis articulation is not enlarged (Figs 1, 2). Most studied species of *Hyloscirtus* have a process on the proximal dorsomedial-third of metacarpal II (Fig. 1B–D) where the m. abductor pollicis longus inserts (see below).

Sesamoids: In the *Hyloscirtus armatus* group there are two medial heterotopic elements that we tentatively identify as sesamoids (see comments under Character 12 below). One is a flat disc positioned medial to the distal epiphysis of metacarpal II. The other is flat and elliptical and lies medial to the dorsoventral expansion of the distal prepollex (Fig. 1K). These elements support the spine-shaped nuptial pad of males.

MUSCULATURE

The musculature associated with the prepollex and related carpal elements was studied in 39 species of Cophomantini, representing all available species groups.

Dorsal musculature: The m. abductor pollicis longus has a fleshy origin on the postaxial surface of the radioulna along the longitudinal axis, and the point of its insertion is variable (Fig. 4). In *Aplastodiscus* and *Hyloscirtus*, this muscle has a single tendinous insertion on metacarpal II. In several species of *Hyloscirtus*, this insertion is on the proximal dorsomedial process of metacarpal II (see above). In *Myersiohyla chamaeleo*, *Bokermannohyla* and *Boana*, it inserts on metacarpal II via a flat tendon and on the distal prepollex via a flat and wider tendon. *Boana semilineata* has two thin tendons of insertion on metacarpal II, one distal to the other, while the insertion on the distal prepollex is absent (Fig. 4D–E). *Boana geographica* is polymorphic, having one or two tendons of insertion on metacarpal II.

We compared qualitatively (i.e. assessed visually under a stereomicroscope, but without measuring size or mass) the m. abductor pollicis longus of adult males and females of 19 species representing all available species groups of *Aplastodiscus*, *Boana* and *Bokermannohyla* (Supporting Information, File S1). In *Aplastodiscus arildae*, *A. cavicola*, *A. perviridis*, *Boana albomarginata*, *Boana faber*, *Boana geographica*, *Boana microderma* and *Boana tepuiana*, the m. abductor pollicis longus is not sexually dimorphic. In contrast, in *Bokermannohyla hylax*, *Bokermannohyla martinsi*, *Bokermannohyla oxente*, *Bokermannohyla saxicola*, *Boana albopunctata*, *Boana boans*, *Boana ericae*, *Boana joaquini*, *Boana punctata*, *Boana rufitela* and *Boana semilineata*, the volume of the m. abductor pollicis longus is qualitatively greater in males than in females.

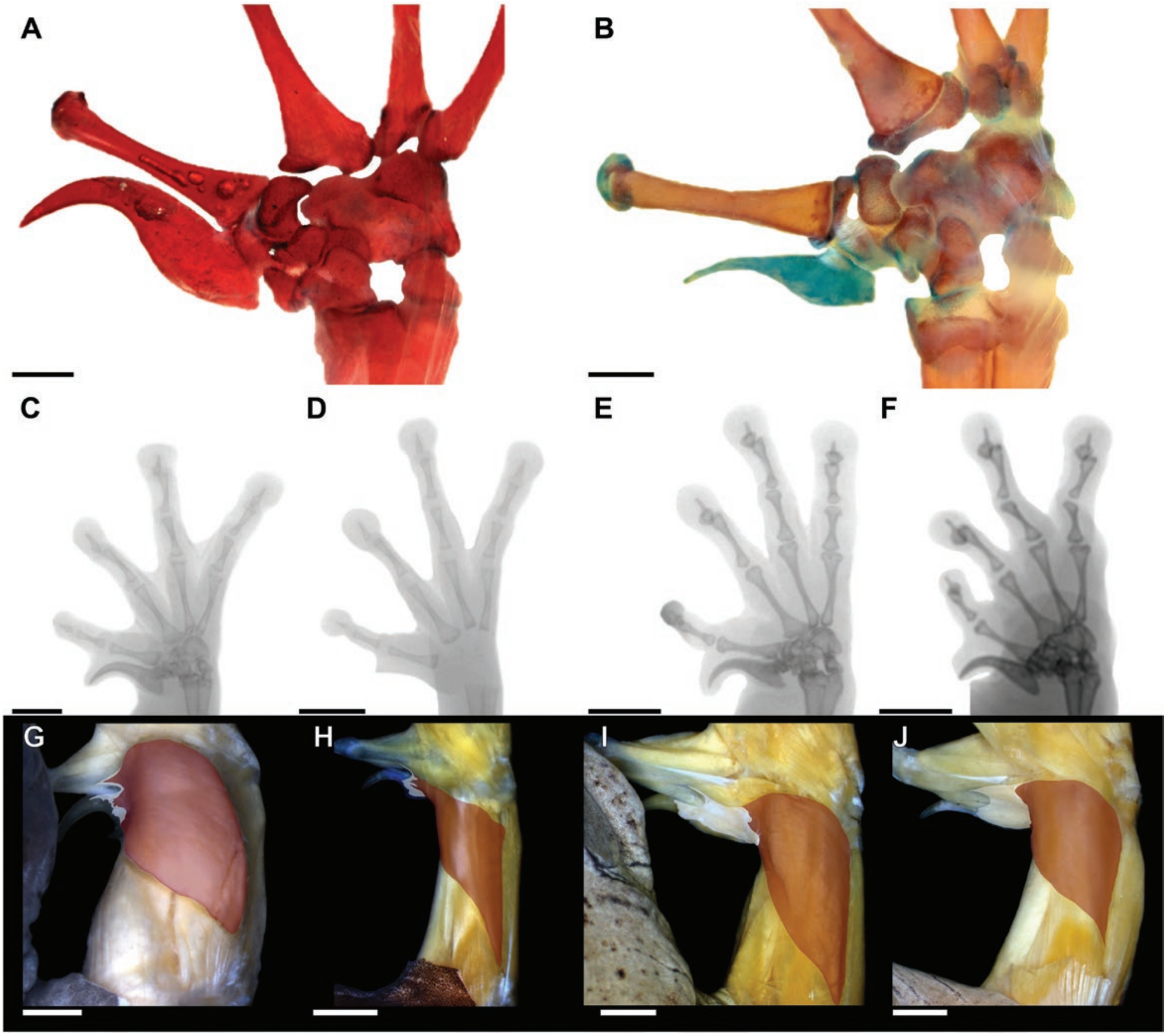


Figure 3. Dorsal view of hands showing sexual dimorphism of the spine-shaped distal prepollex (A–F) and m. abductor pollicis longus (G–J; highlighted in brown; tendons of insertion in white; m. extensor digitorum and m. extensor carpi ulnaris removed). A, B, cleared and stained; C–F, X-ray images (taken from the website Anfíbios del Ecuador; Ron *et al.*, 2019). (A) male (CFBH 11545) and (B) female (CFBH 3620) of *Bokermannohyla hylax*; (C) male (QCAZ 72533) and (D) female (QCAZ 72549) of *Hyloscirtus hillisi*; (E) male (QCAZ 15085) and (F) female (QCAZ 16705) of *H. tapichalaca*. Males of all species with ossified prepollex. Females of *Bokermannohyla hylax* and *H. hillisi* with cartilaginous prepollex, and from *H. tapichalaca* with ossified prepollex. (G) Male (UFMG 19338) and (H) female (UFMG 10680) of *Bokermannohyla martinsi*, showing an evident difference in relative size of m. abductor pollicis longus between sexes; (I) male (MZUSP 140287) and (J) female (MZUSP 140289) of *Boana faber*, with no evident difference in muscle relative size. (A, B, D, F–H) right hand; (C, E, I–J) left hand (reflected for easier comparison with the remaining figures). Scale bar 1 mm (A and B); 5 mm (C–F); 3 mm (G–J).

The m. extensor indicis brevis superficialis and m. extensor indicis brevis medius both arise from the radiale. Their origins are separated by the tendon of the m. extensor carpi radialis that inserts on the element Y (which passes dorsally to the radiale between the origins of the mm. extensores breves superficialis and medius and curves mediad to insert on the element Y). The m. extensor indicis brevis superficialis has two insertions: one fleshy on metacarpal II and the other via a tendon on the metacarpophalangeal joint of digit II. The m. extensor indicis brevis medius has a fleshy insertion on metacarpal II, contiguous

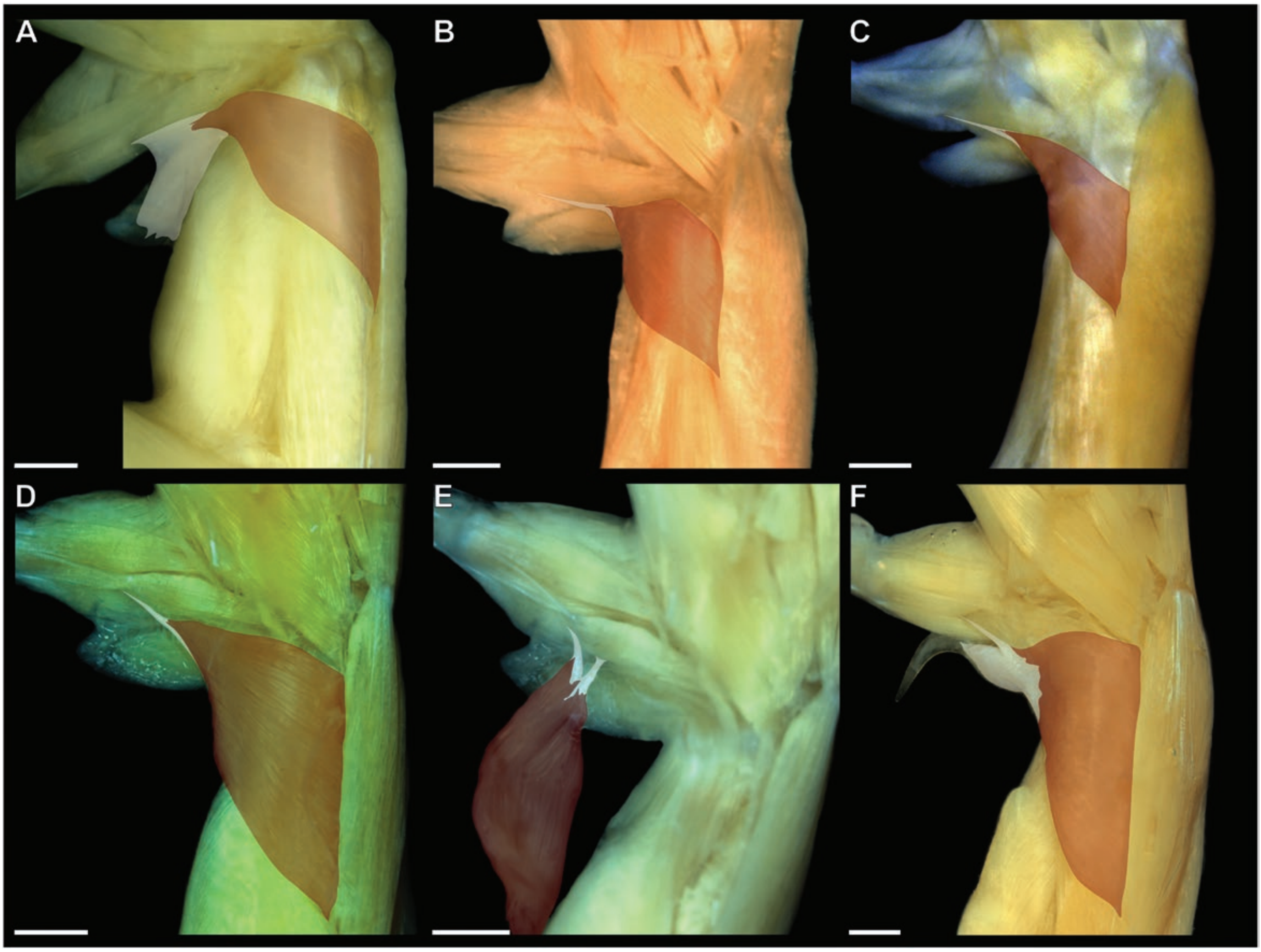


Figure 4. Dorsal hand musculature showing variation on the insertion of the m. abductor pollicis longus (highlighted in brown; tendons of insertion in white; m. extensor digitorum removed). A, *Myersiohyla chamaeleo* MZUSP 159198; B, *Hyloscirtus palmeri* ICN 20087; C, *Aplastodiscus perviridis* UFMG 9851; D–E, *Boana semilineata* CFBH 13013; F, *Boana pombali* CFBH 36791. Two insertions, one on metacarpal II and other, wider, on the prepollex in (A) and (F) ; one tendon on metacarpal II in (B) and (C) ; two tendons on metacarpal II in (D, E). In (D) the muscle is intact and seems to present only one insertion, but after dissecting its origin and deflecting the muscle (E) it is possible to see the two insertions on metacarpal II. (B, D–F) right hand; (A, C) left hand (reflected for easier comparison with the remaining figures). Scale bars 1 mm.

with the insertion of the m. extensor indicis brevis superficialis in all studied species of Cophomantini. In *Myersiohyla chamaeleo*, *Bokermannohyla* and several species of *Boana* and *Aplastodiscus*, the m. extensor indicis brevis medius has a thin second slip with fleshy insertion on the distal prepollex.

The mm. dorsometacarpales indicis proximales (Fig. 5) constitute a group composed of a medial and a lateral muscle. The medial muscle comprises three slips: (1) the medial slip originates on the distal prepollex (present in most species of *Boana* and *Bokermannohyla*); (2) the intermediate slip originates on the medial surface of metacarpal II; and (3) the lateral slip has an origin on the dorsomedial and proximal surface of metacarpal II, contiguous with the lateral muscle. The last two slips are present in all studied species of Cophomantini. The three slips insert via a common tendon on the interphalangeal joint and/or the distal phalanx of digit II (in some species, the lateral slip also inserts partially or completly on the dorsal surface of the metacarpophalangeal joint of digit II via a short tendon). The lateral m. dorsometacarpalis indicis proximalis originates from the laterodorsal surface of metacarpal II (in some exemplars also from the distal carpal 2) and inserts on the interphalangeal joint and/or the distal phalanx of digit II. The m. dorsometacarpalis indicis distalis is absent in all studied specimens of Cophomantini.

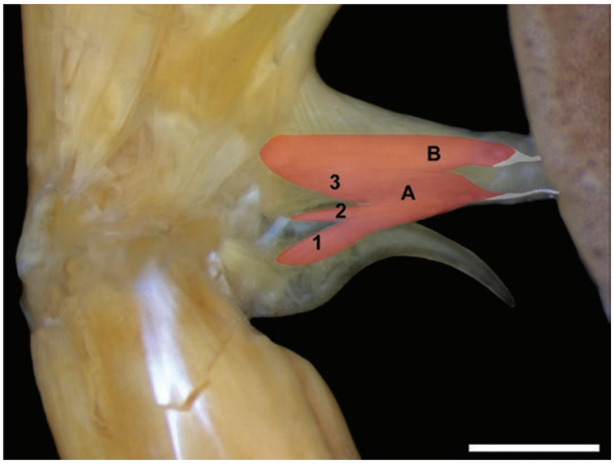


Figure 5. *Bokermannohyla hylax* (UFMG 732), male, left hand. The mm. dorsometacarpales indicis proximales are highlighted in red (tendons of insertion highlighted in white). The medial (A) and lateral (B) muscles are indicated. Different slips of the medial muscle are numbered as follows: (1) medial slip originating on the distal prepollex; (2) intermediate slip originating on the medial surface of the proximal epiphysis of metacarpal II; (3) lateral slip originating on the dorsomedial and proximal surface of metacarpal II, contiguous to the lateral muscle. Scale bar 2 mm.

The m. abductor indicis brevis dorsalis arises from the element Y and has a fleshy insertion on the dorsal surface of the distal prepollex. In *Aplastodiscus sibilatus*, some *Boana* and *Myersiohyla chamaeleo*, the m. abductor indicis brevis dorsalis has a second tiny slip with a fleshy insertion on the proximal and medial region of metacarpal II. In some species, the presence of the insertion on metacarpal II is intraspecifically variable (see Supporting Information, File S3: Ch. 16).

Palmar musculature: Variation in the ventral muscles associated with the digit II and the prepollex is minimal. The m. adductor pollicis arises medially on the ventral surface of distal carpal 3-4-5 and inserts on the ventral surface of the distal prepollex. Some fibres also insert on the integument of the inner metacarpal tubercle in some species (observed in species of *Aplastodiscus*, *Boana* and *Bokermannohyla*). The m. pronator quadratus has a double origin: one from the preaxial tip of the radioulna and the other from the ulnare. It inserts on the post-axial surfaces of the proximal and distal elements of the prepollex, element Y and on the ventral surface of metacarpal II. This last insertion may be through an extremely thin and difficult to detect tendon in some species (the m. adductor pollicis usually must be removed to observe it). The insertion on element Y is deeper to the other insertions and was observed in all studied Cophomantini. In species that have a post-articular process on the distal prepollex (see above; Supporting Information, File S3: Ch. 6.2), the insertion of the m. pronator quadratus on this process can be reinforced by tendinous tissue.

The m. flexor indicis superficialis proprius, m. lumbricalis brevis indicis, m. contrahentis indicis and m. flexor indicis brevis profundus, originate on the ventromedial surface of distal carpal 3-4-5. The m. flexor indicis superficialis proprius inserts via a long tendon on the palmar surface of the distal phalanx of digit II; the m. lumbricalis brevis indicis is medial to the m. flexor indicis superficialis proprius and inserts on the metacarpophalangeal joint of digit II. The m. contrahentis indicis is lateral to the m. flexor indicis superficialis proprius and inserts proximally on the basal phalanx of digit II, via a thin tendon. The m. flexor indicis brevis profundus, which is deeper than the other three muscles, has a fleshy insertion on the palmar surface of metacarpal II.

HYPOTHESES OF HOMOLOGY

Based on the variation described above, we defined the following 17 characters related to the distal prepollex and digit II. For the taxonomic distribution of each character state, see Supporting Information, File S3. For ancestral character-state reconstructions see Figures 6 and 7, and Supporting Information, Files S4 and S5.

0. Distal prepollex, number of elements. (0) One element. (1) Three elements.

State 1 refers to the distal prepollex in *Scinax cruentomma*. This species has an entirely cartilaginous prepollex, formed by one proximal prepollex and with the distal prepollex of adult males formed by three elements of similar size, as described in *S. fuscovarius* and *S. nasicus* (Fabrezi, 2001), but differing in proportions and shape.

It is not possible to infer if the single distal prepollex of Cophomantini is homologous to one element of the distal prepollex of *Scinax* (and in this case, to which one of the three elements) or to all three elements. Besides *Scinax*, Fabrezi (2001) reports several other anuran genera with a prepollex composed by three or more elements.

Character optimization: The distal prepollex formed by three elements is an autapomorphy of *Scinax*.

1. Shape of the distal prepollex formed by a single element. (0) Blade-shaped (Fig. 1). (1) Spine-shaped (Fig. 2).

Character optimization: The blade-shaped distal prepollex is plesiomorphic for Cophomantini (Ch. 1.0), as it is present in all outgroups, except *Scinax* *cruentomma* (non-applicable character). The optimization of the spine-shaped distal prepollex within Cophomantini (Ch. 1.1) is ambiguous, as it could have evolved independently in *Bokermannohyla* and *Boana*, or it could have evolved once in the common ancestor of *Bokermannohyla*, *Boana* and *Aplastodiscus* – in both cases from a plesiomorphic blade-shaped distal prepollex – with a subsequent reversal to blade-shaped distal prepollex in *Aplastodiscus* (see Fig. 6; Supporting Information, File S5). Additionally, the spine-shaped distal prepollex evolved independently, also from a blade-shaped distal prepollex, in the clade including *Hyloscirtus condor*, *H. hillisi*, *H. tapichalaca* and *H. diabolus* [this last taxon was tentatively assigned to this clade by Rivera-Correa *et al.* (2016)]. During the evolutionary history of *Boana*, there was a reversal from the spine-shaped to the blade-shaped distal prepollex in the common ancestor of the *Boana semilineata* complex.

2. Medial dorsoventral expansion of the distal prepollex. (0) Absent (Fig. 1A–J). (1) Present (Fig. 1K).

Character optimization: A medial dorsoventral expansion of the distal prepollex (Ch. 2.1) evolved in the most recent common ancestor of the *Hyloscirtus armatus* group.

3. Dorsal crest on medial margin of the distal prepollex. (0) Absent (Fig. 2C). (1) Present (Fig. 2H).

Character optimization: The optimization of the dorsal crest on the medial margin of the prepollex (Ch. 3.1) is similar to that of spine-shaped distal prepollex (Ch. 1.1). Among the species with a spine-shaped distal prepollex, this crest is absent in *Boana microderma*, *Bokermannohyla oxente* (but it is present in other species of the *Bokermannohyla pseudopseudis* group) and *Hyloscirtus tapichalaca*. The only species that has a blade-shaped distal prepollex and has this crest is *Trachycephalus typhonius*.

4. Medial margin of distal prepollex. (0) Ossified (Fig. 1F). (1) Cartilaginous (Fig. 1E).

Character optimization: In the outgroups, the cartilaginous margin (Ch. 4.1) optimizes as synapomorphy of Hylini, although we recognize the limitations of our sample for this clade. In Cophomantini, it optimizes as synapomorphies of the *Hyloscirtus bogotensis* group (with a reversal in *H. platydactylus*), of an internal clade of the *H. larynopygion* group (the clade including *H. pantostictus*, *H. lindae*, *H. larinopygion*, *H. ptychodactylus*, *H. princecharlesi*, *H. tigrinus*, *H. psarolaimus*, *H. criptico*, *H. staufferorum* and *H. pacha*), and of *Aplastodiscus*. In the *Boana semilineata* group, the character is polymorphic in *Boana geographica*.

5. Lateral margin of blade-shaped distal prepollex. (0) Straight (Fig. 1C). (1) Concave (Fig. 1E).

Character optimization: The straight lateral margin (Ch. 5.0) optimizes as a synapomorphy of Cophomantini, with instances of homoplasy in *Phrynomedusa appendiculata* and *Phyllodytes luteolus*. There are multiple reversals to a concave margin (Ch. 5.1) in *Hyloscirtus alytolylax*, *H. platydactylus*, in the *H. armatus* group and in the *Boana semilineata* complex. In the taxa studied by us, but not represented in the phylogenetic hypothesis employed for the optimization, a concave margin was found in *Hyloscirtus bogotensis* and in *H.* aff. *palmeri*. The character was found to be polymorphic in *Aplastodiscus albosignatus*, *H. antioquia* and *H. torrenticola*.

6. Post-articular process of the distal prepollex. (0) Absent or at most a rudimentary tip (Fig. 2D). (1) Short; in dorsal view, proximal margin not surpassing level of articulation between element Y, proximal prepollex and distal carpal 2 (Fig. 2I). (2) Long; in dorsal view, proximal margin reaching or surpassing level of portion of element Y that articulates with radiale (Fig. 2J).

The post-articular process is ossified (in males) or cartilaginous (females of some species). As it is a posterior prolongation of variable length, we considered it to be additive.

Character optimization: The absence of a post-articular process (Ch. 6.0) is plesiomorphic for Cophomantini. The short post-articular process (Ch. 6.1) evolved in the *Boana semilineata* group (with a reversal in the *Boana semilineata* complex) and independently in *Boana multifasciata*. The short post-articular process (Ch. 6.1) is also a synapomorphy of the clade including *Boana heilprini* and the *Boana pellucens*, *Boana faber*, *Boana claresignata* and *Boana pulchella* groups. The long post-articular process (Ch. 6.2) is a synapomorphy of the *Boana pulchella* group (convergent in the *Bokermannohyla martinsi* group; Bokermann, 1965; Faivovich *et al.*, 2009), which evolved from a short post-articular process (Ch. 6.1).

7. Curvature of spine-shaped distal prepollex. (0) Curved mediad (Fig. 2D). (1) Straight (Fig. 2C).

Character optimization: The straight spine (Ch. 7.1) evolved in *Boana microderma*. It is polymorphic in its sister-species, *Boana nympha*. The character state in *Boana roraima* (sister to *Boana microderma* + *Boana nympha*) is unknown, rendering the optimization ambiguous in the most recent common ancestor of these three species (see Supporting Information, File S5).

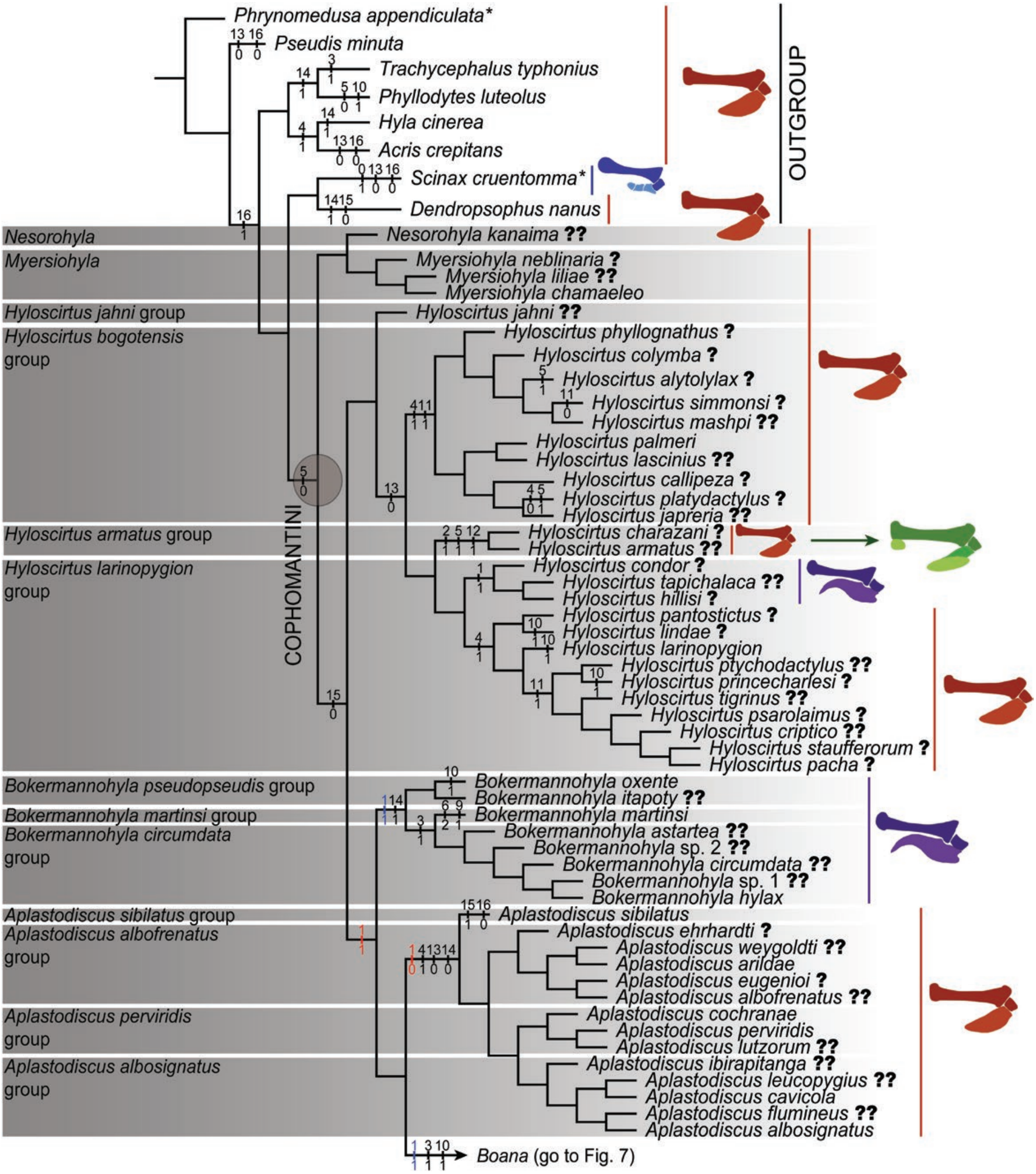


Figure 6. Optimization of 17 characters associated with the prepollex and metacarpal II on the phylogenetic hypothesis of Lyra *et al.* (2020). Numbers above branches refer to characters; numbers below are the character states. For character definitions see the text (Hypotheses of homology). For character 1, competing hypotheses are shown in red and blue, respectively (see text for discussion). One question mark on species name indicates missing entries for myological characters; two question marks indicate missing entries for both myological and osteological characters. An asterisk indicates the original terminal taxa *Boana claresignata*, *Phrynomedusa dryade* and *Scinax staufferi* that were substituted on the present study by *Boana clepsydra*, *P. appendiculata* and *S. cruentomma*, respectively (see Material and Methods). Continued in Figure 7 for *Boana*. See Supporting Information, File S5 for individual character optimizations.

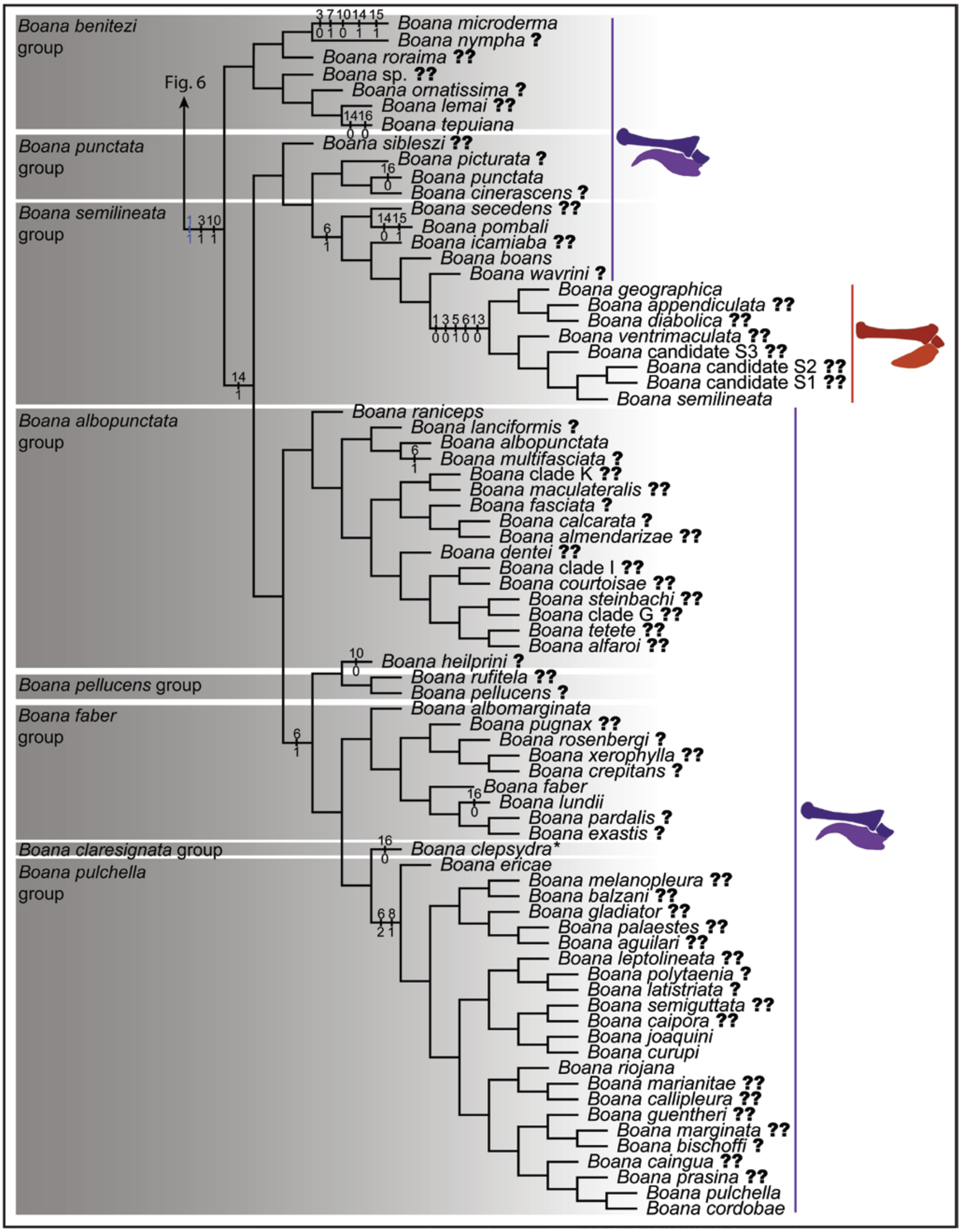


Figure 7. Character optimization on *Boana* (continued from Fig. 6).

8. Shape of curve of spine-shaped distal prepollex in relation to metacarpal II in dorsal view. (0) Directed mediad (Fig. 2F). (1) Directed laterad to pass ventral to metacarpal II and then it turns mediad to end in an acute tip (Fig. 2J, K).

Character optimization: The curve of the spine-shaped distal prepollex passing ventral to metacarpal II (Ch. 8.1) optimizes as a synapomorphy of the *Boana pulchella* group.

9. Distal projection of dorsal crest of spine-shaped distal prepollex forming an additional spine. (0) Absent. (1) Present (Fig. 2B, K).

Character optimization: The presence of this additional spine (Ch. 9.1) optimizes as an autapomorphy of *Bokermannohyla martinsi*. It was also reported for *Bokermannohyla langei* (Bokermann, 1965; Faivovich *et al.*, 2009). This character is polymorphic in *Boana ericae*.

10. Medial expansion of proximal epiphysis of metacarpal II. (0) Absent (Fig. 2C). (1) Present (Fig. 2H).

Character optimization: The medial expansion of the proximal epiphysis of metacarpal II (Ch. 10.1) evolved independently in *Boana* (with reversals on the common ancestor of *Boana heilprini* and the *Boana pellucens* group and in *Boana microderma*), *Bokermannohyla oxente* (also observed in *Bokermannohyla lucianae*), three species of the *Hyloscirtus larinopygion* group (*H. larinopygion*, *H. lindae* and *H. princecharlesi*), and in *Phyllodytes luteolus*.

11. Dorsomedial process on proximal third of metacarpal II. (0) Absent (Fig. 1H). (1) Present (Fig. 1B–D).

Character optimization: This metacarpal process is present (Ch. 11.1) in *Phrynomedusa appendiculata*, the *Hyloscirtus bogotensis* group (with a reversal in *H. simmonsi*; polymorphic in *H. palmeri*) and the sister-taxon of *H. larinopygion*. The character is polymorphic in *Boana riojana*, *H. larinopygion* and *H. lindae*.

12. Sesamoids on the medial surface of the prepollex and distal epiphysis of metacarpal II. (0) Absent. (1) Present (Fig. 1K).

We treat the presence of the two sesamoids in the *Hyloscirtus armatus* group as a single character-state because they do not occur separately. We refer to these heterotopic osseous elements as 'sesamoids' only tentatively. Although they are associated with the prepollex and metacarpal II, respectively, we were unable to confirm their relationship with tendinous tissue (Abdala *et al.*, 2019).

Character optimization: In Cophomantini, the presence of these sesamoids (Ch. 12.1) is a synapomorphy of the *Hyloscirtus armatus* group.

13. Insertion of m. abductor pollicis longus on distal prepollex. (0) Absent (Fig. 4B–D). (1) Present (Fig. 4A, F).

The m. abductor pollicis longus originates from the radioulna (as observed in Cophomantini) and also the humerus in other anuran species, and it inserts on the distal prepollex and/or metacarpal II (e.g. Burton, 1996, 1998; Blotto *et al.*, 2020). As all the species examined in this study possess the insertion on metacarpal II (with the single exception of the outgroup species *Dendropsophus nanus*), we scored here only the insertion on the distal prepollex.

Character optimization: The insertion of the m. abductor pollicis longus on the distal prepollex (Ch. 13.1) is plesiomorphic for Cophomantini. Among the outgroup species, it is absent in *Pseudis minuta*, *Acris crepitans* and *Scinax cruentomma*. Within Cophomantini, the absence of the insertion on the distal prepollex is a synapomorphy of *Aplastodiscus*. Additionally, the insertion on the distal prepollex is absent in all studied species of *Hyloscirtus* (the optimization is ambiguous for the genus because of the unknown condition in *H. jahni*; see Supporting Information, File S5) and the *Boana semilineata* complex (the optimization is ambiguous in that region of the tree due to the unknown condition in *Boana wavrini*).

14. Medial m. dorsometacarpalis indicis proximalis, slip originating from the distal prepollex. (0) Absent. (1) Present (Fig. 5).

This slip originating on the prepollex is, to our knowledge, first reported here (slip 1 in Fig. 5) and is considered to be part of the medial m. dorsometacarpalis indicis proximalis; this muscle is formed by up to three slips in Cophomantini, with the slip originating from the prepollex being medial to the others (see details above in Results).

Character optimization: The absence of the slip from the distal prepollex is plesiomorphic for Cophomantini (Ch. 14.0). In the outgroups, the optimization of this character is ambiguous for some clades. Within Cophomantini it is ambiguous for *Bokermannohyla* + (*Aplastodiscus* + *Boana*) (see Supporting Information, File S5). This basal ambiguity is a consequence of the presence of the slip in *Bokermannohyla* and most *Boana*, its absence in *Aplastodiscus* and missing data for some early diverging clades of *Boana*. The sister-taxon of the

Boana benitezi group has the slip with origin on the distal prepollex, with a reversal in *Boana pombali*.

15. Insertion of m. abductor indicis brevis dorsalis on metacarpal II. (0) Absent. (1) Present.

The m. abductor indicis brevis dorsalis arises from element Y and has a fleshy insertion on metacarpal II, distal prepollex, or on both elements (Burton, 1996, 1998; Blotto *et al.*, 2020; this study). Within Cophomantini, the insertion on the distal prepollex is present in all studied species, with a few specimens also having a fleshy insertion on metacarpal II via a tiny slip. When the insertion on metacarpal II is present, it is similar to that figured by Blotto *et al.* (2020: pl. 3D).

Character optimization: The absence of the insertion of the m. abductor indicis brevis dorsalis on metacarpal II (Ch. 15.0) is a synapomorphy of the clade composed of *Hyloscirtus* + *Bokermannohyla* + *Aplastodiscus* + *Boana* (i.e. all Cophomantini except *Myersiohyla* and *Nesorohyla*), with subsequent independent reversals in *Aplastodiscus sibilatus*, *Boana microderma* and *Boana pombali*. The character is unknown in *Nesorohyla* and polymorphic in *Aplastodiscus arildae*, *A. cochranae* and *Boana punctata*. Among outgroups, the insertion on metacarpal II is absent in *Dendropsophus nanus*.

16. Insertion of m. extensor indicis brevis medius on the distal prepollex. (0) Absent. (1) Present.

The m. extensor indicis brevis medius originates from element Y (or element Y + distal carpal 2 in anurans in which these elements are fused), the radiale, the ulnare or the distal end of the radioulna; it inserts on metacarpal II or by a common tendon with the medial m. dorsometacarpalis indicis proximalis on the distal phalanx of digit II; an additional insertion on the prepollex occurs in some species (Burton, 1996, 1998; Hoyos & Salgar, 2016; Blotto *et al.*, 2020; this study). *Pseudis minuta* is the only species in our taxon sampling in which this muscle originates from element Y and inserts exclusively on the distal phalanx of digit II. This muscle is absent in *Phrynomedusa appendiculata*, *Phyllodytes luteolus* and *Trachycephalus typhonius*.

Character optimization: The insertion on the distal prepollex (Ch. 16.1) is plesiomorphic for Cophomantini. Within the tribe, it was lost independently (Ch. 16.0) in *Aplastodiscus sibilatus*, *Boana clepsydra*, *Boana lundii*, *Boana punctata* and *Boana tepuiana*. It is polymorphic in *Aplastodiscus perviridis*, *Boana albopunctata*, *Boana rufitela* and *Boana semilineata*. Among the outgroups, the insertion on the distal prepollex is absent in *Pseudis minuta* and *Scinax cruentomma*.

DISCUSSION

Prepollex evolution

Our results show notable evolutionary plasticity in the 17 characters associated with the distal prepollex in Cophomantini. The two distinct shapes, blade-shaped and spine-shaped distal prepollices, each evolved more than once within this tribe. However, there are two ambiguities that persist on the ancestral character-state reconstruction of the distal prepollex shape in the common ancestor of *Aplastodiscus*, *Boana* and *Bokermannohyla* and the common ancestor of *Aplastodiscus* and *Boana* (see Ch. 1 optimization in 'Hypotheses of homology'; Fig. 6; Supporting Information, File S5). It should be noted that these ambiguities occur in clades that are recovered in most phylogenetic analyses and with high support values (e.g. Faivovich *et al.*, 2005, 2013; Wiens *et al.*, 2010; Duellman *et al.*, 2016; Pinheiro *et al.*, 2019; Lyra *et al.*, 2020). These ambiguities impose some limitations in the inferences relating to the correlation between the evolution of distinct shapes of prepollex and territoriality, reproductive biology and behaviour at this higher level in Cophomantini. However, they do not affect the inference that, in Cophomantini, the spine-shaped distal prepollex evolved from a blade-shaped distal prepollex. It remains unclear if the blade-shaped distal prepollex in *Aplastodiscus* is plesiomorphic for the tribe or is a reversal from a spine-shaped distal prepollex.

Despite the independent origins of the spine-shaped distal prepollex, there are few differences in this structure between *Boana*, *Bokermannohyla* and *Hyloscirtus*. First, the most evident difference is the absence of a dorsal crest on the medial margin of the spine-shaped distal prepollex in *H. tapichalaca* (present in most *Boana* and *Bokermannohyla*). Second, although there are no discrete differences in the length of the distal prepollex relative to metacarpal II among these three genera, it tends to be smaller in *Boana*: the distal prepollex/metacarpal II ratio is 0.64–1.14 in *Boana*, 0.84–1.35 in *Bokermannohyla* and 1.01–1.31 in *Hyloscirtus* (Table 2). Garcia *et al.* (2001a) hypothesized that the spine-shaped distal prepollex might be larger in mountain-stream dwellers, but our data are inadequate to rigorously test this hypothesis.

In Cophomantini, the dorsal crest on the medial margin of the prepollex (Ch. 3.1), the projection forming an additional spine (Ch. 9.1) and the post-articular process (Ch. 6.1 and 6.2) co-occur in some instances with the spine-shaped distal prepollex. The dorsal crest on the medial margin evolved independently in *Boana* and in a large internal clade of *Bokermannohyla,* and seems to reinforce the insertion of the wide tendon of m. abductor pollicis longus. Although the dorsal crest is absent in *Bokermannohyla oxente*, it is present in other species of the *Bokermannohyla pseudopseudis* group (Supporting Information, File S3) and a more thorough knowledge of the phylogenetic relationships in *Bokermannohyla* is necessary to understand the evolution of the crest in this genus (only six of its 30 species have been included in phylogenetic analyses; Faivovich *et al.*, 2005, 2013; Duellman *et al.*, 2016; Pinheiro *et al.*, 2019; Lyra *et al.*, 2020; Frost, 2021). The dorsal crest was subsequently lost independently in *Boana microderma* and in the *Boana semilineata* complex, in which a reversal from the spine-shaped distal prepollex to the blade-shaped distal prepollex occurs. The only taxon examined by us with a dorsal crest on the medial margin of the blade-shaped distal prepollex is *Trachycephalus typhonius* (tribe Lophyohylini), in which the m. abductor pollicis longus also inserts on the distal prepollex. On the basis of our data, we predict that species with a dorsal crest on the distal prepollex will also have an insertion of the m. abductor pollicis longus on it, but no prediction can be made for species that lack the crest. Our results also point to a possible correlation between the dorsal crest on the medial margin of the distal prepollex and the spine-shaped morphology. An expanded taxon sampling, including taxa from other hylid tribes such as Lophyohylini, could shed light on this question.

The projection forming an additional spine evolved independently in the *Bokermannohyla martinsi* group and in *Boana ericae*, both of which plesiomorphically possess the spine-shaped distal prepollex. The presence of the additional spine in these species was reported previously by Bokermann (1964, 1965), Garcia & Haddad (2008) and Faivovich *et al.* (2009). An additional spine is also known for some species of *Plectrohyla* (Duellman, 1970; Duellman & Campbell, 1992). Our observations agree with the topological description of Garcia & Haddad (2008), although they described the additional spine as being part of the distalmost portion of the crest on the medial margin of the prepollex. In the *Bokermannohyla martinsi* group and *Plectrohyla*, the additional spine has the same position as in *Boana ericae*. However, two male specimens of *Boana ericae* studied by us varied in this character, with the additional spine being present (UFMG 11583) and absent (MZUSP 93852). While there are some specimens with both the crest and the additional spine, no specimen possessed the additional spine without the crest. Ontogenetic studies are necessary to determine if the development of both the additional spine and the crest on the medial margin of the prepollex are related or are independent structures.

The large post-articular process (Ch. 6.2) and the shape of the curve of the prepollex, passing ventral to metacarpal II (Ch. 8.1), are synapomorphies of the *Boana pulchella* group. This finding is especially relevant in light of the relative low support recovered for this group by Faivovich *et al.* (2021). Within the *Boana pulchella* group, some degree of variation in the curvature of the spine was noted by Garcia & Haddad (2008), but its position in relation to metacarpal II was not discussed. They noted that the tip of the spine is oriented almost 90° relative to longitudinal axis of metacarpal II in *Boana ericae*. Although we did not evaluate the angle of orientation of the spine, a possible interpretation is provided below.

The functions of both the post-articular process and the shape of the curve of the spine are unclear. The insertion of the m. pronator quadratus on the post-articular process is reinforced by tendinous tissue in species in which the post-articular process is large (Ch. 6.2), but not in those in which the post-articular process is small (Ch. 6.1) or absent (Ch. 6.0). It is possible that the reinforced insertion enables more efficient contraction of the m. pronator quadratus to support the prepollex during combat. A spine directed orthogonally in relation to metacarpal II [as observed by Garcia & Haddad (2008)] could also have a different effect during fights, compared to species with a lower angle between the spine and metacarpal II. However, a spine just turned 90° medially, could result in a more fragile structure. The curve of the spine passing ventral to metacarpal II before turning mediad might be a structural solution for this apparent fragility. Alternatively, species with distinct shapes of the curve of the spine, might use it in distinct ways during fights. To study this, behavioural observations on the use of the prepollex, together with a careful examination of the bone structure and physiological studies on the associated musculature, would be necessary. Comparisons of the behaviour of species with the different states of both post-articular process and shape of the curve of the spine are essential. To date, the only detailed report on how the hand is positioned during fights is for *Boana curupi*, in which males rotate their wrists in order to hit the back of the opponent with the prepollex (Candaten *et al.*, 2020).

The only reversal to a blade-shaped distal prepollex (from a spine-shaped plesiomorphic morphology) occurred in the well-supported *Boana semilineata* complex (e.g. Peloso *et al.*, 2018; Caminer & Ron, 2020; Lyra *et al.*, 2020). The absence of a spine-shaped distal prepollex was previously proposed as a synapomorphy of this clade by Peloso *et al.* (2018). This reversal is accompanied by the loss of the ossified medial crest

(Ch. 3.0), the post-articular process (Ch. 6.0) and the insertion of the m. abductor pollicis longus on the distal prepollex (Ch. 13.0; Fig. 7; Supporting Information, File S5). No functional hypotheses have been put forth for the different shapes of the distal prepollex. Knowledge on natural history, such as reproductive behaviour and territoriality, for species of this group might be crucial to understand the biological significance of these transformations.

The cartilaginous medial margin (Ch. 4.1) and the additional small distal elements found in the blade-shaped distal prepollex are characters that should be investigated through ontogenetic studies. Both these characters can vary interspecifically and could be related to age. In the case of the cartilaginous medial margin (Ch. 4.1), it evolved from an ossified margin at least four times during the evolution of Cophomantini (Figs 6, 7). Although there is a clear phylogenetic pattern in the taxonomic distribution of this character state (i.e. it is present only in some species with a blade-shaped distal prepollex), as the prepollex is an endochondral element, an ontogenetic study is required to determine if the observed variation is due to sampling different semaphoronts [e.g. Duellman *et al.* (1997) reported one juvenile of *Hyloscirtus armatus* to have a cartilaginous prepollex, whereas it is ossified in the adult female]. Regarding the additional small distal elements, we are unaware if these additional elements fuse ontogenetically at some point with the main element or remain as discrete structures.

We found that the mm. dorsometacarpales indicis proximales are a group composed of medial and lateral muscles. The medial muscle may comprise as many as three slips, two originating from metacarpal II and the third from the distal prepollex. Variation is restricted to the presence of the slip of the medial m. dorsometacarpalis indicis proximalis originating on the distal prepollex. Within Cophomantini, the slip originating on the distal prepollex (Ch. 14.1) was found almost exclusively in species with a spine-shaped distal prepollex (exceptions are *Boana pombali* and *Boana tepuiana*). However, among outgroups the slip originating from the distal prepollex is present in the two species of Lophyohylini and in *Dendropsophus*, all of which possess a blade-shaped distal prepollex (Figs 6, 7; Supporting Information, File S5). This variation precludes any interpretation on the biological significance of the slip originating from the prepollex.

Besides the medial m. dorsometacarpalis indicis proximalis, there is no other variation in musculature that could be associated with either of the two prepollical morphologies. Some of the muscles that insert on the prepollex (e.g. the m. abductor indicis brevis dorsalis, m. adductor pollicis and the m. pronator quadratus) are similar in species with the blade- and spine-shaped distal prepollices. The m. abductor pollicis longus having two insertions (one on the prepollex and other on metacarpal II) is plesiomorphic for Cophomantini. Interestingly, the insertion on the prepollex was lost in the studied species of *Aplastodiscus* and *Hyloscirtus* (all with blade-shaped distal prepollex). Based on the available data, we can see a pattern in which all species with a spine-shaped distal prepollex have the insertion of the m. abductor pollicis longus on the prepollex, whereas in species with the blade-shaped distal prepollex this does not apply. The significance of this loss should be studied and natural history observations could shed light on this topic.

The m. abductor pollicis longus inserts on digit I in several pentadactyl tetrapods (e.g. Diogo *et al.*, 2015, 2018). In anurans, hypothesized to have lost digit I (Fabrezi & Alberch, 1996), this muscle is generally inserted on digit II (Burton, 1996, 1998; Diogo *et al.*, 2015; Blotto *et al.*, 2020). Diogo *et al.* (2015) suggested that the attachments are determined by topological position and not by the identity of the element (i.e. prepollex, digit I, digit II). Under the hypothesis that considers that anurans have lost digit I, the m. abductor pollicis longus is expected to insert on the most preaxial elements, which are the prepollex and digit II in the case of anurans. Possibly, this lack of constraint in the attachment results in the variation in the insertion point observed across clades, favouring the insertion on the prepollex when there are well-developed prepollical elements such as it occurs in Cophomantini. This fact might support the heterotopic shift hypothesis of Diogo *et al.* (2015). However, there is scarce information regarding the variation of the insertion of m. abductor pollicis longus across anurans (Blotto *et al.*, 2020), leaving this problem as an open question for the time being. The m. abductor pollicis longus inserts also on the prepollex in other distant clades, such as in some rodents (e.g. Echeverría *et al.*, 2019). However, the controversy regarding the specific digit lost in anurans (e.g. Diogo & Ziermann, 2014), and the homology of the prepollex among mammals and other tetrapods (e.g. Le Minor, 1994; Kley & Kearney, 2007), imposes limits for further discussion at this point.

Outside Cophomantini, a spine-shaped distal prepollex evolved several times. Among hylids, it also occurs in Hylini, in some species of *Plectrohyla* and in *Ecnomiohyla miliaria* (Duellman, 1970; Duellman & Campbell, 1992). Among other nobleobatrachians (*sensu* Frost *et al.*, 2006), a spine-shaped prepollex occurs in the centrolenids *Centrolene lynchi*, *Cochranella duidaeana*, *Cochranella riveroi*, *Teratohyla spinosa*, *Vitreorana castroviejoi*, *V. gorzulae*, *V. helenae* and *V. ritae* (Taylor, 1949; Flores, 1985; Señaris &

Ayarzagüena, 2005). Contrary to the prepollex of Cophomantini, which includes proximal and distal elements, the prepollex of these centrolenids is formed by a single element (Señaris & Ayarzagüena, 2005).

Among Ranoides, the two species of *Babina* (Ranidae) are known to have a spine-shaped distal prepollex. As in Cophomantini, the prepollex of those species includes a small proximal prepollex and a large spine-shaped distal prepollex (Tokita & Iwai, 2010; Iwai, 2012). Similarly, species of the *Boophis albilabris* group (Mantellidae) and *Anodonthyla*, *Hoplophryne* and *Metaphrynella pollicaris* (Microhylidae) are reported to have a spine-shaped prepollex, at least in males (Boulenger, 1890; Noble, 1931; Cadle, 1995; Andreone *et al.*, 2002; Glaw & Vences, 2005; Vences *et al.*, 2010a, b), but the osteology remains undescribed for most of them. The transformations associated with these independent instances of evolution of the spine-shaped prepollex have not been studied. It is unknown if this morphology of the prepollex always evolves from a plesiomorphic blade-shaped structure, as in Cophomantini, and if the associated musculature differs between these groups.

Other sharp structures are known to occur on the hands of other anuran clades with some similarities to the spine-shaped prepollex. Breeding males of the petropedetids *Petropedetes* (except *P. cameronensis*) and *Arthroleptides martiensseni* have a sharp bony structure on digit II (Scott, 2005; Barej *et al.*, 2010). Scott (2005) considered this spine as a prepollex fused to metacarpal II. However, as noted by Noble (1931), and subsequently evidenced by Barej *et al.* (2010: fig. 15; 2014: fig. A15), the spine of petropedetids is part of metacarpal II.

In *Leptodactylus* (Leptodactylidae), males of several species of the *L. latrans*, *L. melanonotus* and *L. pentadactylus* groups have a robust, conical spine distally on metacarpal II and sometimes a robust and conical spine on the prepollex (Heyer, 1970, 1979, 1994; Lynch, 1971; Shine, 1979). In those species, the robust conical structures provide internal support for external black keratinous spines (Lynch, 1971; de Sá *et al.*, 2014). These keratinous spines do not occur in anuran species having a spine-shaped distal prepollex, as described in this paper. Also, according to Luna *et al.* (2018), those keratinous structures found in leptodactylid spines are not homologous to the papillary epidermal projections found in most other anurans, including some species of Cophomantini. Shine (1979) correlated the presence of all these sharp structures on the hand to territoriality and male–male combat, although they had already been related to the amplexus (e.g. Noble, 1931). The presence of these similar, non-homologous, sharp structures on the hand in all those distinct groups requires study.

PREPOLLICAL ANATOMY, FUNCTION AND BEHAVIOUR

In Cophomantini there are reports of scars in the dorsum of males or aggressive behaviour against the collector in many species that have a spine-shaped distal prepollex (e.g. Pombal & Haddad, 1993; Kizirian *et al.*, 2003; Garcia *et al.*, 2008; Toledo *et al.*, 2011; P. D. P. Pinheiro & C. F. B. Haddad, pers. obs.). Nevertheless, direct observations are less common in the literature and scars serve as indirect evidence of fights among males (see Supporting Information, File S6 for reports on fights in Cophomantini). The only case known to us of scars in a female dorsum is a specimen of *Boana riojana* (FML 3866-5; P. D. P. Pinheiro & J. Faivovich, pers. obs.). On the other hand, there are no reports of scars or physical fights in cophomantines with blade-shaped distal prepollex, that is, *Aplastodiscus*, the *Boana semilineata* complex, most species of *Hyloscirtus*, *Myersiohyla* and *Nesorohyla*.

The spine-shaped distal prepollex is commonly referred to in the literature as a protruding or projecting spine (e.g. Duellman, 1970; Duellman *et al.*, 1997; Blackburn *et al.*, 2009; Rivera-Correa *et al.*, 2016; Peloso *et al.*, 2018; Ron *et al.*, 2018). But these mentions should be understood as a protrusion from the outline of digit II and not as a structure that can be mechanically externalized, as its functional mechanism remains unknown. It is also unknown if there is a channel in the skin through which the spine could be projected or if it simply pierces the skin during fights, healing afterwards. In the case of the ranid *Babina subaspera*, Iwai (2012) reported some male specimens with wounded skin over the tip of the prepollex [see Iwai (2012: fig. 3)].

Our results show that the presence of the insertion of the m. abductor pollicis longus on the distal prepollex is plesiomorphic for Cophomantini. Among the studied taxa, the insertion on the prepollex is lost in most species with a blade-shaped distal prepollex, except for *Myersiohyla chamaeleo*. The insertion of the m. abductor pollicis longus remains unknown in other species of *Myersiohyla*, *Nesorohyla* and in several species of *Hyloscirtus*, all with a blade-shaped distal prepollex. In the clades with a spine-shaped distal prepollex, the insertion on the distal prepollex is via a flat, wide tendon that might protrude the element when the muscle is contracted and possibly generate partial abudction of the distal prepollex, or at least tense the structure during fights. We could not examine the musculature of the *Hyloscirtus* species with the spine-shaped distal prepollex (i.e. *H. condor*, *H. diabolus*, *H. hillisi* and *H. tapichalaca*; Kizirian *et al.*, 2003; Almendáriz *et al.*, 2014; Rivera-Correa *et al.*, 2016; Ron *et al.*, 2018) to understand if the insertion of the m. abductor pollicis longus in these species is convergent with *Bokermannohyla* and *Boana*; this information is necessary to make more robust inferences about the biomechanical and biological significance of the insertion of the m. abductor pollicis longus.

The species with a blade-shaped distal prepollex, instead, have different types of insertion of the m. abductor pollicis longus. *Myersiohyla chamaeleo* has two insertions: on metacarpal II via a flat tendon and on the distal prepollex via a flat, wider tendon. *Hyloscirtus* and *Aplastodiscus* have a single tendon of insertion on metacarpal II. In *Boana semilineata*, there are two thin tendons of insertion on metacarpal II (Fig. 4D, E), whereas in *Boana geographica* there is a polymorphism, with one or two tendons of insertion on metacarpal II. These two insertions on metacarpal II suggest that one of them could be homologous to the insertion on the distal prepollex of other species of *Boana*. This is evidenced by the reversal to a blade-shaped distal prepollex from a spine-shaped one, in which two insertions are present: one on the prepollex and other on metacarpal II. Indeed, the reversal in the *Boana semilineata* complex is the only strongly supported case of such an event. Other species of the *Boana semilineata* complex should be studied regarding the nature of the insertion of the m. abductor pollicis longus in order to understand the taxonomic distribution of this variation and to evaluate the homology of the two tendons inserting on metacarpal II.

In several studied species of *Hyloscirtus*, the m. abductor pollicis longus inserts on a dorsomedial process of metacarpal II. This putative synapomorphy of *Hyloscirtus* (with subsequent reversals) might have evolved as a reinforcement for the insertion of the m. abductor pollicis longus, as in this group the insertion on the distal prepollex is absent. When compared with species having a spine-shaped distal prepollex, the tension of the muscle is divided between two bones, the distal prepollex and metacarpal II (dorsomedial process absent). Biomoechanical approaches are required for testing this hypothesis.

Fabrezi (2001) considered the internal interaction with skin structures as a possible primary function of the prepollex in anurans. Several species studied by us (i.e. *Acris crepitans*, *Dendropsophus nanus*, *Hyla cinerea*, *Phyllodytes luteolus*, *Phrynomedusa appendiculata* and *Trachycephalus typhonius*) have nuptial pads in the skin overlying the prepollex. Within Cophomantini, nuptial pads are present in *Myersiohyla*, *Nesorohyla*, the *Hyloscirtus armatus* group, some species of the *H. larinopygion* group, some species of *Bokermannohyla*, *Aplastodiscus musicus* and in the *Boana claresignata* and *Boana semilineata* groups (Lutz, 1949; Faivovich *et al.*, 2006, 2013; Rivera-Correa & Faivovich, 2013; Peloso *et al.*, 2018; Pinheiro *et al.*, 2019; Lyra *et al.*, 2020; P. D. P. Pinheiro & J. Faivovich pers. obs.).

Luna *et al.* (2018) pointed out that in many cases where there is a nuptial pad present proximally on digit II, it is associated with an enlarged prepollex. However, those authors noted that when nuptial pads co-occur with a spine-shaped distal prepollex, they probably have primarily distinct functions. The species of Cophomantini with both a spine-shaped distal prepollex and nuptial pads, have the pad proximally or more dorsally located on digit II, but never associated with the tip of the spine, corroborating the hypothesis of Luna *et al.* (2018) that the tip of the element has a primary function for fights and its proximal region, which is enlarged, supports the nuptial pads internally.

Garcia *et al.* (2001b) hypothesized the association of the enlarged inner metacarpal tubercles with the construction of subterranean nests, a behaviour considered as a putative synapomorphy of *Aplastodiscus* (Haddad & Sawaya, 2000; Hartmann *et al.*, 2004; Faivovich *et al.*, 2005; Haddad *et al.*, 2005). The inner metacarpal tubercle in this group is internally supported by the blade-shaped distal prepollex. A correlation between these characters is difficult to establish at this point because of the ambiguities regarding the origin of a blade-shaped distal prepollex in *Aplastodiscus* and the absence of information on the reproductive biology of *Hyloscirtus*, *Myersiohyla* and *Nesorohyla*.

In some species of the *Boana faber* group, males use their hands to build mud basins for egg laying (Goeldi, 1895; Lutz, 1960a, b; Kluge, 1981). *Boana boans* and *Boana wavrini* (*Boana semilineata* group) are known to use mud-, sand- or gravel-constructed basins for reproduction, but it remains unknown how those basins are constructed (Duellman, 1970; Crump, 1974; Martins & Moreira, 1991). Anuran species that are hindlimb-first burrowers have several modifications on the prehallux and other hindlimb bones, as well as in foot musculature, that were considered adaptations for this behaviour (Laurent, 1964; Emerson, 1976; Burton, 2001; Fabrezi, 2001; Kley & Kearney, 2007; Blotto *et al.*, 2017). Although those are modifications of the foot, the large distal prepollex of Cophomantini could be the result of a similar adaptation in the hand for the excavation of basins or nests in the soil; however, the lack of information on natural history and reproductive behaviour for *Hyloscirtus*, *Myersiohyla* and *Nesorohyla* precludes further inferences.

In Cophomantini and other hylids, the m. abductor indicis brevis dorsalis inserts dorsally on the distal prepollex, and in some species it also has a small fleshy insertion medially on metacarpal II. Blotto *et al.* (2020) presumed it to abduct metacarpal II, either via a direct insertion on it or indirectly via an insertion on the distal prepollex (which is joined to metacarpal II by connective tissue and both bones, prepollex and metacarpal II, might act as a single structure in this case). In several other clades of Anura, it inserts on metacarpal II medially, to abduct the digit II (Gaupp, 1896; Burton, 1996, 1998). The abduction of the prepollex could be important for different behaviours: (1) digging, acting as a shovel; (2) protruding the bone through the skin or at least tensing the structure during fights, in species with a spine-shaped distal prepollex; (3) steadying/pressing the nuptial pads against the female body, in species with nuptial pads.

Sexual dimorphism

Kluge (1981) had already noted that males of *Boana rosenbergi* have the prepollical spine ossified, since they are postmetamorphic juveniles, while in adult females it is only partially ossified. Goldberg *et al.* (2019), studying the ontogeny of some characters in *Boana riojana*, found that the prepollical element begins to differentiate as a cartilaginous structure at Stage 36 of Gosner (1960). During metamorphosis it remains cartilaginous in both sexes. Juvenile males have an entirely cartilaginous element, whereas in juvenile females the tip is already ossified. This pattern is retained in adult females, whereas in males the prepollex becomes entirely ossified. In general, among the species with a spine-shaped distal prepollex, this element is smaller in females than in males, although still evident externally in both sexes of most species (e.g. Taucce *et al.*, 2015: fig. 3). We studied sexual dimorphism of the spine-shaped distal prepollex in 21 species representing most clades of Cophomantini where it occurs. Whereas in males it is entirely ossified and proportionally larger (Table 2), in females it is partially or entirely cartilaginous and smaller (Fig. 3), corroborating the observations of Kluge (1981) and Goldberg *et al.* (2019).

Cadle (1995) reported a similar dimorphism in the mantellid *Boophis albilabris*, where the prepollex in males is more robust and 'more projecting' (presumably the author means that the spine is osseous and larger) than in females. Also, he observed that the prepollex of females is cartilaginous, except for its tip, which is ossified. Andreone *et al.* (2002) also reported a 'soft prepollex' for a female of *Boophis occidentalis* (also from the *Boophis albilabris* group), suggesting that it is at least partially cartilaginous.

However, in *Hyloscirtus tapichalaca* both male and female have an osseous prepollical spine, as reported by Kizirian *et al.* (2003). Observations of X-ray images from both sexes corroborate this (Fig. 3E, F). Ron *et al.* (2018) reported a curved prepollex protruding as a spine in both sexes of *H. hillisi*; X-ray images of this species suggest that the prepollex is cartilaginous in females (Fig. 3C, D). Both species are nested in a clade that is the sister-taxon of most other species of the *H. larinopygion* group, as is *H. condor* and, presumably, *H. diabolus* (Rivera-Correa *et al.*, 2016; Ron *et al.*, 2018). However, females are unknown for these last two species. Scars have been only reported for males (Kizirian *et al.*, 2003; Rivera-Correa *et al.*, 2016). It is unknown whether in *H. tapichalaca* the osseous prepollical spine in the females has any biological function, such as intraspecific interactions or defense against predators. Outside Cophomantini, both sexes of the hyline *Plectrohyla* and the centrolenids with a spine-shaped prepollex (see above) have a large and ossified element (Duellman, 1970; Hayes & Starret, 1980; Flores, 1985). The report of scars in males of some *Plectrohyla* (Duelman & Campbell, 1992: fig. 16) suggests that they resulted from male–male interactions.

In many Cophomantini species with a spine-shaped distal prepollex, males have commonly been described as having hypertrophied forearms (e.g. Duellman *et al.*, 1997; Garcia *et al.*, 2001a; Nali & Prado, 2012). Studies with androgens have shown their positive correlation with increase in size of male musculature (Müller *et al.*, 1969; Regnier & Herrea, 1993) or with male behaviour directly associated with muscular systems (Mangiamele *et al.*, 2016). However, Oka *et al.* (1984), examining sexually dimorphic forearm muscles in *Bufo japonicus*, concluded that males do not have hypertrophied muscles. Instead, females have the sexually dimorphic muscles presenting fibres with a narrower diameter than the fibres of the non-dimorphic muscles in both sexes and with fewer fibres than the corresponding muscles in males (but see Mi, 2012). However, bufonids are distantly related to hylids, and the anatomical basis of sexual dimorphism in forearm musculature in Cophomantini requires study. In any case, there is a difference in musculature size between the sexes.

Wells (2007) hypothesized that a wider arm could increase chances of fighting success and that it could be positively correlated to wrestling behaviour, at least in some Cophomantini. However, it seems that the sexual dimorphism in forearm width in this tribe could also be related to reproduction in montane streams, as pointed out by Garcia *et al.* (2001a) for species of the *Boana pulchella* group. As a preliminary approach to test this hypothesis, we optimized sexual dimorphism in forearm width (i.e. forearms larger in males than in females or equal between the sexes) and habitat for reproduction (i.e. streams or ponds) for the Cophomantini, using the topology of Lyra *et al.* (2020) (see Supporting Information, File S7). In Cophomantini, we found that a larger forearm in males always evolved together with, or after, the evolution of reproduction in streams. These results are congruent with the hypothesis that the habitat where the species live and reproduce could be a selective pressure favouring the hypertrophy of forearms in this group, supporting the hypothesis of Garcia *et al.* (2001a). However, as we evaluated the forearm width only qualitatively, we recognize that the correlation between those traits should be tested with a broader sampling and formal measurements.

Oka *et al.* (1984) identified five sexually dimorphic forearm muscles in *Bufo japonicus*: m. flexor carpi radialis, m. extensor carpi radialis caput superius, m. abductor pollicis longus (as m. abductor indicis longus), m. flexor antibrachii lateralis superficialis caput superius and m. flexor antibrachii medialis caput superius. From these, only the m. abductor pollicis longus is associated with the prepollex and/or digit II in Cophomantini. In most species of *Bokermannohyla* and *Boana* in which we studied the musculature of both sexes, the m. abductor pollicis longus has an evidently larger volume in males than in females. In *Aplastodiscus*, *Boana albomarginata*, *Boana faber*, *Boana geographica*, *Boana microderma* and *Boana tepuiana* no differences were observed.

Gaupp (1896) reported differences in development of both the m. extensor carpi radialis and m. flexor carpi radialis between sexes of *Pelophylax* cf. *esculenta* (as *Rana esculenta*), being stouter in males than in females. Hoyos & Salgar (2016) found a more developed m. extensor carpi radialis in males of *Dendropsophus luddeckei* (as *D. labialis*). Oka *et al.* (1984) investigated those differences in *Bufo japonicus*, corroborating the observations of Gaupp (1896) in *Pelophylax*, and reported similar differences in another two forelimb muscles. Both Gaupp (1896) and Oka *et al.* (1984) considered that the sexual differences on those muscles are adaptations to the clasping behaviour of males during amplexus. Indeed, a strong arm could be important for an amplectant male to avoid being removed from the female by another male, as commonly occurs in some species of hylids and bufonids (Wells, 2007; C. F. B. Haddad, pers. obs.). Among the species we examined for sexual dimorphism in musculature, we found a clearly larger (only visual examination, no measurements) m. extensor carpi radialis in males than in females of *Boana albomarginata*, *Boana boans*, *Boana ericae*, *Boana joaquini*, *Boana rufitela* and *Bokermannohyla hylax*. Similarly, we found a m. flexor carpi radialis larger in males than in females of *Boana albomarginata*, *Boana albopunctata*, *Boana boans*, *Boana ericae*, *Boana joaquini*, *Boana rufitela*, *Bokermannohyla hylax*, *Bokermannohyla martinsi* and *Bokermannohyla oxente*. The other studied species have no differences between the sexes with regard to these two muscles. As in Cophomantini the differences in volume of both m. extensor carpi radialis and m. flexor carpi radialis are observed only in species with a spine-shaped distal prepollex (although a broader taxon sampling for these characters is necessary, so as proper measurements), it is possible that such differences might be associated not only to the clasping during amplexus, but also to the occurrence of fights between males and/or to life in lotic environments due to selective pressures such as water flow.

CONCLUSION

The prepollex shows a notable evolutionary plasticity in Cophomantini. The two distinct morphologies of the distal prepollex, the blade-shaped and the spine-shaped, evolved more than once, as did many associated characters. However, the ambiguity in the origin of the spine-shaped distal prepollex in *Boana* and in *Bokermannohyla* imposes some limitations in the inferences relating to the correlation between evolution of these distinct morphologies and life history traits such as territoriality, reproductive biology and behaviour within Cophomantini.

The articulation through a medial expansion of the proximal epiphysis of metacarpal II with the prepollex is recovered as a synapomorphy of *Boana*. A large post-articular process is homoplastic in the *Boana pulchella* group and in the *Bokermannohyla martinsi* group, being synapomorphic for each clade. The shape of the curve of the spine, ventral to mecatarpal II, is another synapomorphy of the *Boana pulchella* group.

Muscles that insert on the prepollex (i.e. the m. abductor indicis brevis dorsalis, m. adductor pollicis and the m. pronator quadratus) are similar in species with the blade- or the spine-shaped distal prepollices. The m. abductor pollicis longus, which commonly inserts on metacarpal II among anurans, has an additional insertion on the prepollex in the species with a spine-shaped distal prepollex, although this insertion is plesiomorphically present in Cophomantini, being present in other hylid clades with different prepollical morphologies.

The two prepollical morphologies have differences in anatomical characters, which presumably play distinct biological functions. However, their biological significance is still poorly understood. Natural history data, such as detailed observations of basin-building behaviour, courtship behaviour, territoriality and amplexus, as well as biomechanical studies, probably will help to better understand the functional roles of the prepollex.

ACKNOWLEDGEMENTS

We thank the curators and/or managers N. C. Pupin (CFBH); D. C. Blackburn and C. M. Sheehy III (UF); E. O. Lavilla and S. Kretzschmar (FML); J. D. Lynch (ICN); S. J. Nenda (MACN); L. B. Nascimento (MCNAM); J. Daza (MHUA); S. Torquato (MUFAL); I. De La Riva (MNCN); J. P. Pombal Jr. and U. Caramaschi (MNRJ); A. L. C. Prudente (MPEG); F. A. Juncá (MZUEFS); D. A. Paucar (QCAZ); H. Zaher and A. S. Benetti (MZUSP); C. Almeida (UFMG); R. McDiarmid, W. R. Heyer, and S. Goette (USNM), for allowing access to material. A. Brunetti, F. Centeno, A. C. C. Lourenço, M. Rivera-Correa, M. O. Pereyra, M. Rada and M. T. Rodriguez helped in various ways, sharing photos of critical specimens, preserved specimens and/or literature. M. T. T. Santos read the manuscript and provided useful comments. PDPP was funded by Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG; #5.181/11), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; #158681/2013-4) and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP #2018/18473-6, #2018/15425-0, #2019/25061-9). SRR was funded by Secretaría Nacional de Educación Superior, Ciencia, Tecnología e Innovación del Ecuador SENESCYT (Arca de Noé initiative; SRR and Omar Torres principal investigators) and grants from Pontificia Universidad Católica del Ecuador, Dirección General Académica. PCAG thanks CNPq (481585/2008-7). CFBH and PCAG thanks CNPq for a research fellowship. JF thanks ANPCyT 2015-820 and 2019-346. We thank grants from FAPESP #2012/10000-5, #2013/20423-3, #2013/50741-7, #2014/50342-8, 2015/11237-7. The authors declare no competing interests.

REFERENCES

Abdala V, **Vera MC**, **Amador LI**, **Fontanarrosa G**, **Fratani J**, **Ponssa ML. 2019.** Sesamoids in tetrapods: the origin of new skeletal morphologies. *Biological Reviews* **94:** 2011–2032.

Almendáriz A, **Brito J**, **Batallas D**, **Ron SR. 2014.** Una especie nueva de rana arbórea del género *Hyloscirtus* (Amphibia: Anura: Hylidae) de la Cordillera del Cóndor. *Papéis Avulsos de Zoologia* **54:** 33–49.

Andreone F, **Vences M**, **Guarino FM**, **Glaw F**, **Randrianirina JE. 2002.** Natural history and larval morphology of *Boophis occidentalis* (Anura: Mantellidae: Boophinae) provide new insights into the phylogeny and adaptive radiation of endemic Malagasy frogs. *Journal of Zoology* **257:** 425–438.

Barbour T. 1908. Some new Amphibia Salientia. *Proceedings of the Biological Society of Washington* **21:** 189–190.

Barej MF, **Rödel M**, **Gonwouo LN**, **Pauwels OSG**, **Böhme W**, **Schmitz A. 2010.** Review of the genus *Petropedetes* Reichenow, 1874 in Central Africa with the description of three new species (Amphibia: Anura: Petropedetidae). *Zootaxa* **2340:** 1–49.

Barej MF, **Schmitz A**, **Günther R**, **Loader SP**, **Mahlow K**, **Rödel M-O. 2014.** The first endemic West African vertebrate family – a new anuran family highlighting the uniqueness of the Upper Guinean biodiversity hotspot. *Frontiers in Zoology* **11:** 1–27.

Blackburn DC, **Hanken J**, **Jenkins FA Jr**. **2009.** Concealed weapons: erectile claws in African frogs. *Biology Letters* **4:** 355–357.

Blotto BL, **Pereyra MO**, **Faivovich J**, **Dias PHS**, **Grant T. 2017.** Concentrated evolutionary novelties in the foot musculature of Odontophrynidae (Anura: Neobatrachia), with comments on adaptations for burrowing. *Zootaxa* **4258:** 425–442.

Blotto BL, **Pereyra MO**, **Grant T**, **Faivovich J. 2020.** Hand and foot musculature of Anura: structure, homology, terminology, and synapomorphies for major clades. *Bulletin of the American Museum of Natural History* **443:** 1–156.

Bokermann WCA. 1964. Dos nuevas species de *Hyla* de Minas Gerais y notas sobre *Hyla alvarengai* Bok. (Amphibia, Salientia, Hylidae). *Neotropica* **10:** 67–76.

Bokermann WCA. 1965. *Hyla langei*, a new frog from Paraná, southern Brasil. *Journal of the Ohio Herpetological Society* **5:** 49–51.

Boulenger GA. 1890. List of the reptiles, batrachians, and freshwater fishes collected by Professor Moesch and Mr. Iversen in the district of Deli, Sumatra. *Proceedings of the Zoological Society of London* **1890:** 30–39.

Boulenger GA. 1892. Descriptions of new reptiles and batrachians from the Loo Choo Islands. *Annals and Magazine of Natural History* **10:** 302–304.

Brunetti AE, **Hermida GN**, **Luna MC**, **Barsotti AMG**, **Jared C**, **Antoniazzi MM**, **Rivera-Correa M**, **Berneck BvM**, **Faivovich J. 2015.** Diversity and evolution of sexually dimorphic mental and lateral glands in Cophomantini treefrogs (Anura: Hylidae: Hylinae). *Biological Journal of the Linnean Society* **114:** 12–34.

Burton TC. 1996. Adaptation and evolution in the hand muscles of Australo-Papuan hylid frogs (Anura: Hylidae: Pelodryadinae). *Australian Journal of Zoology* **44:** 611–23.

Burton TC. 1998. Variation in the hand and superficial throat musculature of Neotropical leptodactylid frogs. *Herpetologica* **54:** 53–72.

Burton TC. 2001. Variation in the foot muscles of frogs of the family Myobatrachidae. *Australian Journal of Zoology* **49:** 539–559.

Cadle JE. 1995. A new species of *Boophis* (Anura: Rhacophoridae) with unusual skin glands from Madagascar, and a discussion of variation and sexual dimorphism in *Boophis albilabris* (Boulenger). *Zoological Journal of the Linnean Society* **115:** 313–345.

Caminer MA, **Ron SR. 2020.** Systematics of the *Boana semilineata* species group (Anura: Hylidae), with a description of two new species from Amazonian Ecuador. *Zoologial Journal of the Linnean Society* **190:** 149–180.

Candaten A, **Possenti AG**, **Mainardi AA**, **Rocha MC**, **Palaoro AV. 2020.** Fighting scars: heavier gladiator frogs bear more injuries than lighter frogs. *Acta Ethologica* **23:** 39–44.

Crump ML. 1974. Reproductive strategies in a tropical anuran community. *Miscellaneous Publication, Museum of Natural History, University of Kansas* **61:** 1–68.

Diogo R, **Ziermann JM. 2014.** Development of fore and hindlimb muscles in frogs: Morphogenesis, homeotic transformations, digit reduction, and the forelimb-hindlimb enigma. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* **322:** 86–105.

Diogo R, **Walsh S**, **Smith C**, **Ziermann JM**, **Abdala V. 2015.** Towards the resolution of a long-standing evolutionary question: muscle identity and attachments are mainly related to topological position and not to primordium or homeotic identity of digits. *Journal of Anatomy* **226:** 523–529.

Diogo R, **Ziermann ZM**, **Molnar J**, **Siomava N**, **Abdala V. 2018.** *Muscles of chordates*. Boca Raton: CRC Press.

Duellman WE. 1961. A new species of fringe-limbed tree frog from Mexico. Studies of American hylid frogs. VIII. *Transactions of the Kansas Academy of Science* **64:** 349–352.

Duellman WE. 1968. Descriptions of new hylid frogs from Mexico and Central America. *University of Kansas Publications, Museum of Natural History* **17:** 559–578.

Duellman WE. 1970. Hylid frogs of Middle America. *Monographs of the Museum of Natural History, University of Kansas* **1–2:** 1–753.

Duellman WE. 1972. A review of the Neotropical frogs of the *Hyla bogotensis* group. *Occasional Papers of the Museum of Natural History, University of Kansas* **11:** 1–31.

Duellman WE, **Campbell JA. 1992.** Hylid frogs of the genus *Plectrohyla*: systematics and phylogenetic relationships. *Miscellaneous Publications, Museum of Zoology, University of Michigan* **181:** 1–32.

Duellman WE, **De la Riva I**, **Wild ER. 1997.** Frogs of the *Hyla armata* and *Hyla pulchella* groups in the Andes of South America, with definitions and analyses of phylogenetic relationships of Andean groups of *Hyla*. *Scientific Papers, Natural History Museum, University of Kansas* **3:** 1–41.

Duellman WE, **Marion AB**, **Hedges SB. 2016.** Phylogenetics, classification, and biogeography of the treefrogs (Amphibia: Anura: Arboranae). *Zootaxa* **4104:** 1–109.

Echeverría AI, **Abdala V**, **Longo MV**, **Vassallo AI. 2019.** Functional morphology and identity of the thenar pad in the subterranean genus *Ctenomys* (Rodentia, Caviomorpha). *Journal of Anatomy* **235:** 940–952.

Emerson SB. 1976. Burrowing in frogs. *Journal of Morphology* **149:** 437–458.

Fabrezi M. 1992. El carpo de los anuros. *Alytes* **10:** 1–29.

Fabrezi M. 2001. A survey of prepollex and prehallux variation in anuran limbs. *Zoological Journal of the Linnean Society* **131:** 227–248.

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

Faivovich J, **Haddad CFB**, **Garcia PCA**, **Frost DR**, **Campbell JA**, **Wheeler WC. 2005.** Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History* **294:** 1–240.

Faivovich J, **Moravec J**, **Cisneros-Heredia DF**, **Köhler J. 2006.** A new species of the *Hypsiboas benitezi* group from the western Amazon Basin (Amphibia: Anura: Hylidae). *Herpetologica* **62:** 96–108.

Faivovich J, **Lugli L**, **Lourenço ACC**, **Haddad CFB. 2009.** A new species of the *Bokermannohyla martinsi* group from central Bahia, Brazil with comments on *Bokermannohyla* (Anura: Hylidae). *Herpetologica* **65:** 303–310.

Faivovich J, **McDiarmid RW**, **Myers CW. 2013.** Two new species of *Myersiohyla* (Anura: Hylidae) from Cerro de la Neblina, Venezuela, with comments on other species of the genus. *American Museum Novitates* **3792:** 1–63.

Faivovich J, **Pinheiro PDP**, **Lyra ML**, **Pereyra MO**, **Baldo D**, **Muñoz A**, **Reichle S**, **Brandão RA**, **Giaretta AA**, **Thomé MT**, **Chaparro JC**, **Baêta D**, **Widholzer RL**, **Baldo J**, **Lehr E**, **Wheeler WC**, **Garcia PCA**, **Haddad CFB. 2021.** Phylogenetic relationships of the *Boana pulchella* group (Anura: Hylidae). *Molecular Phylogenetics and Evolution* **155:** 106981.

Farris JS. 1970. Methods for computing Wagner trees. *Systematic Zoology* **19:** 83–92.

Ferro JM, **Cardozo DE**, **Suárez P**, **Boeris JM**, **Blasco-Zúñiga A**, **Barbero G**, **Gomes A**, **Gazoni T**, **Costa W**, **Nagamachi CY**, **Rivera M**, **Parise-Maltempi PP**, **Wiley JE**, **Pieczarka JC**, **Haddad CFB**, **Faivovich J**, **Baldo D. 2018.** Chromosome evolution in Cophomantini (Amphibia, Anura, Hylidae). *PLoS One* **13:** e0192861.

Fitch WM. 1971. Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Zoology* **20:** 406–416.

Flores G. 1985. A new *Centrolenella* (Anura) from Ecuador, with comments on nuptial pads and prepollical spines in *Centrolenella*. *Journal of Herpetology* **19:** 313–320.

Fouquet A, **Marinho P**, **Réjaud A**, **Carvalho TR**, **Caminer MA**, **Jansen M**, **Rainha RN**, **Rodrigues MT**, **Werneck FP**, **Lima AP**, **Hrbek T**, **Giaretta AA**, **Venegas PJ**, **Chávez G**, **Ron S. 2021.** Systematics and biogeography of the *Boana albopunctata* species group (Anura, Hylidae), with the description of two new species from Amazonia. *Systematics and Biodiversity* **19:** 375–399.

Frost DR. 2021. *Amphibian species of the world: an online reference, v.6.1.* New York: American Museum of Natural History. Available at: https://amphibiansoftheworld.amnh.org/index.php (accessed 30 March 2021).

Frost DR, **Grant T**, **Faivovich J**, **Bain RH**, **Haas A**, **Haddad CFB**, **de Sá RO**, **Channing A**, **Wilkinson M**, **Donnellan SC**, **Raxworthy CJ**, **Campbell JA**, **Blotto BL**, **Moler PE**, **Drewes RC**, **Nussbaum RA**, **Lynch JD**, **Green DM**, **Wheeler WC. 2006.** The amphibian tree of life. *Bulletin of the American Museum of Natural History* **297:** 1–370.

Garcia PCA, **Haddad CFB. 2008.** Vocalizations and comments on the relationships of *Hypsiboas ericae* (Amphibia, Hylidae). *Iheringia, Série Zoologia* **98:** 161–166.

Garcia PCA, **Vinciprova G**, **Haddad CFB. 2001a.** Vocalização, girino, distribuição geográfica e novos comentários sobre *Hyla marginata* Boulenger, 1887 (Anura, Hylidae, Hylinae). *Boletim do Museu Nacional* **460:** 1–19.

Garcia PCA, **Caramaschi U**, **Kwet A. 2001b.** O status taxonômico de *Hyla cochranae* Mertens e recaracterização de

Aplastodiscus A. Lutz (Anura, Hylidae). *Revista Brasileira de Zoologia* **18:** 1197–1218.

Garcia PCA, **Peixoto OL**, **Haddad CFB. 2008.** A new species of *Hypsiboas* (Anura: Hylidae) from the Atlantic forest of Santa Catarina, southern Brazil, with comments on its conservation status. *South American Journal of Herpetology* **3:** 27–35.

Gaupp E. 1896. *A. Ecker's und R. Wiedersheim's Anatomie des Frosches. I.* Braunschweig: Friedrich Vieweg und Sohn.

Glaw F, **Vences M. 2005.** A new arboreal microhylid frog of the genus *Anodonthyla* from south-eastern Madagascar. *Spixiana* **28:** 181–189.

Goeldi EO. 1895. Contribution to the knowledge of the breeding-habits of some tree-frogs (Hylidae) of the Serra dos Órgãos, Rio de Janeiro, Brazil. *Proceedings of the Zoological Society of London* **1895:** 89–96.

Goldberg J, **Quinzio SI**, **Cruz JC**, **Fabrezi M. 2019.** Intraspecific developmental variation in the life cycle of the Andean treefrog (*Boana riojana*): a temporal analysis. *Journal of Morphology* **280:** 480–493.

Goloboff PA, **Catalano S. 2016.** TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* **32:** 221–238.

Gosner KL. 1960. A simplified table for staging anuran embryo and larvae with notes on identification. *Herpetologica* **16:** 183–190.

Haddad CFB, **Prado CPA. 2005.** Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. *BioScience* **55:** 207–217.

Haddad CFB, **Sawaya RJ. 2000.** Reproductive modes of Atlantic Forest hylid frogs: a general overview and the description of a new mode. *Biotropica* **32:** 862–871.

Haddad CFB, **Faivovich J**, **Garcia PCA. 2005.** The specialized reproductive mode of the treefrog *Aplastodiscus perviridis* (Anura: Hylidae). *Amphibia-Reptilia* **26:** 87–92.

Hartmann MT, **Hartmann PA**, **Haddad CFB. 2004.** Visual signaling and reproductive biology in a nocturnal treefrog, genus *Hyla* (Anura: Hylidae). *Amphibia-Reptilia* **25:** 395–406.

Hayashi S, **Kobayashi T**, **Yano T**, **Kamiyama N**, **Egawa S**, **Seki R**, **Takizawa K**, **Okabe M**, **Yokoyama H**, **Tamura K. 2015.** Evidence for an amphibian sixth digit. *Zoological Letters* **1:** 17.

Hayes MP, **Starret PH. 1980.** Notes on a collection of centrolenid frogs from the Colombian Chocó. *Bulletin of the Southern California Academy of Sciences* **79:** 89–96.

Heyer WR. 1970. Studies on the frogs of the genus *Leptodactylus* (Amphibia: Leptodactylidae). VI. Biosystematics of the *melanonotus* group. *Contributions in Science* **191:** 1–48.

Heyer WR. 1979. Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology* **301:** 1–43.

Heyer WR. 1994. Variation within the *Leptodactylus podicipinus-wagneri* complex of frogs (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology* **546:** 1–124.

Heyer WR, **Rand AS**, **Cruz CAG**, **Peixoto OL**, **Nelson CE. 1990.** Frogs of Boracéia. *Arquivos de Zoologia* **31:** 231–410.

Hoyos JM, **Salgar L. 2016.** New conditions and intraspecific variation of some muscles of hands and feet of *Dendropsophus labialis* (Peters, 1863) (Anura, Hylidae). *Acta Zoologica* **97:** 143–153.

Iwai N. 2012. Morphology, function and evolution of the pseudothumb in the Otton frog. *Journal of Zoology* **289:** 127–133.

Kizirian D, **Coloma LA**, **Paredes-Recalde A. 2003.** A new treefrog (Hylidae: *Hyla*) from southern Ecuador and a description of its antipredator behavior. *Herpetologica* **59:** 339–349.

Kley NJ, **Kearney M. 2007.** Adaptations for digging and burrowing. In: Hall BK, ed. *Fins into limbs: evolution, development and transformation*. Chicago: University of Chicago Press, 284–309.

Kluge AG. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Miscellaneous Publications, Museum of Zoology, University of Michigan* **160:** 1–170.

Landestoy MAT. 2013. Observations on the breeding behavior of the Hispaniolan green treefrog, *Hypsiboas heilprini*. *IRCF Reptiles & Amphibians* **20:** 160–165.

Laurent RF. 1964. Adaptive modifications in frogs of an isolated highland fauna in central Africa. *Evolution* **18:** 458–467.

Le Minor JM. 1994. The sesamoid bone of the *Musculus abductor pollicis longus* (*Os radiale externum* or Prepollex) in primates. *Acta Anatomica* **150:** 227–231.

Luna MC, **McDiarmid RW**, **Faivovich J. 2018.** From erotic excrescences to pheromone shots: structure and diversity of nuptial pads in anurans. *Biological Journal of the Linnean Society* **124:** 403–446.

Lutz B. 1949 '1948'. Anfibios anuros da coleção Adolpho Lutz. II. Espécies verdes do genero *Hyla* do Leste-Meridional do Brasil. *Memórias do Instituto Oswaldo Cruz* **46:** 551–577.

Lutz B. 1960a. Fighting and an incipient notion of territory in male tree frogs. *Copeia* **1960:** 61–63.

Lutz B. 1960b. The clay nests of *Hyla pardalis* Spix. *Copeia* **1960:** 364–366.

Lutz B. 1973. *Brazilian species of Hyla*. Austin: University of Texas Press.

Lutz B, **Orton GL. 1946.** *Hyla claresignata* Lutz & B. Lutz, 1939. Aspects of the life history and description of the rhyacophilous tadpole. *Boletim do Museu Nacional* **70:** 1–20.

Lynch JD. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Miscellaneous Publication, Museum of Natural History, University of Kansas* **53:** 1–238.

Lyra ML, **Lourenço ACC**, **Pinheiro PDP**, **Pezzuti TL**, **Baêta D**, **Barlow A**, **Hofreiter M**, **Pombal JP Jr**, **Haddad CFB**, **Faivovich J. 2020.** High-throughput DNA sequencing of museum specimens sheds light on the long-missing species of the *Bokermannohyla claresignata* group

(Anura: Hylidae: Cophomantini). *Zoological Journal of the Linnean Society* **190:** 1235–1255.

Malagoli LR, **Pezzuti TL**, **Bang DL**, **Faivovich J**, **Lyra ML**, **Giovanelli JLR**, **Garcia PCA**, **Sawaya RJ**, **Haddad CFB. 2021.** A new reproductive mode in anurans: natural history of *Bokermannohyla astartea* (Anura: Hylidae) with the description of its tadpole and vocal repertoire. *PLoS One* **16:** e0246401.

Mangiamele LA, **Fuxjager MJ**, **Schuppe ER**, **Taylor RS**, **Hödl W**, **Preininger D. 2016.** Increased androgenic sensitivity in the hind limb muscular system marks the evolution of a derived gestural display. *Proceedings of the National Academy of Sciences of the USA* **113:** 5664–5669.

Martins M, **Haddad CFB. 1988.** Vocalizations and reproductive behaviour in the smith frog, *Hyla faber* Wied (Amphibia: Hylidae). *Amphibia-Reptilia* **9:** 49–60.

Martins M, **Moreira G. 1991.** The nest and the tadpole of *Hyla wavrini*, Parker (Amphibia, Anura). *Memórias do Instituto Butantan* **53:** 197–204.

Mi ZP. 2012. Sexual dimorphism in the forelimb muscles of the Asiatic toad *Bufo gargarizans*. *Herpetological Journal* **22:** 219–224.

Montesinos R, **Jeckel AM**, **Pavan SE**, **Targino M. 2021.** Natural history notes: *Boerkamnnohyla gouveai* (Itatiaia Treefrog). Parental care. *Herpetological Review* **52:** 113.

Müller ERA, **Galavazi G**, **Szirmai JA. 1969.** Effect of castration and testosterone treatment on fiber width of the flexor carpi radialis muscle in the male frog (*Rana temporaria*). *General and Comparative Endocrinology* **13:** 275–284.

Nali RC, **Prado CPA. 2012.** Habitat use, reproductive traits and social interactions in a stream-dweller treefrog endemic to the Brazilian Cerrado. *Amphibia-Reptilia* **33:** 337–347.

Noble GK. 1931. *The biology of the Amphibia*. New York and London: McGraw-Hill.

Oka Y, **Ohtani R**, **Satou M**, **Ueda K. 1984.** Sexually dimorphic muscles in the forelimb of the Japanese toad, *Bufo japonicus*. *Journal of Morphology* **180:** 297–308.

Peloso PLV, **Oliveira RM**, **Sturaro MJ**, **Rodrigues MT**, **Lima-Filho GR**, **Bitar YOC**, **Wheeler WC**, **Aleixo A. 2018.** Phylogeny of map tree frogs, *Boana semilineata* species group, with a new Amazonian Species (Anura: Hylidae). *South American Journal of Herpetology* **13:** 150–169.

Pinheiro PDP, **Kok PJR**, **Noonan B**, **Means DB**, **Haddad CFB**, **Faivovich J. 2019.** A new genus of Cophomantini, with comments on the taxonomic status of *Hypsiboas liliae* Kok, 2006 (Anura: Hylidae: Hylinae). *Zoological Journal of the Linnean Society* **185:** 226–245.

Pombal JP Jr, **Haddad CFB. 1993.** *Hyla luctuosa*, a new treefrog from southeastern Brazil (Amphibia: Hylidae). *Herpetologica* **49:** 16–21.

Regnier M, **Herrera AA. 1993.** Changes in contractile properties by androgen hormones in sexually dimorphic muscles of male frogs (*Xenopus laevis*). *Journal of Physiology* **461:** 565–581.

Rivera-Correa M, Faivovich J. 2013. A new species of *Hyloscirtus* (Anura: Hylidae) from Colombia, with a rediagnosis of *Hyloscirtus larinopygion* (Duellman, 1973). *Herpetologica* **63:** 298–313.

Rivera-Correa M, **García-Burneo K**, **Grant T. 2016.** A new red-eyed of stream treefrog of *Hyloscirtus* (Anura: Hylidae) from Peru, with comments on the taxonomy of the genus. *Zootaxa* **4061:** 29–40.

Ron SR, **Caminer MA**, **Varela-Jaramillo A**, **Almeida-Reinoso D. 2018.** A new treefrog from Cordillera del Cóndor with comments on the biogeographic affinity between Cordillera del Cóndor and the Guianan Tepuis (Anura, Hylidae, *Hyloscirtus*). *ZooKeys* **809:** 97–124.

Ron SR, **Merino-Viteri A**, **Ortiz DA. 2019.** *Anfibios del Ecuador, v.2019.0.* Museo de Zoología, Pontificia Universidad Católica del Ecuador. Available at: https://bioweb.bio/faunaweb/amphibiaweb (accessed 8 May 2019).

de Sá RO, **Grant T**, **Camargo A**, **Heyer WR**, **Ponssa ML**, **Stanley E. 2014.** Systematics of the Neotropical genus *Leptodactylus* Fitzinger, 1826 (Anura: Leptodactylidae): phylogeny, the relevance of non-molecular evidence, and species accounts. *South American Journal of Herpetology* **9:** 1–128.

Sabaj MH. 2020. Codes for natural history collections in ichthyology and herpetology. *Copeia* **108:** 593–669.

Scott E. 2005. A phylogeny of ranid frogs (Anura: Ranoidea: Ranidae), based on a simultaneous analysis of morphological and molecular data. *Cladistics* **21:** 507–574.

Señaris JC, **Ayarzagüena J. 2005.** *Revisión taxonómica de la familia Centrolenidae (Amphibia; Anura) de Venezuela*. Sevilla: Publicaciones del Comité Español del Programa Hombre y Biosfera – Red IberoMaB de la UNESCO.

Shine R. 1979. Sexual selection and sexual dimorphism in the Amphibia. *Copeia* **1979:** 297–306.

Shubin N, **Alberch P. 1986.** A morphogenetic approach on the origin and basic organization of the tetrapod limb. *Evolutionary Biology* **20:** 319–387.

Taucce PPG, **Pinheiro PDP**, **Leite FSF**, **Garcia PCA. 2015.** Advertisement call and morphological variation of the poorly known and endemic *Bokermannohyla juiju* Faivovich, Lugli, Lourenço and Haddad, 2009 (Anura: Hylidae) from central Bahia, Brazil. *Zootaxa* **3915:** 99–110.

Taylor EH. 1949. Costa Rican frogs of the genera *Centrolene* and *Centrolenella*. *University of Kansas Science Bulletin* **33:** 257–270.

Taylor WR, **Van Dyke GC. 1985.** Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* **9:** 107–119.

Tokita M, **Iwai N. 2010.** Development of the pseudothumb in frogs. *Biology Letters* **6:** 517–520.

Toledo LF, **Sazima I**, **Haddad CFB. 2011.** Behavioural defences of anurans: an overview. *Ethology Ecology & Evolution* **23:** 1–25.

Van Denburgh J. 1912. Concerning certain species of reptiles and amphibians from China, Japan, the Loo Choo Island, and Formosa. *Proceedings of the California Academy of Sciences* **3:** 187–257.

Vences M, **Andreone F**, **Glos J**, **Glaw F. 2010a.** Molecular and bioacoustic differentiation of *Boophis occidentalis* with description of a new treefrog from north-western Madagascar. *Zootaxa* **2544:** 54–68.

Vences M, **Glaw F**, **Köhler J**, **Wollenberg KC. 2010b.** Molecular phylogeny, morphology and bioacoustics reveal five additional species of arboreal microhylid frogs of the genus *Anodonthyla* from Madagascar. *Contributions to Zoology* **79:** 1–32.

Wells KD. 2007. *The ecology and behavior of amphibians*. Chicago: University of Chicago Press.

Wiens JJ, **Kuczynski CA**, **Hua X**, **Moen DS. 2010.** An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution* **55:** 871–882.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

File S1. List of material examined.
File S2. Details for micro-CT scanned specimens and schematic drawings representing measurements taken for metacarpal II and distal prepollex lengths (for both spine-shaped and blade-shaped morphologies).
File S3. Character matrix for all species employed in the present study, showing states for the characters listed on the Results section – Hypotheses of homology.
File S4. Character matrix for character optimization as implemented on TNT, showing states for the characters listed on the Results section – Hypotheses of homology.
File S5. Ancestral character-reconstruction of the 17 characters from the present study on the tree provided by Lyra *et al.* (2020) given in separate figures.
File S6. Evidence of fights among males in species of Cophomantini.
File S7. Ancestral character-reconstruction of relative width of male forearm and habitat, for species of Cophomantini on the tree provided by Lyra *et al.* (2020).

SUPPORTING INFORMATION S1

List of material examined. An asterisk (*) indicates cleared and double stained specimens; a numeral (#) indicates specimens with X-ray images; the Mu character (µ) indicate micro-CT scanned specimens; the plus sign (+) indicates specimens dissected for the study of hand muscles; specimens without any of these signs were used only for external morphology. Female specimens are indicated by the female sign (♀); metamorphs or juvenile specimens are indicated by JUV; voucher numbers without a ♀ or JUV indication correspond to adult males. Some acronyms refer to personal field series (EMM, GGD, JMR, MAR, MC, MRC, PR, and VR). These specimens are already housed at MACN collection. They have not received an institutional accession number yet due to the COVID-19 pandemic, but they will be deposited at MACN as soon as the conditions allow, maintaining their respective field number tags. EMM: Eliana Muñoz; GGD: Gustavo González; JMR: Juan Manuel Rengifo; MAR: Marco Rada; MC: María Cristina Ardíla-Robayo; MRC: Mauricio Rivera-Correa; PR: Pedro Ruiz-Carranza; VR: José Vicente Rueda-Almonacid.

HYLINAE: COPHOMANTINI: *APLASTODISCUS*: *A. albofrenatus* group.—*A. arildae*, CFBH 1242*, 30829+, UFMG 12054♀+, 13732+; *A. ehrhardti*, CFBH 3183*; *A. eugenioi*, CFBH 3181*. ***A. albosignatus* group.**—*A. albosignatus*, CFBH 4941+, 4944*, 3910*; *A. cavicola*, UFMG 5719+, 6699♀+. ***A. perviridis* group.**—*A. cochranae*, CFBH 2193*, 2987+; *A. perviridis*, CFBH 11206+, MACN 35170+, 34970+, UFMG 9851+, 9862♀+, 21555*. ***A. sibilatus* group.**—*A. sibilatus*, CFBH 32494+, MNRJ 36946*. ***BOANA*: *B. albopunctata* group.**—*B. albopunctata*, CFBH 739*, 4434*, 6051*, 7456+, 22086*, 22087*, 22089*, 45511+, MZUSP 7816♀+, 7872+, UFMG 1174*; *B. caiapo*, MZUSP 139009*; *B. calcarata*, MPEG 25035*, QCAZ 43047#; *B. fasciata*, MPEG 14101*, QCAZ 44029#; *B. heilprini*, UF 57577+, UFMG 8641*; *B. lanciformis*, MZUSP 121577*; *B. multifasciata,* UFMG 5279*; *B. raniceps,* MACN 45053+, UFMG 1547*. ***B. benitezi* group.**—*B. microderma*, MZUSP 159188+, 159193♀+, 159194+*; *B. nympha*, QCAZ 2145*, 6012#, 8707♀#, 24302#, 28184*; *B. ornatissima*, MPEG 20361*; *B. tepuiana,* MZUSP 159179+*, 159181+, 159187♀+. ***B. claresignata* group.**—*B. clepsydra,* MZUSP 112612*, 112615+. ***B. faber* group.**—*B. albomarginata,* CFBH 10596*, 10597*, 10599*, 10602*, 17639*, 34999*, MZUSP 145340+,153794♀+, UFMG 8231*; *B. crepitans,* UFMG 6937*; *B. exastis,* UFMG 11059*; *B. faber,* MZUSP 140287+, 140289♀+, UFMG 3318*; *B. lundii,* CFBH 34316+, UFMG 1637*; *B. pardalis,* UFMG 7730*; *B. rosenbergi* QCAZ 32383♀#. ***B. pellucens* group.**—*B. pellucens,* UF 30660+, QCAZ 7267#, 11596#, 40273♀#; *B. rufitela* UF 108720♀+, 108728+. ***B. pulchella* group.**—*B. bischoffi,* CFBH 1009*; *B. botumirim,* UFMG 3793*; *B. cambui* UFMG 20190+; *B. cipoensis,* UFMG 1218*; *B. cordobae,* MACN 54785+*, 53786+*, 37696+, 48999+; *B. curupi,* MACN 42589+; *B. ericae,* MZUSP 93851♀+, 93852+, UFMG 11583*; *B. freicanecae,* MUFAL 9472*; *B. goiana,* UFMG 8452*, 10346*; *B. joaquini,* CFBH 3592*, 3594*, 3595*, MZUSP 35525♀+, 35527+, UFMG 10005*, UFMG 10037*; *B. marianitae,* MACN 34653, 34661♀, 34662, 34663; *B. polytaenia,* UFMG 1419*, 2991*; *B.* aff. *polytaenia,* UFMG1480*; *B. pulchella,* MACN 40485+, 54563+*, 54564+*; *B. riojana,* FML 3866-5♀, MACN 43664+, 54565+*, 54566+*; *B. stenocephala,* UFMG 11205*. ***B. punctata* group.**—*B. atlantica,* CFBH 13257+, 18725+, UFMG 5744*; *B. cinerascens,* MPEG 10001*, QCAZ 17541♀#; *B. picturata,* QCAZ 230#, 3474♀#, 4055#, 4058#, 4059#, 7233*; *B. punctata,* CFBH 9161*, MACN 40114+, MZUSP 31534+, 34828♀+, 53667*, 140455*, QCAZ 43118♀#. ***B. semilineata* group.**—*B. boans,* MPEG 8863*, MZUSP 26603♀+, 26618+, QCAZ 27029♀#; *B. geographica,* MPEG 17822*, MZUSP 41829♀+, 41880♀+, 41881+, 41931+, 41955+, 41973♀+, QCAZ 44161♀#; *B. pombali,* CFBH 14917*; 36791+; *B.*

semilineata, CFBH 2389*, 10524*, 10528*, 10530*, 10533*, 13013+, MZUSP 127748♀+, 127750+, 127753+, 127757+, 127767+; *B. wavrini*, MPEG 15315*. ***BOKERMANNOHYLA*: *B. circumdata* group.—***B. hylax*, CFBH 3620♀*, 11545+*, UFMG 732+ 20300♀+; *B. lucianae*, MNRJ 40483*; *B. luctuosa*, UFMG 21546*; *B. nanuzae*, UFMG 10940*. ***B. martinsi* group.—***B. langei*, MZUSP 74275#; *B. juiju*, MZUEFS 1900#; *B. martinsi*, MNRJ 49675*, MZUSP 73667#, UFMG 745*, 10680♀+, 19338+. ***B. pseudopseudis* group.—***B. alvarengai*, CFBH 44645*, CFBH 44646♀* MCNAM 3165*; *B. ibitiguara*, CFBH 17323+*, CFBH 40583+; *B. oxente*, CFBH 30145+*, UFMG 4229♀+, 4533+; *B. pseudopseudis*, CFBH 6800+*; *B. saxicola*, CFBH 30901+*, MZUSP 134308+, 134312♀+. ***HYLOSCIRTUS*: *H. armatus* group.—***H. armatus*, MNCN 43516*, USNM 346062♀+, 206715µ,; *H. charazani*, MNCN 44823*. ***H. bogotensis* group.—***H. alytolylax*, QCAZ 16411*, 35295♀#, 37234♀#, 37246♀#, 37250#; *H.* aff. *alytolylax*, PR 16277*; *H. bogotensis*, ICN 4420*; *H. callipeza*, VR 5150*, 5152*; *H. colymba*, MAR 1471*, 1628♀*; *H. denticulentus*, MRC 591*, 610*; *H. lynchi*, PR 16302*; *H. palmeri*, ICN 20087+, MAR 1082*, 1196*, GGD 073*, QCAZ 32054♀#, 32063♀#; *H.* aff. *palmeri*, EMM 263*; *H. phyllognathus* QCAZ 23942#, 42047#, 45679JUV#, 46447#; *H.* aff. *phyllognathus*, MRC 701*, 702*; *H. piceigularis*, ICN 5307*; *H.* aff. *piceigularis*, MC 9748♀*, 9749*; *H. platydactylus*, ICN 10471*, 10472*; *H. simmonsi*, ICN 25906*, 41305*; *H.* aff. *simmonsi* sp. 1, MHUA 4098*, 5017*; *H.* aff. *simmonsi* sp. 2, VR 3293*; *H. torrenticola*, ICN 23614*, MAR 1974*. ***H. larinopygion* group.—***H. antioquia*, ICN 9384*, 9392*; *H. caucanus*, ICN 7074*; *H. condor*, QCAZ 65235#, 65236#, 65237#, 65240JUV#, 65241JUV#; *H. hillisi*, QCAZ 68646JUV#, 68647JUV#, 68646JUV#, 68649♀#, 68650JUV#, 72549♀#, 72750#, 72551# 72553#; *H. larinopygion*, MRC 575*, 576*, ICN 36138+, ICN 31190♀+, QCAZ 29211#, 41826#; *H. lindae*, ICN 49662*, QCAZ 10483*, 41232#, 41296#, 41297#; *H. pacha* QCAZ 48238#, 48240#; *H.*

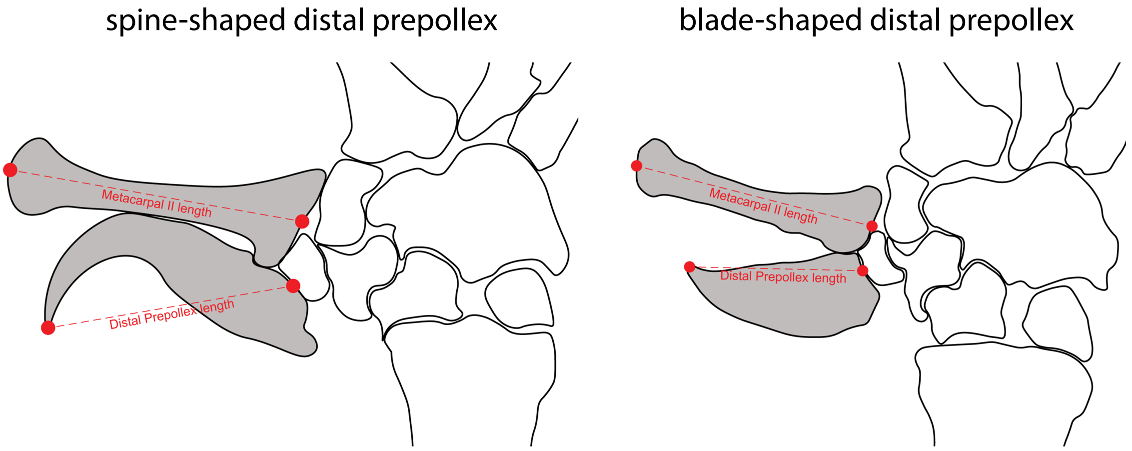
pantostictus QCAZ 46587#, 46588#; *H. princecharlesi*, QCAZ 48075*; *H. psarolaimus* QCAZ 31671#; *H. sarampiona*, JMR 2434, 2888*; *H. staufferorum*, QCAZ 45963#, 45966#, 50381*; *H. tapichalaca*, QCAZ 14611#, 15084#, 15085#, 16704#, 16705♀#, 16706*, 17776#, 17777♀#, 63872♀#. ***MYERSIOHYLA*****:** *M. chamaeleo*, AMNH-A 131173µ, MZUSP 159198+; *M. neblinaria*, USNM 562071µ. **DENDROPSOPHINI:** *Dendropsophus nanus*, MZUSP 95213+. **HYLINI:** *Acris crepitans*, MZUSP 118655+; *Hyla cinerea*, MZUSP 118103+. **LOPHYOHYLINI:** *Phyllodytes luteolus*, MZUSP 78477+; *Trachycephalus typhonius*, MZUSP 139088+. **PSEUDINI:** *Pseudis minuta*, MZUSP 80284+. **SCINAXINI:** *Scinax cruentomma*, MZUSP 70337+. **PHYLLOMEDUSINAE:** *Phryomedusa appendiculata*, MZUSP 75688+.

SUPPORTING INFORMATION S2

1) Scan settings of micro-CT scanned specimens:

- *Hyloscirtus armatus*: voucher USNM 206715. 50kV, 0.5mA, 1.319791 second detector capture time, 4209 projections, voxel resolution 17.42µm.
- *Myersiohyla chamaeleo*: voucher AMNH-A 131173. 170kV, 50mA, 1 second detector capture time, 1400 projections, voxel resolution 44.89908µm.
- *Myersiohyla neblinaria*: USNM 562071. 170kV, 50mA, 1 second detector capture time, 1400 projections, voxel resolution 49.44149µm.

2) Schematic drawings representing measurements taken for metacarpal II and distal prepollex lengths (for both spine-shaped and blade-shaped distal prepollex).



SUPPORTING INFORMATION S3. Character Matrix for species employed in the present study, showing states for the characters listed in Results, Hypotheses of homology section. (**n/a**) character not applicable; (**?**) missing data; two numbers interspaced by a slash "/" indicate a polymorphism. An asterisk points species for which Ch. 0 and 1 were coded infered from the literature (see references below).

Taxa	**Character States**																
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Ingroup																	
***Aplastodiscus albofrenatus* gr.**																	
*Aplastodiscus albofrenatus**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aplastodiscus arildae	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	0/1	1
Aplastodiscus ehrhardti	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Aplastodiscus eugenioi	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
*Aplastodiscus musicus**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Aplastodiscus weygoldti**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Aplastodiscus albosignatus* gr.**																	
Aplastodiscus albosignatus	0	0	0	0	0/1	0/1	0	n/a	n/a	n/a	0	0	0	0	0	0	?
Aplastodiscus cavicola	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	0	1
*Aplastodiscus heterophonicus**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Aplastodiscus flumineus**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Aplastodiscus ibirapitanga**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Aplastodiscus leucopygius**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Aplastodiscus perviridis* gr.**																	
Aplastodiscus cochranae	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	0/1	1
*Aplastodiscus lutzorum**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aplastodiscus perviridis	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	0	0/1
***Aplastodiscus sibilatus* gr.**																	
Aplastodiscus sibilatus	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	1	0
***Boana albopunctata* gr.**																	
Boana albopunctata	0	1	0	1	0	n/a	0	0	0	0	1	0	0	1	1	0	0/1
*Boana alfaroi**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana almendarizae**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana caiapo	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
Boana calcarata	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
*Boana courtoisae**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana dentei**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana eucharis**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana fasciata	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
Boana heilprini	0	1	0	1	0	n/a	1	0	0	0	0	0	0	1	1	0	1
Boana lanciformis	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
*Boana leucocheila**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana maculateralis**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana multifasciata	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?
*Boana paranaiba**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana raniceps	0	1	0	1	0	n/a	0	0	0	0	1	0	0	1	?	0	?
*Boana steinbachi**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana tetete**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Boana benitezi* gr.**																	
*Boana benitezi**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana hobbsi**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana jimenezi**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana lemai**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana microderma	0	1	0	0	0	n/a	0	1	0	0	0	0	0	1	1	1	1
Boana nympha	0	1	0	1	0	n/a	0	0/1	0	0	1	0	0	?	?	?	?
Boana ornatissima	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
*Boana rhythmica**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana roraima**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana tepuiana	0	1	0	1	0	n/a	0	0	0	0	1	0	0	1	0	0	0
***Boana claresignata* gr.**																	
*Boana claresignata**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana clepsydra	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	0
***Boana faber* gr.**																	

Taxa	Character States																
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Boana albomarginata	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	1
Boana crepitans	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?
Boana exastis	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?
Boana faber	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	1
Boana lundii	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	0
Boana pardalis	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?
*Boana platanera**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana pugnax**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana rosenbergi	0	1	0	1	0	n/a	1	0	0	0	?	?	0	?	?	?	?
*Boana xerophylla**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Boana pellucens* gr.**																	
Boana pellucens	0	1	0	1	0	n/a	1	0	0	0	0	0	0	1	1	0	1
*Boana rubracyla**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana rufitela	0	1	0	1	0	n/a	1	0	0	0	0	0	0	1	1	0	0/1
***Boana pulchella* gr.**																	
*Boana aguilari**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana balzani**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana bischoffi	0	1	0	1	0	n/a	2	0	1	0	1	0	0	?	?	?	?
Boana botumirim	0	1	0	1	0	n/a	2	0	1	0	1	0	0	?	?	?	?
*Boana buriti**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana caingua**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana caipora**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana callipleura**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana cambui	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	0	0
Boana cipoensis	0	1	0	1	0	n/a	2	0	1	0	1	0	0	?	?	?	?
Boana cordobae	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	0	?
Boana curupi	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	?	?
*Boana cymbalum**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana ericae	0	1	0	1	0	n/a	2	0	1	0/1	1	0	0	1	1	0	1
Boana freicanecae	0	1	0	1	0	n/a	2	0	1	0	1	0	0	?	?	?	?
*Boana gladiator**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana goiana	0	1	0	1	0	n/a	2	0	1	0	1	0	0	?	?	?	?
*Boana guentheri**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana jaguariaivensis**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana joaquini	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	0	1
*Boana leptolineata**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana marginata**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana marianitae**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana melanopleura**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana palaestes**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana poaju**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana polytaenia	0	1	0	1	0	n/a	2	0	1	0	1	0	0	?	?	?	?
Boama aff. polytaenia	0	1	0	1	0	n/a	2	0	1	0	1	0	0	?	?	?	?
*Boana prasina**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana pulchella	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	0	?
Boana riojana	0	1	0	1	0	n/a	2	0	1	0	1	0/1	0	1	1	?	?
*Boana semiguttata**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana stellae**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana stenocephala	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	?	?
***Boana punctata* gr.**																	
*Boana alemani**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana atlantica	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
Boana cinerascens	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
*Boana gracilis**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana picturata	0	1	0	1	0	n/a	0	0	0	0	?	?	0	?	?	?	?
Boana punctata	0	1	0	1	0	n/a	0	0	0	0	1	0	0	1	1	0/1	0
*Boana sibleszi**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Boana semilineata* gr.**																	
*Boana appendiculata**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana boans	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	1

	Character States																
Taxa	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
*Boana diabolica**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana geographica	0	0	0	0	0/1	1	0	n/a	n/a	n/a	1	0	0	0	1	0	1
*Boana hutchinsi**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana icamiaba**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Boana nigra**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana pombali	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	0	1	1
*Boana secedens**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana semilineata	0	0	0	0	0	1	0	n/a	n/a	n/a	1	0	0	0	1	0	0/1
*Boana ventrimaculata**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana wavrini	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?
***Bokermannohyla circumdata* gr.**																	
*Bokermannohyla ahenea**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla astartea**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla capra**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla caramaschii**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla carvalhoi**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla circumdata**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla diamantina**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla gouveai**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla hylax	0	1	0	1	0	n/a	0	0	0	0	0	0	0	1	1	0	1
*Bokermannohyla ibitipoca**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla izecksohni**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla lucianae	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
Bokermannohyla luctuosa	0	1	0	1	0	n/a	0	0	0	0	0	0	0	?	?	?	?
Bokermannohyla nanuzae	0	1	0	1	0	n/a	0	0	0	0	0	0	0	?	?	?	?
*Bokermannohyla napolii**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla ravida**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla sazimai**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla vulcaniae**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Bokermannohyla martinsi* gr.**																	
Bokermannohyla juiju	0	1	0	1	0	n/a	0	0	0	0	0	0	0	?	?	?	?
Bokermannohyla langei	0	1	0	1	0	n/a	2	0	0	1	0	0	0	?	?	?	?
Bokermannohyla martinsi	0	1	0	1	0	n/a	2	0	0	1	0	0	0	1	1	0	1
***Bokermannohyla pseudopseudis* gr.**																	
Bokermannohyla alvarengai	0	1	0	1	0	n/a	0	0	0	0	0	0	0	?	?	?	?
*Bokermannohyla flavopicta**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla ibitiguara	0	1	0	1	0	n/a	0	0	0	0	0	0	0	1	0	1	1
*Bokermannohyla itapoty**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla oxente	0	1	0	0	0	n/a	0	0	0	0	1	0	0	1	1	0	1
Bokermannohyla pseudopseudis	0	1	0	1	0	n/a	0	0	0	0	0	0	0	1	?	?	?
*Bokermannohyla sagarana**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Bokermannohyla sapiranga**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla saxicola	0	1	0	1	0	n/a	0	0	0	0	0	0	0	1	1	0	1
***Hyloscirtus armatus* gr.**																	
Hyloscirtus armatus	0	0	1	n/a	0	1	0	n/a	n/a	n/a	0	0	1	0	0	?	?
Hyloscirtus charazani	0	0	1	n/a	0	1	0	n/a	n/a	n/a	0	?	1	?	?	?	?
*Hyloscirtus chlorosteus**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Hyloscirtus bogotensis* gr.**																	
*Hyloscirtus albopunctulatus**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus alytolylax	0	0	0	0	1	1	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus aff. *alytolylax*	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Hyloscirtus bogotensis	0	0	0	0	1	1	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus callipeza	0	0	0	0	1	0	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus colymba	0	0	0	0	1	0	0	n/a	n/a	n/a	0	1	0	?	?	?	?
*Hyloscirtus conscientia**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus denticulentus	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
*Hyloscirtus japreria**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Hyloscirtus lascinius**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus lynchi	0	0	0	0	1	0	0	n/a	n/a	n/a	0	1	0	?	?	?	?
*Hyloscirtus mashpi**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Taxa	**Character States**																
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Hyloscirtus palmeri	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0/1	0	0	?	0	?
Hyloscirtus aff. *palmeri*	0	0	0	0	1	1	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Hyloscirtus phyllognathus	0	0	?	?	1	0	?	n/a	n/a	n/a	0	?	0	?	?	?	?
Hyloscirtus aff. *phyllognathus*	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Hyloscirtus piceigularis	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Hyloscirtus aff. *piceigularis*	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Hyloscirtus platydactylus	0	0	0	0	0	1	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus simmonsi	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Hyloscirtus aff. *simmonsi* 1	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0/1	0	?	?	?	?
Hyloscirtus aff. *simmonsi* 2	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Hyloscirtus torrenticola	0	0	0	0	1	0/1	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus jahni **gr.**																	
*Hyloscirtus jahni**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus larinopygion **gr.**																	
Hyloscirtus antioquia	0	0	0	0	1	0/1	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus caucanus	0	0	0	0	1	0	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus condor	0	1	0	?	0	n/a	0	0	0	0	0	?	0	?	?	?	?
*Hyloscirtus criptico**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Hyloscirtus diabolus**	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus hillisi	0	1	0	?	0	n/a	0	0	0	0	0	?	0	?	?	?	?
Hyloscirtus larinopygion	0	0	0	0	1	0	0	n/a	n/a	n/a	1	0/1	0	0	0	0	?
Hyloscirtus lindae	0	0	0	0	1	0	0	n/a	n/a	n/a	1	0/1	0	?	?	?	?
Hyloscirtus pacha	0	0	0	0	?	0	0	n/a	n/a	n/a	0	?	0	?	?	?	?
Hyloscirtus pantostictus	0	0	0	0	?	0	0	n/a	n/a	n/a	0	?	0	?	?	?	?
Hyloscirtus princecharlesi	0	0	0	0	1	0	0	n/a	n/a	n/a	1	1	0	?	?	?	?
Hyloscirtus psarolaimus	0	0	0	0	?	0	0	n/a	n/a	n/a	0	?	0	?	?	?	?
*Hyloscirtus ptychodactylus**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus sarampiona	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Hyloscirtus staufferorum	0	0	0	0	1	0	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus tapichalaca	0	1	0	0	0	n/a	0	0	0	0	0	0	0	?	?	?	?
*Hyloscirtus tigrinus**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Myersiohyla																	
*Myersiohyla aromatica**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Myersiohyla chamaeleo	0	0	0	0	0	0	0	n/a	n/a	n/a	0	0	0	1	0	1	1
*Myersiohyla inparquesi**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Myersiohyla liliae**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Myersiohyla loveridgei**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Myersiohyla neblinaria	0	0	0	0	?	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Nesorohyla																	
*Nesorohyla kanaima**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Insertae sedis **species of Cophomantini**																	
*"Hyla" nicefori**	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Outgroup																	
Acris crepitans	0	0	0	0	1	1	0	n/a	n/a	n/a	0	0	0	0	0	1	1
Dendropsophus nanus	0	0	0	0	0	1	0	n/a	n/a	n/a	0	0	0	1	1	0	1
Hyla cinerea	0	0	0	0	1	1	0	n/a	n/a	n/a	0	0	0	1	1	1	1
Phrynomedusa appendiculata	0	0	0	0	0	0	0	n/a	n/a	n/a	0	1	0	1	0	1	n/a
Phyllodytes luteolus	0	0	0	0	0	0	0	n/a	n/a	n/a	1	0	0	1	1	1	n/a
Pseudis minuta	0	0	0	0	0	1	0	n/a	n/a	n/a	0	0	0	0	0	1	0
Scinax cruentoma	1	n/a	0	0	0	n/a	0	n/a	n/a	n/a	0	0	0	0	0	1	0
Trachycephalus typhonius	0	0	0	1	0	1	0	n/a	n/a	n/a	0	0	0	1	1	1	n/a

REFERENCES

Antunes AP, Faivovich J, Haddad CFB. 2008. A new species of *Hypsiboas* from the Atlantic Forest of southeastern Brazil (Amphibia: Anura: Hylidae). *Copeia* **2008:** 170–190.

Ayarzagüena J, Señaris JC. 1994 "1993". Dos nuevas especies de *Hyla* (Anura; Hylidae) para las cumbres Tepuyanas del Estado Amazonas, Venezuela. *Memoria. Sociedad de Ciencias Naturales La Salle* **53:** 127–146.

Berneck BM, Giaretta AA, Brandão RA, Cruz CAG, Haddad CFB. 2017. The first species of *Aplastodiscus* endemic to the Brazilian Cerrado (Anura, Hylidae). *ZooKeys* **642:** 115–130.

Bokermann WCA. 1963. Una nueva especie de *Hyla* del sudeste Brasileño. *Neotropica* **9:** 27–30.

Bokermann WCA. 1967a. Nova espécie de *Hyla* do Amapá (Amphibia, Hylidae). *Revista Brasileira de Biologia* **27:** 109–112.

Bokermann WCA. 1967b. *Hyla astartea*, nova espécie da Serra do Mar em São Paul (Amphibia, Hylidae). *Revista Brasileira de Biologia* **27:** 157–158.

Boulenger GA. 1882. *Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum*. Second Edition. London: Taylor and Francis.

Brandão RA, Magalhães RF, Garda AA, Campos LA, Sebben A, Maciel. AO. 2012. A new species of *Bokermannohyla* (Anura: Hylidae) from highlands of central Brazil. *Zootaxa* **3527:** 28–42.

Braun PC, Braun CAS. 1977. Nova espécie de *Hyla* do estado do Rio Grande do Sul, Brasil (Anura, Hylidae). *Revista Brasileira de Biologia* **37:** 853–857.

Caminer MA, Ron SR. 2014. Systematics of treefrogs of the *Hypsiboas calcaratus* and *Hypsiboas fasciatus* species complex (Anura, Hylidae) with the description of four new species. *ZooKeys* **370:** 1–68.

Caminer MA, Ron SR. 2020. Systematics of the *Boana semilineata* species group (Anura: Hylidae), with a description of two new species from Amazonian Ecuador. *Zoologial Journal of the Linnean Society* **190:** 149–180.

Caramaschi U, Cruz CAG. 1999. Duas espécies novas do grupo de *Hyla polytaenia* Cope, 1870 do Estado de Minas Gerais, Brasil. *Boletim do Museu Nacional. Nova Serie, Zoologia* **403:** 1–10.

Caramaschi U, Feio RN. 1990. A new species of *Hyla* (Anura, Hylidae) from southern Minas Gerais, Brazil. *Copeia* **1990:** 542–546.

Caramaschi U, Niemeyer H. 2003. New species of the *Hyla albopunctata* group from central Brazil (Amphibia, Anura, Hylidae). *Boletim do Museu Nacional. Nova Serie, Zoologia* **504:** 1–8.

Caramaschi U, Cruz CAG, Segalla MV. 2010. A new species of *Hypsiboas* of the *H. polytaenius* clade from the state of Paraná, southern Brazil (Anura: Hylidae). *South American Journal of Herpetology* **5:** 169–174.

Caramaschi U, Napoli MF, Bernardes AT. 2001. Nova espécie do grupo do *Hyla circumdata* (Cope, 1870) do Estado de Minas Gerais, Brasil (Amphibia, Anura, Hylidae). *Boletim do Museu Nacional. Nova Serie, Zoologia* **457:** 1–11.

Cardoso AJ, Andrade GV. 1982. Nova espécie de *Hyla* do Parque Nacional Serra da Canastra (Anura, Hylidae). *Revista Brasileira de Biologia* **42:** 589–593.

Carrizo GR. 1991 "1990". Sobre los hílidos de Misiones, Argentina, con la descripción de una nueva especie *Hyla caingua* n. sp. *Cuadernos de Herpetología* **5:** 32–39.

Carvalho TR, Giaretta AA, Facure KG. 2010. A new species of *Hypsiboas* Wagler (Anura: Hylidae) closely related to *H. multifasciatus* Günther from southeastern Brazil. *Zootaxa* **2521:** 37–52.

Carvalho TR, Giaretta AA, Magrini L. 2012. A new species of the *Bokermannohyla circumdata* group (Anura: Hylidae) from southeastern Brazil, with bioacoustic data on seven species of the genus. *Zootaxa* **3321:** 37–55.

Cochran DM, Goin CJ. 1970. Frogs of Colombia. *Bulletin of the United States National Museum* **288:** 1–655.

Coloma LA, Carvajal-Endara S, Dueñas JF, Paredes-Recalde A, Morales-Mite MA, Almeida-Reinoso D, Tapia EE, Hutter CR, Toral-Contreras E, Guayasamin JM. 2012. Molecular phylogenetics of stream treefrogs of the *Hyloscirtus larinopygion* group (Anura: Hylidae), and description of two new species from Ecuador. *Zootaxa* **3364:** 1–78.

Cope ED. 1871 "1870". Eighth contribution to the herpetology of tropical America. *Proceedings of the American Philosophical Society* **11:** 553–559.

Cruz CAG, Peixoto OL. 1985 "1984". Espécies verdes de *Hyla*: o complexo "*Albosignata*" (Amphibia, Anura, Hylidae*). Arquivos de Universidade Federal Rural do Rio de Janeiro* **7:** 31–47.

Cruz CAG, Peixoto OL. 1987 "1985". Espécies verdes de *Hyla*: o complexo "*Albofrenata*" (Amphibia, Anura, Hylidae). *Arquivos de Universidade Federal Rural do Rio de Janeiro* **8:** 59–70.

Cruz CAG, Pimenta BVS, Silvano DL. 2003. Duas novas espécies pertencentes ao complexo de *Hyla albosignata* Lutz & Lutz, 1938, do leste do Brasil (Amphibia, Anura, Hylidae). *Boletim do Museu Nacional. Nova Serie, Zoologia* **503:** 1–13.

Duellman WE, De la Riva I, Wild ER. 1997. Frogs of the *Hyla armata* and *Hyla pulchella* group in the Andes of South America, with definitions and analyses of phylogenetic relationships of Andean group of *Hyla*. *Scientific Papers. Natural History Museum, University of Kansas* **3:** 1–41.

Escalona Sulbarán M, La Marca E, Castellanos M, Fouquet A, Crawford AJ, Rojas-Runjaic FJM, Giaretta AA, Señaris JC, Castroviejo-Fisher S. 2021. Integrative taxonomy reveals a new but common Neotropical treefrog, hidden under the name *Boana xerophylla*. *Zootaxa* **4981:** 401–448.

Faivovich J, De la Riva I. 2006. On "*Hyla*" *chlorostea* Reynolds and Foster, 192, a hylid of uncertain relationships, with some comments on *Hyloscirtus* (Anura: Hylidae). *Copeia* **2006:** 785–791.

Faivovich J, Moravec J, Cisneros-Heredia DF, Köhler J. 2006. A new species of the *Hypsiboas benitezi* group from the western Amazon Basin (Amphibia: Anura: Hylidae). *Herpetologica* **62:** 96–108.

Faivovich J, McDiarmid RW, Myers CW. 2013. Two new species of *Myersiohyla* (Anura: Hylidae) from Cerro de la Neblina, Venezuela, with comments on other species of the genus. *American Museum Novitates* **3792:** 1–63.

Fouquet A, Marinho P, Réjaud A, Carvalho TR, Caminer MA, Jansen M, Rainha RN, Rodrigues MT, Werneck FP, Lima AP, Hrbek T, Giaretta AA, Venegas PJ, Chávez G, Ron S. 2021. Systematics and biogeography of the *Boana albopunctata* species group (Anura, Hylidae), with the description of two new species from Amazonia. *Systematics and Biodiversity* **19:** 375–399.

Fouquette MJ Jr. 1961. Status of the frog *Hyla albomarginata* in Central America. *Fieldiana. Zoology* **39:** 595–601.

Garcia PCA, Peixoto OL, Haddad CFB. 2008. A new species of *Hypsiboas* (Anura: Hylidae) from the Atlantic Forest of Santa Catarina, southern Brazil, with comments on its conservation status. *South American Journal of Herpetology* **3:** 27–35.

Guayasamin JM, Rivera-Correa M, Arteaga-Navarro AF, Culebras J, Bustamante L, Pyron RA, Peñafiel N, Morochz C, Hutter CR. 2015. Molecular phylogeny of stream treefrogs (Hylidae: *Hyloscirtus bogotensis* Group), with a new species from the Andes of Ecuador. *Neotropical Biodiversity* **1:** 2–21.

Jim J, Caramaschi U. 1979. Uma nova espécie de *Hyla* da região de Botucatu, São Paulo, Brasil (Amphibia, Anura). *Revista Brasileira de Biologia* **40:** 717–719.

Kluge AG. 1979. The gladiator frogs of Middle America and Colombia—a reevaluation of their systematics (Anura: Hylidae). *Occasional Papers of the Museum of Zoology, University of Michigan* **688:** 1–24.

Köhler J, Koscinski D, Padial JM, Chaparro JC, Handford P, Lougheed SC, De la Riva I. 2010. Systematics of the Andean gladiator frogs of the *Hypsiboas pulchellus* species group (Anura, Hylidae). *Zoologica Scripta* **39:** 572–590.

Kok PJR. 2006. A new species of *Hypsiboas* (Amphibia: Anura: Hylidae) from Kaieteur National Park, eastern edge of the Pakaraima Mountains, Guyana. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* **76:** 191–200.

Kwet A. 2008. New species of *Hypsiboa*s (Anura: Hylidae) in the *pulchellus* group from southern Brazil. *Salamandra* **44:** 1–14.

Lehr E, Faivovich J, JungferK-H. 2010. A new Andean species of the *Hypsiboas pulchellus* group: adults, calls, and phylogenetic relationships. *Herpetologica* **66:** 296–307.

Leite FSF, Pezzuti TL, Drummond LO. 2011. A new species of *Bokermannohyla* from the Espinhaço range, state of Minas Gerais, southeastern Brazil. *Herpetologica* **67:** 440–448.

Leite FSF, Pezzuti TL, Garcia PCA. 2012. A new species of the *Bokermanohyla pseudopseudis* group from the Espinhaço Range, central Bahia, Brazil (Anura: Hylidae). *Herpetologica* **68:** 401–409.

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

Lutz B, Orton GL. 1946. *Hyla claresignata* Lutz & B. Lutz, 1939. Aspects of the life history and description of the rhyacophilous tadpole. *Boletim do Museu Nacional. Nova Serie, Zoologia* **70:** 1–20.

Lynch JD. 2008. A taxonomic revision of frogs of the genus *Cryptobatrachus* (Anura: Hemiphractidae). *Zootaxa* **1883:** 28–68.

Mueses-Cisneros JJ, M. Anganoy-Criollo MA. 2008. Una nueva especie del grupo *Hyloscirtus larinopygion* (Amphibia: Anura: Hylidae) del suroccidente de Colombia. *Papéis Avulsos de Zoologia* **48:** 129–138.

Myers CW, Donnelly MA. 2008. The summit herpetofauna of Auyantepui, Venezuela: report from the Robert G. Goelet American Museum–Terramar Expedition. *Bulletin of the American Museum of Natural History* **308:** 1–147.

Napoli MF. 2005. A new species allied to *Hyla circumdata* (Anura: Hylidae) from Serra da Mantiqueira, southeastern Brazil. *Herpetologica* **61:** 63–69.

Napoli MF, Caramaschi U. 2004. Two new species of the *Hyla circumdata* group from Serra do Mar and Serra da Mantiqueira, southeastern Brazil, with description of the advertisement call of *Hyla ibitipoca* (Anura, Hylidae). *Copeia* **2004:** 534–545.

Napoli MF, Juncá FA. 2006. A new species of the *Bokermannohyla circumdata* group (Amphibia: Anura: Hylidae) from Chapada Diamantina, State of Bahia, Brazil. *Zootaxa* **1244:** 57–68.

Napoli MF, Pimenta BVS. 2009. A new species of the *Bokermannohyla circumdata* Group (Anura: Hylidae) from the coastal forests of Bahia, northeastern Brazil. *Copeia* **2009:** 674–683.

Ouboter PE, Jairam R. 2012. *Amphibians of Suriname*. Leiden: Brill.

Peixoto OL. 1981. Nova especie de *Hyla* da Serra dos Órgãos, Estado do Rio de Janeiro, Brasil (Amphibia, Anura, Hyldiae). *Revista Brasileira de Biologia* **41:** 515.

Peixoto OL, Cruz CAG. 1992. New species of *Hyla* from the "Serra da Mantiqueira, Itatiaia, Rio de Janeiro" State—(Amphibia, Anura, Hylidae). *Memórias do Instituto Oswaldo Cruz* **87:** 197–200.

Peloso PLV, Oliveira RM, Sturaro MJ, Rodrigues MT, Lima-Filho GR, Bitar YOC, Wheeler WC, Aleixo A. 2018. Phylogeny of map tree frogs, *Boana semilineata* species group, with a new Amazonian Species (Anura: Hylidae). *South American Journal of Herpetology* **13:** 150–169.

Pinheiro PDP, Kok PJR, Noonan B, Means DB, Haddad CFB, Faivovich J. 2019. A new genus of Cophomantini, with comments on the taxonomic status of *Hypsiboas liliae* Kok, 2006 (Anura: Hylidae: Hylinae). *Zoological Journal of the Linnean Society* **185:** 226–245.

Pinheiro PDP, Pezzuti TL, Berneck BvM, Lyra ML, Lima RCL, Leite FSF. 2021. A new cryptic species of the *Aplastodiscus albosignatus* group (Anura: Hylidae). *Salamandra* **57:** 27–43.

Pyburn WF. 1978. The voice and relationship of the treefrog *Hyla hobbsi* (Anura: Hylidae). *Proceedings of the Biological Society of Washington* **91:** 123–131.

Rivera-Correa M, García-Burneo K, Grant T. 2016. A new red-eyed of stream treefrog of *Hyloscirtus* (Anura: Hylidae) from Peru, with comments on the taxonomy of the genus. *Zootaxa* **4061:** 29–40.

Rivero JA. 1961. Salientia of Venezuela. *Bulletin of the Museum of Comparative Zoology* **126:** 1–207.

Rivero JA. 1964. Salientios (Amphibia) en la collecion de la Sociedad de Ciencias Naturales La Salle de Venezuela. *Caribbean Journal of Science* **4:** 297–305.

Rivero JA. 1970 "1969". A new species of *Hyla* (Amphibia, Salientia) from the region of Paramo de Tama, Venezuela. *Caribbean Journal of Science* **9:** 145–150.

Rivero JA. 1972 "1971". Notas sobre los anfibios de Venezuela: 1. Sobre los hilidos de la Guayana Venezolana. *Caribbean Journal of Science* **11:** 181–193.

Rojas-Runjaic FJM, Infante-Rivero EE, Salerno PE, Meza-Joya FL. 2018. A new species of *Hyloscirtus* (Anura, Hylidae) from the Colombian and Venezuelan slopes of Sierra de Perijá, and the phylogenetic position of *Hyloscirtus jahni* (Rivero, 1961). *Zootaxa* **4382:** 121–146.

Señaris JC, Ayarzagüena. 2002. A new species of *Hyla* (Anura: Hylidae) from the highlands of Venezuelan Guyana. *Journal of Herpetology* **36:** 634–640.

Señaris JC, Ayarzagüena. 2006. A new species of *Hypsiboas* (Amphibia; Anura; Hylidae) from the Venezuelan Guayana, with notes on *Hypsiboas sibleszi* (Rivero 1972). *Herpetologica* **62:** 308–319.

Sturaro MJ, Costa JCL, Maciel AO, Lima GR Filho, Rojas-Runjaic FJM, Mejia DP, Ron SR, Peloso PLV. 2020. Resolving the taxonomic puzzle of *Boana cinerascens* (Spix, 1824), with resurrection of *Hyla granosa gracilis* Melin, 1941 (Anura: Hylidae). *Zootaxa* **4750:** 1–30.

Vasconcelos EG, Giaretta AA. 2005 "2003". A new species of *Hyla* (Anura: Hylidae) from southeastern Brazil. *Revista Española de Herpetología* **17:** 21–27.

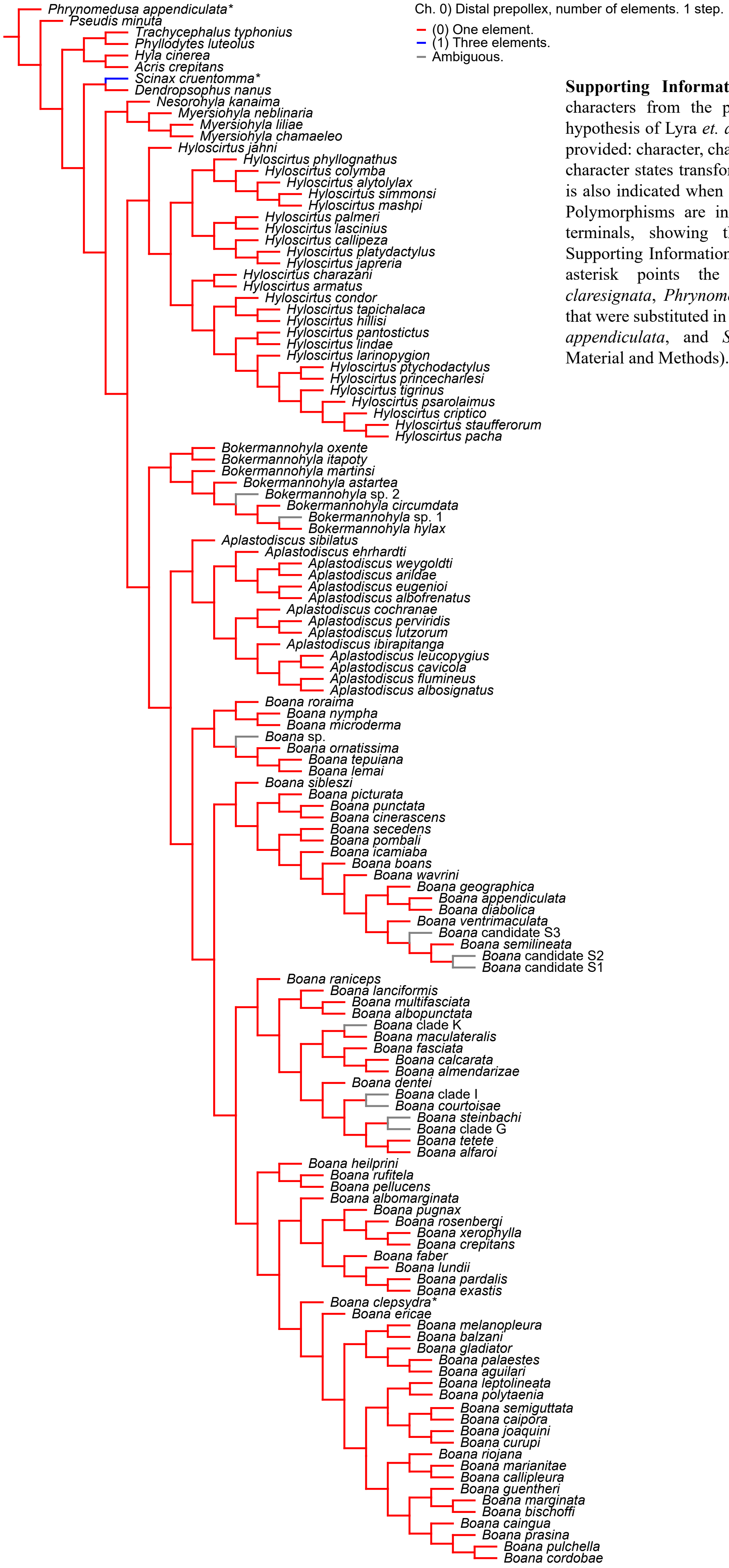
Yánez-Muñoz MH, Reyes-Puig JP, Batallas-Revelo D, Broaddus C, Urgilés-Merchán M, Cisneros-Heredia DF, Guayasamin JM. 2021. A new Andean treefrog (Amphibia: *Hyloscirtus bogotensis* group) from Ecuador: An example of community involvement for conservation. *PeerJ* **9:** e11914.

SUPPORTING INFORMATION S4. Character Matrix as implemented on TNT for character optimization, showing states for the chracters listed in Results, Hypotheses of homology section. (**n/a**) character not applicable; (**?**) missing data; two numbers interspaced by a slash "/" indicate a polymorphism.

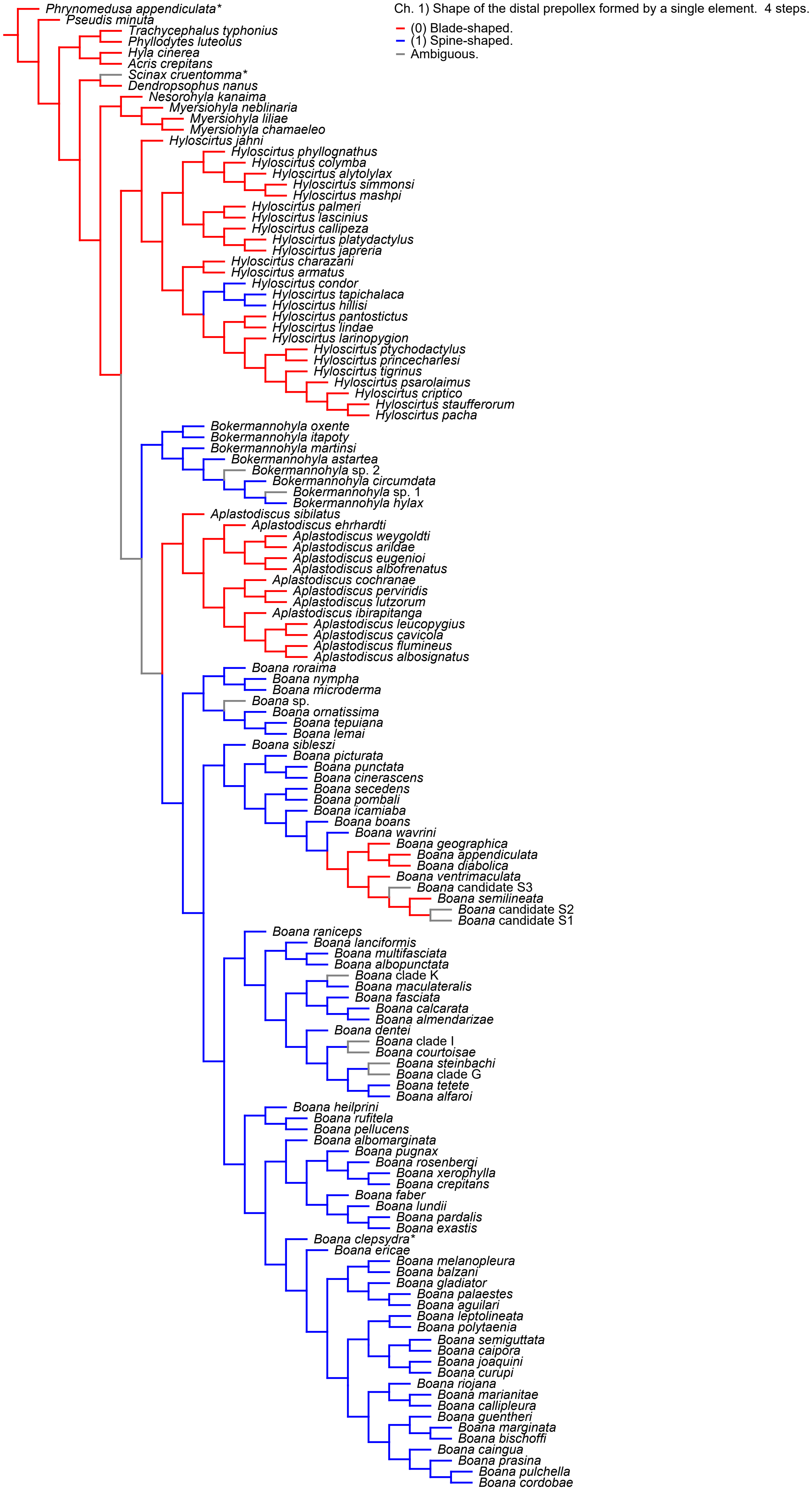
Taxa	**Character States**																
											1	**1**	**1**	**1**	**1**	**1**	**1**
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**
Ingroup																	
***Aplastodiscus albofrenatus* gr.**																	
Aplastodiscus albofrenatus	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aplastodiscus arildae	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	0/1	1
Aplastodiscus ehrhardti	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Aplastodiscus eugenioi	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Aplastodiscus weygoldti	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Aplastodiscus albosignatus* gr.**																	
Aplastodiscus albosignatus	0	0	0	0	0/1	0/1	0	n/a	n/a	n/a	0	0	0	0	0	0	?
Aplastodiscus cavicola	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	0	1
Aplastodiscus flumineus	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aplastodiscus ibirapitanga	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aplastodiscus leucopygius	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Aplastodiscus perviridis* gr.**																	
Aplastodiscus cochranae	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	0/1	1
Aplastodiscus lutzorum	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aplastodiscus perviridis	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	0	0/1
***Aplastodiscus sibilatus* gr.**																	
Aplastodiscus sibilatus	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	0	0	1	0
***Boana albopunctata* gr.**																	
Boana albopunctata	0	1	0	1	0	n/a	0	0	0	0	1	0	0	1	1	0	0/1
Boana alfaroi	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana almendarizae	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana calcarata	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
Boana courtoisae	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana dentei	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana fasciata	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
Boana heilprini	0	1	0	1	0	n/a	1	0	0	0	0	0	0	1	1	0	1
Boana lanciformis	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
Boana maculateralis	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana multifasciata	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?
Boana raniceps	0	1	0	1	0	n/a	0	0	0	0	1	0	0	1	?	0	?
Boana steinbachi	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana tetete	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana clade G	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana clade I	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana clade K	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Boana benitezi* gr.**																	
Boana lemai	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana microderma	0	1	0	0	0	n/a	0	1	0	0	0	0	0	1	1	1	1
Boana nympha	0	1	0	1	0	n/a	0	0/1	0	0	1	0	0	?	?	?	?
Boana ornatissima	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
Boana roraima	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana tepuiana	0	1	0	1	0	n/a	0	0	0	0	1	0	0	1	0	0	0
Boana sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Boana claresignata* gr.**																	
Boana clepsydra	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	0
***Boana faber* gr.**																	
Boana albomarginata	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	1
Boana crepitans	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?
Boana exastis	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?

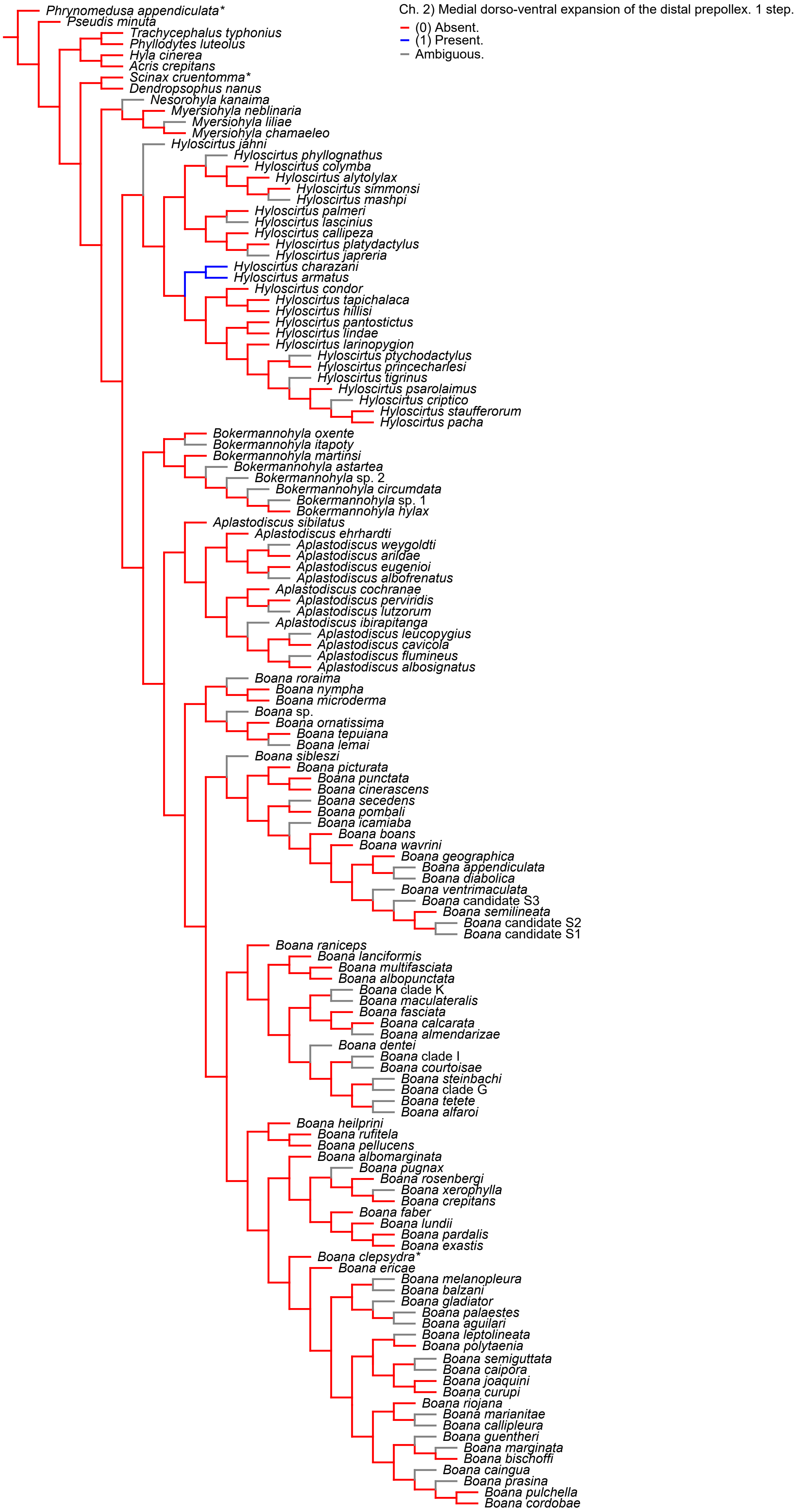
Taxa	Character States																
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Boana faber	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	1
Boana lundii	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	0
Boana pardalis	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?
Boana pugnax	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana rosenbergi	0	1	0	1	0	n/a	1	0	0	0	?	?	0	?	?	?	?
Boana xerophylla	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Boana pellucens* gr.**																	
Boana pellucens	0	1	0	1	0	n/a	1	0	0	0	0	0	0	1	1	0	1
Boana rufitela	0	1	0	1	0	n/a	1	0	0	0	0	0	0	1	1	0	0/1
***Boana pulchella* gr.**																	
Boana aguilari	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana balzani	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana bischoffi	0	1	0	1	0	n/a	2	0	1	0	1	0	0	?	?	?	?
Boana caingua	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana caipora	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana callipleura	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana cordobae	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	0	?
Boana curupi	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	?	?
Boana ericae	0	1	0	1	0	n/a	2	0	1	0/1	1	0	0	1	1	0	1
Boana gladiator	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana guentheri	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana joaquini	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	0	1
Boana leptolineata	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana marginata	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana marianitae	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana melanopleura	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana palaestes	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana polytaenia	0	1	0	1	0	n/a	2	0	1	0	1	0	0	?	?	?	?
Boana prasina	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana pulchella	0	1	0	1	0	n/a	2	0	1	0	1	0	0	1	1	0	?
Boana riojana	0	1	0	1	0	n/a	2	0	1	0	1	0/1	0	1	1	?	?
Boana semiguttata	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Boana punctata* gr.**																	
Boana cinerascens	0	1	0	1	0	n/a	0	0	0	0	1	0	0	?	?	?	?
Boana picturata	0	1	0	1	0	n/a	0	0	0	0	?	?	0	?	?	?	?
Boana punctata	0	1	0	1	0	n/a	0	0	0	0	1	0	0	1	1	0/1	0
Boana sibleszi	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Boana semilineata* gr.**																	
Boana appendiculata	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana boans	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	1	0	1
Boana diabolica	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana geographica	0	0	0	0	0/1	1	0	n/a	n/a	n/a	1	0	0	0	1	0	1
Boana icamiaba	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana pombali	0	1	0	1	0	n/a	1	0	0	0	1	0	0	1	0	1	1
Boana secedens	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana semilineata	0	0	0	0	0	1	0	n/a	n/a	n/a	1	0	0	0	1	0	0/1
Boana ventrimaculata	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana wavrini	0	1	0	1	0	n/a	1	0	0	0	1	0	0	?	?	?	?
Boana candidate S1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana candidate S2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boana candidate S3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
***Bokermannohyla circumdata* gr.**																	
Bokermannohyla astartea	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla circumdata	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla hylax	0	1	0	1	0	n/a	0	0	0	0	0	0	0	1	1	0	1

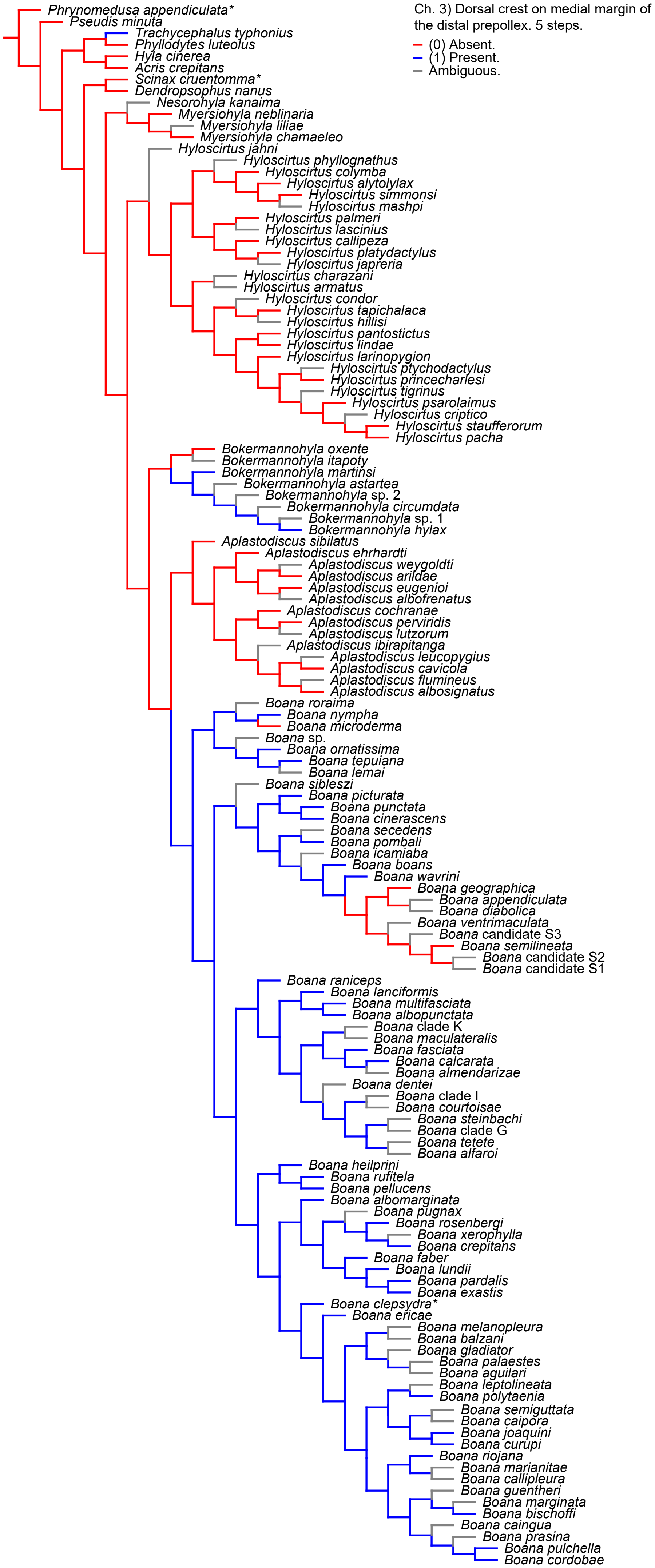
Taxa	**Character States**																
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Bokermannohyla sp. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla sp. 2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla martinsi **gr.**																	
Bokermannohyla martinsi	0	1	0	1	0	n/a	2	0	0	1	0	0	0	1	1	0	1
Bokermannohyla pseudopseudis **gr.**																	
Bokermannohyla itapoty	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bokermannohyla oxente	0	1	0	0	0	n/a	0	0	0	0	1	0	0	1	1	0	1
Hyloscirtus armatus **gr.**																	
Hyloscirtus armatus	0	0	1	n/a	0	1	0	n/a	n/a	n/a	0	0	1	0	0	?	?
Hyloscirtus charazani	0	0	1	n/a	0	1	0	n/a	n/a	n/a	0	?	1	?	?	?	?
Hyloscirtus bogotensis **gr.**																	
Hyloscirtus alytolylax	0	0	0	0	1	1	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus callipeza	0	0	0	0	1	0	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus colymba	0	0	0	0	1	0	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus japreria	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus lascinius	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus mashpi	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus palmeri	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0/1	0	0	?	0	?
Hyloscirtus phyllognathus	0	0	?	?	1	0	?	n/a	n/a	n/a	0	?	0	?	?	?	?
Hyloscirtus platydactylus	0	0	0	0	0	1	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Hyloscirtus simmonsi	0	0	0	0	1	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Hyloscirtus jahni **gr.**																	
Hyloscirtus jahni	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus larinopygion **gr.**																	
Hyloscirtus condor	0	1	0	?	0	n/a	0	0	0	0	0	?	0	?	?	?	?
Hyloscirtus criptico	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus hillisi	0	1	0	?	0	n/a	0	0	0	0	0	?	0	?	?	?	?
Hyloscirtus larinopygion	0	0	0	0	1	0	0	n/a	n/a	n/a	1	0/1	0	0	0	0	?
Hyloscirtus lindae	0	0	0	0	1	0	0	n/a	n/a	n/a	1	0/1	0	?	?	?	?
Hyloscirtus pacha	0	0	0	0	?	0	0	n/a	n/a	n/a	0	?	0	?	?	?	?
Hyloscirtus pantostictus	0	0	0	0	?	0	0	n/a	n/a	n/a	0	?	0	?	?	?	?
Hyloscirtus princecharlesi	0	0	0	0	1	0	0	n/a	n/a	n/a	1	1	0	?	?	?	?
Hyloscirtus psarolaimus	0	0	0	0	?	0	0	n/a	n/a	n/a	0	?	0	?	?	?	?
Hyloscirtus ptychodactylus	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus tapichalaca	0	1	0	0	0	n/a	0	0	0	0	0	0	0	?	?	?	?
Hyloscirtus tigrinus	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyloscirtus staufferorum	0	0	0	0	1	0	0	n/a	n/a	n/a	0	1	0	?	?	?	?
Myersiohyla																	
Myersiohyla chamaeleo	0	0	0	0	0	0	0	n/a	n/a	n/a	0	0	0	1	0	1	1
Myersiohyla liliae	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Myersiohyla neblinaria	0	0	0	0	?	0	0	n/a	n/a	n/a	0	0	0	?	?	?	?
Nesorohyla																	
Nesorohyla kanaima	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Outgroup																	
Acris crepitans	0	0	0	0	1	1	0	n/a	n/a	n/a	0	0	0	0	0	1	1
Dendropsophus nanus	0	0	0	0	0	1	0	n/a	n/a	n/a	0	0	0	1	1	0	1
Hyla cinerea	0	0	0	0	1	1	0	n/a	n/a	n/a	0	0	0	1	1	1	1
Phrynomedusa appendiculata	0	0	0	0	0	0	0	n/a	n/a	n/a	0	1	0	1	0	1	n/a
Phyllodytes luteolus	0	0	0	0	0	0	0	n/a	n/a	n/a	1	0	0	1	1	1	n/a
Pseudis minuta	0	0	0	0	0	1	0	n/a	n/a	n/a	0	0	0	0	0	1	0
Scinax cruentomma	1	n/a	0	0	0	n/a	0	n/a	n/a	n/a	0	0	0	0	0	1	0
Trachycephalus typhonius	0	0	0	1	0	1	0	n/a	n/a	n/a	0	0	0	1	1	1	n/a

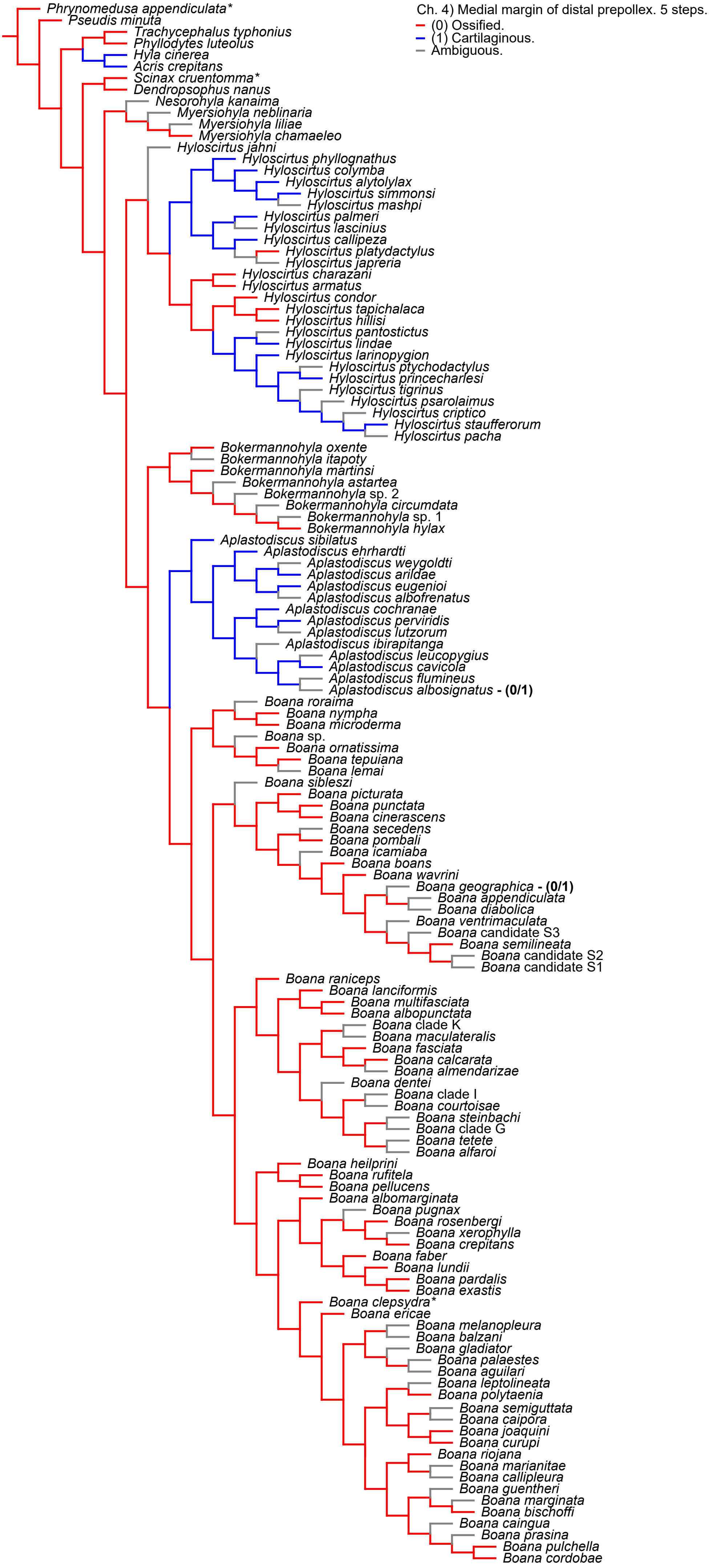


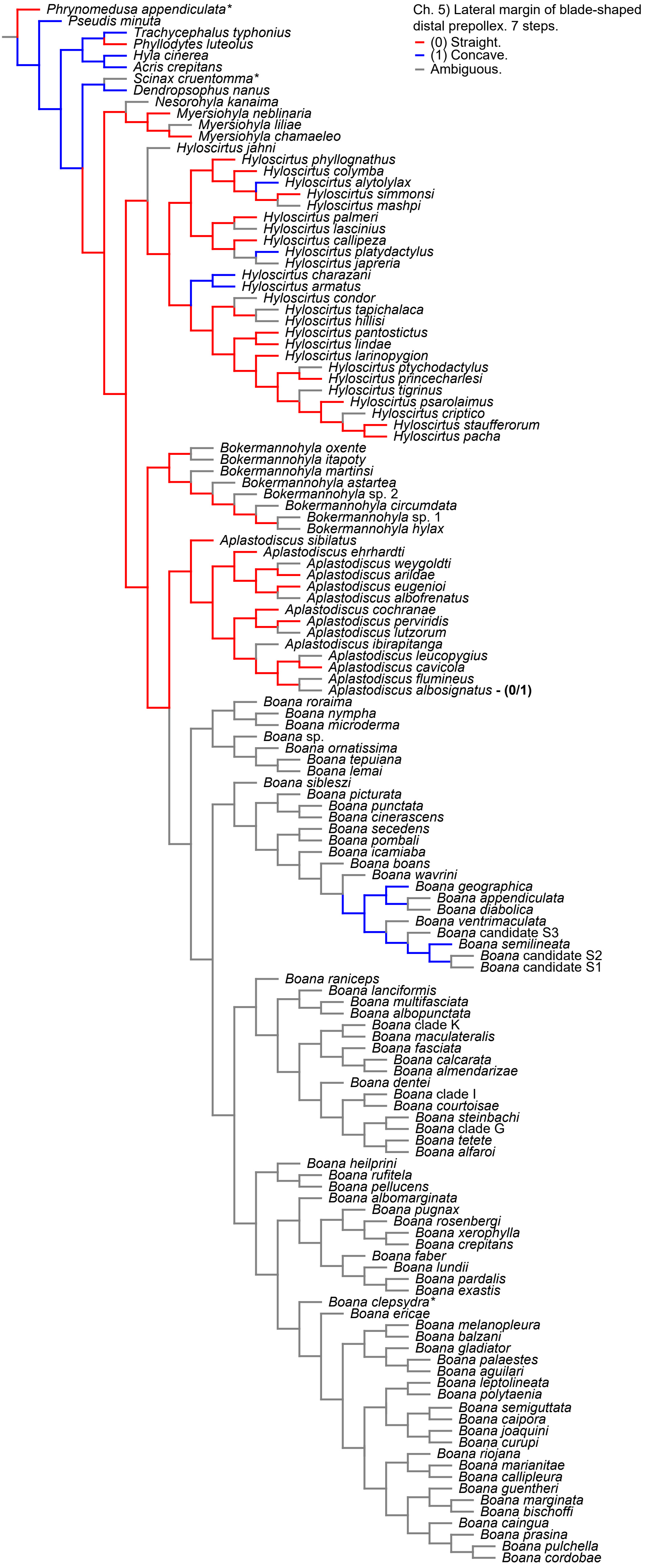
Supporting Information S5. Optimization of the 17 characters from the present study on the phylogenetic hypothesis of Lyra *et. al* (2020). For each optimization are provided: character, character states, and number of steps of character states transformation. For multistate characters it is also indicated when they are considered additive or not. Polymorphisms are indicated in bold on the respective terminals, showing the different states present. See Supporting Information S4 for inapplicable characters. An asterisk points the original terminal taxa *Boana claresignata*, *Phrynomedusa dryade*, and *Scinax staufferi* that were substituted in the present study by *B. clepsydra*, *P. appendiculata*, and *S. cruentomma*, respectively (see Material and Methods).

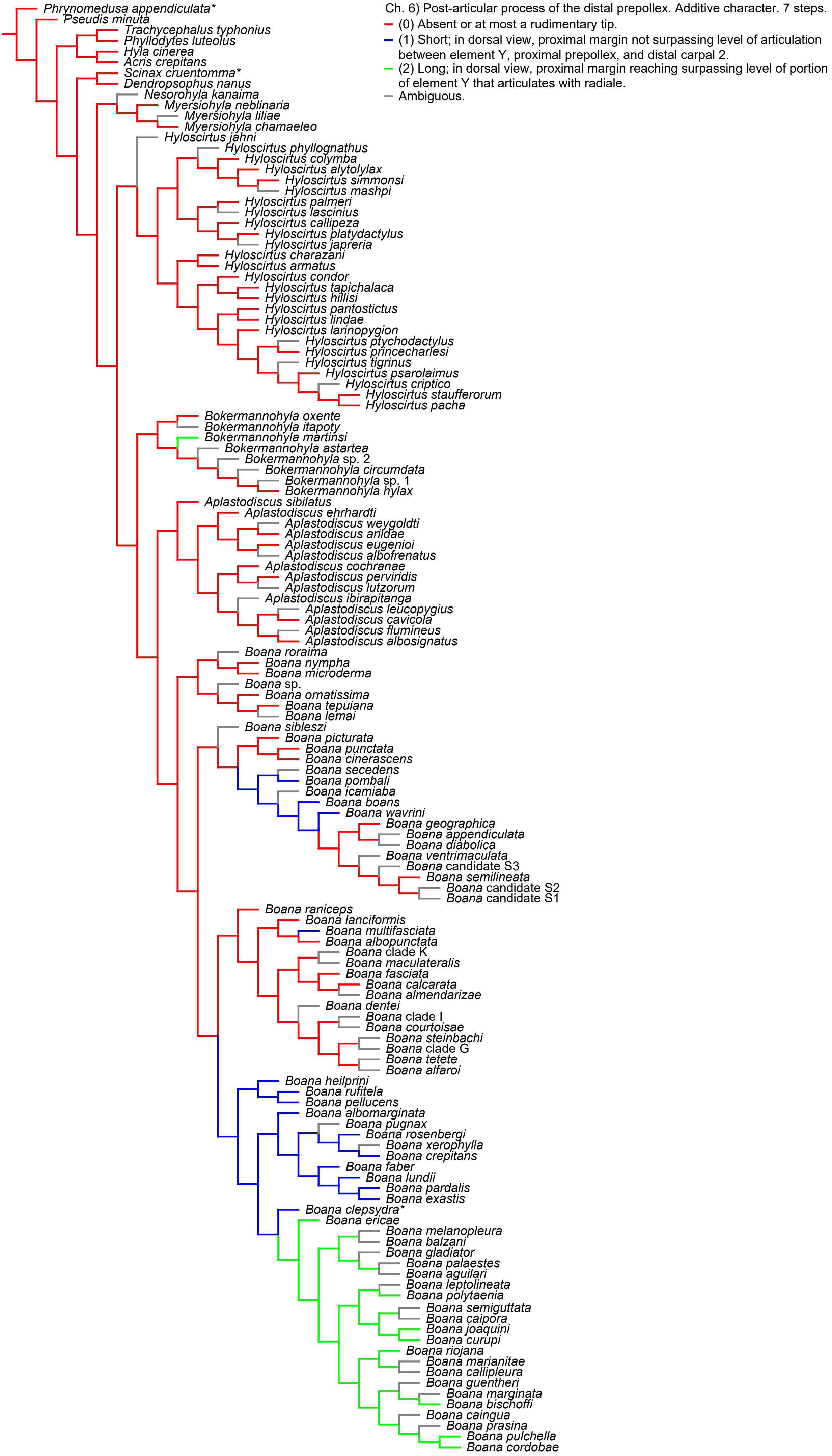

Ch. 1) Shape of the distal prepollex formed by a single element. 4 steps.
(0) Blade-shaped.
(1) Spine-shaped.
Ambiguous.
Phrynomedusa appendiculata*
Pseudis minuta
Trachycephalus typhonius
Phyllodytes luteolus
Hyla cinerea
Acris crepitans
Scinax cruentomma*
Dendropsophus nanus
Nesorohyla kanaima
Myersiohyla neblinaria
Myersiohyla liliae
Myersiohyla chamaeleo
Hyloscirtus jahni
Hyloscirtus phyllognathus
Hyloscirtus colymba
Hyloscirtus alytolylax
Hyloscirtus simmonsi
Hyloscirtus mashpi
Hyloscirtus palmeri
Hyloscirtus lascinius
Hyloscirtus callipeza
Hyloscirtus platydactylus
Hyloscirtus japreria
Hyloscirtus charazani
Hyloscirtus armatus
Hyloscirtus condor
Hyloscirtus tapichalaca
Hyloscirtus hillisi
Hyloscirtus pantostictus
Hyloscirtus lindae
Hyloscirtus larinopygion
Hyloscirtus ptychodactylus
Hyloscirtus princecharlesi
Hyloscirtus tigrinus
Hyloscirtus psarolaimus
Hyloscirtus criptico
Hyloscirtus staufferorum
Hyloscirtus pacha
Bokermannohyla oxente
Bokermannohyla itapoty
Bokermannohyla martinsi
Bokermannohyla astartea
Bokermannohyla sp. 2
Bokermannohyla circumdata
Bokermannohyla sp. 1
Bokermannohyla hylax
Aplastodiscus sibilatus
Aplastodiscus ehrhardti
Aplastodiscus weygoldti
Aplastodiscus arildae
Aplastodiscus eugenioi
Aplastodiscus albofrenatus
Aplastodiscus cochranae
Aplastodiscus perviridis
Aplastodiscus lutzorum
Aplastodiscus ibirapitanga
Aplastodiscus leucopygius
Aplastodiscus cavicola
Aplastodiscus flumineus
Aplastodiscus albosignatus
Boana roraima
Boana nympha
Boana microderma
Boana sp.
Boana ornatissima
Boana tepuiana
Boana lemai
Boana sibleszi
Boana picturata
Boana punctata
Boana cinerascens
Boana secedens
Boana pombali
Boana icamiaba
Boana boans
Boana wavrini
Boana geographica
Boana appendiculata
Boana diabolica
Boana ventrimaculata
Boana candidate S3
Boana semilineata
Boana candidate S2
Boana candidate S1
Boana raniceps
Boana lanciformis
Boana multifasciata
Boana albopunctata
Boana clade K
Boana maculateralis
Boana fasciata
Boana calcarata
Boana almendarizae
Boana dentei
Boana clade I
Boana courtoisae
Boana steinbachi
Boana clade G
Boana tetete
Boana alfaroi
Boana heilprini
Boana rufitela
Boana pellucens
Boana albomarginata
Boana pugnax
Boana rosenbergi
Boana xerophylla
Boana crepitans
Boana faber
Boana lundii
Boana pardalis
Boana exastis
Boana clepsydra*
Boana ericae
Boana melanopleura
Boana balzani
Boana gladiator
Boana palaestes
Boana aguilari
Boana leptolineata
Boana polytaenia
Boana semiguttata
Boana caipora
Boana joaquini
Boana curupi
Boana riojana
Boana marianitae
Boana callipleura
Boana guentheri
Boana marginata
Boana bischoffi
Boana caingua
Boana prasina
Boana pulchella
Boana cordobae


Ch. 2) Medial dorso-ventral expansion of the distal prepollex. 1 step.


Ch. 3) Dorsal crest on medial margin of
the distal prepollex. 5 steps.


Ch. 4) Medial margin of distal prepollex. 5 steps.
(0) Ossified.
(1) Cartilaginous.
Ambiguous.
Phrynomedusa appendiculata*
Pseudis minuta
Trachycephalus typhonius
Phyllodytes luteolus
Hyla cinerea
Acris crepitans
Scinax cruentomma*
Dendropsophus nanus
Nesorohyla kanaima
Myersiohyla neblinaria
Myersiohyla liliae
Myersiohyla chamaeleo
Hyloscirtus jahni
Hyloscirtus phyllognathus
Hyloscirtus colymba
Hyloscirtus alytolylax
Hyloscirtus simmonsi
Hyloscirtus mashpi
Hyloscirtus palmeri
Hyloscirtus lascinius
Hyloscirtus callipeza
Hyloscirtus platydactylus
Hyloscirtus japreria
Hyloscirtus charazani
Hyloscirtus armatus
Hyloscirtus condor
Hyloscirtus tapichalaca
Hyloscirtus hillisi
Hyloscirtus pantostictus
Hyloscirtus lindae
Hyloscirtus larinopygion
Hyloscirtus ptychodactylus
Hyloscirtus princecharlesi
Hyloscirtus tigrinus
Hyloscirtus psarolaimus
Hyloscirtus criptico
Hyloscirtus staufferorum
Hyloscirtus pacha
Bokermannohyla oxente
Bokermannohyla itapoty
Bokermannohyla martinsi
Bokermannohyla astartea
Bokermannohyla sp. 2
Bokermannohyla circumdata
Bokermannohyla sp. 1
Bokermannohyla hylax
Aplastodiscus sibilatus
Aplastodiscus ehrhardti
Aplastodiscus weygoldti
Aplastodiscus arildae
Aplastodiscus eugenioi
Aplastodiscus albofrenatus
Aplastodiscus cochranae
Aplastodiscus perviridis
Aplastodiscus lutzorum
Aplastodiscus ibirapitanga
Aplastodiscus leucopygius
Aplastodiscus cavicola
Aplastodiscus flumineus
Aplastodiscus albosignatus - (0/1)
Boana roraima
Boana nympha
Boana microderma
Boana sp.
Boana ornatissima
Boana tepuiana
Boana lemai
Boana sibleszi
Boana picturata
Boana punctata
Boana cinerascens
Boana secedens
Boana pombali
Boana icamiaba
Boana boans
Boana wavrini
Boana geographica - (0/1)
Boana appendiculata
Boana diabolica
Boana ventrimaculata
Boana candidate S3
Boana semilineata
Boana candidate S2
Boana candidate S1
Boana raniceps
Boana lanciformis
Boana multifasciata
Boana albopunctata
Boana clade K
Boana maculateralis
Boana fasciata
Boana calcarata
Boana almendarizae
Boana dentei
Boana clade I
Boana courtoisae
Boana steinbachi
Boana clade G
Boana tetete
Boana alfaroi
Boana heilprini
Boana rufitela
Boana pellucens
Boana albomarginata
Boana pugnax
Boana rosenbergi
Boana xerophylla
Boana crepitans
Boana faber
Boana lundii
Boana pardalis
Boana exastis
Boana clepsydra*
Boana ericae
Boana melanopleura
Boana balzani
Boana gladiator
Boana palaestes
Boana aguilari
Boana leptolineata
Boana polytaenia
Boana semiguttata
Boana caipora
Boana joaquini
Boana curupi
Boana riojana
Boana marianitae
Boana callipleura
Boana guentheri
Boana marginata
Boana bischoffi
Boana caingua
Boana prasina
Boana pulchella
Boana cordobae





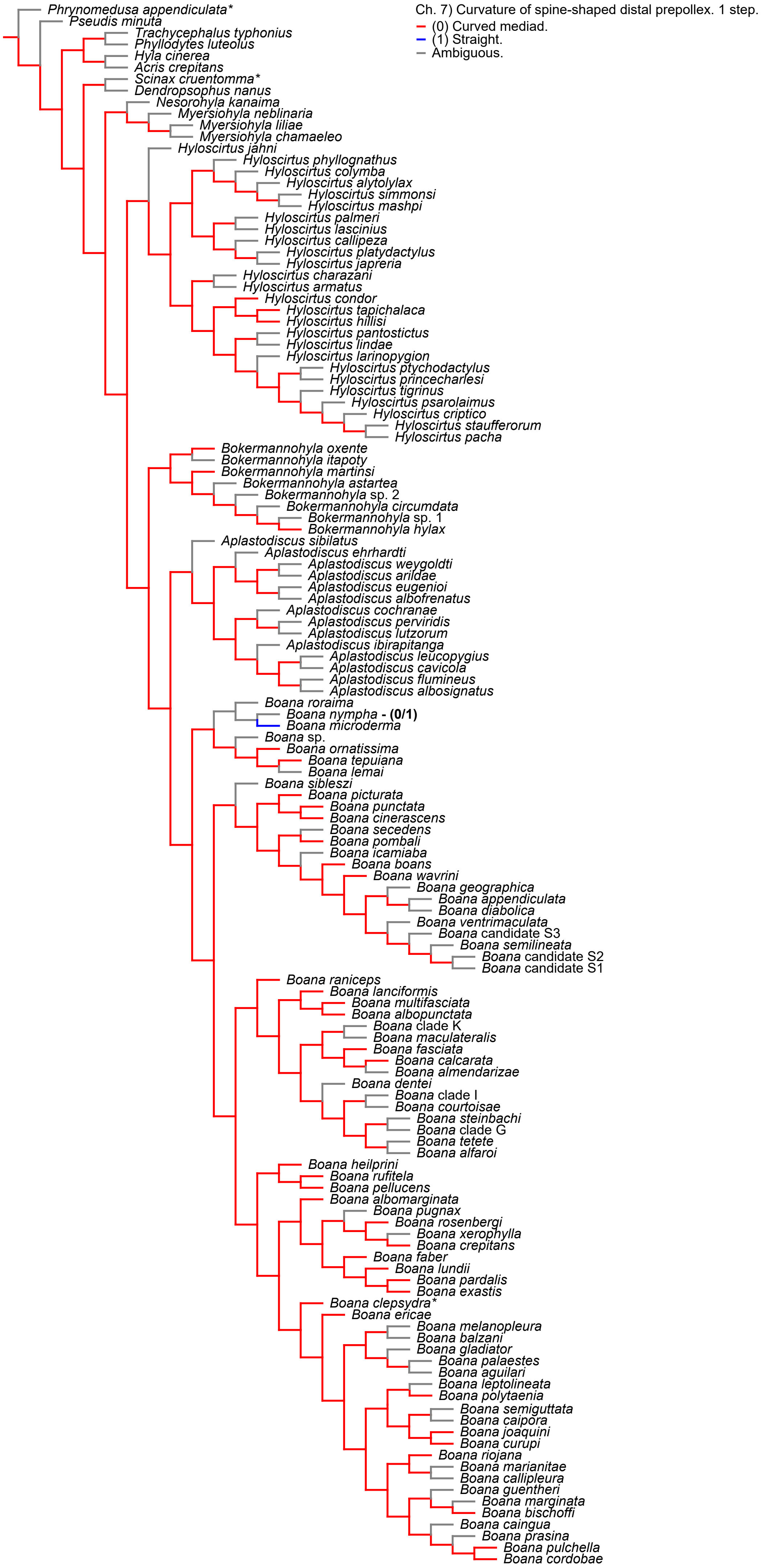
Ch. 6) Post-articular process of the distal prepollex. Additive character. 7 steps.

🟥 (0) Absent or at most a rudimentary tip.

🟦 (1) Short; in dorsal view, proximal margin not surpassing level of articulation between element Y, proximal prepollex, and distal carpal 2.

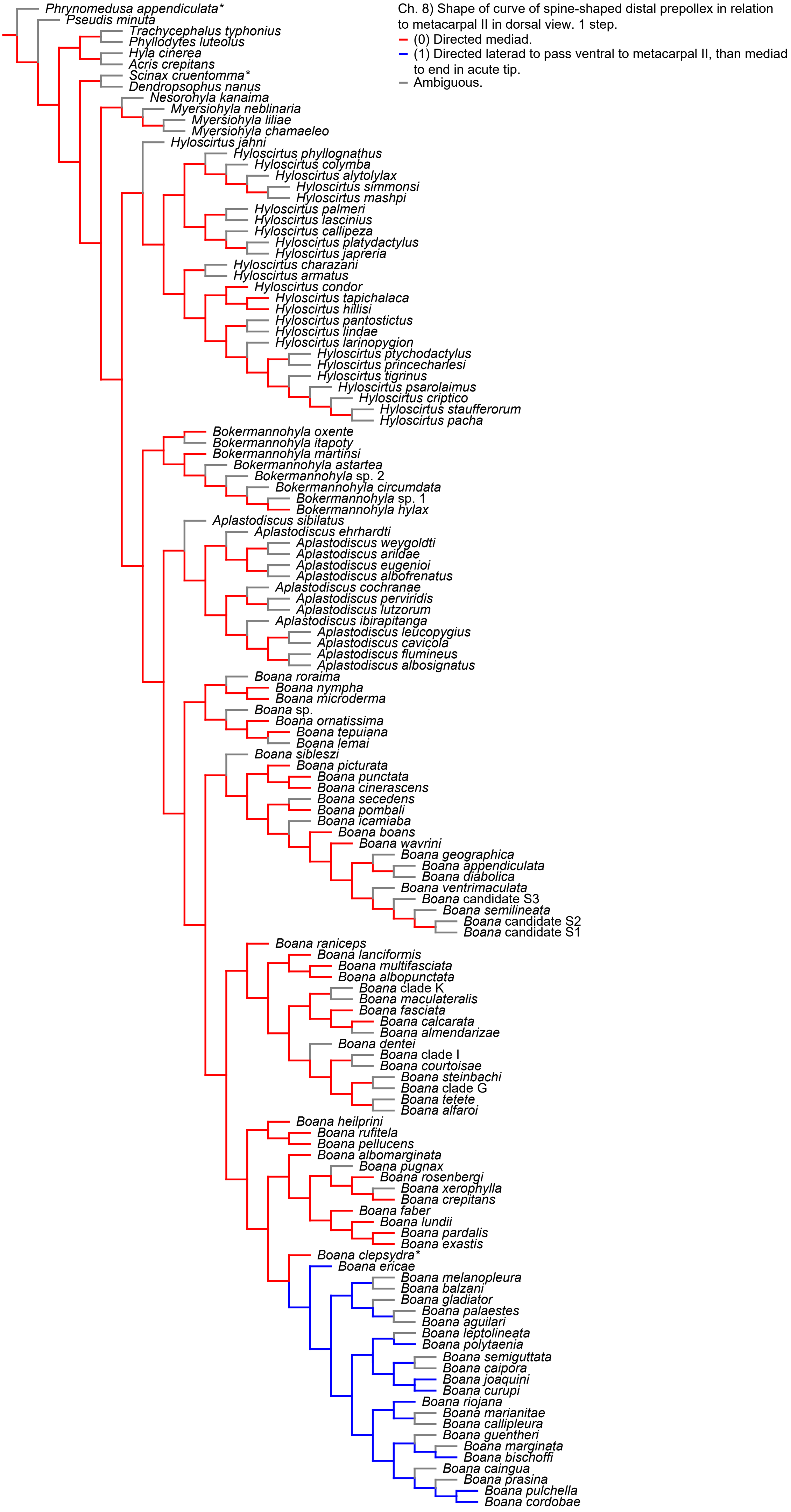
🟩 (2) Long; in dorsal view, proximal margin reaching surpassing level of portion of element Y that articulates with radiale.

▬ Ambiguous.



Ch. 7) Curvature of spine-shaped distal prepollex. 1 step.

— (0) Curved mediad.
— (1) Straight.
— Ambiguous.



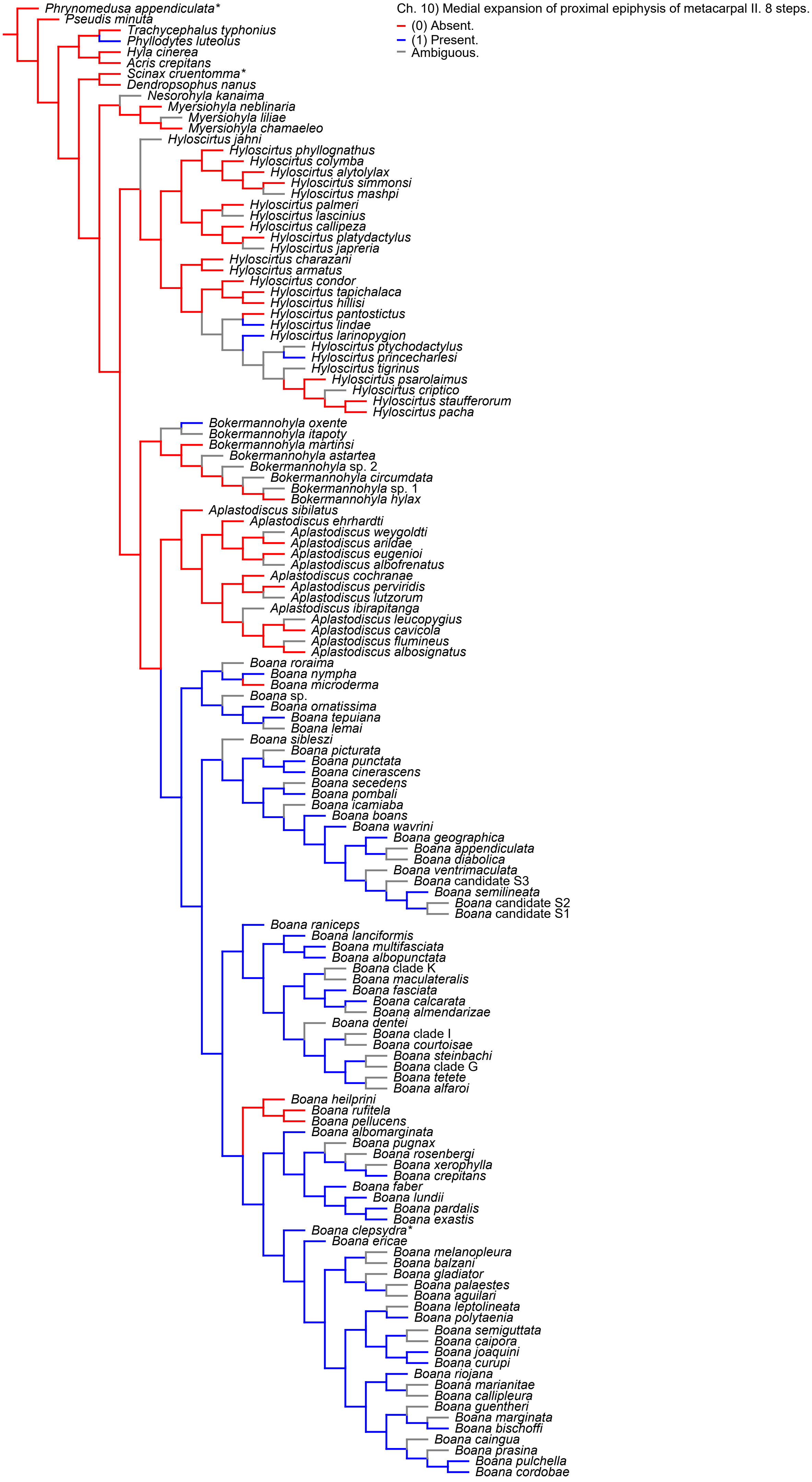
Ch. 8) Shape of curve of spine-shaped distal prepollex in relation to metacarpal II in dorsal view. 1 step.

🟥 (0) Directed mediad.

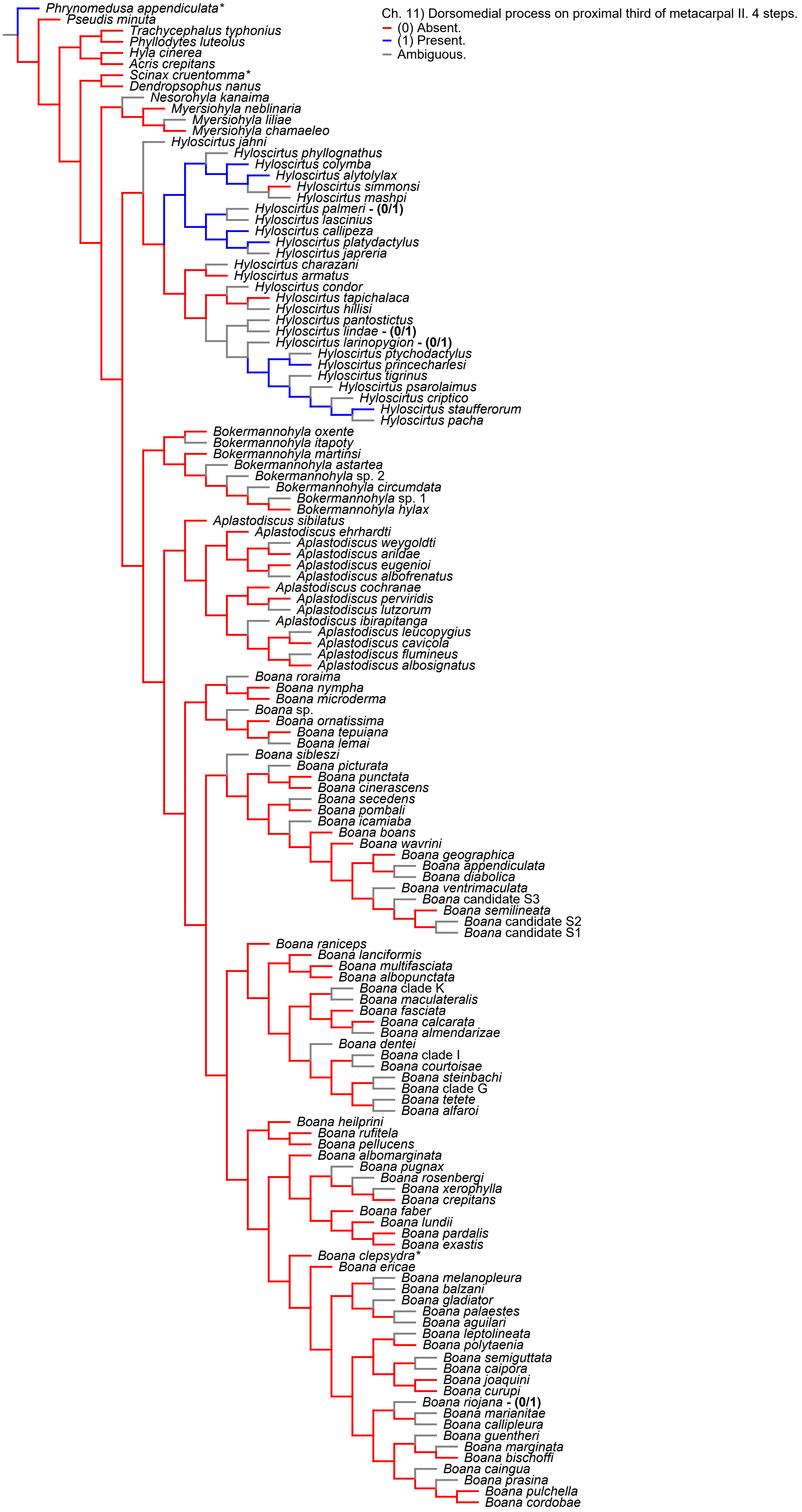
🟦 (1) Directed laterad to pass ventral to metacarpal II, than mediad to end in acute tip.

▨ Ambiguous.

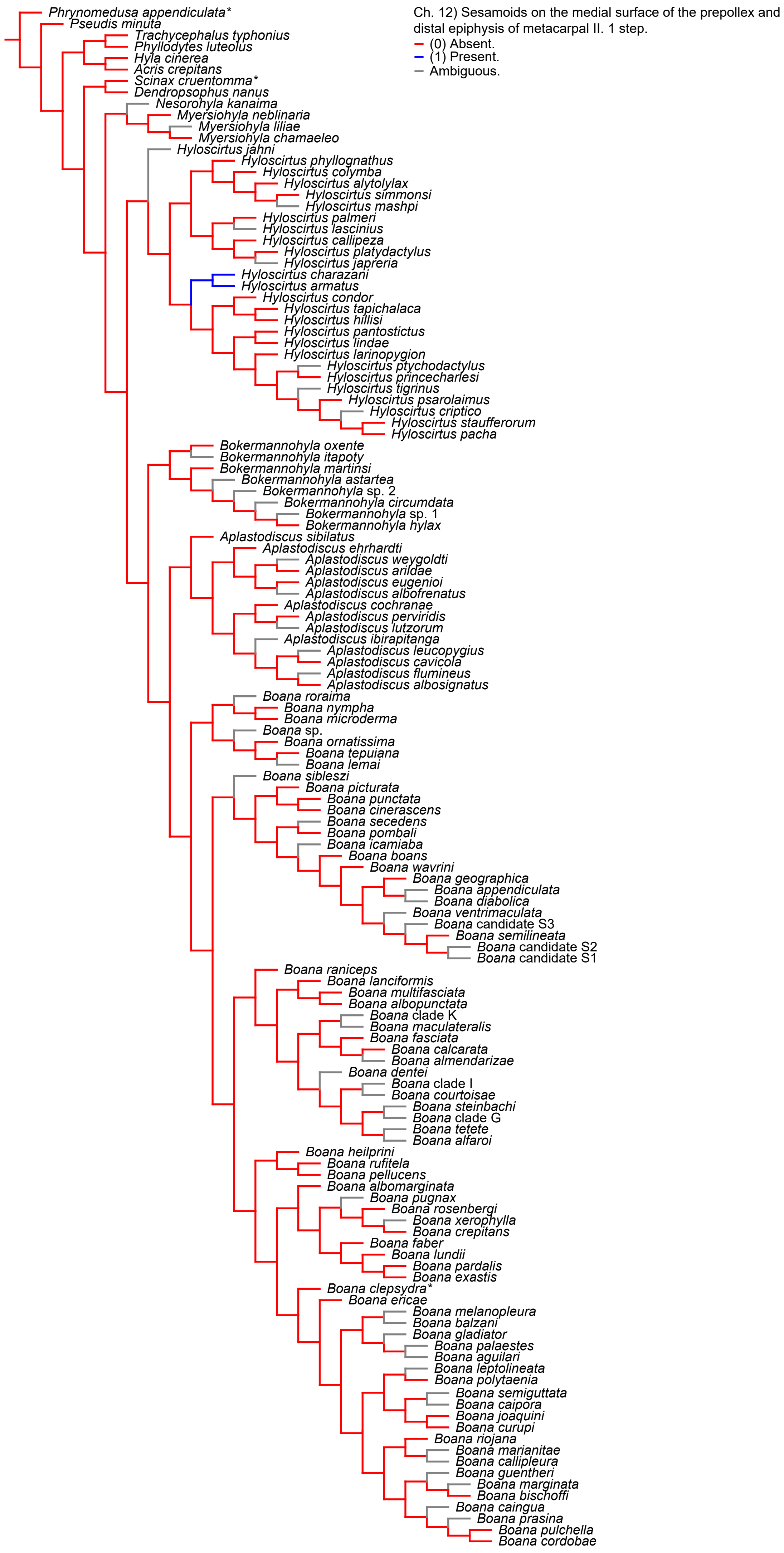

Ch. 9) Distal projection of dorsal crest of spine-shaped distal prepollex forming an additional spine. 1 step.

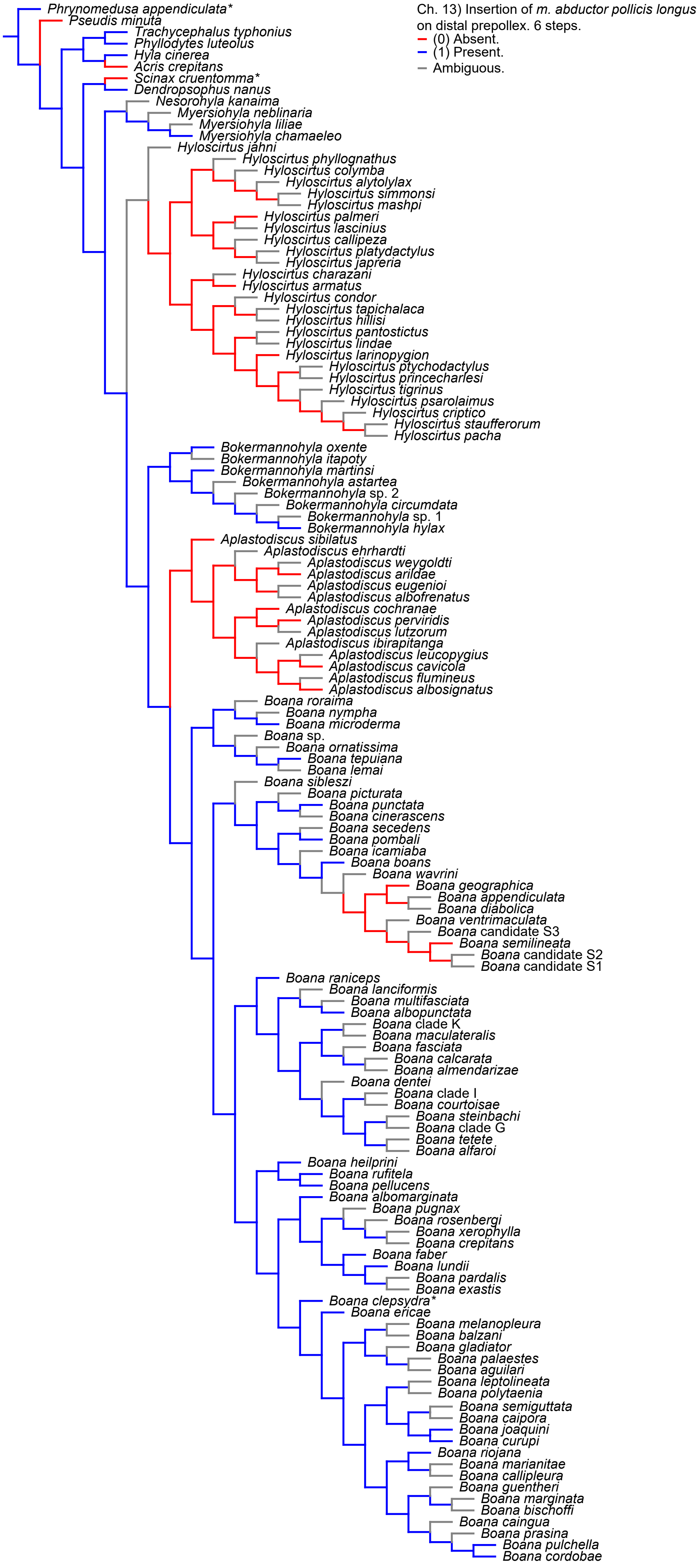


Ch. 10) Medial expansion of proximal epiphysis of metacarpal II. 8 steps.



Ch. 11) Dorsomedial process on proximal third of metacarpal II. 4 steps.

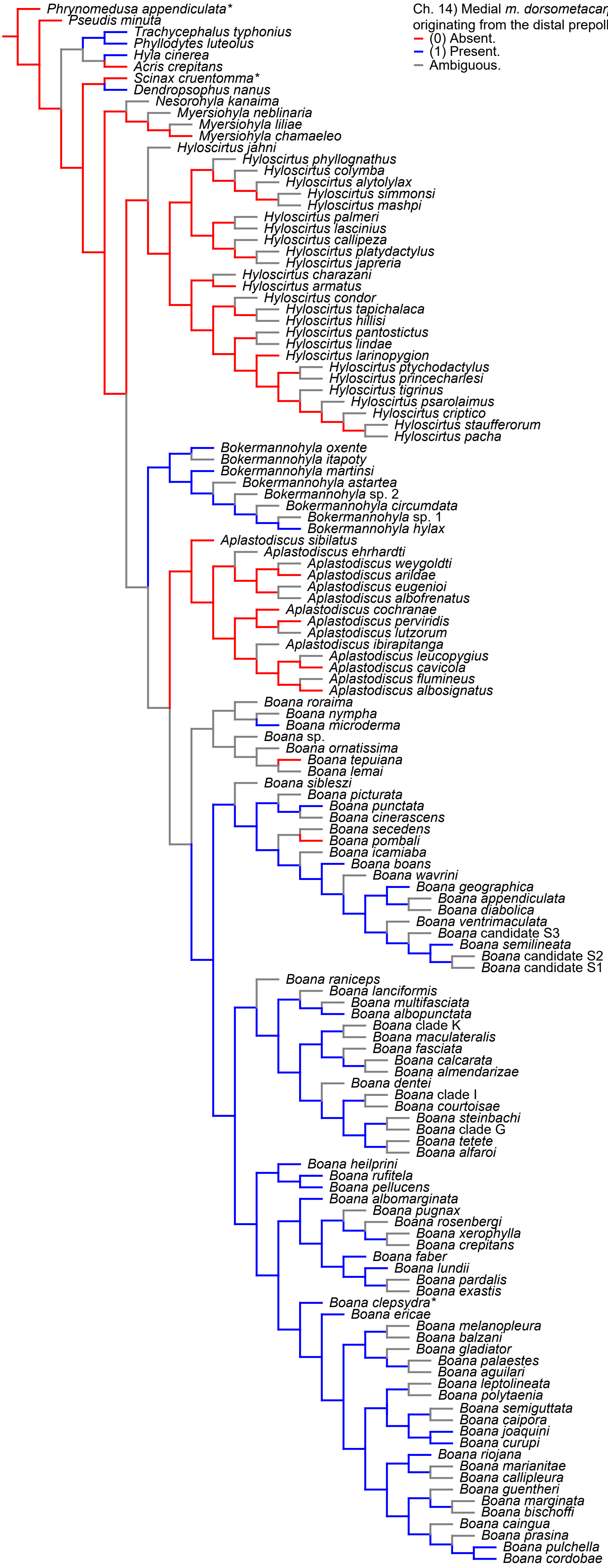

Ch. 12) Sesamoids on the medial surface of the prepollex and distal epiphysis of metacarpal II. 1 step.

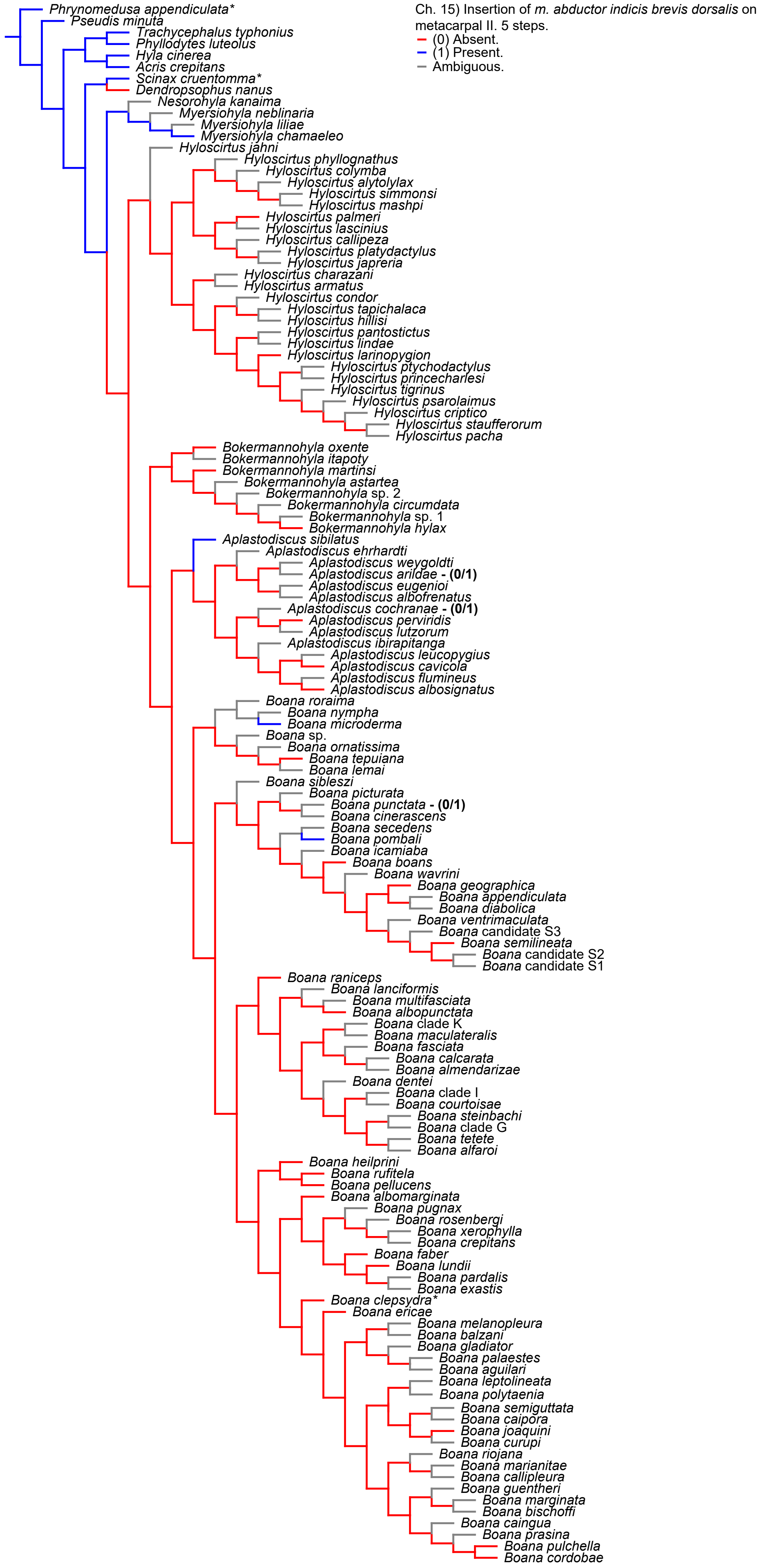


Ch. 13) Insertion of *m. abductor pollicis longus* on distal prepollex. 6 steps.

🟥 (0) Absent.
🟦 (1) Present.
▨ Ambiguous.

Ch. 14) Medial *m. dorsometacarpalis indicis proximalis*, originating from the distal prepollex. 7 steps.
🟥 (0) Absent.
🟦 (1) Present.
— Ambiguous.





Ch. 15) Insertion of *m. abductor indicis brevis dorsalis* on metacarpal II. 5 steps.

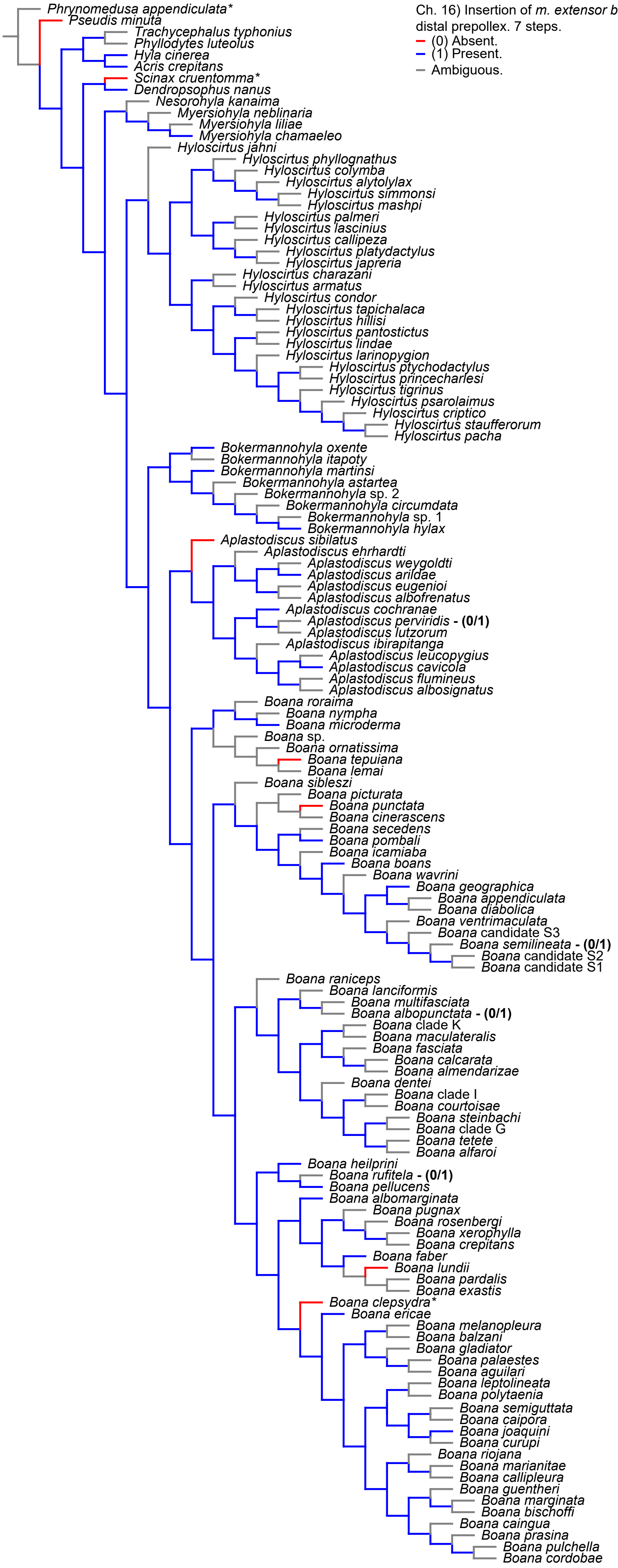
🟥 (0) Absent.

🟦 (1) Present.

▬ Ambiguous.

Ch. 16) Insertion of *m. extensor brevis indicis medius* on the distal prepollex. 7 steps.

🟥 (0) Absent.
🟦 (1) Present.
⬜ Ambiguous.



SUPPORTING INFORMATION S6

Evidence of male-male fights in species of Cophomantini (all listed have a spine-shaped prepollex). Evidence might be direct (reports of fights) or indirect (presence of scars); for the same species is provided a qualitative comparison between male and female forearm width; and habitat.

Species	**Fights / Scars**	**Forearm width in males**	**Habitat**	**References**
Boana aguilari	Scars	Similar to females	Ponds/slow flowing streams	Lehr *et al.* (2010)
Boana albomarginata	Fight	Similar to females	Ponds	Giasson & Haddad (2007)
Boana albopunctata	Fight	Similar to females	Ponds	Toledo *et al.* (2007)
Boana bischoffi	Fight	Similar to females	Ponds	Toledo *et al.* (2007)
Boana boans	Fight	Wider than in females*	Ponds/streams	Duellman (1997, 2005)
Boana caipora	Scars	Wider than in females	Streams	Antunes *et al.* (2008)
Boana cambui	Scars	Similar to females	Ponds	Pinheiro *et al.* (2016)
Boana cipoensis	Scars*	Similar to females*	Slow flowing streams	Eterovick & Sazima (2004)
Boana cordobae	Scars*	Wider than in females	Streams	P.D.P. Pinheiro pers. obs.; Barrio (1965)
Boana curupi	Fight	Wider than in females	Streams	Garcia *et al.* (2007); Candaten *et al.* (2020)
Boana ericae	Scars	Similar to females	Ponds/slow flowing streams *	Garcia & Haddad (2008)
Boana exastis	Scars	Similar to females*	Streams	Caramaschi & Rodrigues (2003); Loebmann *et al.* (2008)
Boana faber	Scars	Similar to females	Ponds	Martins *et al.* (1988)
Boana gladiator	Scars	Wider than in females	Streams	Köhler *et al.* (2010)
Boana goiana	Scars	Similar to females	Ponds/slow flowing streams*	Menin *et al.* (2004)
Boana joaquini	Scars	Wider than in females	Streams	Garcia *et al.* (2003)
Boana leptolineata	Scars*	Similar to females*	Ponds*	P.D.P. Pinheiro pers. obs.

Boana leucocheila	Scars**	Similar to females	Streams	Pansonato *et al.* (2011)
Boana lundii	Fight	Similar to females	Ponds/slow flowing streams	Pimenta *et al.* (2014)
Boana marginata	Scars	Wider than in females	Streams	Garcia *et al.* (2001)
Boana marianitae	Scars	Wider than in females*	Streams	Köhler (2000)
Boana melanopleura	Scars	Similar to females	Streams and ponds	Lehr & von May (2004)
Boana paranaiba	Scars	Similar to females	Streams	Carvalho *et al.* (2010)
Boana pardalis	Scars	Similar to females*	Ponds	Lutz (1973)
Boana poaju	Scars	Wider than in females	Streams	Garcia *et al.* (2008)
Boana polytaenia	Scars*	Similar to females	Ponds/slow flowing streams*	P.D.P. Pinheiro pers. obs.
Boana pugnax	Fight	Similar to females	Streams	Kluge (1979)
Boana punctata	Fight	Similar to females	Ponds	Brunetti *et al.* (2014)
Boana riojana	Scars**	Wider than in females	Streams	Barrio (1965)
Boana rosenbergi	Fight	Similar to females	Streams	Kluge (1981)
Boana secedens	Scars**	Similar to females	Streams	Weber *et al.* (2009)
Boana semiguttata	Scars	Wider than in females	Streams	Garcia *et al.* (2007)
Boana stellae	Scars	Wider than in females	Streams	Kwet (2008)
Boana wavrini	Scars	Similar to females	Ponds	Hoogmoed (1990)
Boana xerophylla	Fight	Similar to females	Ponds	Kluge (1979)
Bokermannohyla alvarengai	Scars*	Greatly wider than in females*	Streams	Eterovick & Sazima (2004)
Bokermannohyla astartea	Scars***	Wider than in females	Bromeliads in streams	Bokermann (1967)
Bokermannohyla caramaschii	Scars**	Wider than in females	Streams	Napoli (2005)
Bokermannohyla ibitiguara	Scars	Wider than in females	Streams	Nali & Prado (2012)
Bokermannohyla itapoty	Fight	Wider than in females	Streams	Lugli & Haddad (2006)
Bokermannohyla martinsi	Scars	Greatly wider than in females	Streams	Magalhães *et al.* (2018)

Bokermannohyla nanuzae	Scars**	?	Streams	Bokermann & Sazima (1973)
Bokermannohyla napolii	Scars	Wider than in females	Streams	Carvalho *et al.* (2012)
Bokermannohyla pseudopseudis	Scars	Wider than in females	Streams	Magalhães *et al.* (2016)
Bokermannohyla ravida	Scars**	Wider than in females	Streams	Caramaschi *et al.* (2001)
Hyloscirtus diabolus	Scars	Greatly wider than in females	Streams	Rivera-Correa *et al.* (2016)
Hyloscirtus tapichalaca	Scars	Greatly wider than in females	Streams	Kizirian *et al.* (2003)

*P.D.P. Pinheiro pers. obs.

**Evidence from fotos on Bokermann & Sazima (1973); Caramaschi *et al*. (2001); Caramaschi & Niemeyer (2003); Napoli (2005); Weber *et al*. (2009); Köhler *et al.* (2010)

***L. Malagoli, per. comm.

LITERATURE CITED

Antunes AP, Faivovich J, Haddad CFB. 2008. A New Species of *Hypsiboas* from The Atlantic Forest of Southeastern Brazil (Amphibia: Anura: Hylidae). *Copeia* **2008:** 179-190.

Barrio A. 1965. Las subspecies de *Hyla pulchella* Duméril y Bibron (Anura, Hylidae). *Physis* **25:**115-128.

Bokermann WCA. 1967. *Hyla astartea*, nova espécie da Serra do Mar em São Paulo (Amphibia, Hylidae). *Revista Brasileira de Biologia* **27:** 157-158.

Bokermann WCA, Sazima I. 1973. Anfíbios da Serra do Cipó, Minas Gerais, Brasil. 1—Espécies novas de *Hyla* (Anura, Hylidae). *Revista Brasileira de Biologia* **33:** 329-336.

Brunetti AE, Taboada C, Faivovich J. 2014. The reproductive biology of *Hypsiboas punctatus* (Anura: Hylidae): male territoriality and the possible role of different signals during female choice. *Salamandra* **50:** 215-224.

Candaten A, Possenti AG, Mainardi AA, Rocha MC, Palaoro AV. 2020. Fighting scars: heavier gladiator frogs bear more injuries than lighter frogs. *Acta Ethologica* **23:** 39–44.

Caramaschi U, Niemeyer H. 2003. New species of the *Hyla albopunctata* group from Central Brazil (Amphibia, Anura, Hylidae). *Boletim do Museu Nacional, Zoologia* **504:** 1-8.

Caramaschi U, Rodriques MT. 2003. A new large species, genus *Hyla* Laurenti, 1768, from Souther Bahia, Brazil (Amphibia, Anura, Hylidae). *Arquivos do Museu Nacional* **61:** 255-260.

Caramaschi U, Napoli MF, Bernardes AT. 2001. Nova espécie do grupo de *Hyla circumdata* (Cope, 1870) do Estado de Minas Gerais, Brasil (Amphibia, Anura, Hylidae). *Boletim do Museu Nacional, Zoologia* **457:** 1-11.

Carvalho TR, Giaretta AA, Facure KG. 2010. A new species of *Hypsiboas* Wagler (Anura: Hylidae) closely related to *H. multifasciatus* Günther from southeastern Brazil. *Zootaxa* **2521:** 37-52.

Carvalho TR, Giaretta AA, Magrini L. 2012. A new species of the *Bokermannohyla circumdata* group (Anura: Hylidae) from southeastern Brazil, with bioacoustic data on seven species of the genus. *Zootaxa* **3321:** 37-55.

Duellman WE. 1997. Amphibians of La Escalera region, southeastern Venezuela: taxonomy, ecology, and biogeography. *Scientific Papers. Natural History Museum, University of Kansas* **2:** 1–52.

Duellman WE. 2005. Cuzco Amazónico: The Lives of Amphibians and Reptiles in the Amazonian Rain Forest. Ithaca: Cornell University Press.

Duellman WE, De la Riva I, Wild ER. 1997. Frogs of the *Hyla armtata* and *Hyla pulchella* Groups in the Andes of South America, with definitions and analyses of phylogenetic relationships of andean groups of *Hyla*. *Scientific Papers, Natural History Museum, University of Kansas* **3:** 1–41.

Eterovick PC, Sazima I. 2004. Anfíbios da Serra do Cipó/Amphibians from the Serra do Cipó—Minas Gerais – Brasil. Belo Horizonte: Editora PUC Minas.

Garcia PCA, Haddad CFB. 2008. Vocalizations and comments on the relationships of *Hypsiboas ericae* (Amphibia, Hylidae). *Iheringia, Zoologia,* **98:** 161–166.

Garcia PCA, Vinciprova G, Haddad CFB. 2001. Vocalização, girino, distribuição geográfica e novos comentários sobre *Hyla marginata* Boulenger, 1887 (Anura, Hylidae, Hylinae). *Boletim do Museu Nacional, Zoologia* **460:** 1–19.

Garcia PCA, Vinciprova G, Haddad CFB. 2003. The taxonomic status of *Hyla pulchella joaquini* (Anura: Hylidae) with description of its tadpole and vocalization. *Herpetologica* **59:** 350–363.

Garcia PCA, Faivovich J, Haddad CFB. 2007. Redescription of *Hypsiboas semiguttatus*, with the description of a new species of the *Hypsiboas pulchellus* group. *Copeia* **2007:** 933–951.

Garcia PCA, Peixoto OL, Haddad CFB. 2008. A new species of *Hypsiboas* (Anura: Hylidae) from the Atlantic forest of Santa Catarina, southern Brazil, with comments on its conservation status. *South American Journal of Herpetology* **3:** 27-35.

Giasson LOM, Haddad CFB. 2007. Mate choice and reproductive biology of *Hypsiboas albomarginatus* (Anura: Hylidae) in the Atlantic Forest, Southeastern Brazil. *South American Journal of Herpetology* **2:** 157-164.

Hoogmoed MS. 1990. Resurrection of *Hyla wavrini* Parker (Amphibia: Anura: Hylidae), a gladiator frog from northern South America. *Zoologishe Mededelingen* **64:** 71–93.

Kizirian D, Coloma LA, Paredes-Recalde A. 2003. A new treefrog (Hylidae: *Hyla*) from southern Ecuador and a description of its antipredator behavior. *Herpetologica* **59:** 339–349.

Kluge AG. 1979. The gladiator frogs of Middle America and Colombia—a reevaluation of their systematics (Anura: Hylidae). *Occasional Papers of the Museum of Zoology, University of Michigan* **688:** 1–24.

Kluge AG. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Miscelaneous Publications, Museum of Zoology, University of Michigan* **160:** 1-170.

Köhler J. 2000. Amphibian diversity in Bolivia: a study with special reference to montane forest regions. *Bonner Zoologische Monographien* **48:** 1–243.

Köhler J, Koscinski D, Padial JM, Chaparro JC, Handford P, Lougheed SC, De la Riva I. 2010. Systematics of Andean gladiator frogs of the *Hypsiboas pulchellus* species group (Anura, Hylidae). *Zoologica Scripta* **39:** 572–590.

Kwet A. 2008. New species of *Hypsiboas* (Anura: Hylidae) in the *pulchellus* group from southern Brazil. *Salamandra* **44:** 1–14.

Lehr E, Faivovich J, Jungfer K-H. 2010. A new Andean species of the *Hypsiboas pulchellus* group: Adults, calls, and phyllogenetic relationships. *Herpetologica* **66:** 296–307.

Lehr E, von May R. 2004. Rediscovery of *Hyla melanopleura* Boulenger, 1912 (Amphibia: Anura: Hylidae). *Salamandra* **40:** 51–58.

Loebmann D, Zina J, Araújo OGS, Toledo LF, Haddad CFB. 2008. Acoustic repertory of *Hypsiboas exastis* (Caramaschi and Rodrigues, 2003) (Amphibia, Hylidae). *South American Journal of Herpetology* **3:** 96–100.

Lugli L, Haddad CFB. 2006. New Species of *Bokermannohyla* (Anura, Hylidae) from Central Bahia, Brazil. *Journal of Herpetology* **40:** 7-15.

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

Magalhães RF, Garda AA, Marques NCS, Brandão RA. 2016. Sexual dimorphism and resource utilisation by the Veadeiros waterfall frog *Bokermannohyla pseudopseudis* (Anura: Hylidae). *Salamandra* **52:** 171-177.

Magalhães RF, Lacerda JVL, Reis LP, Garcia PCA, Pinheiro PDP. 2018. Sexual dimorphism in *Bokermannohyla martinsi* (Bokermann, 1964) (Anura, Hylidae) with a report of male–male combat. *South American Journal of Herpetology* **13:** 202–209.

Martins M, Haddad CFB. 1988. Vocalizations and reproductive behaviour in the smith frog, *Hyla faber* Wied (Amphibia: Hylidae). Amphibia-*Reptilia* **9:** 49-60.

Menin M, Silva RA, Giaretta AA. 2004. Reproductive biology of *Hyla goiana* (Anura, Hylidae). *Iheringia* **94:** 49–52.

Napoli MF. 2005. A new species allied to *Hyla circumdata* (Anura: Hylidae) from Serra da Mantiqueira, Southeastern Brazil. *Herpetologica* **61:** 63-69.

Pansonato A, Ávila RW, Kawashita-Ribeiro RA, Morais DG. 2011. Advertisement call and new distribution records of *Hypsiboas leucocheilus* (Anura: Hylidae). *Salamandra* **47:** 55–58.

Pimenta B, Costa D, Murta-Fonseca R, Pezzuti TL. 2014. Anfíbios—Alvorada de Minas, Conceição do Mato Dentro, Dom Joaquim, Minas Gerais. Belo Horizonte: Bicho do Mato Editora.

Pinheiro PDP, Pezzuti TL, Leite FSF, Garcia PCA, Haddad CFB, Faivovich J. 2016. A new species of the *Hypsiboas pulchellus* group from the Serra da Mantiqueira, Southeastern Brazil (Amphibia: Anura: Hylidae). *Herpetologica* **72:** 256-270.

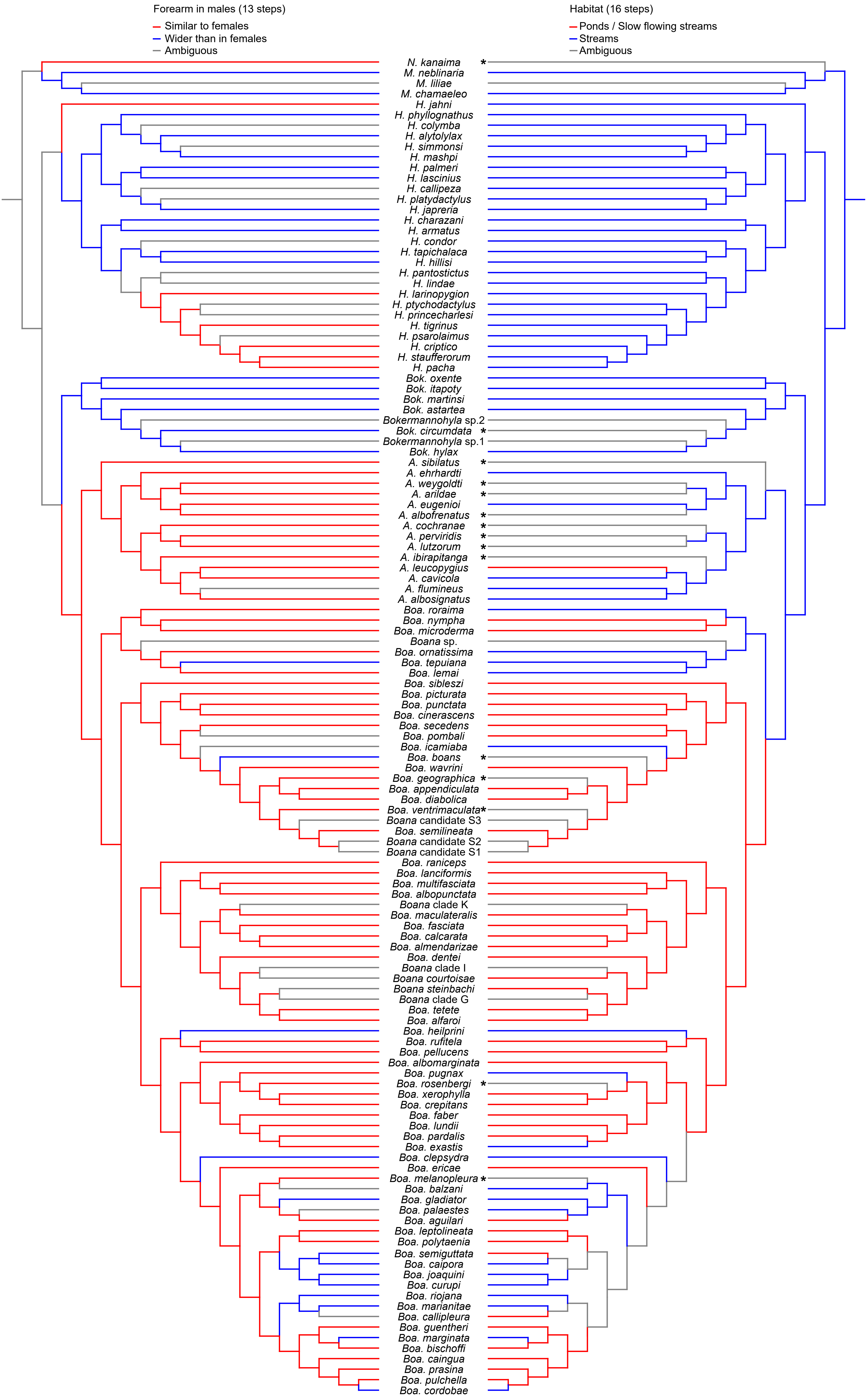
Toledo LF, Araújo OGS, Guimarães L, Lingnau R, Haddad CFB. 2007. Visual and acoustic signaling in three species of Brazilian nocturnal tree frogs (Anura, Hylidae). *Phyllomedusa* **6:** 61–68.

Rivera-Correa M, García-Burneo K, Grant T. 2016. A new red-eyed of stream treefrog of *Hyloscirtus* (Anura: Hylidae) from Peru, with comments on the taxonomy of the genus. *Zootaxa* **4061:** 29–40.

Weber LN, Silva-Soares T, Salles ROL. 2009. Amphibia, Anura, Hylidae, *Hypsiboas secedens*: Reassessment of type locality coordinates and distribution extension. *Check List* **5:** 218–221.

SUPPORTING INFORMATION S7

Ancestral character state reconstruction of the relative forearm width (left) and of the habitat (right), for species of Cophomantini. Phylogenetic hypothesis pruned from the tree provided by Lyra *et al.* (2020). An * on terminals of habitat optimization points polymorphism. Below it is provided a table with citations followed by the list of references used to collect data for these reconstructions. Species absent from the table have no information for both characters. A ? indicates missing information for the respective character.



Species	**Forearm width**	**Habitat**
Aplastodiscus albofrenatus	P.D.P. Pinheiro pers. obs.	Heyer *et al.* (1990); Cruz & Peixoto (1985)
Aplastodiscus albosignatus	P.D.P. Pinheiro pers. obs.	Lutz & Lutz (1938)
Aplastodiscus arildae	P.D.P. Pinheiro pers. obs.	Cruz & Peixoto (1987)
Aplastodiscus cavicola	P.D.P. Pinheiro pers. obs.	Cruz & Peixoto (1985)
Aplastodiscus cochranae	P.D.P. Pinheiro pers. obs.	Garcia *et al.* (2001)
Aplastodiscus ehrhardti	P.D.P. Pinheiro pers. obs.	Conte *et al.* (2005)
Aplastodiscus eugenioi	Carvalho-e-Silva & Carvalho-e-Silva (2005)	Carvalho-e-Silva & Carvalho-e-Silva (2005)
Aplastodiscus flumineus	?	Cruz & Peixoto (1985)
Aplastodiscus ibirapitanga	P.D.P. Pinheiro pers. obs.	Cruz *et al.* (2003)
Aplastodiscus leucopygius	Haddad & Sawaya (2000)	Haddad & Sawaya (2000)
Aplastodiscus lutzorum	Berneck *et al.* (2017)	Berneck *et al.* (2017)
Aplastodiscus perviridis	P.D.P. Pinheiro pers. obs.	Haddad *et al.* (2005)
Aplastodiscus sibilatus	P.D.P. Pinheiro pers. obs.	Cruz *et al.* (2003)
Aplastodiscus weygoldti	Cruz & Peixoto (1987)	Cruz & Peixoto (1987)
Boana aguilari	Lehr *et al.* (2010)	Lehr *et al.* (2010)
Boana albomarginata	Giasson & Haddad (2007)	Giasson & Haddad (2007)
Boana albopunctata	Toledo *et al.* (2007)	Toledo *et al.* (2007)
Boana alfaroi	Caminer & Ron (2014)	Caminer & Ron (2014)
Boana almendarizae	Caminer & Ron (2014)	Caminer & Ron (2014)
Boana appendiculata	Caminer & Ron (2020)	Caminer & Ron (2020)
Boana balzani	?	Duellman *et al.* (1997)
Boana bischoffi	Toledo *et al.* (2007)	Toledo *et al.* (2007)
Boana boans	P.D.P. Pinheiro pers. obs.	Duellman (1997, 2005)
Boana caingua	P.D.P. Pinheiro pers. obs.	Zaracho *et al.* (2012)
Boana caipora	Antunes *et al.* (2008)	Antunes *et al.* (2008)
Boana calcarata	Caminer & Ron (2014)	Caminer & Ron (2014)
Boana callipleura	?	Reynolds & Foster (1992)
Boana cinerascens	Ron *et al.* (2019); Sturaro *et al.* (2020)	Ouboter & Jairam (2012)
Boana clepsydra	P.D.P. Pinheiro pers. obs.	Bokermann (1972)
Boana cordobae	P.D.P. Pinheiro pers. obs.	Barrio (1965)
Boana courtoisae	?	Fouquet *et al.* (2021)
Boana crepitans	P.D.P. Pinheiro pers. obs.	Pimenta *et al.* (2014)
Boana curupi	Garcia *et al.* (2007)	Garcia *et al.* (2007); Candaten *et al.* (2020)
Boana dentei	Marinho *et al.* (2020)	Marinho *et al.* (2020)
Boana diabolica	Fouquet *et al.* (2016)	Fouquet *et al.* (2016)
Boana ericae	Garcia & Haddad (2008)	P.D.P. Pinheiro pers. obs.
Boana exastis	P.D.P. Pinheiro pers. obs.	Loebmann *et al.* (2008)
Boana faber	Martins *et al.* (1988)	Martins *et al.* (1988)
Boana fasciata	Caminer & Ron (2014)	Caminer & Ron (2014)
Boana geographica	Fouquet *et al.* (2016)	Marquez (1993); Schulze *et al.* (2015)

Species	Forearm width	Habitat
Boana gladiator	Köhler *et al.* (2010)	Köhler *et al.* (2010)
Boana guentheri	P.D.P. Pinheiro pers. obs.	Kwet *et al.* (2010)
Boana heilprini	Noble (1923)	Landestoy (2013)
Boana icamiaba	?	Peloso *et al.* (2018)
Boana joaquini	Garcia *et al.* (2003)	Garcia *et al.* (2003)
Boana lanciformis	P.D.P. Pinheiro pers. obs.	Duellman (1978)
Boana lemai	Myers & Donnely (2008)	Duellman (1997)
Boana leptolineata	P.D.P. Pinheiro pers. obs.	P.D.P. Pinheiro pers. obs.
Boana lundii	Pimenta *et al.* (2014)	Pimenta *et al.* (2014)
Boana maculateralis	Caminer & Ron (2014)	Caminer & Ron (2014)
Boana marginata	Garcia *et al.* (2001)	Garcia *et al.* (2001)
Boana marianitae	P.D.P. Pinheiro pers. obs.	Köhler (2000)
Boana melanopleura	Lehr & von May (2004)	Lehr & von May (2004)
Boana microderma	P.D.P. Pinheiro pers. obs.	Pyburn (1977)
Boana multifasciata	P.D.P. Pinheiro pers. obs.	de Sá (1996); Duellman (1997)
Boana nympha	Faivovich *et al.* (2006)	Faivovich *et al.* (2006)
Boana ornatissima	Hoogmoed (1979)	Hoogmoed (1979)
Boana palaestes	?	Duellman *et al.* (1997)
Boana pardalis	P.D.P. Pinheiro pers. obs.	Lutz (1973)
Boana pellucens	Venegas *et al.* (2008)	Venegas *et al.* (2008)
Boana picturata	Ron *et al.* (2019)	Vargas *et al.* (2000)
Boana polytaenia	P.D.P. Pinheiro pers. obs.	P.D.P. Pinheiro pers. obs.
Boana pombali	?	Caramaschi *et al.* (2004)
Boana prasina	P.D.P. Pinheiro pers. obs.	Kwet *et al.* (2010)
Boana pugnax	Kluge (1979)	Kluge (1979)
Boana pulchella	P.D.P. Pinheiro pers. obs.	Kwet *et al.* (2010); Zaracho *et al.* (2012)
Boana punctata	Brunetti *et al.* (2014)	Brunetti *et al.* (2014)
Boana raniceps	P.D.P. Pinheiro pers. obs.	Uetanabaro *et al.* (2008)
Boana riojana	Barrio (1965)	Barrio (1965)
Boana roraima	MacCulloch & Latrop (2005)	Myers & Donnely (2008)
Boana rosenbergi	Kluge (1981)	Kluge (1981); Höbel (2000)
Boana rufitela	P.D.P. Pinheiro pers. obs.	Savage (2002)
Boana secedens	Vrcibradic *et al.* (2016)	Weber *et al.* (2009); Vrcibradic *et al.* (2016)
Boana semiguttata	Garcia *et al.* (2007)	Garcia *et al.* (2007)
Boana semilineata	P.D.P. Pinheiro pers. obs.	P.D.P. Pinheiro pers. obs.
Boana sibleszi	Rivero (1972); Hoogmoed (1979)	Rivero (1972); Hoogmoed (1979)
Boana steinbachi	?	Fouquet *et al.* (2021)
Boana tepuiana	P.D.P. Pinheiro pers. obs.	Barrio-Amorós & Brewer-Carias (2008)
Boana tetete	Caminer & Ron (2014)	Caminer & Ron (2014)
Boana ventrimaculata	Caminer & Ron (2020)	Caminer & Ron (2020)

Species	**Forearm width**	**Habitat**
Boana wavrini	Hoogmoed (1990)	Hoogmoed (1990)
Boana xerophylla	Kluge (1979)	Kluge (1979)
Bokermannohyla astartea	L. Malagoli, per. comm.	Bokermann (1967)
Bokermannohyla circumdata	P.D.P. Pinheiro pers. obs.	Carvalho *et al.* (2012)
Bokermannohyla hylax	P.D.P. Pinheiro pers. obs.	Heyer *et al.* (1990)
Bokermannohyla itapoty	Lugli & Haddad (2006a)	Lugli & Haddad (2006a)
Bokermannohyla martinsi	Magalhães *et al.* (2018)	Magalhães *et al.* (2018)
Bokermannohyla oxente	P.D.P. Pinheiro pers. obs.	Lugli & Haddad (2006b)
Hyloscirtus alytolylax	Ron *et al.* (2019)	Duellman (1972)
Hyloscirtus armatus	Duellman *et al.* (1997)	Guayasamin *et al.* (2015)
Hyloscirtus callipeza	?	Duellman (1989)
Hyloscirtus charazani	Duellman *et al.* (1997)	Guayasamin *et al.* (2015)
Hyloscirtus colymba	?	Duellman (1970)
Hyloscirtus condor	?	Almendáriz *et al.* (2014)
Hyloscirtus criptico	Coloma *et al.* (2012)	Coloma *et al.* (2012)
Hyloscirtus hillisi	Ron *et al.* (2018)	Ron *et al.* (2018)
Hyloscirtus jahni	Rojas-Runjaic *et al.* (2018)	Guayasamin *et al.* (2015)
Hyloscirtus japreria	Rojas-Runjaic *et al.* (2018)	Rojas-Runjaic *et al.* (2018)
Hyloscirtus larinopygion	Mueses-Cisneros & Anganoi-Criollo (2008)	Guayasamin *et al.* (2015)
Hyloscirtus lascinius	Rojas-Runjaic *et al.* (2016)	Guayasamin *et al.* (2015)
Hyloscirtus lindae	?	Duellman & Altig (1978)
Hyloscirtus mashpi	Guayasamin *et al.* (2015)	Guayasamin *et al.* (2015)
Hyloscirtus pacha	Ron *et al.* (2019)	Duellman & Hillis (1990)
Hyloscirtus palmeri	Acosta-Galvis (2019)	Guayasamin *et al.* (2015)
Hyloscirtus pantostictus	?	Duellman & Berger (1982)
Hyloscirtus phyllognathus	Ron *et al.* (2019)	Duellman (1972)
Hyloscirtus platydactylus	?	Duellman (1972)
Hyloscirtus princecharlesi	?	Coloma *et al.* (2012)
Hyloscirtus psarolaimus	?	Duellman & Hillis (1990)
Hyloscirtus ptychodactylus	?	Duellman & Hillis (1990)
Hyloscirtus simmonsi	?	Duellman (1989)
Hyloscirtus staufferorum	Ron *et al.* (2019)	Duellman & Coloma (1993)
Hyloscirtus tapichalaca	Kizirian *et al.* (2003)	Kizirian *et al.* (2003)
Hyloscirtus tigrinus	Mueses-Cisneros & Anganoi-Criollo (2008)	Mueses-Cisneros & Anganoi-Criollo (2008)
Myersiohyla chamaeleo	Faivovich *et al.* (2013)	Faivovich *et al.* (2013)
Myersiohyla neblinaria	Faivovich *et al.* (2013)	Faivovich *et al.* (2013)
Nesorohyla kanaima	MacCulloch & Latrop (2005)	MacCulloch & Latrop (2005)

REFERENCES

Acosta-Galvis AR. 2019. Lista de los Anfibios de Colombia: Referencia en linea Version 09.2019. Batrachia, Villa de Leyva, Boyacá, Colombia, http://www.batrachia.com (accessed 08 November 2020).

Almendáriz A, Brito J, Batallas D, Ron SR. 2014. Una especie nueva de rana arbórea del género *Hyloscirtus* (Amphibia: Anura: Hylidae) de la Cordillera del Cóndor. *Papéis Avulsos de Zoologia* **54:** 33–49.

Antunes AP, Faivovich J, Haddad CFB. 2008. A New Species of *Hypsiboas* from The Atlantic Forest of Southeastern Brazil (Amphibia: Anura: Hylidae). *Copeia* **2008:** 179–190.

Barrio A. 1965. Las subspecies de *Hyla pulchella* Duméril y Bibron (Anura, Hylidae). *Physis* **25:** 115–128.

Barrio-Amorós CL, Brewer-Carias C. 2008. Herpetological results of the 2002 expedition to Sarisariñama, a tepui in Venezuelan Guayana, with the description of five new species. *Zootaxa* **1942:** 1–68.

Berneck BvM, Giaretta AA, Brandão RA, Cruz CAG, Haddad CFB. 2017. The first species of *Aplastodiscus* endemic to the Brazilian Cerrado (Anura, Hylidae). *ZooKeys* **642:** 115–130.

Bokermann WCA. 1967. *Hyla astartea*, nova espécie da Serra do Mar em São Paulo (Amphibia, Hylidae). *Revista Brasileira de Biologia* **27:** 157-158.

Bokermann WCA. 1972. Notas sobre *Hyla clepsydra* A. Lutz (Anura, Hylidae). *Revista Brasileira de Biologia* **32:** 291–295.

Brunetti AE, Taboada C, Faivovich J. 2014. The reproductive biology of *Hypsiboas punctatus* (Anura: Hylidae): male territoriality and the possible role of different signals during female choice. *Salamandra* **50:** 215–224.

Caminer MA, Ron SR. 2014. Systematics of treefrogs of the *Hypsiboas calcaratus* and *Hypsiboas fasciatus* species complex (Anura, Hylidae) with the description of four new species. *ZooKeys* **370:** 1–68.

Caminer MA, Ron SR. 2020. Systematics of the *Boana semilineata* species group (Anura: Hylidae), with a description of two new species from Amazonian Ecuador. *Zoologial Journal of the Linnean Society* **190:** 149–180.

Candaten A, Possenti AG, Mainardi AA, Rocha MC, Palaoro AV. 2020. Fighting scars: heavier gladiator frogs bear more injuries than lighter frogs. *Acta Ethologica* **23:** 39–44.

Caramaschi U, Pimenta BVS, Feio RN. 2004. Nova espécie do grupo de *Hyla geographica* Spix, 1824 da floresta Atlântica, Brasil (Amphibia, Anura, Hylidae). *Boletim do Museu Nacional. Nova Série, Zoologia* **518:** 1–14.

Carvalho TR, Giaretta AA, Magrini L. 2012. A new species of the *Bokermannohyla circumdata* group (Anura: Hylidae) from southeastern Brazil, with bioacoustic data on seven species of the genus. *Zootaxa* **3321:** 37–55.

Carvalho-e-Silva AMPT, Carvalho-e-Silva SP. 2005. New species of the *Hyla albofrenata* group, from the states of Rio de Janeiro and São Paulo, Brazil (Anura, Hylidae). *Journal of Herpetology* **39:** 73–81.

Coloma LA, Carvajal-Endara S, Dueñas JF, Paredes-Recalde A, Morales-Mite MA, Almeida-Reinoso D, Tapia EE, Hutter CR, Toral-Contreras E, Guayasamin JM. 2012. Molecular phylogenetics of stream treefrogs of the *Hyloscirtus larinopygion* group (Anura: Hylidae), and description of two new species from Ecuador. *Zootaxa* **3364:** 1–78.

Conte CE, Lingnau R, Kwet A. 2005. Description of the advertisement call of *Hyla ehrhardti* Müller, 1924 and new distribution records (Anura: Hylidae). *Salamandra* **41:** 147–151.

Cruz CAG, Peixoto OL. 1985 [1984]. Espécies verdes de *Hyla*: o complexo "*Albosignata*" (Amphibia, Anura, Hylidae). *Arquivos de Universidade Federal Rural do Rio de Janeiro* **7:** 31–47.

Cruz CAG, Pimenta BVS, Silvano DL. 2003. Duas novas espécies pertencentes ao complexo de *Hyla albosignata* Lutz & Lutz, 1938, do leste do Brasil (Amphibia, Anura, Hylidae). *Boletim do Museu Nacional. Nova Serie, Zoologia* **503:** 1–13.

de Sá RO. 1996. *Hyla multifasciata*. *Catalogue of American Amphibians and Reptiles* **624:** 1–4.

Duellman WE. 1970. Hylid frogs of Middle America. *Monographs of the Museum of Natural History, University of Kansas* **1–2:** 1–753.

Duellman WE. 1972. A review of the neotropical frogs of the *Hyla bogotensis* group. *Occasional Papers of the Museum of Natural History, University of Kansas* **11:** 1–31.

Duellman WE. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publication. Museum of Natural History, University of Kansas* **65:** 1–352.

Duellman WE. 1989. New species of hylid frogs from the Andes of Colombia and Venezuela. *Occasional Papers of the Museum of Natural History, University of Kansas* **131:** 1–12.

Duellman WE. 1997. Amphibians of La Escalera region, southeastern Venezuela: taxonomy, ecology, and biogeography. *Scientific Papers. Natural History Museum, University of Kansas* **2:** 1–52.

Duellman WE. 2005. Cuzco Amazónico: The Lives of Amphibians and Reptiles in the Amazonian Rain Forest. Ithaca: Cornell University Press.

Duellman WE, Altig RI. 1978. New species of tree frogs (family Hylidae) from the Andes of Colombia and Ecuador. *Herpetologica* **34:** 177–185.

Duellman WE, Berger TJ. 1982. A new species of Andean treefrog (Hylidae). *Herpetologica* **38:** 456–460.

Duellman WE, Coloma LA. 1993. *Hyla staufferorum,* a new species of treefrog in the Hyla larinopygion group from the cloud forest of Ecuador. *Occasional Papers of the Museum of Natural History, University of Kansas* **161:** 1–11.

Duellman WE, Hillis DM. 1990. Systematics of the *Hyla larinopygion* group. *Occasional Papers of the Museum of Natural History, University of Kansas* **134:** 1–23.

Duellman WE, De la Riva I, Wild ER. 1997. Frogs of the *Hyla armtata* and *Hyla pulchella* Groups in the Andes of South America, with definitions and analyses of phylogenetic relationships of andean groups of *Hyla*. *Scientific Papers, Natural History Museum, University of Kansas* **3:** 1–41.

Faivovich J, Moravec J, Cisneros-Heredia DF, Köhler J. 2006. A new species of the *Hypsiboas benitezi* group from the western Amazon Basin (Amphibia: Anura: Hylidae). *Herpetologica* **62:** 96–108.

Faivovich J, McDiarmid RW, Myers CW. 2013. Two new species of *Myersiohyla* (Anura: Hylidae) from Cerro de la Neblina, Venezuela, with comments on other species of the genus. *American Museum Novitates* **3792:** 1–63.

Fouquet A, Martinez Q, Zeidler L, Courtois EA, Gaucher P, Blanc M, Lima JD, Souza SM, Rodrigues MT, Kok PJR. 2016. Cryptic diversity in the *Hypsiboas semilineatus* species group (Amphibia, Anura) with the description of a new species from the eastern Guiana Shield. *Zootaxa* **4084:** 79–104.

Fouquet A, Marinho P, Réjaud A, Carvalho TR, Caminer MA, Jansen M, Rainha RN, Rodrigues MT, Werneck FP, Lima AP, Hrbek T, Giaretta AA, Venegas

PJ, Chávez G, Ron S. 2021. Systematics and biogeography of the *Boana albopunctata* species group (Anura, Hylidae), with the description of two new species from Amazonia. *Systematics and Biodiversity* **19:** 375–399.

Garcia PCA, Haddad CFB. 2008. Vocalizations and comments on the relationships of *Hypsiboas ericae* (Amphibia, Hylidae). *Iheringia, Zoologia,* **98:** 161–166.

Garcia PCA, Vinciprova G, Haddad CFB. 2001. Vocalização, girino, distribuição geográfica e novos comentários sobre *Hyla marginata* Boulenger, 1887 (Anura, Hylidae, Hylinae). *Boletim do Museu Nacional, Zoologia* **460:** 1–19.

Garcia PCA, Vinciprova G, Haddad CFB. 2003. The taxonomic status of *Hyla pulchella joaquini* (Anura: Hylidae) with description of its tadpole and vocalization. *Herpetologica* **59:** 350–363.

Garcia PCA, Faivovich J, Haddad CFB. 2007. Redescription of *Hypsiboas semiguttatus*, with the description of a new species of the *Hypsiboas pulchellus* group. *Copeia* **2007:** 933–951.

Giasson LOM, Haddad CFB. 2007. Mate choice and reproductive biology of *Hypsiboas albomarginatus* (Anura: Hylidae) in the Atlantic Forest, Southeastern Brazil. *South American Journal of Herpetology* **2:** 157–164.

Guayasamin JM, Rivera-Correa M, Arteaga-Navarro AF, Culebras J, Bustamante L, Pyron RA, Peñafiel N, Morochz C, Hutter CR. 2015. Molecular phylogeny of stream treefrogs (Hylidae: *Hyloscirtus bogotensis* Group), with a new species from the Andes of Ecuador. *Neotropical Biodiversity* **1:** 2–21.

Haddad CFB, Sawaya R. 2000. Reproductive modes of Atlantic Forest hylid Frogs: a general overview and the description of a new mode. *Biotropica* **32:** 862–871.

Haddad CFB, Faivovich J, Garcia PCA. 2005. The specialized reproductive mode of the treefrog *Aplastodiscus perviridis* (Anura: Hylidae). *Amphibia-Reptilia* **26:** 87–92.

Heyer WR, Rand AS, Cruz CAG, Peixoto OL, Nelson CE. 1990. Frogs of Boracéia. *Arquivos de Zoologia* **31:** 231–410.

Höbel G. 2000. Reproductive ecology of *Hyla rosenbergi* in Costa Rica. *Herpetologica* **56:** 446–454.

Hoogmoed MS. 1979. Resurrection of *Hyla ornatissima* Noble (Amphibia, Hylidae) and remarks on related species of green tree frogs from the Guiana area. Notes on the herpetofauna of Surinam VI. *Zoologische Verhandelingen* **172:** 1–46.

Hoogmoed MS. 1990. Resurrection of *Hyla wavrini* Parker (Amphibia: Anura: Hylidae), a gladiator frog from northern South America. *Zoologishe Mededelingen* **64:** 71–93.

Kizirian D, Coloma LA, Paredes-Recalde A. 2003. A new treefrog (Hylidae: *Hyla*) from southern Ecuador and a description of its antipredator behavior. *Herpetologica* **59:** 339–349.

Kluge AG. 1979. The gladiator frogs of Middle America and Colombia—a reevaluation of their systematics (Anura: Hylidae). *Occasional Papers of the Museum of Zoology, University of Michigan* **688:** 1–24.

Kluge AG. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Miscelaneous Publications, Museum of Zoology, University of Michigan* **160:** 1-170.

Köhler J. 2000. Amphibian diversity in Bolivia: a study with special reference to montane forest regions. *Bonner Zoologische Monographien* **48:** 1–243.

Köhler J, Koscinski D, Padial JM, Chaparro JC, Handford P, Lougheed SC, De la Riva I. 2010. Systematics of Andean gladiator frogs of the *Hypsiboas pulchellus* species group (Anura, Hylidae). *Zoologica Scripta* **39:** 572–590.

Kwet A, Lingnau R, Di-Bernardo M. 2010. Pró Mata: Anfíbios da Serra Gaúcha, sul do Brasil. Porto Alegre: EDIPUCRS.

Landestoy MA. 2013. Observations on the breeding behavior of the Hispaniolan Green Treefrog, *Hypsiboas heilprini*. *IRCF Reptiles & Amphibians* **20:** 160–165.

Lehr E, von May R. 2004. Rediscovery of *Hyla melanopleura* Boulenger, 1912 (Amphibia: Anura: Hylidae). *Salamandra* **40:** 51–58.

Lehr E, Faivovich J, Jungfer K-H. 2010. A new Andean species of the *Hypsiboas pulchellus* group: Adults, calls, and phyllogenetic relationships. *Herpetologica* **66:** 296–307.

Loebmann D, Zina J, Araújo OGS, Toledo LF, Haddad CFB. 2008. Acoustic repertory of *Hypsiboas exastis* (Caramaschi and Rodrigues, 2003) (Amphibia, Hylidae). *South American Journal of Herpetology* **3:** 96–100.

Lugli L, Haddad CFB. 2006a. New Species of *Bokermannohyla* (Anura, Hylidae) from Central Bahia, Brazil. *Journal of Herpetology* **40:** 7–15.

Lugli L, Haddad CFB. 2006b. A new species of the *Bokermannohyla pseudopseudis* group from central Bahia, Brazil (Amphibia, Hylidae). *Herpetologica* **62:** 453–465.

Lutz A, Lutz B. 1938. I. On *Hyla aurantiaca* Daudin and *Sphoenorhynchus* Tschudi and on two allied Hylae from south-eastern Brazil. II. Two new hylae: *H. albosignata* n. sp. & *H. pickeli*. *Anais da Academia Brasileira de Ciências* **10:** 175–194.

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

MacCulloch RD, Lathrop A. 2005. Hylid frogs from Mount Ayanganna, Guyana: new species, redescriptions, and distributional records. *Phyllomedusa* **4:** 17–37.

Magalhães RF, Lacerda JVL, Reis LP, Garcia PCA, Pinheiro PDP. 2018. Sexual dimorphism in *Bokermannohyla martinsi* (Bokermann, 1964) (Anura, Hylidae) with a report of male–male combat. *South American Journal of Herpetology* **13:** 202–209.

Marinho P, Costa-Campos CE, Pezzuti TL, Magalhães RF, Souza MRD, Haddad CFB, Giaretta AA, Carvalho TR. 2020. The Amapá treefrog *Boana dentei* (Bokermann, 1967): diagnosis and redescription (Hylinae: Cophomantini). *Journal of Natural History* **54:** 971–990.

Marquez R, De la Riva I, Bosch J. 1993. Advertisement calls of Bolivian species of *Hyla* (Amphibia, Anura, Hylidae). *Biotropica* **25:** 426–443.

Martins M, Haddad CFB. 1988. Vocalizations and reproductive behaviour in the smith frog, *Hyla faber* Wied (Amphibia: Hylidae). *Amphibia-Reptilia* **9:** 49–60.

Mueses-Cisneros JJ, Anganoy-Criollo MA. 2008. Una nueva especie del grupo *Hyloscirtus larinopygion* (Amphibia: Anura: Hylidae) del suroccidente de Colombia. *Papéis Avulsos de Zoologia* **48:** 129–138.

Myers CW, Donnelly MA. 2008. The summit herpetofauna of Auyantepui, Venezuela: report from the Robert G. Goelet American Museum–Terramar Expedition. *Bulletin of the American Museum of Natural History* **308:** 1–147.

Noble GK. 1923. Six new batrachians from the Dominican Republic. *American Museum Novitates* **61:** 1–6.

Ouboter PE, Jairam R .2012. Amphibians of Suriname. Leiden: Brill.

Peloso PLV, Oliveira RM, Sturaro MJ, Rodrigues MT, Lima-Filho GR, Bitar YOC, Wheeler WC, Aleixo A. 2018. Phylogeny of map tree frogs, *Boana semilineata* species group, with a new Amazonian Species (Anura: Hylidae). *South American Journal of Herpetology* **13:** 150–169.

Pimenta B, Costa D, Murta-Fonseca R, Pezzuti TL. 2014. Anfíbios—Alvorada de Minas, Conceição do Mato Dentro, Dom Joaquim, Minas Gerais. Belo Horizonte: Bicho do Mato Editora.

Pyburn WF. 1977. A new hylid frog (Amphibia, Anura, Hylidae) from the Vaupés River of Colombia with comments on related species. *Journal of Herpetology* **11:** 405–410.

Reynolds RP, Foster M. 1992. Four new species of frogs and one new species of snake from the Chapare region of Bolivia, with notes on other species. *Herpetological Monographs* **6:** 83–104.

Rivero JA. 1972 [1971]. Notas sobre los anfibios de Venezuela: 1. Sobre los hilidos de la Guayana Venezolana. *Caribbean Journal of Science* **11:** 181–193.

Rojas-Runjaic FJM, Infante-Rivero EE, Barrio-Amorós CL. 2016. New records, range extension and call description for the stream-breeding frog *Hyloscirtus lascinius* (Rivero, 1970) in Venezuela. *Amphibian & Reptile Conservation* **10:** 34–39.

Rojas-Runjaic FJM, Infante-Rivero EE, Salerno PE, Meza-Joya FL. 2018. A new species of *Hyloscirtus* (Anura, Hylidae) from the Colombian and Venezuelan slopes of Sierra de Perijá, and the phylogenetic position of *Hyloscirtus jahni* (Rivero, 1961). *Zootaxa* **4382:** 121–146.

Ron SR, Caminer MA, Varela-Jaramillo A, Almeida-Reinoso D. 2018. A new treefrog from Cordillera del Cóndor with comments on the biogeographic affinity between Cordillera del Cóndor and the Guianan Tepuis (Anura, Hylidae, *Hyloscirtus*). *ZooKeys* **809:** 97–124.

Ron SR, Merino-Viteri A, Ortiz DA. 2019. Anfibios del Ecuador. Version 2019.0. Museo de Zoología, Pontificia Universidad Católica del Ecuador, https://bioweb.bio/faunaweb/amphibiaweb (accessed 08 May 2019).

Savage JM. 2002. The Amphibians and Reptiles of Costa Rica. Chicago: University of Chicago Press.

Schulze A, Jansen M, Köhler G. 2015. Tadpole diversity of Bolivia's lowland anuran communities: molecular identification, morphological characterisation, and ecological assignment. *Zootaxa* **4016:** 1–111.

Sturaro MJ, Costa JCL, Maciel AO, Lima GR, Filho, Rojas-Runjaic FJM, Mejia DP, Ron SR, Peloso PLV. 2020. Resolving the taxonomic puzzle of *Boana cinerascens* (Spix, 1824), with resurrection of *Hyla granosa gracilis* Melin, 1941 (Anura: Hylidae). *Zootaxa* **4750:** 1–30.

Toledo LF, Araújo OGS, Guimarães L, Lingnau R, Haddad CFB. 2007. Visual and acoustic signaling in three species of Brazilian nocturnal tree frogs (Anura, Hylidae). *Phyllomedusa* **6:** 61–68.

Uetanabaro M, Prado CPA, Rodrigues DJ, Gordo M, Campos Z. 2008. Guia de campo dos Anuros do Pantanal e planaltos de entorno. Campo Grande: Editora UFMS / Cuiabá: Editora UFMT.

Vargas F, Bolaños ME, Berrío H. 2000. Notas sobre la ecologia reproductiva de *Agalychnis spurrelli* (Anura: Hylidae) en una población de Anchicayá, Pacifico Colombiano. *Revista de la Academia Colobiana de Ciencias Exatas, Físicas y Naturales* **24:** 85–99.

Venegas PJ, Siu-Ting K, Jordán JC. 2008. Amphibia, Hylidae, *Hypsiboas pellucens*: First country record, Peru. *Check List. A Journal of Species Lists and Distribution* **4:** 214–217.

Vrcibradic D, Nascimento BB, Diniz BLT, Fusinatto LA. 2016. Observations on the natural history and body size of the poorly known Brazilian treefrog *Hypsiboas secedens* (Hylidae: Hylinae: Cophomantini). *Salamandra* **52:** 204–206.

Weber LN, Silva-Soares T, Salles ROL. 2009. Amphibia, Anura, Hylidae, *Hypsiboas secedens*: Reassessment of type locality coordinates and distribution extension. *Check List. A Journal of Species Lists and Distribution* **5:** 218–221.

Zaracho VH, Céspedez JA, Álvarez BB, Lavilla EO. 2012. Guía de campo para la identificación de los anfibios de la provincia de Corrientes (Argentina). San Miguel de Tucumán: Fundación Miguel Lillo.