

PAULO DURÃES PEREIRA PINHEIRO

**CONTRIBUIÇÕES AO ESTUDO DE
TAXONOMIA E SISTEMÁTICA DO GÊNERO
Boana Gray, 1825 (ANURA: HYLIDAE)**



**RIO CLARO - SP
Agosto - 2017**

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SISTEMÁTICA DO GÊNERO *BOANA* GRAY, 1825
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**Tese apresentada ao Instituto de Biociências
do Campus de Rio Claro, Universidade
Estadual Paulista Júlio de Mesquita Filho,
como parte dos requisitos para obtenção do
título de Doutor em Ciências Biológicas
(Zoologia)**

Orientador: Julián Faivovich

Co-orientador: Célio F. B. Haddad

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“Quando você se aproxima do ponto onde ela está, o som pára. Mas fique quieto, e ele voltará em pouco tempo. Você descobrirá uma perereca em uma touceira de capim, em uma folha, ou na lama.”

(Emílio A. Goeldi, 1895)

“Admiranda tibi levium spectacula rerum”

(Virgílio, 29 a.C.)

RESUMO

A tribo Cophomantini inclui espécies de pererecas que dentre outras características, possuem um pré-polex ósseo e avantajado. Atualmente inclui cinco gêneros. Seu maior gênero em riqueza de espécies, e também um dos mais diversos da família Hylidae, o gênero *Boana* contem atualmente 92 táxons formalmente descritos. No entanto, até o presente aproximadamente 60% de sua diversidade taxonômica foi analisada em filogenias mais inclusivas. O gênero *Boana* é dividido em sete grupos de espécies. Muitas de suas espécies são associadas a estes grupos através de caracteres fenotípicos. Alguns destes grupos, todavia encontram-se pouco suportados molecularmente, e apesar de várias espécies agruparem-se por fenótipos, os agrupamentos filogenéticos carecem de sinapomorfias fenotípicas. Na presente tese, foram amostradas seqüências de 83 espécies de *Boana*, bem como de espécimes pertencentes ao gênero, porém de taxonomia indefinida, totalizando 256 terminais para o gênero. Inserimos seqüências de DNA representando fragmentos de até dez genes por terminal do nosso banco de dados. Recuperamos *Boana liliae* inserida em *Myersiohyla*, outro gênero de Cophomantini. A análise filogenética das 83 espécies de *Boana* resultou em uma melhoria para o suporte de muitos dos seus relacionamentos internos, mas curiosamente, apesar da densa amostragem taxonômica, muitos agrupamentos permanecem pouco suportados. Finalmente, fizemos um estudo comparativo do pré-polex na tribo Cophomantini. Investigamos o elemento e estruturas osteológicas e musculares associadas, estabelecemos hipóteses de homologia, e otimizamos os caracteres levantados na árvore mais parcimoniosa recuperada anteriormente. O pré-polex das espécies desta tribo possui considerável plasticidade evolutiva, e suas duas morfologias generalizadas evoluíram diversas vezes na tribo Cophomantini.

Palavras-chave: *Boana*, Hylidae, Sistemática, Pré-polex, Taxonomia.

ABSTRACT

The tribe Cophomantini includes treefrog species which, among other traits, have an osseous and enlarged prepollex. Currently it includes five genera. The genus *Boana* is the most diverse of the tribe, and also one of the richest genera of Hylidae, including 92 formally described taxa. However, approximately 60% of its taxonomic diversity was analyzed in more inclusive phylogenies. The genus *Boana* is divided into seven groups of species. Many of its species are assigned to their respective groups through phenotypical characters. Some of those groups are still poorly supported molecularly. Even being many species assigned to their respective groups through phenotypes, many groupings remain without phenotypical synapomorphies. On the present thesis, we sampled sequences of 83 species of *Boana*, as well specimens of undetermined taxonomy, totalizing 256 terminals for the genus. Each terminal have sequences of up to ten gene fragments. We recovered *Boana liliae* nested within the genus *Myersiohyla*, also from the tribe Cophomantini. The phylogenetic analysis of the 83 species of *Boana* resulted in better supports for many of its internal relationships. Curiously, besides the dense taxonomic sampling, many groupings remain poorly supported. Finally, we made a comparative study of the prepollex within the tribe Cophomantini. We surveyed this element and osteological and myological structures associated, established homology hypothesis, and optimize the resulted characters on the most parsimonious tree previously recovered. The prepollex of species of this tribe have a considerable evolutionary plasticity, and its two basic morphologies evolved many times on the tribe Cophomantini.

Key Words: *Boana*, Hylidae, Systematics, Prepollex, Taxonomy.

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INTRODUÇÃO GERAL

Já se passou pouco mais de uma década desde que o gênero *Hypsiboas* Wagler, 1830 foi recuperado da sinonímia de *Hyla* Laurenti, 1768. Naquele trabalho, Faivovich et al. (2005) fizeram uma extensa revisão da subfamília Hyalinae, e dentre as diversas modificações e proposições taxonômicas que surgiram de seus resultados, muitas foram relacionadas ao, até então, enorme gênero *Hyla*. Para o grupo que passou a ser identificado como *Hypsiboas*, outro nome que havia era *Boana* Gray, 1825, cujo uso já foi proposto por outros autores, sem discussões a respeito (Duellman, 2001; Savage, 2002; Wiens et al., 2005). Faivovich et al. (2005), no entanto, ao revisar o confuso trabalho de Gray (1825), concluíram que *Boana* seria um nome inválido, já que na prática nunca foi usado em uma combinação como nome específico, determinando-o como *nomen oblitum*.

Porém, bem recentemente, Dubois (2017) revisou Gray (1825) e concluiu que na verdade *Boana* é um nome genérico válido, e que, portanto, a interpretação de Faivovich et al. (2005) foi errônea. Sendo assim, os arranjos sistemáticos dentro do grupo seguem os mesmos, porém o gênero passa a ser identificado por *Boana* Gray, e não mais por *Hypsiboas* Wagler. É importante comentar, que quando este projeto iniciou-se, usava-se o nome *Hypsiboas*, e como se pode imaginar, até há pouco, este nome seguiu em uso. Por isso, alguns trabalhos que foram publicados no decorrer de nossas atividades, e que encontram-se no corpo desta tese, usaram o nome *Hypsiboas* em seu conteúdo.

Na revisão de Hyalinae, Faivovich et al. (2005) com uma amostragem que representava aproximadamente 62% da diversidade de *Boana* (naquele momento, mas que hoje representa 49% da mesma; como *Hypsiboas*), demonstraram não só a monofilia de *Boana*, como também propuseram uma série de rearranjos taxonômicos que permanecem seguidos até hoje. Apesar do grande déficit amostral para o gênero naquele momento, nos anos seguintes foram

poucas as alterações taxonômicas que se sucederam, e pouco se avançou sobre a sistemática do grupo.

Boana é um gênero pertencente à família Hylidae. Esta é atualmente uma das mais diversas famílias de anuros em número de espécies, representando cerca de 10-15% da ordem, dependendo do esquema classificatório sendo seguido (Frost, 2017; Faivovich et al., 2005; Duellman et al., 2016). Faivovich et al. (2005) ao fazer uma revisão molecular do grupo, definiram Hylidae como dividida em três subfamílias: Hylinae, Phyllomedusinae e Pelodriadinae. Estas, por sua vez, subdivididas em diversas tribos. Recentemente, Duellman et al., (2016) fizeram uma nova análise filogenética, incluindo a maioria das seqüências de hílideos publicadas subsequente ao trabalho de Faivovich et al. (2005). Apesar do incremento taxonômico, os resultados obtidos não trouxeram grandes novidades nas relações filogenéticas do grupo. Porém, mesmo assim, Duellman et al. (2016) elevaram as três subfamílias reconhecidas por Faivovich et al. (2005) ao nível de família; suas respectivas tribos ao nível de subfamília; além da descrição e revalidação de diversos gêneros. Os autores fizeram tais mudanças sem nenhum argumento sistemático, i.e., sem apresentar sinapomorfias, nem propor características diagnósticas para os novos agrupamentos. Portanto, optamos na presente tese, por manter o esquema classificatório de Faivovich et al. (2005).

O foco deste trabalho encontra-se na tribo Cophomantini, que por sua vez encontra-se inserida em Hylinae. A tribo é composta pelos cinco gêneros (Faivovich et al., 2005): *Aplastodiscus* Lutz, 1950; *Boana* Gray, 1825; *Bokermannohyla* Faivovich, Haddad, Garcia, Frost, Campbell, & Wheeler, 2005; *Hyloscirtus* Peters, 1882; e *Myersiohyla* Faivovich, Haddad, Garcia, Frost, Campbell, & Wheeler, 2005, relacionados da seguinte maneira: (*Myersiohyla* (*Hyloscirtus* (*Bokermannohyla* (*Aplastodiscus*; *Boana*))).

Até o ano de 2005 as espécies hoje alocadas em *Boana*, juntamente com várias outras pertencentes à tribo Cophomantini, eram agrupadas com base em evidências de distintas

naturezas. Em poucos casos os agrupamentos se basearam em possíveis sinapomorfias. Na maioria dos casos, porém, eram feitos por morfologia geral dos táxons sendo comparados. Muitos destes arranjos foram desfeitos por Faivovich et al. (2005), e novos agrupamentos foram propostos, embasados em uma hipótese filogenética. Para um breve histórico dos antigos arranjos taxonômicos, não só do que hoje se entende por *Boana*, mas também se estendendo a toda a família Hylidae, ver a introdução de Faivovich et al. (2005), pags. 14 à 43.

Faivovich et al. (2005), com base em seqüências de DNA, reconheceram sete principais grupos monofiléticos para o gênero. Os grupos de *Boana albopunctata*, *B. benitezi*, *B. faber*, *B. pellucens*, *B. pulchella*, *B. punctata*, e *B. semilineata*. As espécies que não foram testadas foram associadas aos seus respectivos grupos com base em sua morfologia e também em seus trabalhos taxonômicos originais. Além disto, naquele momento *Boana fuentei* (Goin & Goin, 1968) e *B. varelae* (Carrizo, 1992) não foram alocadas em nenhum grupo.

Diversos outros trabalhos com filogenia, utilizando diferentes critérios de otimização, surgiram desde então. De uma maneira geral, os resultados alcançados por Wiens et al. (2005, 2006, 2010), Pyron and Wiens (2011), Faivovich et al. (2013) e Duellman et al. (2016) encontram os mesmos agrupamentos de Faivovich et al. (2005), porém podendo variar o relacionamento entre os mesmos.

Além disso, várias novas espécies de *Boana* foram descritas nos últimos doze anos, e foram alocadas aos seus respectivos grupos tanto com seqüências de DNA (e.g., Antunes et al., 2008; Caminer & Ron, 2014; Fouquet et al., 2016), quanto através da taxonomia alfa clássica (e.g., Garcia et al. 2008; Kwet 2008; Carvalho et al., 2010). Ainda, alguns rearranjos taxonômicos foram feitos. Por exemplo, *Boana hutchinsi* (Pyburn and Hall, 1984) foi transferida de grupo devido a possíveis sinapomorfias morfológicas (Faivovich et al. 2006), e *B. ornatissimus* (Noble, 1923), devido à seqüências de DNA (Faivovich et al., 2013). Orrico

et al. (2017) com seqüências de DNA e características morfológicas retiraram *Boana xerophylla* (Duméril & Bibron, 1841) da sinonímia de *Boana crepitans* (Wied-Neuwied, 1824) e ainda incluíram *Boana fuentei* (Goin & Goin, 1968) na sinonímia de *B. xerophylla*, solucionando o problema taxonômico deste último nome.

Considerando todas as novidades taxonômicas dos últimos anos, hoje *Boana* compreende 92 espécies (Frost, 2017). Apesar de os agrupamentos propostos por Faivovich et al. (2005) se manterem, a relação de algumas espécies permanece pouco suportada—e.g., *Boana sibleszi* (Rivero, 1972), *B. picturata* (Boulenger, 1899)—assim como a posição dos grupos de *B. benitezi*, *B. punctata*, *B. semilineata* segue incerta. Para melhor compreensão destas relações, comparar os resultados obtidos por Faivovich et al. (2005, 2013), Wiens et al. (2005, 2006, 2010), Pyron and Wiens (2011), e Duellman et al. (2016).

Outro ponto importante é a carência de sinapomorfias morfológicas para *Boana*. Faivovich et al. (2005) discute uma série de sinapomorfias putativas para os agrupamentos infra-genéricos de *Boana*, porém, no que tange a definição do gênero, o único comentário feito é acerca do pré-polex desenvolvido em um espinho. Mas devido a este estado de caráter ser comum a *Bokermannohyla*, e a estes dois gêneros sequer serem irmãos, nada foi concluído. Seguindo as proposições de Duellman et al. (1997) os autores consideram ainda que o pré-polex bem desenvolvido poderia vir a constituir uma sinapomorfia da tribo Cophomantini, e chamam a atenção para a necessidade de um estudo profundo definindo caracteres envolvendo esta estrutura.

Considerando então, a necessidade de testar o posicionamento filogenético de diversas espécies de *Boana* até então relacionadas somente por fenética; a necessidade de estudos de natureza taxonômica para resolver problemas relacionados a alguns nomes; e a necessidade de estudos de evolução dentro do gênero, foi desenvolvida a presente tese. Nossos objetivos foram: (i) realizar uma análise filogenética molecular do gênero *Boana* contemplando o maior

número possível de espécies do gênero; (ii) aprimorar o conhecimento sobre o relacionamento entre e dentro dos grupos de *Boana*; (iii) resolver problemas de diferentes instâncias relacionados a taxonomia do grupo; (iv) aumentar o conhecimento sobre a diversidade do gênero; (v) estudar a diversidade morfológica e evolução do pré-pólex no contexto de Cophomantini.

Para tal, optamos por dividir esta tese em duas seções abrangendo diferentes propósitos. Em cada uma encontram-se distintos trabalhos que foram desenvolvidos no decorrer dos últimos quatro anos. Alguns se encontram já publicados, outros submetidos, e os demais em preparação para submissão a distintos periódicos acadêmicos. Portanto, devido às regras das diferentes revistas serem variadas, os trabalhos por nós aqui apresentados encontram-se com distintas formatações.

Na Seção 1, intitulada “Contribuições taxonômicas ao gênero *Boana*”, encontram-se descrições de espécies do gênero, bem como avaliações sobre os status taxonômicos de alguns nomes. Na Seção 2, “Estudos de sistemática e evolução de Cophomantini”, encontram-se estudos de cunho filogenético contemplando a sistemática e evolução do grupo, bem como da estrutura do pré-pólex.

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Seção 1

Contribuições taxonômicas ao gênero *Boana*

1 **The identity of *Hyla leucotaenia* Burmeister, 1861 (Anura: Hylidae)**

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15
16 The German naturalist Carl Hermann Conrad Burmeister (1807–1892) had a prolific scientific
17 career, spanning multiple taxa from diverse insect groups and trilobites to temnospondyls, birds,
18 and extant and fossil mammals (see Berg, 1895). His contributions to anuran taxonomy are
19 concentrated in two books, “*Erläuterungen zur Fauna Brasiliensis...*” (Burmeister, 1856) and
20 “*Reise durch die La Plata-Staaten...*” (Burmeister, 1861). The latter is an account of his travels
21 in Argentina and Uruguay from 1857–1860 and includes descriptions of three new species of
22 frogs: *Leiuperus nebulosus*, *Cystignathus mystacinus*, and *Hyla leucotaenia*. While the first two
23 names currently designate valid species, with the combinations *Pleurodema nebulosum* and
24 *Leptodactylus mystacinus* respectively, the last name has had a more complex taxonomic
25 history. It involves confusions involving a homonym, its consideration as a junior synonym of
26 *Hypsiboas pulchellus* (Duméril & Bibron, 1841)—a widely distributed species in eastern
27 Argentina, southeastern Brazil, and Uruguay (Frost, 2014)—and its actual identity
28 corresponding to another widespread species in the same geographic area, with which it has
29 never before been associated: *Scinax squalirostris* (A. Lutz, 1925). All these issues are
30 discussed in this paper.

Burmeister (1861) described *Hyla leucotaenia*, from “Paraná”, at that time the capital of Argentina and since 1883 the capital of the province of Entre Rios, on the eastern bank of the Rio Paraná. Subsequently, on the basis of a single specimen, Günther (1868) described a homonym from “Rio Grande”, referring to Rio Grande do Sul, Brazil. The fact that *Hyla leucotaenia* Günther, 1868 was preoccupied by *Hyla leucotaenia* Burmeister, 1861 was noticed by Boulenger (1886), who coined the replacement name *Hyla guentheri* for the former. Langone (1997) provided a detailed account of the taxonomic history of *Hyla guentheri* Boulenger, 1886 (now with the combination *Hypsiboas guentheri*). *Hyla leucotaenia* Burmeister was treated as a valid species, without comment, by Weyenberg (1876) and Avé-Lallemant (1895).

Berg (1896) considered *Hyla leucotaenia* Burmeister to be a junior synonym of *Hyla raddiana* Fitzinger, 1826. After describing variation in adults and juveniles, Berg (1896) states that “Probably *Hyla leucotaenia* Burm. was established in presence of equally young specimens” (translated from the Spanish). This proposal was followed by subsequent authors (Nieden, 1923; Miranda-Ribeiro, 1926; Barrio, 1965; Lutz, 1973; Gorham, 1974; Duellman, 1977; Ceí, 1980; Klappenbach & Langone, 1992; Lavilla, 1992) who included that name as a junior synonym of *Hyla raddiana* Fitzinger, 1826 or *Hyla pulchella* Duméril & Bibron, 1841, after Bokermann (1966) demonstrated that the latter name was the correct one to be applied for that species. The only comment on the synonymy, subsequent to Berg (1896), was by Lutz (1973) who stated that “*Hyla leucotaenia* Burmeister (1861) seems to be correctly interpreted by most authors as the juvenile of *Hyla pulchella*”.

The brief description by Burmeister (1861: p. 531–532) states that:

“Of the look and size of the *H. leucophyllata* (D. B. VIII, 607), but more slender, the head sharper with a rounded and truncated snout overhanging the mouth. – Vomer teeth on two little round knobs between the choanae backwards; tongue at the back not notched, but free; the tympanum small, but clearly visible. The color of the little animal with a snout vent length of 1 Zoll [= 2.54 cm], whose long, thin legs possess distinct calves, is dorsally a light reddish brown, which becomes darker towards the sides, taking there a silvery white stripe that extends from the nostril,

through the eye to the angle of the thigh, which is accompanied on each side by a brown band. The ventral surface plays into a grey-white coloration. As I am not able to find the species of this small treefrog anywhere, I allocate to him a new name assuming that the small animal does not grow larger as my specimens are all the same size.” (translated from the German).

Several aspects of this description, like the “rounded and truncated snout overhanging the mouth” or the “silvery white stripe that extends from the nostril, through the eye to the angle of the thigh, which is accompanied on each side by a brown band” are definitely not characters of juveniles of *Hypsiboas pulchellus* (voucher specimens MACN-HE 14953–963; See Appendix below).

While Burmeister (1861) makes no reference to type material of *Hyla leucotaenia*, he refers to the existence of at least two, but possibly more, specimens in his description, which, therefore, must be considered as syntypes. However, Duellman (1977) and Lavilla (1992) list ZMB (Museum für Naturkunde, Berlin) 7376 as the “holotype” specimen. Given the original description clearly states that it was based on more than one specimen, according to Art. 74.5 of the ICZN, Duellman’s (1977) mere use of the term holotype does not constitute a valid lectotype designation. Besides the ZMB, amphibians described by Burmeister are housed in the Zoological collections of the University of Halle, where a recent survey yielded no specimens that could be considered syntypes of *Hyla leucotaenia* (Grosse et al., in press; Grosse pers. com. to A. Kwet, June 14, 2014).

ZMB 7376 (Figs. 1A–C) is the only known specimen used in the description of *Hyla leucotaenia* Burmeister. Furthermore, in the original type catalogue, ZMB 7376 is clearly marked as a type specimen by an asterisk (hand-written by Wilhelm Peters; Tillack pers. com. to A. Kwet, June 24, 2014) and a red underline. Additionally, a red spot, which is normally used for type material in the ZMB collection, is on the jar, and an asterisk is noted on the jar label. A photograph of this specimen is also available on-line at <http://www.biologie.uni-ulm.de/systax/>. As we are not aware of the current housing of the additional type specimens, we designate ZMB 7376 as the lectotype of *Hyla leucotaenia* Burmeister, 1861.

The information provided by Burmeister (1861) is suggestive, and the syntype specimen evacuates any doubt, that *Hyla leucotaenia* is not a junior synonym of *Hypsiboas pulchellus*, but designates the same species known today as *Scinax squalirostris* (A. Lutz, 1925; Fig. 1D–F). Supporting its placement in *Scinax*, ZMB 7376 presents the two adult external morphological synapomorphies that support the genus: truncated adhesive disks of the hand, and the webbing between Toes I and II that does not extend beyond the subarticular tubercle of Toe I (Faivovich, 2002). Among the 112 described species of *Scinax* (Frost, 2014), *S. squalirostris* is unique by its elongated snout. The presence of this character together with a dorso-lateral silvery white stripe promptly distinguishes ZMB 7376 from any other species of the genus.

As ZMB 7376 corresponds with *Scinax squalirostris* and there is no possible confusion with any other described species, we consider *Hyla leucotaenia* Burmeister, 1861 a senior synonym of *Scinax squalirostris* (Lutz, 1925). Having established that, the usage of these names needs to be sorted out.

Article 23.9.1 of the ICZN states that prevailing usage should be maintained when (Art. 23.9.1.1) the senior synonym has not been used as a valid name after 1899, and (Art. 23.9.1.2) the junior synonym or homonym has been used, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of no less than 10 years. Both conditions are met in this case. *Hyla leucotaenia* has been considered a junior synonym of *Hyla pulchella* Dumeril & Bibron, 1841 since Berg (1896) and to our knowledge was never employed as a valid name since that time. The junior synonym *Hyla squalirostris* A. Lutz 1925, or the combinations *Oloolygon squalirostris* (A. Lutz, 1925) or *Scinax squalirostris* (A. Lutz, 1925), have been used in many more than 25 publications, from numerous authors, between 1965 and 2014: Bokermann (1966; 1967); Pyburn & Fouquette (1971); Lutz (1973); Duellman (1977); Fouquette & Delahoussaye (1977); Cei (1980); Prigioni & Langone (1984); Gallardo (1982; 1987); Gayer *et al.* (1988); Haddad *et al.* (1988); Basso (1990); Carvalho e Silva & Peixoto (1991); Klappenbach & Langone (1992); Lavilla (1992); Langone (1994); Pombal *et al.* (1995); Vega & Bellagamba (1996); Brandão *et al.* (1997); De la Riva *et al.* (2000); Natale *et al.* (2000); Lavilla & Cei (2001); Maneyro & Langone (2001); Faivovich

(2002); Achaval & Olmos (2003); Alcalde & Rosset (2003); Cacciali (2004); Costa *et al.* (2004); Núñez *et al.* (2004); Alcalde (2005); Faivovich *et al.* (2005); Kwet (2005); Brusquetti & Lavilla (2006); Caramaschi & Cardoso (2006); Canelas & Bertoluci (2007); Leite *et al.* (2008); Borteiro *et al.* (2009); Motte *et al.* (2009); Silva & Toledo (2010); Cardozo *et al.* (2011); Pombal *et al.* (2011); Fonte & Volkmer (2013); Attademo *et al.* (2014); and Brusquetti *et al.* (2014).

These conditions establish the prevailing usage of *Hyla squalirostris* A. Lutz, 1925 over *Hyla leucotaenia* Burmeister, 1861, in accordance with Art. 23.9.1 and its precedence over its senior synonym. As such, *Hyla squalirostris* A. Lutz, 1925 is a *nomen protectum*, and *Hyla leucotaenia* Burmeister, 1861 a *nomen oblitum*.

Scinax squalirostris (A. Lutz, 1925) is a highly variable, broadly distributed species, that occurs in southeastern, southern and central Brazil; northern La Paz in Bolivia; southern, central and eastern Paraguay; Uruguay; and central and northeastern Argentina (Frost, 2014). If a taxonomic revision of this species were to show that populations in its southern range are a distinct species from those from the vicinity of the type locality (Fazenda do Bonito, Serra da Bocaina, São José do Barreiro, São Paulo, Brazil), the name *Hyla leucotaenia* Burmeister, 1861 is available for them, following Art. 23.9.2 of the ICZN, as are the names *Hyla lindneri* Müller & Hellmich, 1936 and *Hyla evelynae* Schmidt, 1944.

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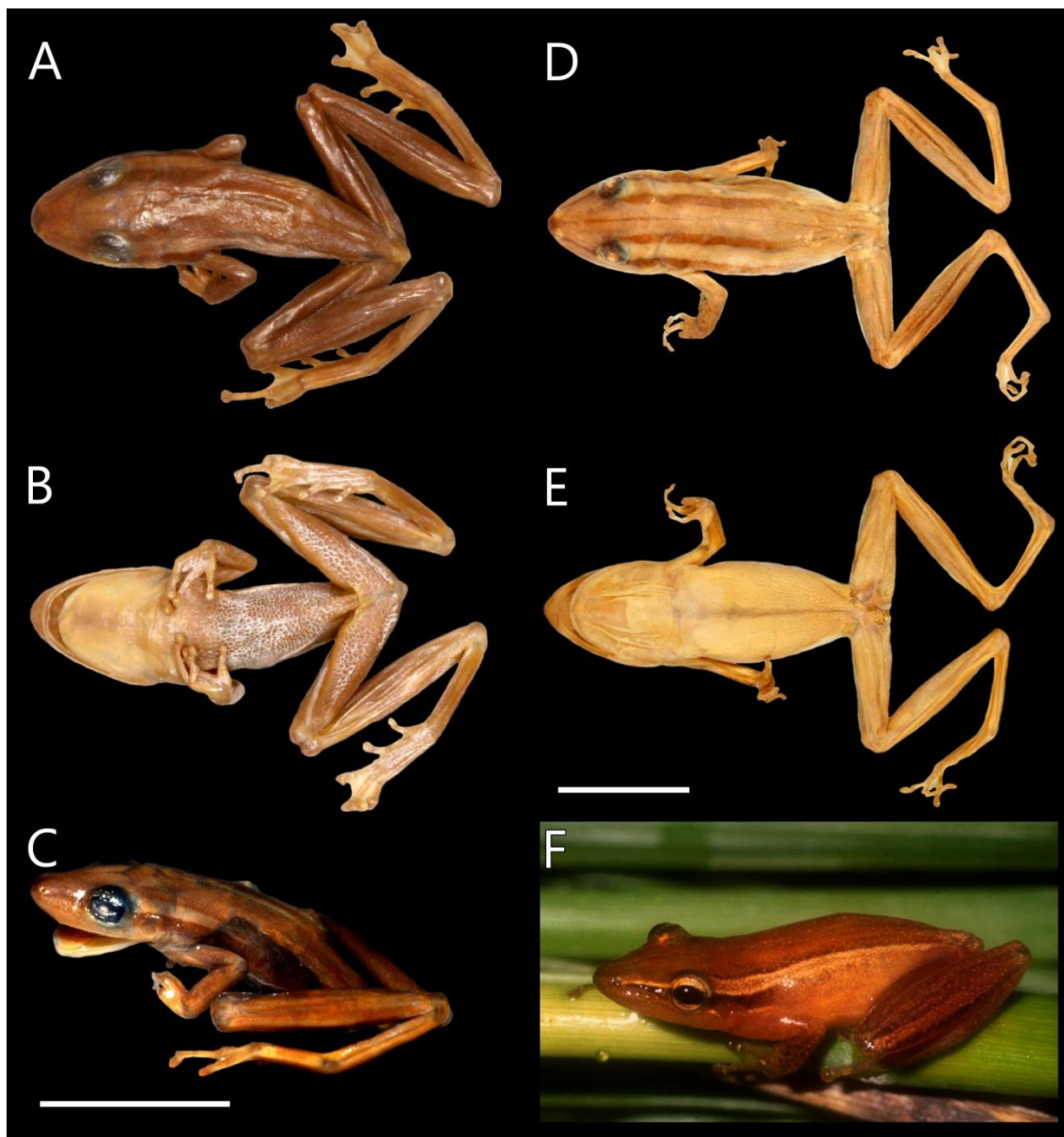
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- APPENDIX.** Examined specimens.
- Hyla leucotaenia*—ARGENTINA: ENTRE RÍOS: Paraná (ZMB 7376 [Museum für Naturkunde, Berlin]).
- Hypsiboas pulchellus*—ARGENTINA: CORRIENTES: Manatiales (MACN-HE 14953–963, juveniles [Herpetological Collection of Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires]).

Scinax squalirostris—BRAZIL: SÃO PAULO: Bonito, Serra da Bocaina (AL-MN 954 [Adolfo Lutz Collection, Museu Nacional, Rio de Janeiro]); ARGENTINA: ENTRE RÍOS: Basavilbaso (MACN-HE 38248 [Herpetological Collection of Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires]).

Figure 1. A–C: Syntype of *Hyla leucotaenia* Burmeister, 1861, ZMB 7376, here designated lectotype. **D–E:** Syntype of *Scinax squalirostris* (Lutz, 1925), AL-MN 954. **F:** adult male; MACN 38248, from Basavilbaso, Entre Rios, Argentina, 170 KM SE of Paraná, Entre Rios, the type locality of *Hyla leucotaenia*. Scale bars 10 mm. Photos: **A** and **B:** Frank Tillack; **C:** Axel Kwet; **D** and **E:** Marcos Bilate; **F:** Boris L. Blotto.

345

346 **Figure 1.**

**A New Species of the *Hypsiboas pulchellus* Group from the Serra da Mantiqueira,
Southeastern Brazil (Amphibia: Anura: Hylidae)**

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RRH: PINHEIRO ET AL.—A NEW SPECIES OF *HYPYSIBOAS*

ABSTRACT: A new species of the *Hypsiboas pulchellus* group is described from the Mantiqueira range, in the Município de Rio Preto, State of Minas Gerais, Brazil. We describe adults, tadpoles and the advertisement call. The new species is morphologically similar to *H. freicanecae*, a species known from a few localities in the states of Alagoas and Pernambuco, northeastern Brazil, ~1640 km north. Adults differ from *H. freicanecae* in having a slender body, smaller male size, larger calcar, and hidden surfaces of thighs and feet orange in life. Tadpoles have a ventral oral disc, with labial tooth row formula 2(2)/3–4(1), with one to three narrow posterior gaps on the marginal papillae located on the oral disc emarginations. The advertisement call is composed by two non-pulsed notes with dominant frequency at the second harmonic. The species is known only from its type locality, in an unprotected area.

Key words: Cophomantini; Species description; Tadpoles; Taxonomy; Treefrogs; Vocalization

THE *HYPYSIBOAS pulchellus* group is the most species-rich of the seven species groups of *Hypsiboas* Wagler 1830 (Faivovich et al. 2005). The group currently includes 38 species, representing more than one third of the described species in the genus (91 spp.; Frost 2016). The monophyly of the group has been corroborated by several analyses on the basis of molecular data (Faivovich et al. 2004, 2005, 2013; Wiens et al. 2010; Pyron and Wiens 2011). The only putative phenotypic synapomorphy known for the group, so far is the absence of the slip of the *m. depressor mandibulae* of scapular origin (Faivovich et al. 2005).

The species of the *H. pulchellus* group inhabit both streams and lentic water bodies in forests and grasslands, from northeastern Brazil in the State of Pernambuco to the pampean grasslands of Argentina, and westward to the eastern slopes of the Andes, from northern Argentina to central Peru. Phylogenetic analyses of the group (Faivovich et al. 2004, 2005, 2013;

Köhler et al. 2010; Lehr et al. 2010) show two Andean clades including four species each, while the bulk of the species included in the group are distributed in the Atlantic Forest in Brazil (20 species; only two reach adjacent areas in Argentina and Paraguay), seven species are distributed in the Cerrado formations, one mostly in pampean grasslands, and one in the Central Sierras of Argentina.

During a field trip in the mountains of Serra Negra, part of the Serra da Mantiqueira (Mantiqueira mountain range) in the State of Minas Gerais, Brazil, we collected a new species of the *H. puchellus* group, morphologically similar to *H. freicanecae* (Carnaval and Peixoto 2004). In this paper, we describe its adult and larval morphology and its advertisement call, and provide comments on the conservation status of Serra Negra.

MATERIALS AND METHODS

Adult Morphology and Species Description

Adults were euthanized in 5% lidocaine, fixed in 10% formalin, and preserved in 70% ethanol. Voucher specimens are housed in the Celio F.B. Haddad Amphibian Collection, Rio Claro, São Paulo, Brazil (CFBH); Amphibian Collection of Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil (UFMG); and Museu de Zoologia João Moojen de Oliveira, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil (MZUFV). Additional specimens used for comparisons are listed in the Appendix; museum acronyms follow Sabaj Pérez (2014). We measured specimens to the nearest 0.1 mm using digital calipers under a Zeiss Stemi SV 11 stereomicroscope. Measurements follow Duellman (1970): SVL (snout–vent length), HL (head length), HW (head width), ED (eye diameter), EN (eye–nostril distance), IND (internarial distance), EW (eyelid width), IOD (interorbital distance), TD (tympanum diameter), TL (tibia length), TAL (tarsal length), and FL

(foot length). We also measured SL (snout length; Cei 1980); THL (thigh length; Heyer et al. 1990); 3FD (Finger III disc diameter), and 4TD (Toe IV disc diameter; Napoli and Caramaschi 1999). Additionally, we measured CAL (calcar length; distance from the base to the tip of the calcar). Terminology for external morphology follows Duellman (1970), except for the dorsal outline of the snout, which follows Heyer et al. (1990). Webbing formulae follows Savage and Heyer (1967) as modified by Myers and Duellman (1982). Sex was determined by the development of a prepollex, vocalization, or presence of vocal slits in males, and presence of mature oocytes in the female specimen.

Tadpoles

Tadpoles were collected in the same pond where the adults were collected, euthanized in 5% lidocaine solution, then preserved in 10% formalin (one specimen was preserved in ethanol 95% as tissue for DNA analysis). Voucher lots are housed in the CFBH collection. To confirm the identity of the tadpoles, we used sequences of cytochrome oxidase c subunit I (COI; primers AnF1 and AnR1; Jungfer et al. 2013; GenBank accessions KX241479—KX241481 (tadpole, holotype, and recorded male paratype, respectively) showing 100% of similarity between adult and larva. Descriptions, measurements, and proportions of tadpole external morphology are based on six tadpoles in Gosner's (1960) stages 34–36 (lots CFBH 39392, 39405). In order to assess ontogenetic variation, 23 specimens in stages 25–39 were also analyzed (lots CFBH 39392, 39405). Measurements and terminology follow Altig and McDiarmid (1999): TL (total length), BL (body length), TAL (tail length), MTH (maximum tail height), IND (internarial distance), IOD (interorbital distance), TMW (tail muscle width), and TMH (tail muscle height); Lavilla and Scrocchi (1986): BW (body width), BWN (body width at narial level), BWE (body width at eyes level), BH (body height), ESD (eye–snout distance), END (eye–nostril distance), NSD (nostril–snout distance), ED (eye diameter), ND (narial diameter), SSD (snout–spiracular distance), and

ODW (oral disc width). We also measured DFH (dorsal fin height) and VFH (ventral fin height; Grosjean 2005); SL (spiracle length), SDH (spiracle distal edge height), and DF_iA (dorsal-fin insertion angle; Pinheiro et al. 2012); ODP (oral-disc position; angle formed by the tangent of the extended line connecting the anterior and posterior lips and the plane of longitudinal axes of the tadpole, characterized as ventral [$0^\circ < \times < 30^\circ$] and anteroventral [$31^\circ < \times < 80^\circ$]; adapted from Altig and Johnston 1989). Tadpoles were measured using ImageTool v3.00 (Wilcox et al. 1996) on digital photographs. To obtain high quality photos we used an adjustable platform for the support of the tadpoles immersed in water (Schacht and McBrayer 2009). Lateral line system terminology and descriptions follow Lannoo (1987) and Kolenc et al. (2008). Terminology for tooth morphology follows Vera Candioti and Altig (2010).

Recording and Vocalization Analysis

We recorded two specimens of the new species, at the same locality where we collected the entire series, using a Marantz PMD 660 digital recorder coupled to a Sennheiser K6/ ME66 microphone at 44.1 kHz with 16 bit sampling size. Air temperature was measured with an alcohol thermometer. The data were analyzed using software Raven Pro 64 v1.4 (Cornell Lab of Ornithology, Ithaca, NY). Spectrograms and power spectra were produced with window size of 256 samples, 75% overlap, hop size of 64 samples, and window type Hann. Resolution, contrast, and brightness were those of the default settings. Voucher specimens and recordings are housed at CFBH (Recordings CFBH/PDPP_1 and CFBH/PDPP_2).

The following acoustic parameters were considered: number of notes, note duration (time from the beginning to the end of one note, measured on the oscillogram), interval between notes (time from the end of one note to the beginning of the following note, measured on the oscillogram), interval between calls (time from the end of last note of one call to the beginning of the first note of the following call, measured on the oscillogram), dominant frequency range

(band of frequency in which the energy of the note is concentrated, measured on the spectrogram), and peak frequency (the specific frequency with higher energy of the note, accessed directly from Raven Pro software). Note definition follows Duellman and Trueb (1986). For all parameters we analyzed eight calls from two males (four calls from each male).

SPECIES ACCOUNT

Hypsiboas cambui sp. nov.

(Table 1; Figs. 1–3)

Holotype.—CFBH 39397, an adult male from Brazil: State of Minas Gerais: Município de Rio Preto: Vilarejo do Funil (22°0'19"S, 43°53'20"W, 905 m above sea level; datum = WGS84), collected on 27 February 2015 by P.D.P. Pinheiro, B. Blotto and B. Lisboa.

Paratypes.—All adults (15 males, one female), collected in the type locality. CFBH 39393 (female); CFBH 39394–39396, 39398–39402 (males), collected with the holotype. CFBH 39403, 39404 (males), collected on 6 March 2015 by P.D.P. Pinheiro and F. A. Brusquetti. UFMG 12449–12451 (males) collected on 27 January 2007 by B.G. Pacheco. MZUFV 9016–9017 (males) collected between 30 November and 4 December 2008 by E.F. Oliveira, J.T. Santos and I.G. Dias.

Diagnosis.—A member of the *H. pulchellus* group, as indicated by the absence of a scapular origin of the *m. depressor mandibulae*. This new species is distinguished by the following combination of characters: Male SVL 26.3–32.8 ($n = 16$), single known female SVL 32.7; slender body; palpebral membrane almost entirely translucent; large, triangular calcar (CAL / TAL 0.07–0.11); dorsum pale to dark brown, with a whitish cream (female) to pale and light brown (males) dorsolateral band on each side of the dorsum, that contours the posterior outer half of the eyelid and expand anteriorly into a triangle that covers the dorsal surface between the

orbits and the tip of the snout (Figs. 1–3); hidden parts of thighs orange; absence of bars and spots on flanks and hidden surfaces of thighs; nuptial pads absent; vomerine teeth in two short and transverse series; tadpoles with oral disc 33–39% of body width; labial tooth row formula (LTRF) 2(2)/3–4(1), with P2 larger than P1, and P4 one fourth of P3; row of marginal papillae with anterior gap and small posterior gaps on the oral disc emarginations; spiracle free distally; tail muscle cream colored, finely reticulated with melanophores contrasting with rounded light, unpigmented spots; fins translucent with scattered small light blotches; advertisement call composed of two non-pulsed notes of equal duration, with the dominant frequency at the second harmonics.

Comparisons.—The coloration pattern with a dorsolateral band on each side of the dorsum, that contours the posterior outer half of the eyelid and expand anteriorly into a triangle that covers the dorsal surface between the orbits and the tip of the snout in *H. cambui* resembles that of *H. freicanecae* (Carnaval and Peixoto 2004) and promptly distinguishes these two species from all other species of the *H. pulchellus* group. The new species differs from *H. freicanecae* by having a more slender body (robust in *H. freicanecae*), a smaller male SVL (26.3–32.8; 37.3–42.2 in *H. freicanecae*), a larger calcar (CAL / TAL 0.07–0.11; 0.03 in *H. freicanecae*; see also Carnaval and Peixoto 2004) and hidden surfaces of thighs and feet orange in life (pale cream in *H. freicanecae*).

Male SVL also differentiates *H. cambui* (26.3–32.8) from *H. aguilari* (33.7–43.8), *H. alboniger* (47.0–56.0), *H. balzani* (33.3–49.9), *H. bischoffi* (36.0–47.0), *H. callipleura* (37.2–43.3), *H. cordobae* (39.0–50.0), *H. cymbalum* (44.8–46.2), *H. gladiator* (35.3–49.4), *H. guentheri* (33.0–40.0), *H. joaquina* (40.3–56.4), *H. latistriatus* (34.9–40.6), *H. marginatus* (37.5–53.6), *H. marianitae* (36.5–56.8), *H. melanopleura* (43.6–50.0), *H. palaestes* (36.2–50.4), *H. poaju* (33.5–42.7), *H. prasinus* (41.0–47.0), *H. pulchellus* (37.0–49.0), *H. riojanus* (48.0–56.0), *H. secedens*

(55.0–57.0), *H. semiguttatus* (36.1–45.2), and *H. stellae* (40.7–49.9; Boulenger 1912; Bokermann 1963; Lutz 1963; Barrio 1965; Lutz 1973; Heyer et al. 1990; Duellman et al. 1997; Garcia et al. 2001, 2003, 2007, 2008; Caramaschi and Cruz 2004; Kwet 2008; Köhler et al. 2010; Lehr et al. 2010).

The absence of vertical bars or spots on hidden parts of thighs differentiates *H. cambui* from *H. alboniger* (Nieden 1923), *H. balzani* (Boulenger 1898), *H. bischoffi* (Boulenger 1887), *H. caingua* (Carrizo 1991), *H. callipleura* (Boulenger 1902), *H. cordobae* (Barrio 1965), *H. curupi* (Garcia et al. 2007), *H. cymbalum* (Bokermann 1963), *H. gladiator* (Köhler et al. 2010), *H. guentheri* (Boulenger 1886), *H. marianitae* (Carrizo 1992), *H. prasinus* (Burmeister 1856), *H. pulchellus* (Duméril and Bibron 1841), *H. riojanus* (Koslowsky 1895), *H. secedens* (Lutz 1963), and *H. stellae* (Kwet 2008; vertical bars or spots on hidden parts of thighs present in these species). The absence of vertical bars or spots on flanks differentiates *H. cambui* from *H. aguilari* (Lehr et al. 2010), *H. alboniger* (Nieden 1923), *H. balzani* (Boulenger 1898), *H. caingua* (Carrizo 1991), *H. caipora* (Antunes et al. 2008), *H. callipleura* (Boulenger 1902), *H. curupi* (Garcia et al. 2007), *H. cymbalum* (Bokermann 1963), *H. ericae* (Caramaschi and Cruz 2000), *H. gladiator* (Köhler et al. 2010), *H. guentheri* (Boulenger 1886), *H. joaquini* (Lutz 1968a), *H. marianitae* (Carrizo 1992), *H. melanopleura* (Boulenger 1912), *H. poaju* (Garcia et al. 2008), *H. prasinus* (Burmeister 1856), *H. pulchellus* (Duméril and Bibron 1841), *H. riojanus* (Koslowsky 1895), *H. secedens* (Lutz 1963), *H. semiguttatus* (Lutz 1925), and *H. stellae* (Kwet 2008; vertical bars or spots on flanks present in these species).

The new species can be distinguished from *H. bandeirantes* (Caramaschi and Cruz 2013), *H. beckeri* (Caramaschi and Cruz 2004), *H. bischoffi*, *H. botumirim* (Caramaschi et al. 2009), *H. buriti* (Caramaschi and Cruz 1999), *H. caingua*, *H. cipoensis* (Lutz 1968b), *H. goianus* (Lutz 1968b), *H. guentheri*, *H. jaguariaivensis* (Caramaschi et al. 2010), *H. latistriatus* (Caramaschi

and Cruz 2004), *H. leptolineatus* (Braun and Braun 1977), *H. phaeopleura* (Caramaschi and Cruz 2000), *H. polytaenius* (Cope 1870), and *H. stenocephalus* (Caramaschi and Cruz 1999) by the absence of longitudinal stripes and lines on dorsum (dorsal stripes and lines present in all these species).

The calcar is a character that *H. cambui* shares only with *H. bischoffi*, *H. freicanecae*, *H. polytaenius*, and *H. secedens*. It is also present in some specimens of *H. caingua* (e.g., CFBH 8605). *Hypsiboas cambui* does not have nuptial pads on the thumbs or reticulations on the palpebrae, and its vomerine teeth series are short and transverse whereas *H. secedens* has nuptial excrescences on thumbs, reticulations on the inferior portion of the palpebrae and vomerine teeth series long and oblique, forming an inverted “V”.

Description of the holotype.—Adult male; SVL 32.8; body slender; head wider than body, nearly as wide as long ($HW / HL = 0.94$); snout rounded in dorsal view ($SL / HL = 0.43$; $SL / HW = 0.43$), round in profile (Fig. 3A,B); eye–nostril distance shorter than eye diameter ($EN / ED = 0.75$); canthus rostralis slightly curved in dorsal view and rounded in cross section; loreal region slightly concave; lips thin, not flared; internarial region barely depressed; nostrils not protuberant, dorsolaterally directed; interorbital area flat, shorter than eye diameter ($IOD / ED = 0.79$), more than three times shorter than head width ($IOD / HW = 0.28$). Eyes large and protuberant ($ED / HL = 0.33$; $ED / HW = 0.35$); palpebral membrane translucent, without reticulations, and its lower portion poorly pigmented. Supratympanic fold poorly developed, covering the upper portion of tympanic ring, extending to arm insertion. Tympanum small ($TD / ED = 0.46$), distinct, directed dorsolaterally, separated from eye by a distance slightly longer than tympanum diameter.

Arm slender, not hypertrophied, lacking an axillary membrane; a row of small and juxtaposed ulnar tubercles extend from proximal limit of hand to the elbow. Fingers long, bearing

round discs; disc diameter on Finger III slightly narrower than tympanum ($TD / 3FD = 1.05$); relative finger length $I < II < IV < III$; webbing formula $I-II\ 2-3^{1/2}\ III\ 3-2^{1/2}\ IV$; presence of lateral fringes on fingers; subarticular tubercles distinct, non-bifid, and rounded in ventral view; subarticular tubercles conical in profile on fingers I and II and flat on III and IV; supernumerary tubercles present; inner metacarpal tubercle flat and elongated; outer metacarpal tubercle bifid, flat, and large (Fig. 3C). Nuptial pad absent; prepollex enlarged and pointed as a bony spine that is evident under the skin.

Hind limbs long and slender ($THL / SVL = 0.47$; $TL / SVL\ 0.51$); tarsal fold present, extending from inner metatarsal tubercle to the heel; calcars large ($CAL / TAL = 0.09$) and triangle shaped in dorsal view. Toes long, bearing round discs, slightly smaller than those on fingers ($4TD / 3FD = 0.93$); relative toe length $I < II < III = V < IV$; webbing formula $I\ 1-2\ II\ 1-2\ III\ 1^{1/2}-2^+\ IV\ 2^+-1^+\ V$; presence of lateral fringes on toes; presence of a thickened layer of tissue at midline of webbing between toes IV and V. Subarticular tubercles moderately large, round in ventral view, slightly conical in profile; supernumerary tubercles present; outer metatarsal tubercle absent; inner metatarsal tubercle distinct, flat, and elliptical in ventral view (Fig. 3D).

Skin smooth except pectoral and abdominal areas, and ventral surfaces of thighs, where it is granular. Pectoral fold absent. Cloacal opening directed posteroventrally at upper level of thighs; cloacal sheath absent; a white, supracloacal dermal ridge present; cloacal tubercles present, scattered, extending to midlevel of thighs.

Tongue ovoid, barely free behind; dentigerous processes of vomers prominent, in two separate, nearly straight series converging medially, bearing six (right) and eight (left) teeth. Choanae large, almost rounded, spaced 2.4 mm from each other. Vocal slits moderately long,

extending from midlateral base of tongue, almost reaching the angle of jaws. Vocal sac single, median, subgular.

Measurements of holotype (in mm).—SVL 32.8, HL 10.9, HW 10.8, ED 3.8, EN 2.9, IND 2.0, EW 2.7, IOD 3.1, TD 1.6, TL 16.7, TAL 9.3, FL 13.6, SL 4.7, THL 15.9, 3FD 1.6, 4TD 1.3, CAL 1.1.

Coloration.—In life, at night, dorsum dark brown, with light brown dots (Fig. 1). Dorsum dark brown with a light brown dorsolateral band on each side, that contours the posterior outer half of the eyelid and expand anteriorly into a triangle that covers the dorsal surface between the orbits and the tip of the snout (for simplicity, we hereinafter refer to this pattern as “dorsolateral bands and triangle”). A cream line delimits the dorsolateral bands internally, and the triangle, running along the canthus rostralis, and extending anteriorly to the tip of the snout where it joins a labial stripe. Upper part of loreal region dark brown, like the dorsum of the body, with the limit between it and the labial stripe with a gradual change in colors. Palpebral membrane translucent with its lower portion partially pigmented, following the pattern of the loreal region. Laterally, a dark brown band ventrally delimited by a cream line extends from behind the eye, covering the upper portion of tympanum, to inguinal region. Ulnar tubercles, tip of calcar, and cloacal crest whitish cream. Dorsally, limbs and thickened layer of tissue at midline of webbing between toes IV and V light brown. Small, irregular dark blotches on dorsal surface of tibia. Hidden surfaces of thigh and foot webbing orange. Posterior region of elbow and ankle, and dorsal region of cloaca dark brown. Ventral surfaces of arm and body cream. Iris copper to golden, with fine black reticulation. Bones green, visible through the skin.

During the day, the colors are paler and the contrast between dark and light colors decreases. Also, it is possible to see tiny red dots all over the dorsal surfaces.

In preservative, the colors fade, turning into pale tones, with scattered melanophores. The red dots disappear, and the light brown dots of the dorsum become whitish. The orange colors of the hidden surfaces of thighs and webbing turn paler or completely vanish. The contrast between the dorsolateral bands and triangle, and the dorsum also diminishes (Fig. 2).

Variation.—Some measurements and body proportions are provided in Table 1. Webbing formulae on hands varies as follows I—II ($2-2^+$)—($3-3^{1/2}$) III ($2^{1/2}-3$)—($2-2^{1/2}$) IV, while webbing on feet varies as I ($1^-1^{1/2}$)—(2^-2^+) II ($1-1^+$)—($2-2^+$) III ($1-1^{1/2}$)—($2-2^{1/2}$) IV ($2^+-2^{1/2}$)—($1-1^+$) V. Light dots on dorsum can vary in number or might be absent in some specimens (CFBH 39394, 39396, 39398, 39399; UFMG 12250–12251; variation illustrated in Fig. 1B–D). The dorsolateral bands and triangle, and dorsum of limbs can be yellowish (CFBH 39400); some males that were collected during vocal activity showed pale tones and weaker contrast with the dorsum (CFBH 39403). The cream line that contours the dorsolateral bands and triangle can be absent (CFBH 39400; UFMG 12449–12251; MZUFV 9017). The loreal region can have a well defined upper dark brown band, with the limit between it and the labial stripe marked with a sinuous pattern, and not a gradual change in colors as in the holotype (CFBH 39400). In some specimens, the dorsolateral bands and triangle have small dark brown spots or blotches (CFBH 39400; UFMG 12249, 12250; MZUFV 9016). In one specimen (CFBH 39400), forearm with a lateral dark brown blotch, and tibia with a lateral dark brown stripe. Dark brown blotches on tibia may be absent (CFBH 39394).

The only known female (CFBH 39393) has the dorsolateral bands and triangle, spots on dorsum, and dorsal parts of arms and legs whitish cream. The lateral dark brown stripe covers the entire tympanum; and the tibia presents a dark brown lateral stripe (Fig. 1E). There is no difference in SVL or development of forearms between sexes, but the female has a less developed prepollex than the males.

Etymology.—“Cambuí” is a Portuguese word derived from the tupi “Kābu’i,” attributed to many species of small to medium size, twisted trees of Myrtaceae, that occur close to streams and wet soils, like those of the locality where we found the species. Also, the local people know the area where the animals were collected with the name “Cambuí.” The name is used here as a noun in apposition.

Tadpole.—(stages 34–36; lots CFBH 39392, 39405; Table 2; Fig. 4) Body depressed (BH / BW = 0.91–0.95; Fig. 4A,B), BL 0.31–0.36 times TL; elliptical in dorsal view; in lateral view, ventral contour flat in peribranchial region, slightly convex in abdominal region. Snout oval in dorsal view (BWN / BWE = 0.74–0.77) and rounded in lateral view. Nostrils large (ND / BL = 0.06–0.07), elliptical, dorsolaterally directed, with a triangular fleshy projection on the medial margin that gives it a reniform appearance (Fig. 4E); nostrils dorsally located (IND / BWN = 0.44–0.51), closer to snout than to the eyes (NSD / ESD = 0.43–0.48). Eyes medium-sized (ED / BWE = 0.23–0.25), dorsally located (IOD / BWE = 0.82–0.90), dorsolaterally directed. Spiracle sinistral, lateral, visible in dorsal and lateral views (SDH / BH = 0.38–0.60), medium-sized (SL / BL = 0.10–0.13), posteriorly projected; its inner wall barely free from the body and slightly longer than the external wall; opening located at the posterior third of the body (SSD / BL = 0.75–0.86; Fig. 4B,D).

Lateral line system barely distinct, with the infra-orbital and middle lines (in the dorsal body region) being the most noticeable series. Cumuli of neuromasts anterolaterally to the base of the vent tube are also barely noticeable (Fig. 4F). Intestinal tube circularly coiled; its switchback point located at the center of abdominal region. Vent tube large with dextral opening; its mid-ventral portion fused to ventral fin (Fig. 4G).

Tail moderately high (MTH / TAL = 0.31–0.39), slightly higher than body (MTH / BH = 1.03–1.17); tail musculature slightly robust (TMH / BH = 0.44–0.53) reaching the tip of the

pointed tail. Dorsal fin moderately high ($DFH / TAL = 0.11\text{--}0.14$), with the free margin convex, emerging on posterior third of the body at a low slope ($DFiA = 4.4^\circ\text{--}15.13^\circ$); its maximum height at the anterior third of the tail. Ventral fin moderately high ($VFH / TAL = 0.08\text{--}0.12$) with its free margin almost parallel to the longitudinal axis of tail muscle; origin concealed by vent tube.

Oral disc (Fig. 5A,B) ventrally positioned ($ODP = 18.9^\circ\text{--}28.2^\circ$), medium-sized ($ODW / BW = 0.35\text{--}0.39$, measured with oral disc folded), with three posterior emarginations (one medial and two lateral); a single row of 99–121 conical marginal papillae with bases offset throughout the oral disc; presence of an anterior narrow gap (about 0.15 of ODW), and from one to three narrow posterior gaps located on the emarginations (corresponding to the absence of two to four papillae; Fig. 5A–C); one to six submarginal papillae located laterally in the angular region. Labial tooth row formula 2(2)/4(1); gaps in A-2 and P-1 about 0.27 and 0.08 mm, respectively; A-1 and A-2 of the same length; P-2 longer than P-1 and P-3, which are equal in length; P4 smaller than the others, consisting of 4–32 labial teeth; teeth density on P1 35–39 teeth/mm; presence of flaps with labial teeth laterally in the oral disc; teeth continuously curved from base to tip, with an obtuse oral angle; sheath 6.6 times wider than tip; body marked; head long, flattened, and curved with 6–8 marginal cusps; cusps from the tip higher than those from the base (Fig. 5D). Narrow jaw-sheaths darkly pigmented and finely serrated on the margins (34 to 48 triangular serrations on the upper jaw-sheath); upper jaw-sheath arc-shaped, lower jaw-sheath “V” shaped. Measurements for developmental stages 34–36 and 37–39 are shown in Table 2.

Coloration of tadpole in life.—Body with brownish background and marbled with black. Black dots and sparse silver blotches scattered dorsally over the body. Distal portion of spiracle lighter than the rest of the body. Intestinal coil visible ventrally. Tail musculature cream, finely reticulated with melanophores contrasting with rounded unpigmented spots; fins translucent with scattered, small light blotches. Dorsal region of dorsal fin reddish brown. A dark longitudinal

stripe starting from posterior end of body and extends posteriorly between dorsal and ventral caudal myotomes, reaching the proximal fourth of tail; dorsal margin of the caudal musculature with an interrupted, narrow brown line. Iris centrally copper to gold and peripherally with greenish tones. A golden rim surrounds the pupil. The anterior, posterior, dorsal and ventral areas of iris are dark.

Coloration of tadpole in preservative.—Silver blotches might disappear in the majority of specimens; the brownish background is paler, and the spiracle is whitish. The intestinal mass is visible both ventrally and laterally. The reddish brown on dorsal fin is paler or might totally disappear. Iris black (Fig. 4A–C).

Morphological variation in tadpoles.—The inner wall of the spiracle is totally fused to the body in Stage 25; it grows and separates during subsequent development. The switchback point of the intestine is dislocated anteriorly and to the left in two specimens in Stage 29, one in Stage 31, and one in Stage 37. ODW / BW varies between 0.33–0.39 when measures of specimens between stages 37–39 are included. The row of marginal papillae is aligned anteriorly in Stage 25. The presence of narrow posterior gaps in the row of marginal papillae, can be variable: four specimens in stages 28 (1), 34 (1), and 35 (2), have only the posterolateral gaps, and do not possess the medial one; five individuals (in stages 28, 29, 30, 30, and 39) have only the medial gap; posterior gaps are absent in two specimens in stages 28 and 29. Flaps with labial teeth are absent in eight specimens in stages 28 (3), 29 (2), 30 (1), 35 (1), and 39 (1). One specimen in Stage 39 presents one medial flap, between A1 and A2 labial tooth rows. P4 is reduced (approximately $\frac{1}{4}$ of P3 length) in two specimens (stages 36 and 39); laterally to it, some papillae bear few teeth. In one specimen in Stage 28 and four in Stage 31, P3 is smaller than P2. One specimen in Stage 29 presents P3 fused to P2 on its mid portion. Seven specimens with

LTRF 2(2)/3(1) in stages 28 (3), 29 (2), 30 (1), and 31 (1). The black line on the tail muscle axis is absent in some specimens (mostly in stages 25–28).

Comparison with tadpoles of other species of the *H. pulchellus* group.—From the 38 described species of the *H. pulchellus* group, the tadpoles of 15 remain undescribed. These include: *H. alboniger*, *H. beckeri*, *H. botumirim*, *H. buriti*, *H. callipleura*, *H. cymbalum*, *H. ericae*, *H. gladiator*, *H. guentheri*, *H. jaguariaivensis*, *H. phaeopleura*, *H. prasinus*, *H. secedens*, *H. stellae*, and *H. stenocephalus*. From the remaining 23 species, the tadpole of *H. cambui* is distinguished from those of *H. bischoffi*, *H. caipora*, *H. curupi*, *H. joaquini*, *H. marianitae*, and *H. poaju* by the relative width of the oral-disc (OD / BW 0.33–0.39 in *H. cambui* and OD / BW > 0.45 in the others; Heyer et al. 1990; Faivovich 1996; Lötters et al. 1999; Garcia et al. 2003, 2008; Antunes et al. 2008). As with most species of the *H. pulchellus* group, *H. cambui* has an anterior gap in the row of marginal papillae (the exception is *H. curupi* which has complete marginal papillation in the oral disc; Faivovich 1996). The presence of narrow posterior gaps in the row of marginal papillae, as described for *H. cambui*, has been reported only in two species of the *H. pulchellus* group (*H. freicanecae*, Carnaval and Peixoto 2004; *H. marianitae*, Lötters et al. 1999).

The LTRF in species of the *H. pulchellus* group varies commonly from 2(1,2)/3–4(1,2), reaching 2(2)/5(1) in *H. poaju* (Garcia et al. 2008), 3(1,2)/4(1) in *H. balzani* (Duellman et al. 1997), and 3(1,3)/5(1) in *H. curupi* (Faivovich 1996). With respect to species with LTRF 2/3–4, *H. cambui* has gaps on the A2 and P1 rows of labial teeth, whereas in addition to these two gaps, *H. caingua*, *H. goianus*, *H. latistriatus*, and *H. polytaenius* have a gap on A1 (Eterovick et al. 2002; Orrico et al. 2007; Kolenc et al. 2008; Pinheiro et al. 2012); *H. bandeirantes* has a gap on P2 (Heyer et al. 1990, as *Hyla polytaenia*); *Hypsiboas palaestes* can show gaps on A1, P2, and P3 (Duellman et al. 1997) and *H. pulchellus* can show gap on P2 (Fernández 1927). *Hypsiboas*

cambui has P2 longer than P1, whereas *H. aguilari*, *H. balzani*, *H. bandeirantes*, *H. bishoffi*, *H. caingua*, *H. caipora*, *H. cordobae*, *H. curupi*, *H. goianus*, *H. melanopleura*, *H. palaestes*, *H. poaju*, *H. polytaenius*, *H. pulchellus*, *H. riojanus*, and *H. semiguttatus* have P2 equal to P1 in length (Heyer et al. 1990; Faivovich 1996; Duellman et al. 1997; Eterovick et al. 2002; Garcia et al. 2007, 2008; Antunes et al. 2008; Kolenc et al. 2008; Lehr et al. 2011; Pinheiro et al. 2012). As with most species of the group, *H. cambui* has, polymorphically in this case, flaps with labial teeth laterally in the oral disc.

Hypsiboas cambui has a spiracle with only the distal portion of its inner wall free from the body (but see the variation reported for tadpoles in Stage 25), whereas *H. caingua* possesses an inner wall entirely free (Kolenc et al. 2008) and *H. cipoensis*, *H. goianus*, *H. leptolineatus*, *H. marginatus*, and *H. palaestes* have the inner wall entirely fused to the body (Duellman et al. 1997; Garcia et al. 2001; Eterovick et al. 2002; Both et al. 2007). The tadpoles of *H. cambui* can be differentiated from those of *H. freicanecae* by a shorter P4 (in *H. freicanecae*, P4 is ~50% of P3, while in *H. cambui* it reaches only 30% of P3), and a different pattern of tail coloration (*H. freicanecae* has dark brown to black coloration, with large dark brown to black spots on tail; Carnaval and Peixoto 2004).

We found adults of *H. faber* and larvae of *H. albomarginatus* in the same pond where we found the new species. Both *H. albomarginatus* and *H. faber* present a tube-like spiracle with its inner-wall entirely free from the body, differing from *H. cambui*, in which only the distal end of inner wall is free (Lutz 1973; Peixoto and Cruz 1983; Kolenc et al. 2008). Also, tadpoles of *H. albomarginatus* have smaller nostrils (ND / BL 0.03–0.05; $n = 12$; stages 28–36; lots UFMG 1854, 1855; see Appendix). The tadpoles of *H. faber* have much more noticeable cumuli of neuromasts, a brown to black tail, and fins with dark blotches (Kolenc et al. 2008).

Advertisement call.—(Recordings CFBH/PDPP_1 and CFBH/PDPP_2) The call

described here is probably the advertisement call of the species (as defined by Wells 1977). We infer this because the two males were found vocalizing in isolated situations—the first individual started its activity around 2030 h (air temperature = 19°C) and the second individual at 2300 h (air temperature = 17°C). In both cases, no other males were calling nor, as far as we could see, perched nearby. The males were found calling perched on grass and a branch, 20 and 40 cm above water level, respectively, in the middle of a swampy pond. Values are reported as range (mean $\pm$ 1 SD).

The call of *H. cambui* (Fig. 6) is composed of one (25% of analyzed calls) or two non-pulsed notes (75% of analyzed calls). Note duration is 23–54 ms (34 ± 9 ms; $n = 14$). When composed by two notes, the interval between them varies between 69–121 ms (88 ± 19 ms; $n = 6$). The fundamental frequency of the note is 2062.5 Hz. The dominant frequency is on the second harmonic and ranges between 3382.6–5076.7 Hz, and the peak frequency is normally at 4125 Hz ($n = 11$; one male presented the peak frequency of three notes at 4312.5 Hz). Other harmonics, with less energy than the fundamental and dominant frequencies, were found at 6187.5, 8250, and 10312.5 Hz. Interval between calls varies between 2.13–4.73 s (3.39 ± 1.24 s; $n = 4$).

Comparison with advertisement calls of other species of the *Hypsiboas pulchellus*

group.—From the 38 described species of the *H. pulchellus* group, the advertisement call of 12 remain undescribed: *H. alboniger*, *H. buriti*, *H. caingua*, *H. cipoensis*, *H. cymbalum*, *H. freicanecae*, *H. guentheri*, *H. jaguariaivensis*, *H. latistriatus*, *H. leptolineatus*, *H. secedens*, and *H. stenocephalus*. Although calls of *H. latistriatus* and *H. leptolineatus* are undescribed, they have a very similar structure to the calls of *H. bandeirantes*, *H. beckeri*, and *H. polytaenius* (P.D.P. Pinheiro, personal observation). The non-pulsed notes of *H. cambui* are distinct from those of *H. aguilari*, *H. balzani*, *H. bandeirantes*, *H. beckeri*, *H. bischoffi*, *H. botumirim*, *H.*

caipora, *H. callipleura*, *H. curupi*, *H. ericae*, *H. gladiator*, *H. joaquini*, *H. latistriatus*, *H. leptolineatus*, *H. marginatus*, *H. marianitae*, *H. melanopleura*, *H. palaestes*, *H. poaju*, *H. polytaenius*, *H. prasinus*, *H. semiguttatus*, and *H. stellae*, which emit pulsed notes (Barrio 1965; Heyer et al. 1990; Márquez et al. 1993; Duellman et al. 1997; Garcia et al. 2001, 2007, 2008; Köhler et al. 2006, 2010; Acioli and Toledo 2008; Antunes et al. 2008; Garcia and Haddad 2008; Kwet 2008; Caramaschi et al. 2009; Lehr et al. 2010; Pinheiro et al. 2012; Delgado and Haddad 2015).

The dominant frequency in the advertisement call of *H. cambui* is on the second harmonic, between 3382.6–5076.6 Hz, whereas *H. cordobae*, *H. goianus*, *H. phaeopleura*, *H. pulchellus*, and *H. riojanus* have the dominant frequency coincident with the fundamental frequency, between 1160–2450, 2925–3694, 2557.3–3554.8, 1203–3428, and 1700–2800 Hz, respectively (Barrio 1962, 1965; Márquez et al. 1993; Di Tada et al. 1996; Salas et al. 1998; Guimarães et al. 2001; Menin et al. 2004; Baraquet et al. 2007, 2013; Köhler et al. 2010; Pinheiro et al. 2012). The ability of an individual to change the emphasized frequencies has been documented in at least two species of *Hypsiboas*, however, as shown by Napoli and Cruz (2005) and Brunetti et al. (2015) for *H. atlanticus* and *H. punctatus*, respectively. Therefore, the dominant frequency on the second harmonic of all calls compared above could be biased by the small sample size. Whereas there is no difference in note duration in *H. cambui*, the last note of calls emitted by *H. cordobae* and *H. pulchellus* is longer than the first, and the first note is longer than the subsequent ones in *H. riojanus* (Márquez et al. 1993; Di Tada et al. 1996; Salas et al. 1998; Baraquet et al. 2007, 2013).

Natural history.—We found the new species in a swampy pond (Fig. 7B) completely covered by vegetation, at the side of a stream locally known as “Riacho do Funil”. The area is a fragment of primary forest in an area known by local people as Cambuí. At 2030 h, a few males

were calling from grass directly above the water, or from lianas and shrubs at the margin of the pond (air temperature = 19°C). These males were perched 0.4–2.0 m above the water surface. One specimen was bitter to the taste (P.D.P. Pinheiro, personal observation). Shortly after 2030 h, a rain fell on the area and the vocal activity of the frogs increased. Individuals started calling from > 3 m high, which suggests that they take shelter at the treetop when not active. The single female was found perched 1.6 m above the soil, approximately 5 m away from the pond. During this first night, there was no contact between the river and the pond. Also, we did not find any fish in the pond. Besides the adults and larvae of *H. cambui*, other species present include adults of *Rhinella crucifer*, *Hypsiboas faber*, *H. polytaenius*, *Dendropsophus berthalutzae*, *D. microps*, *D. cf. oliveirai*, and *Scinax argyreornatus*, and tadpoles of *H. albomarginatus*, *D. microps*, *Dendropsophus* sp., *Scinax* sp. 1 (*S. catharinae* group) and *Scinax* sp. 2 (*S. ruber* clade).

After a week of continuous rain (6 March 2015), with air temperature ~17°C, the activity at the pond was reduced compared to the previous observation. The water level of both river and pond had increased and there were two points of contact between them. Very few tadpoles were found and there were small fish in the pond. The only two males that were calling alone were recorded as described above in the advertisement call section. Those males were perched over grass and lianas, 20 and 40 cm above the water surface, respectively.

DISCUSSION

Hypsiboas cambui is morphologically more similar to *H. freicanecae* than to any other species of the *H. pulchellus* group. Interestingly, *H. freicanecae* has a distribution that is isolated from all other species of the group, being known only from the mountain forests in northeastern Brazil (Carnaval and Peixoto 2004; Cardoso et al. 2006), at Borborema Plateau. The

southernmost known population of *H. freicanecae* is from Município de Murici, State of Alagoas (Cardoso et al. 2006), which is ~1640 km north from the type locality of *H. cambui*.

The Serra da Mantiqueira is one of the most prominent Brazilian mountain ranges fully inserted in the Atlantic Forest biome. It is characterized by a high degree of endemism among the anuran fauna (Cruz and Feio 2007), where narrowly distributed species restricted to a single, or few, localities are common (e.g., Lutz 1958; Lutz and Carvalho 1958; Heyer 1982, 1983). *Hypsiboas cambui* is known from a single locality in the mountains of Serra Negra, part of the Serra da Mantiqueira, Município de Rio Preto, State of Minas Gerais, close to the border with the State of Rio de Janeiro (Fig. 7A). To our knowledge, *H. cambui* does not occur within protected areas. In addition to *H. cambui*, Serra Negra also harbors two narrowly distributed Mantiqueira endemic anurans, namely, *Physalaemus rupestris* Caramaschi, Carcerelli and Feio 1991 and *Hyloides perere* Silva and Benmaman 2008 (Oliveira et al. 2009). The former also occurs in the Parque Estadual do Ibitipoca (Caramaschi et al. 1991), a neighboring reserve located 32 km north of Serra Negra. The latter occurs 7.2 km northeast of the type locality of *H. cambui*, and is also known only from Serra Negra.

The Atlantic Forest is one of the most threatened tropical rain forests of the world (Mittermeier et al. 2005) where ~90% of the original vegetation has been removed (Ribeiro et al. 2009). Because of difficulty in access, mountainous regions of higher elevations within the Serra da Mantiqueira mountain range (e.g., Serra do Itatiaia, Serra Fina, Serra do Ibitipoca, Serra do Brigadeiro, Serra de Campos do Jordão, Serra do Papagaio, in the states of Minas Gerais, Rio de Janeiro, and São Paulo) harbor some of the larger forest remnants of southeastern Brazil. At the same time, the difficult access to some areas of Serra da Mantiqueira also hampers comprehensive amphibian inventories (as well as for other taxa). Thus, as exemplified by *H. cambui* at Serra Negra, many Mantiqueira anurans still wait to be discovered.

The rarity and endemism of these unexplored mountain forest patches reinforce the relevance of the Serra da Mantiqueira mountain range for the conservation of the Atlantic Forest biome. Having identified Serra Negra as the type locality for a vertebrate species, we hope to increase the scientific and conservation concern for this region, and stimulate a more committed stance of the Brazilian government concerning the conservation of this biodiversity heritage. The implementation of most conservation actions in the Serra da Mantiqueira has been delayed for years, however, jeopardizing the future of these highland remnants (Becker et al. 2013). The establishment of a reserve at Serra Negra is imperative to ensure the conservation of its unique biota.

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867 RESUMO: Uma nova espécie do grupo de *Hypsiboas pulchellus* é descrita da Serra da
868 Mantiqueira, Município de Rio Preto, Minas Gerais. Descrevemos adultos, girinos e o canto de
869 anúncio. A nova espécie é morfologicamente similar a *H. freicanecae*, espécie conhecida para
870 poucas localidades nos estados de Alagoas e Pernambuco, nordeste do Brasil, ~1640 km ao norte.
871 Os adultos diferem de *H. freicanecae* por possuírem corpo delgado, menor comprimento dos
872 machos, apêndice calcâneo grande e superfícies ocultas das coxas e pés de tons alaranjados em
873 vida. Girinos possuem disco oral ventral, fórmula de dentes labiais 2(2)/3–4(1) e presença de uma
874 a três pequenas interrupções posteriores na fileira de papilas marginais, localizadas nas
875 emarginações do disco oral. O canto de anúncio é composto por duas notas não pulsadas com
876 frequência dominante no segundo harmônico. A espécie é conhecida apenas da sua localidade
877 tipo, em uma área não protegida.

878
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1122

1123

APPENDIX

Specimens Examined

- 1124
- 1125
- 1126 *Hypsiboas albomarginatus* (larvae).—BRAZIL: MINAS GERAIS: Rio Preto, Vilarejo do
- 1127 Funil: UFMG 1854, 1855.
- 1128 *Hypsiboas bandeirantes*.—BRAZIL: SÃO PAULO: Itapeccerica da Serra: CFBH 36181,
- 1129 36182. BRAZIL: SÃO PAULO: São José do Barreiro, Serra da Bocaina: CFBH 36064, 36065,
- 1130 36067, 36080.
- 1131 *Hypsiboas beckeri*.—BRAZIL: MINAS GERAIS: Botelhos: CFBH 35786, 35787. BRAZIL:
- 1132 MINAS GERAIS: Poços de Caldas: CFBH 35880–35882.
- 1133 *Hypsiboas bischoffi*.—BRAZIL: PARANÁ: Cruz Machado: CFBH 18261. BRAZIL: RIO
- 1134 GRANDE DO SUL: Itati, Reserva Biológica Estadual Mata Paludosa: CFBH 14595. BRAZIL:
- 1135 SANTA CATARINA: Imbituba: CFBH 33732. BRAZIL: SÃO PAULO: Piedade, Vila Elvio CFBH
- 1136 15988.
- 1137 *Hypsiboas botumirim*.—BRAZIL: MINAS GERAIS: Botumirim: UFMG 3793.
- 1138 *Hypsiboas buriti*.—BRAZIL: DISTRITO FEDERAL: Brasília, Fazenda Água Limpa: CFBH
- 1139 22785–22787, 22794.
- 1140 *Hypsiboas caingua*.—BRAZIL: RIO GRANDE DO SUL: Cerro Largo, Vila Santo Antônio:
- 1141 CFBH 12036, 12039. BRAZIL: SÃO PAULO: Assis: CFBH 18692, 20042. BRAZIL: SÃO PAULO:
- 1142 Guapiara: CFBH 14697. BRAZIL: SÃO PAULO: Pilar do Sul: CFBH 8605.
- 1143 *Hypsiboas caipora*.—BRAZIL: SÃO PAULO: São Miguel Arcanjo, Parque Estadual Carlos
- 1144 Botelho: CFBH 38435, 38461, 38462.
- 1145 *Hypsiboas cipoensis*.—BRAZIL: MINAS GERAIS: Santana do Riacho: CFBH 286, 35057.
- 1146 *Hypsiboas curupi*.—ARGENTINA: MISIONES: San Vicente: CFBH 3444, 3445, 4908.
- 1147 BRAZIL: SANTA CATARINA: Campos Novos: CFBH 23854. BRAZIL: SANTA CATARINA: São

- 1148 Domingos: CFBH 9559, 9561. BRAZIL: SANTA CATARINA: Vargem Bonita: UFMG 3267.
- 1149 BRAZIL: SANTA CATARINA: Xanxerê: BRAZIL: CFBH 21144. SANTA CATARINA: Xavantina:
- 1150 CFBH 20803, 21141.
- 1151 *Hypsiboas cymbalum*.—BRAZIL: SÃO PAULO: Santo André, Campo Grande da Serra:
- 1152 MZUSP 73697, 74194.
- 1153 *Hypsiboas ericae*.—BRAZIL: GOIÁS: Alto Paraíso de Goiás: CFBH 3599, 3600, 3602,
- 1154 3603, 6762–6764.
- 1155 *Hypsiboas freicanecae*.—BRAZIL: ALAGOAS: Murici, Estação Ecológica de Murici:
- 1156 MUFAL 9472, 9475.
- 1157 *Hypsiboas goianus*.—BRAZIL: GOIÁS: São João d'Aliança, Córrego Jatobazinho: UFMG
- 1158 10347. BRAZIL: GOIÁS: Silvânia: CFBH 2666, 4167, 4168, 9510.
- 1159 *Hypsiboas guentheri*.—BRAZIL: RIO GRANDE DO SUL: Terra de Areia: CFBH 3384,
- 1160 3385, 3387. BRAZIL: SANTA CATARINA: Urussanga: CFBH 9855.
- 1161 *Hypsiboas joaquina*.—BRAZIL: SANTA CATARINA: Urubici, Morro da Igreja: CFBH
- 1162 3279, 3282, 3288, 3627, 3628.
- 1163 *Hypsiboas latistriatus*.—BRAZIL: MINAS GERAIS: Itamonte, Brejo da Lapa: CFBH 139.
- 1164 BRAZIL: RIO DE JANEIRO: Itatiaia, Brejo da Lapa: CFBH 9866. BRAZIL: RIO DE JANEIRO:
- 1165 Maromba, Parque Nacional do Itatiaia: CFBH 35776.
- 1166 *Hypsiboas leptolineatus*.—BRAZIL: RIO GRANDE DO SUL: São Francisco de Paula:
- 1167 CFBH 3056, 3060, 8505, 19246, 19247.
- 1168 *Hypsiboas marginatus*.—BRAZIL: RIO GRANDE DO SUL: Cambará do Sul, road of access
- 1169 to Parque Nacional Aparados da Serra, Itaimbezinho: CFBH 3050, 3051. BRAZIL: RIO GRANDE
- 1170 DO SUL: São Francisco de Paula: CFBH 3413. BRAZIL: SANTA CATARINA: Treviso: CFBH 8495.

- 1171 *Hypsiboas phaeopleura*.—BRAZIL: GOIÁS: Alto Paraíso de Goiás, Rio dos Couros:
 1172 CFBH 3598; UFMG 10346.
- 1173 *Hypsiboas poaju*.—BRAZIL: SANTA CATARINA: Anitápolis: CFBH 20263, 20264.
 1174 BRAZIL: SANTA CATARINA: Rancho Queimado: CFBH 3335, 3336, 3610, 5398.
- 1175 *Hypsiboas polytaenius*.—BRAZIL: MINAS GERAIS: Belo Horizonte: UFMG 13713,
 1176 13714. BRAZIL: MINAS GERAIS: Muriaé: CFBH 39040. BRAZIL: RIO DE JANEIRO: Nova
 1177 Friburgo: CFBH 36396, 36404. BRAZIL: RIO DE JANEIRO: Petrópolis: UFMG 11545. BRAZIL:
 1178 RIO DE JANEIRO: Teresópolis: UFMG 11564.
- 1179 *Hypsiboas prasinus*.—BRAZIL: RIO DE JANEIRO: Nova Friburgo: 36409. BRAZIL: SÃO
 1180 PAULO: Apiaí, Parque Estadual Turístico do Alto Ribeira: CFBH 25604. BRAZIL: SÃO PAULO:
 1181 Jundiaí, Serra do Japi: CFBH 729. BRAZIL: SÃO PAULO: Mairiporã, old road from São Paulo to
 1182 Mairiporã: CFBH 9507.
- 1183 *Hypsiboas pulchellus*.—BRAZIL: RIO GRANDE DO SUL: São Francisco de Paula: CFBH
 1184 3376, 3377, 8533, 8544, 8545.
- 1185 *Hypsiboas riojanus*.—ARGENTINA: SAN MIGUEL DE TUCUMÁN: Burruyacú: CFBH
 1186 4037–4040.
- 1187 *Hypsiboas secedens*.—BRAZIL: Rio de Janeiro: Cachoeiras de Macacu, Reserva
 1188 Ecológica de Guapiaçú: MNRJ 61476, 61477, 86331–86334, 86897–86899.
- 1189 *Hypsiboas semiguttatus*.—BRAZIL: PARANÁ: Piraquara, Mananciais da Serra: CFBH
 1190 3579, 3705, 5000. BRAZIL: SANTA CATARINA: Rio Vermelho: UFMG 13164, 13165. BRAZIL:
 1191 SANTA CATARINA: São Bento do Sul: UFMG 13875, 13888.
- 1192 *Hypsiboas stellae*.—BRAZIL: RIO GRANDE DO SUL: Road RS 471, 10 km from
 1193 bifurcation to Herveiras: CFBH 25716.

- 1194 *Hypsiboas stenocephalus*.—BRAZIL: MINAS GERAIS: Poços de Caldas: CFBH 98.
- 1195 BRAZIL: MINAS GERAIS: São Roque de Minas, Serra da Canastra: 2946–2948; UFMG 15144,
- 1196 15150, 15163, 15179.

1197 TABLE 1.—Some measurements and proportions of the type series of *Hypsiboas cambui*. Values (mm) are reported as ranges
 1198 (mean $\pm$ 1 SD). See text for explanation of measurements abbreviations.

1199

	Measurement			Body ratios	
	Males ($n = 16$)	Female ($n = 1$)		Males ($n = 11$)	Female ($n = 1$)
SVL	26.3–32.8 (30.3 ± 1.7)	32.7	HW / HL	0.90–1.00	0.97
HL	9.3–11.3 (10.6 ± 0.5)	11.8	HL / SVL	0.33–0.36	0.36
HW	9.2–10.8 (10.2 ± 0.4)	11.5	HW / SVL	0.32–0.35	0.35
ED	3.2–3.9 (3.5 ± 0.2)	3.5	EN / ED	0.69–0.89	0.90
EN	2.4–3.0 (2.8 ± 0.2)	3.1	IOD / ED	0.75–1.09	0.84
IND	1.8–2.1 (1.9 ± 0.1)	2.1	IOD / HL	0.27–0.34	0.25
EW	2.1–3.0 (2.6 ± 0.2)	2.8	IOD / HW	0.28–0.36	0.25
IOD	2.6–3.5 (3.1 ± 0.2)	2.9	ED / HL	0.31–0.38	0.29
TD	1.3–1.7 (1.5 ± 0.1)	1.8	ED / HW	0.32–0.39	0.30
TL	14.0–16.8 (16.0 ± 0.7)	16.9	EW / HL	0.20–0.27	0.24
TAL	8.3–10.3 (9.4 ± 0.5)	10.3	TD / 3FD	0.88–1.26	1.20
FL	11.6–14.1 (13.2 ± 0.6)	14.0	TD / ED	0.38–0.47	0.53

SL	4.0–4.8 (4.5 ± 0.2)	4.9	TD / HL	0.12–0.15	0.16
THL	12.7–15.9 (14.8 ± 0.9)	15.9	TAL / SVL	0.29–0.33	0.31
3FD	1.2–1.6 (1.4 ± 0.1)	1.5	FL / SVL	0.42–0.45	0.43
4TD	1.1–1.5 (1.3 ± 0.1)	1.3	SL / HL	0.41–0.47	0.42
CAL	0.6–1.1 (0.9 ± 0.1)	1.1	SL / HW	0.42–0.48	0.43
			THL / SVL	0.46–0.52	0.48
			TL / SVL	0.50–0.55	0.52
			CAL / TAL	0.07–0.11	0.11
			4TD / 3FD	0.78–0.99	0.87

1201 TABLE 2.—Measurements (in mm) of tadpoles of *Hypsiboas cambui* in two groups of stages of
 1202 Gosner (1960). Values (mm) are reported as ranges (mean $\pm$ 1 SD). See text for explanation of
 1203 measurements abbreviations.

1204

	Stages 34–36 ($n = 6$)	Stages 37–39 ($n = 4$)
TL	38.8–44.7 (41.1 ± 2.0)	48.8–54.5 (51.9 ± 2.9)
BL	13.4–15.1 (14.0 ± 0.7)	15.5–16.9 (16.3 ± 0.6)
TAL	24.6–30.5 (27.1 ± 1.9)	32.5–37.6 (35.3 ± 2.6)
MTH	8.2–10.6 (9.5 ± 0.8)	10.2–11.9 (11.3 ± 0.8)
IND	2.7–3.0 (2.8 ± 0.1)	3.0–3.2 (3.1 ± 0.1)
IOD	6.1–7.4 (6.8 ± 0.4)	7.3–8.3 (7.8 ± 0.4)
TMW	3.2–4.3 (3.6 ± 0.4)	4.5–5.2 (4.8 ± 0.3)
TMH	3.8–5.0 (4.2 ± 0.5)	5.1–5.6 (5.3 ± 0.2)
BW	8.5–10.3 (9.2 ± 0.6)	10.5–11.7 (11.0 ± 0.5)
BWN	5.5–6.7 (6.0 ± 0.5)	6.5–7.2 (6.8 ± 0.3)
BWE	7.4–8.9 (7.9 ± 0.6)	8.7–9.2 (9.0 ± 0.2)
BH	7.9–9.5 (8.5 ± 0.6)	9.2–10.8 (10.1 ± 0.7)
ESD	5.2–6.3 (5.6 ± 0.4)	6.2–6.4 (6.4 ± 0.1)
END	2.7–3.3 (3.1 ± 0.3)	3.4–3.8 (3.6 ± 0.2)
NSD	2.4–2.9 (2.6 ± 0.2)	2.5–3.1 (2.8 ± 0.2)
ED	1.7–2.0 (1.9 ± 0.1)	2.0–2.3 (2.2 ± 0.1)
ND	0.8–1.0 (0.9 ± 0.1)	0.9–1.1 (1.0 ± 0.1)
SSD	10.1–11.9 (11.3 ± 0.6)	11.5–13.3 (12.7 ± 0.8)

ODW	3.1–3.7 (3.4 ± 0.2)	3.6–4.0 (3.9 ± 0.2)
DFH	2.9–3.5 (3.3 ± 0.2)	3.0–4.4 (3.8 ± 0.7)
VFH	2.2–3.1 (2.7 ± 0.3)	2.9–3.1 (3.0 ± 0.1)
SL	1.5–1.9 (1.8 ± 0.1)	1.9–2.1 (2.0 ± 0.1)
SDH	3.4–5.7 (4.4 ± 0.8)	4.3–5.7 (5.0 ± 0.6)
DFiA	4.4–15.1 (10.2 ± 4.7)	10.9–12.9 (12.0 ± 0.9)
ODP	19.0–28.2 (24.0 ± 3.8)	23.8–26.9 (24.8 ± 1.5)

FIGURE CAPTIONS

FIG. 1.—(A) *Hypsiboas cambui*, holotype in life (CFBH 39397; snout-vent length [SVL] = 32.8 mm). Photo: Barnagleison S. Lisboa. (B–E) Variation in coloration pattern of adults; B–D are males. (B) CFBH 39398 (SVL = 30.2 mm), with no light spots on dorsum, and many tiny red dots on dorsal surfaces of body and limbs. (C) CFBH 39400 (SVL = 31.6 mm) with absence of the cream line that contours the dorsolateral bands and triangle, and irregular border between loreal coloration and labial stripe. (D) CFBH 39403 (SVL = 30.6 mm) with poor differentiation of the dorsolateral bands and triangle. (E) Female, CFBH 39393 (SVL = 32.7 mm), dorsolateral bands and triangle cream and a dark lateral stripe on tibia. A color version of this figure is available on-line.

FIG. 2.—*Hypsiboas cambui*, holotype (CFBH 39397). (A) Dorsal view. (B) Ventral view. Scale bar = 10 mm. A color version of this figure is available on-line.

FIG. 3.—*Hypsiboas cambui*, holotype (CFBH 39397). (A) Head in dorsal view. (B) Head in lateral view. (C) Left hand in ventral view. (D) Left foot in ventral view. Scale bar = 5 mm.

FIG. 4.—Tadpole of *Hypsiboas cambui* in Stage 35 (lot CFBH 39392). (A) Lateral view. (B) Dorsal view. (C) Ventral view. Scale bar = 10 mm. (D) Detail of spiracular aperture in a specimen in Stage 36. Scale bar = 1 mm. (E) Detail of the margin of the left nostril with

1230 triangular fleshy projection in a specimen in Stage 36. Scale bar = 0.2 mm. (F) Details of vent
 1231 tube and cumuli of neuromasts (white arrows) in a specimen in Stage 35, in ventral view. Scale
 1232 bar = 2 mm. (G) Dextral vent tube in lateral view of a specimen in Stage 35. Scale bar = 2 mm. A
 1233 color version of this figure is available on-line.

1234
 1235
 1236 FIG. 5.—Oral disc of *Hypsiboas cambui* (lot CFBH 39392). (A) Stage 36. (B) Stage 34.
 1237 Scale bar = 1 mm. (C) A detail of the posterolateral gap of an individual in Stage 36. Scale bar =
 1238 0.2 mm. The arrows show the variable position of the narrow posterior gaps in the row of
 1239 marginal papillae. (D) A portion of A2 labial tooth row an individual in Stage 36, showing the
 1240 general shape of the labial teeth. Scale bar = 0.2 mm. On inset at right bottom, lateral view of a
 1241 typical A1 labial tooth. Scale bar = 0.05 mm.

1242
 1243
 1244 FIG. 6.—Advertisement call of *Hypsiboas cambui*. (A) Spectrogram (top) and waveform
 1245 (bottom) of the two note call. (B) Power spectrum of the second note in (A). Recording
 1246 CFBH/PDPP_1; voucher specimen CFBH 39403. Recorded at Vilarejo do Funil, Município de
 1247 Rio Preto, State of Minas Gerais, Brazil, on 6 March 2015 at 2300 h (air temperature = 17°C).

1248
 1249
 1250 FIG. 7.—(A) Map showing type locality of *Hypsiboas cambui* at Vilarejo do Funil,
 1251 Município de Rio Preto, State of Minas Gerais (highlighted in gray on right top), Brazil
 1252 (22°0'19"S, 43°53'20"W, 905 m above sea level; datum = WGS84). (ES) Espírito Santo, (MG)

1253 Minas Gerais, (RJ) Rio de Janeiro and (SP) São Paulo. (B) Pond where the new species was
1254 found. A color version of this figure is available on-line.
1255

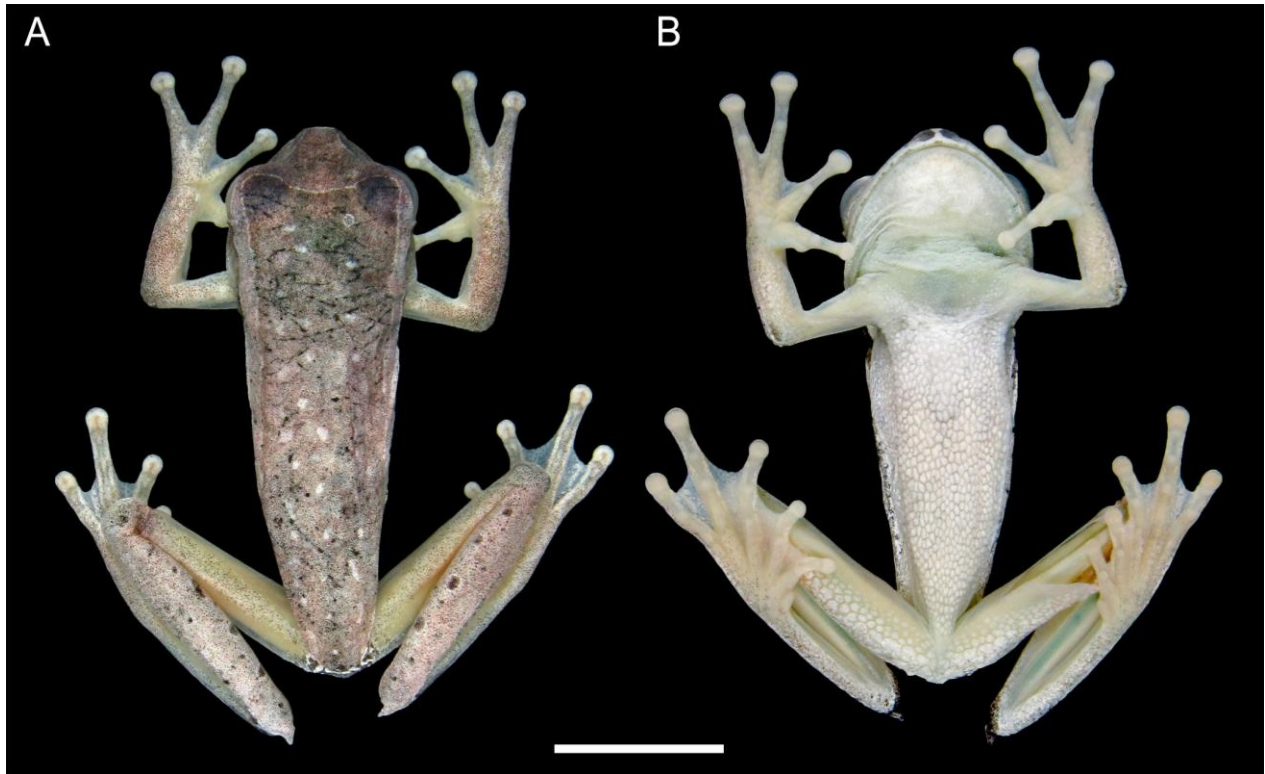
1256 **Fig. 1.**

1257

1258



1259 **Fig. 2.**



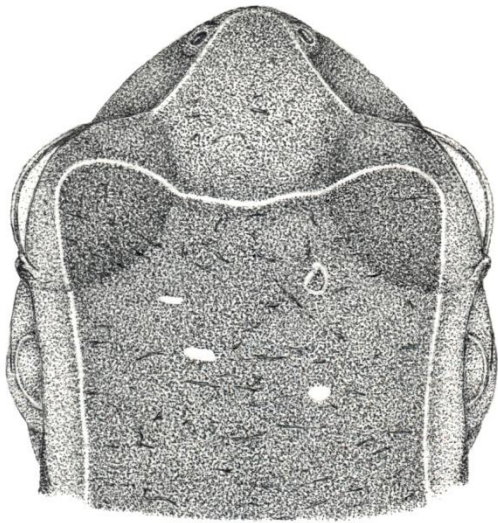
1260

1261

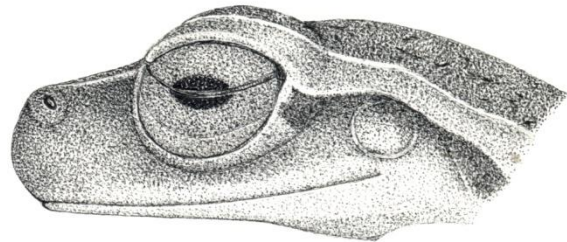
1262

1263 **Fig. 3.**

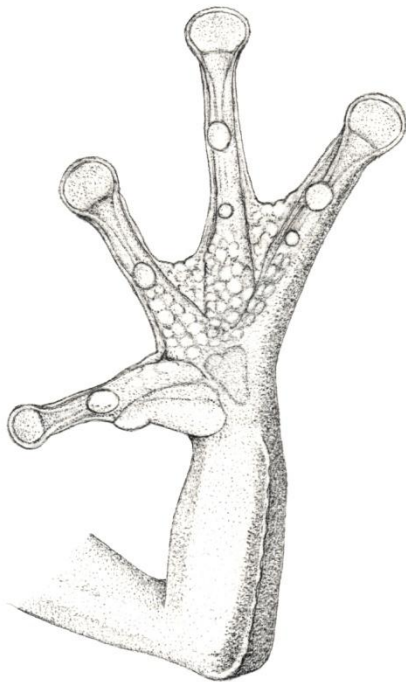
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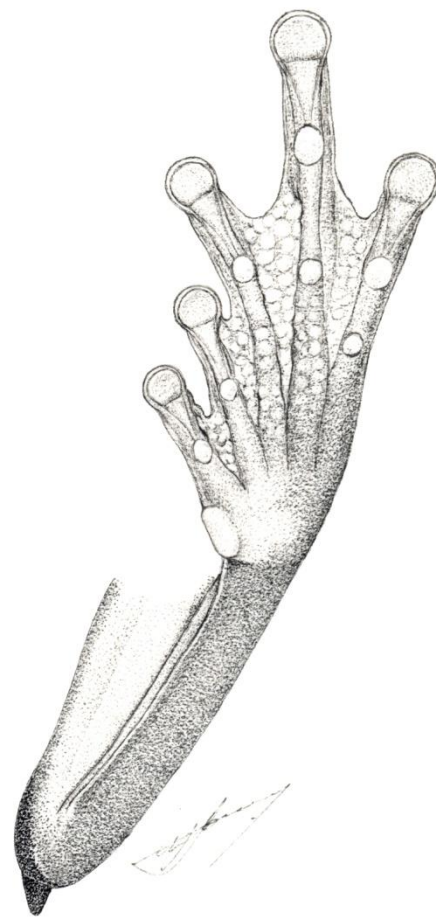
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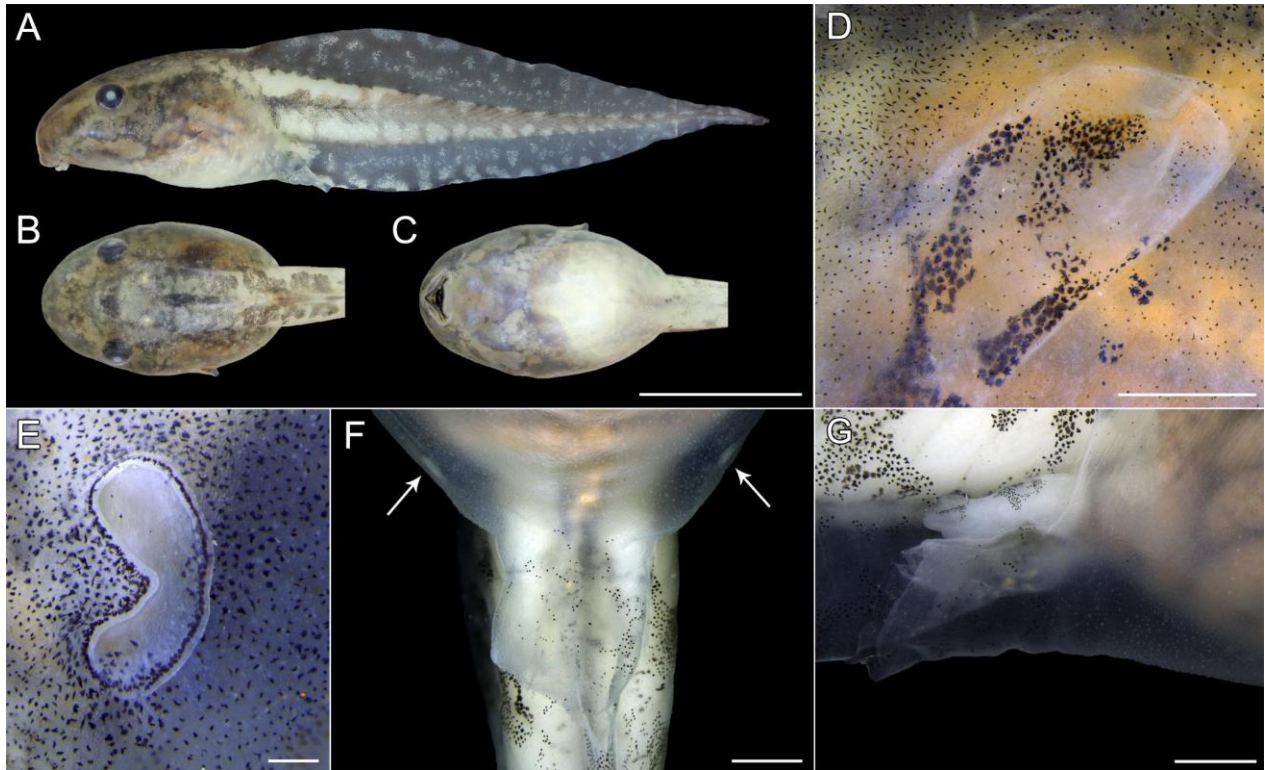


C



D



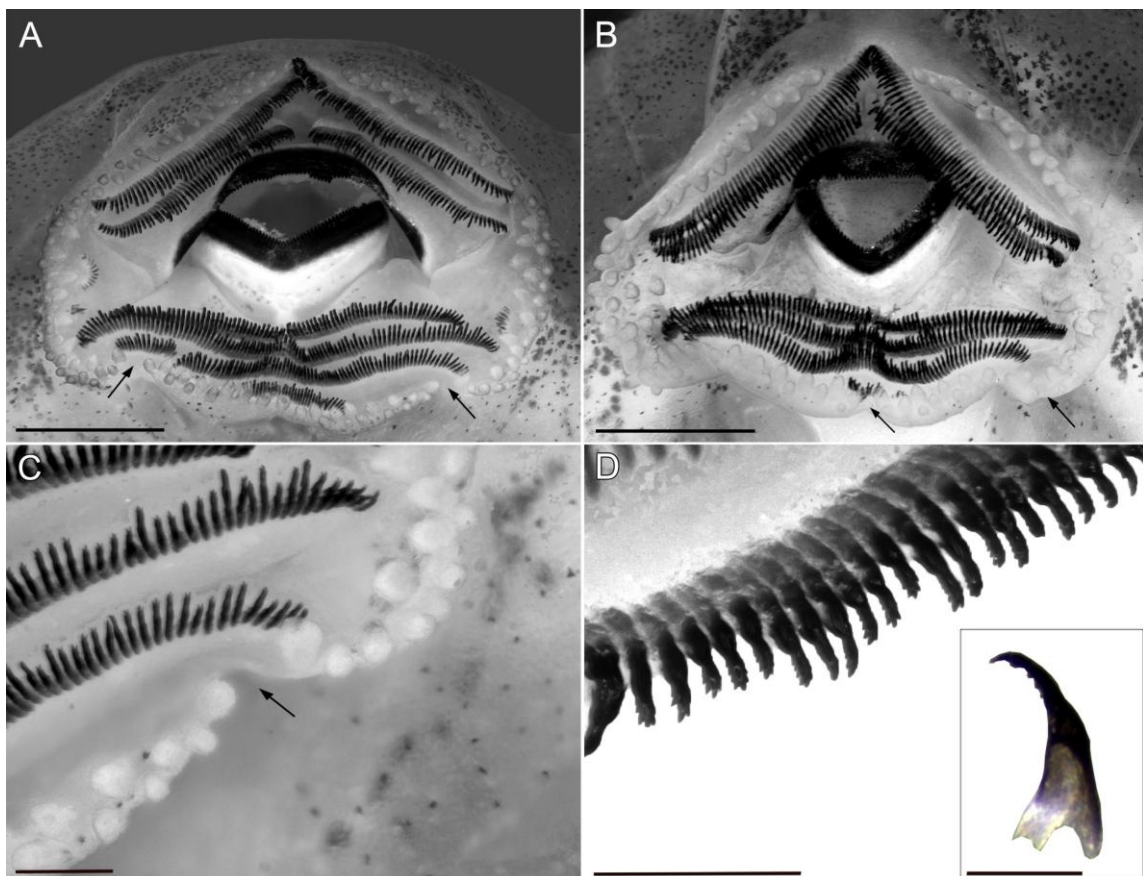
1265 **Fig. 4.**

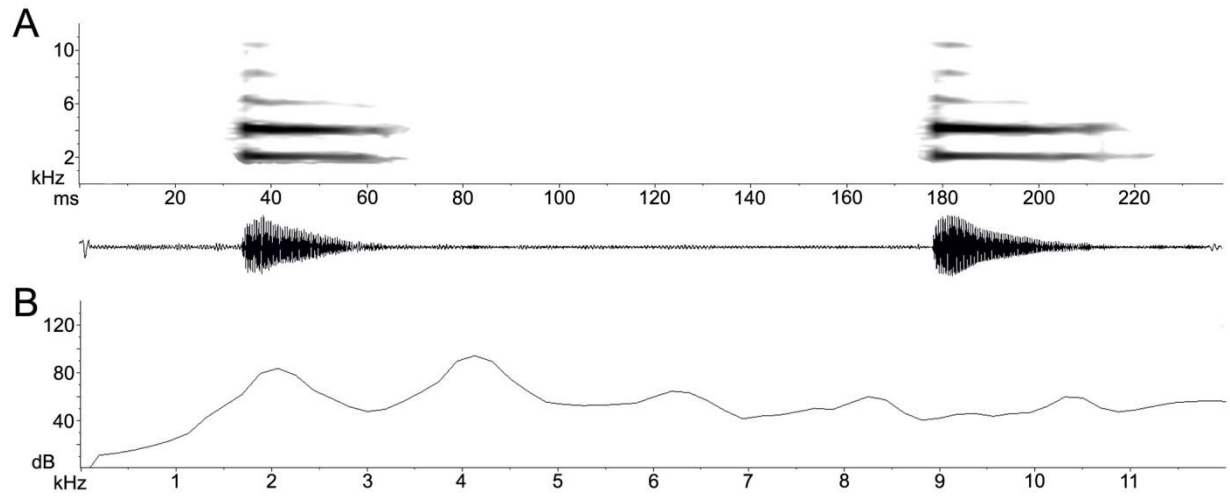
1266

1267 **Fig. 5.**

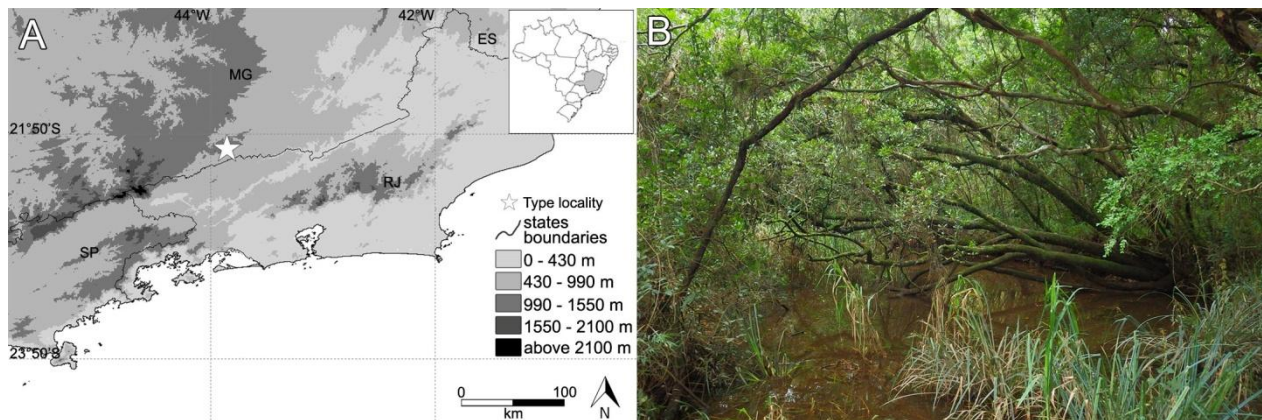
1268

1269



1270 **Fig. 6.**

1271

1272 **Fig. 7.**

1273

1274 **A New Species of the *Boana albopunctata* Group (Anura: Hylidae) from the Cerrado of**
 1275 **Brazil**

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1277

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1298

1299 **Abstract**

1300 We describe a new species of *Boana* endemic to the Araguaia-Tocantins Basin in the center of
 1301 the Brazilian Cerrado, which has previously been confused with species of the *B. pulchella*
 1302 group. The new species is included in the *B. albopunctata* group based on morphological and
 1303 bioacoustics traits. The new species is characterized by a rounded head in dorsal view; dorsal
 1304 color pattern consisting of three beige longitudinal stripes interspersed by two dark-brown
 1305 stripes; posterior surfaces of thighs purple with dark-brown spots; and absence of a calcar.
 1306 Males have a pulsed advertisement call, with the end of the first note possessing an
 1307 uncountable number of pulses. The new species is distinct from species of the *B. pulchella*
 1308 group by the presence of a slip of the *m. depressor mandibulae* of scapular origin, presence of
 1309 anterolateral processes of the hyoid and a distal prepollex with a weakly developed or absent
 1310 post-articulation process.

1311 **Keywords:** Amphibia; Bioacoustics; Neotropics; Systematics; Taxonomy.

1312 **Resumo**

1313 Descrevemos aqui uma nova espécie de *Boana* endêmica da Bacia do Araguaia-Tocantins, no
 1314 Cerrado Central brasileiro, e previamente confundida com espécies do grupo de *B. pulchella*.
 1315 A nova espécie é tentativamente incluída no grupo de *B. albopunctata* com base em caracteres
 1316 morfológicos e de canto. É caracterizada pela cabeça arredondada em vista dorsal; padrão de
 1317 coloração dorsal composto por três faixas longitudinais de cor bege intercaladas por outras
 1318 duas de tom marrom-escuro; superfície posterior das coxas roxa, com pontos marrom-escuro;
 1319 calcar ausente. Machos apresentam o canto pulsado, cujos pulsos da porção final da primeira
 1320 nota são incontáveis. Se separa do grupo de *B. pulchella* pela presença do braço muscular de
 1321 origem escapular do *m. depressor mandibulae*, presença do processo antero-lateral do hioide e
 1322 pré-polex distal com processo posterior à articulação pouco evidente ou ausente.

1323 **Palavras-chave:** Amphibia; Bioacústica; Neotrópicos; Sistemática; Taxonomia.

1324

INTRODUCTION

The *Boana albopunctata* group contains 15 described species distributed throughout South and Central America: *Boana albopunctata* (Spix, 1824); *B. alfaroi* (Caminer and Ron, 2014); *B. almendarizae* (Caminer and Ron, 2014); *B. calcarata* (Troschel, 1848); *B. dentei* (Bokermann, 1967); *B. fasciatus* (Günther, 1858a); *B. heilprini* (Noble, 1923); *B. lanciformis* (Cope, 1871 [1870]); *B. leucocheila* (Caramaschi and Niemeyer, 2003); *B. maculateralis* (Caminer and Ron, 2014); *B. multifasciata* (Günther, 1858b); *B. paranaiba* (Carvalho and Giaretta, 2010); *B. raniceps* (Cope, 1862); *B. steinbachi* (Boulenger, 1905); and *B. tetete* (Caminer and Ron, 2014) (Faivovich et al., 2005; Frost, 2016). The group is defined by 43 transformations in nuclear and mitochondrial proteins, and in ribosomal genes (Faivovich et al., 2005). However, some few species remain without a phylogenetic test: *B. leucocheila*, *B. paranaiba*, and *B. steinbachi*—but see Caminer and Ron (2014) for this last one. They were just tentatively assigned to the *B. albopunctata* group, based on overall morphological similarities with other species included on it. According to Faivovich et al. (2005) the group remains without any morphological synapomorphy.

Among the species of the group, *Boana albopunctata*, *B. multifasciata*, and *B. raniceps* possess broad distributions throughout Brazil, occurring in both open and forest environments of many Brazilian biomes (Carvalho et al., 2010; Zina et al., 2010; Prado et al., 2012); *B. paranaiba* is known from central Brazil (Carvalho et al., 2010); *B. alfaroi*, *B. almendarizae*, *B. calcarata*, *B. dentei*, *B. fasciata*, *B. lanciformis*, *B. leucocheila*, *B. maculateralis*, *B. steinbachi* and *B. tetete* occur in the Amazon Basin, and thus in forest environments (Caminer and Ron, 2014; Frost, 2016); and *B. heilprini* is restricted to forested streams of Hispaniola and the West Indies in the Caribbean (Stuart et al., 2008). Among the species that occur in Brazil, only *B. albopunctata*, *B. multifasciata*, *B. paranaiba*, and *B. raniceps* can be found in the Cerrado (neotropical savanna).

During fieldwork in the southwestern portion of the state of Goiás, we identified specimens of a new species of *Boana*. These specimens possess morphological characters resembling both the *B. pulchella* and *B. albopunctata* groups. Examining additional material recovered from herpetological collections, we found this species to be distributed throughout the states of Goiás, Mato Grosso, and Tocantins, in areas within the Cerrado morphoclimatic domain (Ab'Saber, 1977). Herein we describe this new species and present data about its habits, habitat and call; and discuss its phylogenetic relationships.

MATERIAL AND METHODS

We examined vouchers of the following species: *Boana albopunctata*, *B. alfaroi*, *B. calcarata*, *B. dentei*, *B. cf. fasciata*, *B. heilprini*, *B. lanciformis*, *B. leucocheila*, *B. multifasciata* and *B. raniceps* (*B. albopunctata* group); *B. tepuiana* (Barrio-Amorós and Brewer-Carias, 2008) (*B. benitezi* group); *B. albomarginata* (Spix, 1824), *B. crepitans* (Wied-Neuwied, 1824), *B. faber* (Wied-Neuwied, 1821), and *B. lundii* (Burmeister, 1856) (*B. faber* group); *B. boans* (Linnaeus, 1798), *B. pombali* (Caramaschi, Pimenta, and Feio, 2004), and *B. semilineata* (Spix, 1824) (*B. semilineata* group); *B. ericae* (Caramaschi and Cruz, 2000), *B. leptolineata* (Braun and Braun, 1977), *B. poaju* (Garcia, Peixoto, and Haddad, 2008), *B. polytaenia* (Cope, 1870 [1869]), *B. prasina* (Burmeister, 1856), *B. pulchella* (Duméril and Bibron, 1841), and *B. riojana* (Koslowsky, 1895) (*B. pulchella* group); and *B. atlantica* (Caramaschi and Velosa, 1996), *B. cinerascens* (Spix, 1824), *B. pellucens* (Werner, 1901) (*B. pellucens* group) and *B. punctata* (Schneider, 1799) (*B. punctata* group). Specimens used in this study are presented on Appendix.

Abbreviations for collections follow Sabaj (2016). Webbing formula follows Savage and Heyer (1967), as modified by Myers and Duellman (1982). Standards for describing the dorsal outline and profile of the snout followed Heyer et al. (1990). Measurements (in mm)

1375 follow Duellmann (1970): snout-vent length (SVL), head length (HL), head width (HW), eye
 1376 diameter (ED), eye to nostril distance (END), internarial distance (IND), nostril to tip of snout
 1377 distance (NSD), eyelid width (EW), tympanum diameter (TD), tibia length (TL), foot length
 1378 (FL); Heyer et al. (1990): hand length (HAL), thigh length (THL), tarsal length (TAL);
 1379 Duellman et al. (1997): forearm length (FAL); Napoli and Caramaschi (1999): third finger
 1380 disk diameter (3FD) fourth toe disk diameter (4TD); and Garcia et al. (2003): anterior margins
 1381 of eyes distance (AMD). SVL, HL, HW, TL, FL, FAL, HAL and THL were measured with a
 1382 Mytutoyo digital caliper up to 0.01mm, under a stereomicroscope. ED, END, IND, NSD,
 1383 UEW, TD, TAL, 3FD, 4TD and AMD were measured with the help of an ocular micrometer
 1384 coupled to a Nikon stereomicroscope.

1385 Calls were recorded with a Marantz PMD 660 digital recorder, carried out at 44.100
 1386 Hz on 16 bit sampling size, and coupled to a Sennheiser K6/ ME66 microphone, analyzed
 1387 with Raven 1.4 beta (The Cornell Lab Ornithology, Bioacoustics Research Program).
 1388 Spectrograms were produced with a FFT of 256 points, 75% overlap and window Hann.
 1389 Resolution, while contrast and brightness settings were the default of the software. We
 1390 measured note length, interval between notes, number of pulses per note, dominant frequency
 1391 range (band of frequency in which the energy of the note is concentrated, measured on the
 1392 spectrogram), and peak frequency (the specific frequency with the highest note energy as
 1393 assessed directly from Raven Pro software; called dominant frequency by Cocroft and Ryan,
 1394 1995). Temporal parameters were measured in milliseconds (ms) and spectral parameters in
 1395 Hertz (Hz).

1396

1397 **SPECIES ACCOUNT**

1398 ***Boana caiapo* sp. nov.**

1399 **(Tables 1 and 2; Figs. 1-8)**

1400 *Hypsiboas* aff. *leucocheilus*—Valdujo et al. (2012).

1401 **Holotype (Figs. 1A, 5, and 6)**

1402 MZUSP 138987, an adult male, from Brazil: state of Goiás: municipality of Aragarças
1403 (15°53'39"S, 51°49'23"W; 309 m a.s.l.), collected by C.E.D. Cintra on 10 December 2007.

1404 **Paratypes (*n* = 26 [24 adult males and two juveniles])**

1405 MZUSP 138988–139009, adult males, collected together with the holotype
1406 (topotypes). MZUSP 139004 without skin and MZUSP 139009 cleared and doubled stained.
1407 UFMG 3281 and 3918, adult males, from Brazil: state of Goiás: municipality of Montes
1408 Claros de Goiás: Mina de Níquel Votorantin (16°01'53"S, 51°21'11"W; 446 m a.s.l.),
1409 collected by F.S.F. Leite on 20 March 2007. UFMG 3282–3283, juveniles, from Brazil: state
1410 of Goiás: municipality of Montes Claros de Goiás: Fazenda Carolina (15°49'17"S,
1411 51°37'16"W, 327 m a.s.l.), collected by F.S.F. Leite on 14 June 2007.

1412 **Etymology**

1413 Both holotype and topotypic paratypes were collected in lakes and backwaters of small
1414 rivulets in the Caiapó River Basin. The Caiapó River originates in the municipality of
1415 Caiapônia, state of Goiás, Brazil, and flows into the Araguaia River between the
1416 municipalities of Aragarças and Montes Claros de Goiás. The name “caiapo” is used here as a
1417 noun in apposition.

1418 **Diagnosis**

1419 A species of the *Boana albopunctata* group characterized by: 1) medium-size males
1420 (SVL 42.4–51.2; females remain unknown); 2) head rounded in dorsal view (as long as wide);
1421 3) calcar absent or rudimentary; 4) dorsal color pattern consisting of three beige longitudinal
1422 stripes interspersed by two dark-brown stripes, from the snout to urostyle region; 5) posterior
1423 surfaces of thighs purple with dark-brown spots; 6) presence of a slip of the *m. depressor*
1424 *mandibulae* originating from dorsal fascia, at the level of the *m. dorsalis scapularis* (Fig. 2);

7) presence of anterolateral processes of the hyoid (Fig. 3); 8) absence of a post-articulation process of the distal prepollex (Fig. 4); 9) absence of a mental gland; 10) absence of a reticulated pattern on palpebrae; 11) advertisement call with a pulsed structure; 12) end portion of the first note with an uncountable number of pulses; and 13) notes with ascending frequency modulation (Fig. 7).

Comparison with other *Boana* species groups

The new species has the following features that resemble species of the *Boana pulchella* group: head rounded in dorsal view (as long as wide); presence of dorsal longitudinal blotches, frequently as longitudinal stripes, which might resemble some dorsal patterns found in, for example, species of the clade of *Boana semiguttata*, (Garcia et al., 2003, 2007; Antunes et al., 2008; Kwet, 2008). However, it differs from the *B. pulchella* group by the presence of a slip of the *m. depressor mandibulae* originating from dorsal fascia, at the level of the *m. dorsalis scapularis* (absent in species of *B. pulchella* group; see Faivovich et al., 2005; Fig. 2); presence of anterolateral processes of the hyoid (absent in *B. pulchella* group; Fig. 3, see material examined). It also differs from *B. faber*, *B. pellucens*, and *B. pulchella* groups by the absence of a post-articulation process of the distal prepollex (strongly developed in species of *B. pulchellus* group; see Garcia and Haddad, 2008: figs. 13–15; and moderately developed in species of *B. faber* and *B. pellucens* groups; Fig 4; see material examined in Appendix). It is distinguished from the *B. semilineata* group by the absence of a reticulated pattern on the palpebral membrane (present in *B. semilineata* group; see Faivovich et al., 2005, 2006). From *B. pellucens* and *B. punctatus* groups it is promptly distinguished by its general color pattern consisting of three beige longitudinal stripes interspersed by two dark-brown stripes from the snout to urostyle region (species with overall green coloration in *B. pellucens* and *B. punctata* groups; dorsum violet, with cream-colored spots edged with purplish red in *B. picturata* [Boulenger, 1899]); Boulenger, 1899; Duellman, 1971;

1450 Hoogmoed 1979; Caramaschi and Velosa, 1996). From the *B. benitezi* group it is
 1451 distinguished by the absence of a mental gland (present in *B. benitezi* group; Faivovich et al.,
 1452 2005, 2006).

1453 All the character states listed above for *Boana caiapo* are shared with species of the *B.*
 1454 *albopunctata* group. Based on these observations, and in the absence of morphological
 1455 synapomorphies for the *B. albopunctata* group (Faivovich et al., 2005), we tentatively include
 1456 *Boana caiapo* in this group.

1457 **Comparison with other species of the *Boana albopunctata* group**

1458 *Boana caiapo* differs from all other species of the *B. albopunctata* group, except *B.*
 1459 *maculateralis* and *B. steinbachi*, by its dorsal longitudinal stripes (dorsum with transversal
 1460 stripes in *B. albopunctata*, *B. alfaroi*, *B. almendarizae*, *B. calcarata*, *B. dentei*, *B. fasciata*, *B.*
 1461 *heilprini*, *B. leucocheila*, *B. multifasciata*, *B. paranaiba*, *B. raniceps*, and *B. tetete*; Cope,
 1462 1862; Boulenger, 1905; Noble, 1923; Cochran, 1955; Bokermann, 1967; Lutz, 1973; De Sá,
 1463 1995, 1996; Caramaschi and Niemeyer, 2003; Carvalho et al., 2010; Caminer and Ron, 2014).
 1464 Additionally, it differs from *B. alfaroi*, *B. almendarizae*, *B. calcarata*, *B. dentei*, *B. fasciata*,
 1465 *B. maculateralis*, *B. steinbachi* and *B. tetete* by the absence of a calcar (present as a small
 1466 tubercle in *B. alfaroi* and *B. tetete*; more developed in the others species; Boulenger, 1905;
 1467 Bokermann, 1967; Caminer and Ron, 2014). From *B. albopunctata*, *B. almendarizae*, *B.*
 1468 *calcarata*, *B. heilprini*, *B. lanciformis*, *B. leucocheila*, *B. multifasciata*, and *B. raniceps* it
 1469 differs by possessing dark-brown spots on the posterior surface of thighs (absence of marks
 1470 on posterior surface of thighs in *B. lanciformis*, *B. leucocheila*, and *B. multifasciata*; presence
 1471 of yellow or cream spots in *B. albopunctata*; and transversal dark-brown bars or strips in *B.*
 1472 *almendarizae*, *B. calcarata*, *B. heilprini*, and *B. raniceps*; Spix, 1824; Cope, 1862, 1871
 1473 [1870]; Noble, 1923; De Sá, 1995, 1996; Caramaschi and Niemeyer, 2003; Caminer and Ron,
 1474 2014); from *B. alfaroi*, *B. maculateralis*, and *B. tetete* it differs by possessing a purple

background color of the posterior surface of the thighs (pale cream, creamy white or brown in these species; Caminer and Ron, 2014). From *B. alfaroi*, *B. fasciata*, *B. maculateralis*, *B. steinbachi*, and *B. tetete* it differs by having a larger SVL of males (SVL 42.4–51.2 mm in males of *B. caiapo*; 27.9–36.2 mm in males of *B. alfaroi*, 32.6–37.7 mm in males of *B. fasciata*, 31.8–39.1 mm in males of *B. maculateralis*, 35 mm in *B. steinbachi* and 31.1–32.2 in males of *B. tetete*; Boulenger, 1905; Caminer and Ron, 2014).

Description of the holotype (MZUSP 138987)

A robust, medium-sized treefrog (SVL = 47.6); head length slightly larger than width (HW/HL = 0.89), about a 1/3 of SVL; snout rounded in dorsal view and profile (Figs. 5 and 6); canthus rostralis distinct and slightly curved; loreal region slightly concave; nostrils slightly protuberant, rounded, directed laterally; distance from nostril to tip of snout less than the inter-nostril distance (NSD/IND = 0.64) and eye-nostril distance (NSD/END = 0.84). Eyes of moderate size (ED/HL = 0.29), lateral and directed slightly anteriorly; pupil horizontal; tympanum distinct, diameter approximately half of eye diameter (TD/ED = 0.48); supratympanic fold distinct, covering upper part of tympanic annulus, but short, not reaching the level of the arm. Vocal sac single, median, subgular, well expanded externally; vocal slits large, located laterally under tongue; tongue large, cordiform, approximately 3/4 of the mouth floor, free and notched posteriorly. Dentigerous processes of vomers slightly curved posteriorly, the right rudimentary and without teeth and the left bearing nine teeth.

Arms robust; forearm slightly more robust than upper arm but not hypertrophied (Figs. 5 and 6); ulnar fold on external margin of forearm, weakly developed; hands large (HAL/SVL = 0.28), their length less than head length (HAL/HL 0.81); fingers slender; adhesive disks of moderate-size, disk on finger I smaller than the others; disk on finger III slightly smaller than tympanum diameter (3FD/TD 0.87 TD); relative finger lengths I = II < IV < III; hand webbing formula, **I—II2—3^{1/2}III3—2^{1/2}IV**; prepollex prominent, ending in a curved osseous

1500 spine; inner metacarpal tubercle slightly distinct, elongated and ventral to the distal prepollex;
 1501 outer metacarpal tubercles indistinct; subarticular tubercles single, protruding; large number
 1502 of small supernumerary metacarpal tubercles present.

1503 Legs long and slender; thigh length almost equal to tibia length (THL/TL = 1.01), and
 1504 almost half of SVL (THL/SVL 0.51); tarsus slightly longer than half the thigh length
 1505 (TAL/THL 0.61); foot relatively small (Fig. 6), less than half of SVL (FL/SVL 0.42), with
 1506 slender toes and developed disks (4TD/3FD = 1.00); relative toe lengths I < II < V < III < IV;
 1507 foot webbing formula $\text{I}1^{1/2}-2^{+}\text{II}1-2^{1/2}\text{III}1^{+}-3\text{IV}3-1^{+}\text{V}$; inner metatarsal tubercle
 1508 developed, oval, visible from dorsal view; outer metatarsal tubercle absent; subarticular
 1509 tubercles present, single; some small supernumerary tarsal tubercles present; inner tarsal fold
 1510 present but poorly developed, beginning at internal metatarsal tubercle and ending at the tibia-
 1511 tarsus articulation. Dorsal and lateral skin texture smooth; ventral skin finely granular.

1512 **Coloration in life**

1513 Dorsum color pattern consisting of three beige longitudinal stripes interspersed by two
 1514 dark-brown stripes, which extend from the level of the eyes to the cloacal region. A thin,
 1515 longitudinal, and interrupted dark-brown line passes over the most lateral beige stripe. Three
 1516 longitudinal dark-brown interrupted lines pass over the central beige stripe. Body laterally
 1517 marked by a longitudinal dark-brown stripe, bordered dorsally and ventrally by a light
 1518 caramel-colored line, which extends from anterior region of nostril to inguinal region, passing
 1519 over the eye and tympanum. Upper lip margin slightly lighter, whitish. Lower lip margin
 1520 distinctly white in color, which extends until the level of the tympanum. Limbs beige
 1521 dorsally, with irregular dark-brown blotches. Lateral surfaces of shanks and forearms dark-
 1522 brown. Anterior and posterior surfaces of thighs violet; posterior surfaces with dark-brown
 1523 spots. Inguinal region with small light-brown blotches. Ventrolateral margin of forearms and
 1524 tarsus with thin cream stripe extending to the tip of fourth finger and fifth toe, respectively;

1525 ventrally a larger, darker stripe passes along forearm and tarsus. Venter of body cream-
 1526 colored. Vocal sac yellowish. Mental region with discrete dark-brown flecks. Iris silver, with
 1527 copper-colored dorsal margin and thin black reticulations (Fig. 1).

1528 **Coloration in preservative**

1529 The colors vanish, but the general pattern is retained. The violet color of the anterior
 1530 and posterior surfaces of the thighs disappears, as do the silvery and copper tones of the iris
 1531 (Fig. 5).

1532 **Variation**

1533 See Tables 1 and 2 for measurements and proportions of the type series. There is
 1534 variation in both hand and foot webbing formulae: hand $\text{I—II}(2-2^+)—3^{1/2}\text{III}(3^--3^+)—$
 1535 $(2^{1/2}-3)\text{IV}$; foot $\text{I}(1^{1/2}-2^-)—2^+\text{II}(1-1^{1/2})—(2^{1/2}-3^-)\text{III}(1^+-2^-)—3\text{IV}(3^--3)—(1^+-1^{1/2})\text{V}$. The
 1536 dorsal color varies from pale to caramel-brown; in some specimens the dorsal longitudinal
 1537 stripes are imperceptible (Fig. 1B), while in others they are extremely fragmented or
 1538 anastomosed. In some specimens there are irregularly distributed dark-brown blotches on the
 1539 dorsum. The spots on the posterior surfaces of the thighs vary in size and shape, from spots to
 1540 blotches, and in color, from light to dark-brown. Some specimens possess scars on the
 1541 dorsum, probably originating from agonistic interactions between males.

1542 **Osteology (cleared and stained MZUSP 139009 specimen)**

1543 Tympanic ring with a slender and elongate *pars externa plectri*. Optic and zygomatic
 1544 rami of squamosal equal in length. Mandibular articulation slightly anterior to the level of the
 1545 occipital condyle in dorsal view. Dentigerous processes of vomers arched with eight teeth on
 1546 the left and ten on the right. Hyoid apparatus with an oval and elongate arytenoid cartilage
 1547 (length almost two times the width). Cardiac process of cricoid cartilage with a “W”-shaped
 1548 invagination. Hyoid with both anterolateral and posterolateral processes present (Fig. 3A).

Ventral crest of humerus slight developed, with its length being 0.44 times that of the humerus; lateral crest of humerus weakly developed. Distal prepollex ossified and developed into a projecting spine with no post-articulation process (Fig. 4A). Distal prepollex shorter than metacarpus II.

Diapophysis of sacral vertebrae axe-shaped, similar to that of *Hypsiboas ericae* (Garcia and Haddad, 2008). Prehallux composed of four elements on the left foot, and five on the right; in both the two proximal elements are partially ossified, while the distal elements are completely cartilaginous.

Vocalization

Call recordings were made at the type locality on 08 November 2008, at 21:23 h, with an air temperature of 23°C and relative humidity of 85%. The recorded male called while perched on vegetation at 1.0 m above the ground, ca. 2.0 m from an artificial lake (ca. 250 m wide, 700 m length, 1.5 m deep) in anthropogenic areas (pasture), in the municipality of Aragarças near the roadside of BR 070.

Two types of notes were identified, here referred to as “A” and “B” (Fig. 7A). The two types are very similar in structure and frequency, but note A is shorter in duration and number of pulses. Additionally, the end portion of note A possesses pulses that are juxtaposed such that is difficult to count them. Also, at the end of note A there is an increase in intensity that is clear both to the ear and on the audio-spectrogram. The pulses of note B are arranged in groups that gradually increase in intensity until the last third of the note, when the intensity may decrease or remain steady. The frequency of the two notes exhibits ascending modulation. Note A is more commonly emitted, and is sometimes emitted together with note B; we believe that this composition could function as a territorial call. Rarely was note B emitted alone. Values are presented as min-max ($X \pm SD$; n).

Note A (Fig. 7B) is composed of 69–122 pulses (92.7 ± 10.1 ; 107), until the uncountable portion, with note length of 406–789 ms (533 ± 65 ; 107); dominant frequency ranges 1390.7–3078.5 Hz. The peak frequency varies from 1875 Hz at the beginning of a note to 2437.5 Hz at the end.

Note B (Fig. 7C) is composed of 106–147 pulses (132.7 ± 8.4 ; 37) arranged in 8–12 groups (10.1 ± 0.87 ; 37), with note length of 584–906 ms (771 ± 68 ; 37); dominant frequency ranges 1434.6–2922.3 Hz. The peak frequency varies from 1875 Hz at the beginning of a note to 2062.5 Hz at the end.

When A notes are emitted alone, the interval between notes ranges 320–5815 ms (1844 ± 771 ; 61). When the call composed of both notes A and B is emitted, the interval between calls ranges 1281–3191 ms (1919 ± 458 ; 35) and the interval between the notes A and B within the call ranges 282–363 ms (326 ± 21 ; 35).

Comparison with calls of other *Boana albopunctata* group species

Among all species described for this group, only *Boana dentei* and *B. steinbachi* lack formal descriptions of their vocalizations. However, Lescure and Marty (2000) make a brief comment on the call of *B. dentei*, stating that males call sporadically and their vocalization closely resembles the call of *Boana fasciata*.

The presence of intense and uncountable pulses at the end of note A of *Boana caiapo* promptly distinguishes it from the call of all other species of the group (uncountable end portion absent in the vocalization of *Boana albopunctata*, *B. alfaroi*, *B. almendarizae*, *B. calcarata*, *B. faciata*, *B. heilprini*, *B. lanciformis*, *B. leucocheila*, *B. maculateralis*, *B. multifasciata*, *B. paranaiba*, *B. raniceps*, and *B. tetete*; Duellman, 1973; Hödl, 1977; Cardoso and Vielliard, 1990; Heyer et al., 1990; De Sá, 1995, 1996; Guimarães et al., 2001; Guimarães and Bastos, 2003; Carvalho et al., 2010; Pansonato et al., 2011; Landestoy, 2013; Caminer and Ron, 2014). Because of the comment of Lescure and Marty (2000) mentioned above, we

1598 believe that this character is also likely absent in *B. dentei*. The ascending frequency
 1599 modulation of the notes of *B. caiapo* distinguishes it from the notes of *B. albopunctata*, *B.*
 1600 *calcarata*, *B. fasciata*, *B. heilprini*, *B. leucocheila*, *B. multifasciata*, *B. paranaiba*, *B.*
 1601 *raniceps*, and *B. tetete* (no frequency modulation; Duellman, 1973; Heyer et al., 1990; De Sá,
 1602 1995, 1996; Guimarães et al., 2001; Guimarães and Bastos, 2003; Carvalho et al., 2010;
 1603 Pansonato et al., 2011; Landestoy, 2013; Caminer and Ron, 2014). The pulsed structure of the
 1604 call of *B. caiapo* distinguishes it from the non-pulsed calls of *B. alfaroi*, *B. maculateralis*, and
 1605 *B. tetete* (Caminer and Ron, 2014).

1606 **Natural history**

1607 Individuals of *Boana caiapo* were found in open areas along the banks of aquatic
 1608 habitats such as marshes or shrub wetlands, margins of natural and permanent lakes covered
 1609 by grasses and shrubs, or backwaters of small rivulets, as well as in moderately disturbed
 1610 areas, such as flooded rangelands covered by shrubs. Despite search efforts, no individuals
 1611 were found in forested environments. Males were found calling on the ground, perched on
 1612 shrubs, or on fallen vegetation. The height of perched males varied from 10 to 100 cm above
 1613 the ground. Vocally active males were typically found spaced from each other and did not
 1614 form a chorus. In Barra do Garças, other species found calling at the same site where *B.*
 1615 *caiapo* was collected included *Pseudis tocantins*, *Scinax fuscomarginatus*, *Dendropsophus*
 1616 *anataliasiasi*, *Boana raniceps*, *Leptodactylus pustulatus*, *Elachistocleis cesarii*, and an
 1617 undescribed species of *Physalaemus*.

1618

1619 **Geographic distribution**

1620 All our records of *Boana caiapo* are restricted to the Tocantins-Araguaia River Basin.
 1621 Its southernmost distribution is in the municipality of Montes Claros de Goiás, state of Goiás,
 1622 and its northernmost distribution is in the municipality of Conceição do Araguaia, state of

Pará, about 892 km straight-line distance. To the east the species also occurs in the state of Tocantins, and to the west it occurs in the eastern portions of the state of Mato Grosso (Fig. 8). Besides being restricted to a single river basin, another remarkable pattern of the distribution of *B. caiapo* is its elevation range, which is between 180 and 450 m a.s.l. The complete absence of records of *H. caiapo* from either mountains or the plateaus that surround its distribution range, despite search efforts, indicates that these geographic features likely act as barriers, isolating the populations of this species to the lowlands. See the Appendix for material not included in the type series.

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APPENDIX

Material examined

- 1808 *Boana albomarginata* ($n = 1$): BRAZIL: **Espírito Santo**: Vitória: UFMG 8231.
 1809 *Boana albopunctata* ($n = 2$): BRAZIL: **Minas Gerais**: Rio acima: UFMG 1155; Belo
 1810 Horizonte: UFMG 1174.
 1811 *Boana alfaroi* ($n = 11$): BRAZIL: **Amazonas**: MZUSP 75651; **Mato Grosso**: Aripuanã:
 1812 MZUSP 80790–80794; **Rondônia**: MZUSP 107178–107181; COLOMBIA: **Caquetá**:
 1813 MZUSP 107184.
 1814 *Boana atlantica* ($n = 1$): BRAZIL: **Alagoas**: Maceió: UFMG 5744.
 1815 *Boana boans* ($n = 1$): BRAZIL: **Rondônia**: Pimenta Bueno: MPEG 8863.
 1816 *Boana caiapo* ($n = 75$): BRAZIL: **Goiás**: Britania: CHUNB 24000, 24002, 24003, 24005,
 1817 24006, 30365, 30370; **Mato Grosso**: Barra do Garças: MZUSP 143795-143800, 152332;
 1818 Cocalinho: MZUSP 29, 52, 103, 114, 125, 167, 186, 4231, 4232, 4233, 4234, 4235, 4236,
 1819 4237, 4238, 4239, 10929, 54473, 91898-91906; Santa Terezinha: CHUNB 10722, 10724;

- 1820 **Pará:** Conceição do Araguaia: CHUNB 43163, 43186, 43188, 43189, 43231-43235;
- 1821 **Tocantins:** Araguacema: Road between Araguacema and Fazenda Entre Ríos: CFBH 10256,
- 1822 10287; Dois Irmãos: Fazenda Vera Cruz: CFBH 10271; Guaraí: MZUSP 127074; Lagoa da
- 1823 Confusão: MZUSP 33866; Palmas: CHUNB: 11250-11252. 11254, 24264, 24231-24235,
- 1824 24328, 25101, 25406; Pedro Afonso: CHUNB 43187.
- 1825 *Boana calcarata* ($n = 12$): BRAZIL: **Roraima:** Rorainópolis: Santa Maria do Boiaçu,
- 1826 MZUSP 68272–68274; **Mato Grosso:** Apiacás: MZUSP 80764; Aripuanã: MZUSP 87681:
- 1827 Juruena: MZUSP 86070–86074; **Pará:** Belém: MZUSP 119518; ECUADOR: **Napo:**
- 1828 MZUSP119521.
- 1829 *Boana cinerascens* ($n = 1$): BRAZIL: **Pará:** Oriximiná: MPEG 10001.
- 1830 *Boana crepitans* ($n = 1$): BRAZIL: **Minas Gerais:** Catas Altas: UFMG 6937.
- 1831 *Boana dentei* ($n = 1$): BRAZIL: **Amapá:** Serra do Navio: MZUSP 74195.
- 1832 *Boana ericae* ($n = 1$): BRAZIL: **Goiás:** Alto Paraíso de Goiás: UFMG 11583.
- 1833 *Boana faber* ($n = 1$): BRAZIL: **São Paulo:** Americana: CFBH 3761.
- 1834 *Boana* cf. *fasciata* ($n = 3$): BRAZIL: **Pará:** Rio Xingu, MZUSP 66211–66213.
- 1835 *Boana heilprini* ($n = 1$): HAITI: **Ouest:** Kenscoff: Furcy, MZUSP 106704.
- 1836 *Boana lanciformis* ($n = 3$): BRAZIL: **Amazonas:** São Gabriel da Cachoeira: Taracuá,
- 1837 MZUSP 121575–121577.
- 1838 *Boana leptolineata* ($n = 1$): BRAZIL: **Rio Grande do Sul:** Cambará do Sul: UFMG 10016.
- 1839 *Boana leucocheila* ($n = 5$): BRAZIL: **Mato Grosso:** Aripuanã: MZUSP 80609; Apiacás:
- 1840 MZUSP 80798–80801.
- 1841 *Boana lundii* ($n = 2$): BRAZIL: **São Paulo:** Descalvado: CFBH 3907; **Minas Gerais:**
- 1842 Cabeceira Grande: UFMG 1396.
- 1843 *Boana multifasciata* ($n = 6$): BRAZIL: **Amazonas:** Reserva do Instituto Nacional de
- 1844 Pesquisas da Amazonia-World Wildlife Fund (INPA/WWF), MZUSP 64544–64546; **Goiás:**

- 1845 Montes Claros de Goiás: UFMG 5279; **Pará**: Oriximiná: MZUSP 69612; Kenpore, MZUSP
- 1846 69856.
- 1847 *Boana pellucens* ($n = 2$): ECUADOR: **Esmeraldas**: Durango: QCAZ 7267; Bosque Protector
- 1848 La Chiquita, a 30 km de San Lorenzo vía Ibarra: QCAZ 11596.
- 1849 *Boana poaju* ($n = 1$): BRAZIL: **Santa Catarina**: Rancho Queimado: UFMG 1417.
- 1850 *Boana polytaenia* ($n = 1$): BRAZIL: Minas Gerais: São Gonçalo do Rio Abaixo: UFMG
- 1851 1471, 1480.
- 1852 *Boana pombali* ($n = 1$): BRAZIL: **Espírito Santo**: Sooretama: Reserva Biológica de
- 1853 Sooretama, CFBH 14917.
- 1854 *Boana prasina* ($n = 1$): BRAZIL: **Paraná**: Jaguariaíva: UFMG 10050.
- 1855 *Boana pulchella* ($n = 1$): URUGUAY: **Maldonado**: Sierra de las Ánimas, MCN 4419.
- 1856 *Boana punctata* ($n = 1$): BRAZIL: **Mato Grosso/Mato Grosso do Sul**: UHE Ponte de Pedra,
- 1857 MZUSP 140455.
- 1858 *Hypsiboas raniceps* ($n = 9$): BRAZIL: **Goiás**: UHE Serra da Mesa, MZUSP 89164–89166;
- 1859 **Mato Grosso**: Barra do Garças: Pindaíba, MZUSP 91026-91029. **Mato Grosso do Sul**:
- 1860 Corumbá: UFMG 5603. **Minas Gerais**: Uberlândia: UFMG 1547.
- 1861 *Boana riojana* ($n = 1$): ARGENTINA: **Jujuy**: Tumbaya: Purmamarca, UFMG 5758.
- 1862 *Boana semilineata* ($n = 1$): BRAZIL: **Bahia**: Valença: UFMG 1551.
- 1863 *Boana tepuiana* ($n = 1$): BRAZIL: **Roraima**: Vila Pacaraíma: MZUSP 67057.
- 1864

1865 **Table 1.** Measurement (in mm) of the 25 adult males of the type series of *Boana caiapo* sp. nov (holotype in **bold** and marked with an *). See
 1866 Material and Methods section for abbreviations.

Collection Number	SVL	HL	HW	ED	END	IND	NSD	EW	TD	TL	FL	HAL	THL	TAL	FAL	3FD	4TD	AMD
MZUSP 138987*	47.6	16.3	14.4	4.8	3.2	4.2	2.7	3.9	2.3	23.8	19.8	13.3	24.0	14.7	7.2	2.0	2.0	8.8
MZUSP 138988	47.7	16.7	15.3	4.9	3.3	4.2	2.4	4.2	2.8	25.2	19.8	13.8	25.3	14.7	7.8	1.8	1.8	8.8
MZUSP 138989	43.8	14.7	13.9	4.8	3.1	3.9	2.2	4.1	2.5	22.6	17.9	12.2	23.4	13.5	6.8	1.5	1.5	8.0
MZUSP 138990	44.3	14.9	13.9	4.4	3.3	3.9	2.5	4.3	2.5	21.6	18.0	12.3	22.0	13.0	7.0	1.6	1.6	7.6
MZUSP 138991	49.4	15.9	15.3	4.9	3.4	4.1	2.4	4.2	2.3	24.5	21.6	14.4	25.7	15.1	8.1	1.7	1.6	8.6
MZUSP 138992	44.6	15.4	14.5	5.2	3.4	4.1	2.5	4.2	2.7	24.6	18.7	12.4	25.5	13.0	7.3	1.6	1.5	8.7
MZUSP 138993	51.2	16.5	15.4	4.8	3.5	4.1	2.3	4.2	2.6	25.2	20.0	13.8	25.9	14.3	7.8	1.8	1.6	8.7
MZUSP 138994	46.6	16.3	15.2	4.6	3.2	4.0	2.5	4.2	2.3	23.6	19.3	12.6	24.5	14.1	7.4	1.8	1.4	8.9
MZUSP 138995	46.3	14.8	14.2	4.4	3.3	4.0	2.4	3.9	2.5	22.8	18.7	12.2	23.9	13.5	8.0	1.6	1.5	8.3
MZUSP 138996	48.3	16.1	15.9	4.7	3.3	4.0	2.2	4.2	2.6	25.4	20.5	13.7	26.5	14.4	7.5	1.9	1.6	9.0
MZUSP 138997	43.4	15.9	15.3	4.8	3.5	4.1	2.3	4.5	2.5	23.7	19.1	12.4	23.8	13.6	7.2	1.9	1.8	8.7
MZUSP 138998	44.7	15.3	14.9	4.6	3.5	4.0	2.6	4.3	2.5	23.4	19.3	13.2	24.4	14.1	7.4	1.6	1.5	8.5

MZUSP 138999	42.5	14.8	14.1	4.5	3.2	4.0	2.3	3.5	2.6	23.1	18.7	12.5	23.3	14.1	6.6	1.8	1.6	8.5
MZUSP 139000	45.5	15.4	14.8	5.4	3.5	4.0	2.8	4.4	2.9	23.2	19.0	12.8	23.4	13.1	7.4	2.4	1.5	8.5
MZUSP 139001	44.9	15.3	14.1	4.5	3.2	4.1	2.3	3.5	2.5	24.1	18.7	12.9	24.4	13.7	7.2	1.8	1.6	8.5
MZUSP 139002	43.8	15.1	14.7	5.3	3.5	3.6	2.9	3.5	2.8	23.3	17.8	11.8	21.3	13.5	7.6	1.6	1.4	7.9
MZUSP 139003	45.3	15.7	15.3	5.1	3.0	4.0	2.5	4.1	2.9	23.9	18.8	12.4	22.9	13.6	8.0	1.6	1.8	8.1
MZUSP 139004	42.5	14.7	13.8	4.6	3.6	3.5	1.9	3.5	2.8	23.4	18.5	12.8	23.4	13.5	7.2	2.4	1.6	7.9
MZUSP 139005	45.3	15.5	14.6	5.0	2.9	3.9	2.5	4.1	2.4	23.8	19.7	12.6	23.3	13.9	7.8	1.8	1.6	8.4
MZUSP 139006	42.2	15.2	14.1	5.1	3.5	3.8	2.7	4.1	2.6	22.7	18.0	11.6	22.1	12.7	6.9	1.7	1.5	8.5
MZUSP 139007	43.8	15.4	13.6	4.9	3.1	3.8	2.3	3.5	2.5	23.4	18.5	11.7	22.6	13.4	7.9	1.9	1.7	8.8
MZUSP 139008	43.4	15.4	14.8	5.0	3.5	3.6	2.1	3.5	3.1	24.5	18.7	12.5	24.9	14.2	7.2	1.8	1.6	8.3
MZUSP 139009	42.7	14.4	13.4	4.5	2.6	3.9	2.1	3.6	2.3	22.0	18.2	11.6	22.2	13.2	7.4	2.0	2.0	8.5
UFMG 3281	43.3	15.0	13.8	4.7	3.5	3.4	2.5	4.9	2.5	21.1	17.2	13.3	19.2	12.1	6.6	1.5	1.5	7.5
UFMG 3918	43.9	14.9	14.3	5.1	3.4	3.8	2.4	4.0	2.8	23.1	19.5	12.1	21.6	13.2	7.6	1.8	1.5	8.5

Table 2. Minimum and maximum values of some of the ratios between measurements shown in Table 1, for the 25 adult males of the type series of *Boana caiapo* sp. nov. See Material and Methods section for abbreviations.

Proportions	Min-Max
HW/HL	0.89-0.99
HL/SVL	0.32-0.37
HW/SVL	0.30-0.35
NSD/IND	0.54-0.79
NSD/END	0.52-0.87
IND/HL	0.23-0.27
END/ED	0.58-0.79
END/HL	0.18-0.25
ED/HL	0.28-0.35
EW/HL	0.23-0.33
AMD/HW	0.53-0.64
TD/ED	0.47-0.63
TD/HL	0.14-0.20
HAL/SVL	0.26-0.31
HAL/HL	0.76-0.91
FAL/SVL	0.15-0.18
3FD/TD	0.56-0.87
3FD/HAL	0.11-0.19
THL/TL	0.91-1.05
THL/SVL	0.44-0.57
TAL/SVL	0.28-0.33

TAL/THL	0.51-0.63
TL/SVL	0.49-0.56
FL/SVL	0.39-0.44
4TD/3FD	0.63-1.08

FIGURE CAPTIONS

Fig. 1. Live specimens of (A) Holotype of *Boana caiapo* sp. nov. (MZUSP 138987); (B) paratype (MZUSP 139000).

Fig. 2. *M. depressor mandibulae* (highlighted) of (A) *Boana caiapo* sp. nov. (MZUSP 139004); (B) *B. raniceps* (UFMG 5603); and (C) *B. riojanus* (UFMG 5758). Note its slip of scapular origin present in “A” and “B” and absent in “C” (white arrows). Scale bars = 2 mm.

Fig. 3. Hyolaryngeal apparatus of (A) *Boana caiapo* sp. nov. (MZUSP 139009); (B) *B. albopunctata* (UFMG 2205); (C) *B. lundii* (CFBH 3907); and (D) *B. polytaenia* (UFMG 1471). Arrows indicate anterolateral processes of hyoid. Scale bars = 2 mm.

Fig. 4 Dorsal view of the right Prepollex of: (A) *Boana caiapo* sp. nov. (MZUSP 139009); (B) *B. albopunctata* (UFMG 2205); (C) *B. lundii* (CFBH 3907); and (D) *B. polytaenius* (UFMG 1471). It is composed of two elements: the proximal prepolex (**pprox**) and the distal prepolex (**pdist**); Arrows indicate the postaxial process of the distal Pprepollex, absent in **A**, reduced in **B**, moderately developed in **C**, and extremely developed in **D**. Scale bars 1 = mm (A, B, and C); and = 500 μ m (D).

Fig. 5. Dorsal (A) and ventral (B) views of the preserved holotype of *Boana caiapo* sp. nov. (MZUSP 138987). Scale bar = 10 mm.

Fig. 6. Lateral profile of the snout (A) and ventral views of left hand (B) and left feet (C), respectively, of the preserved holotype of *Boana caiapo* sp. nov. (MZUSP 138987). Scale bars = 5 mm.

Fig. 7. **(A)** Audio-spectrogram of notes A and B of *Boana caiapo* sp. nov. **(B-C)**

Details of notes “A” and “B”, respectively, with of some of the parameters used in the call description indicated. Recordings were made at the type locality of the species in the municipality of Aragarças, state of Goiás, Brazil.

Fig. 8. Map showing the known geographic distribution of *Boana caiapo* sp. nov, spread throughout the Tocantins-Araguaia River Basin (delimited by a white line, and also marked by dark grey on the inset). The white star marks the type locality, white asterisks mark the localities of other paratypes, and white circles represent other records. Abbreviations for states are: Bahia (BA), Goiás (GO), Maranhão (MA), Mato Grosso (MT), Mato Grosso do Sul (MS), Minas Gerais (MG), Pará (PA), Piauí (PI), and Tocantins (TO), and Distrito Federal (DF).

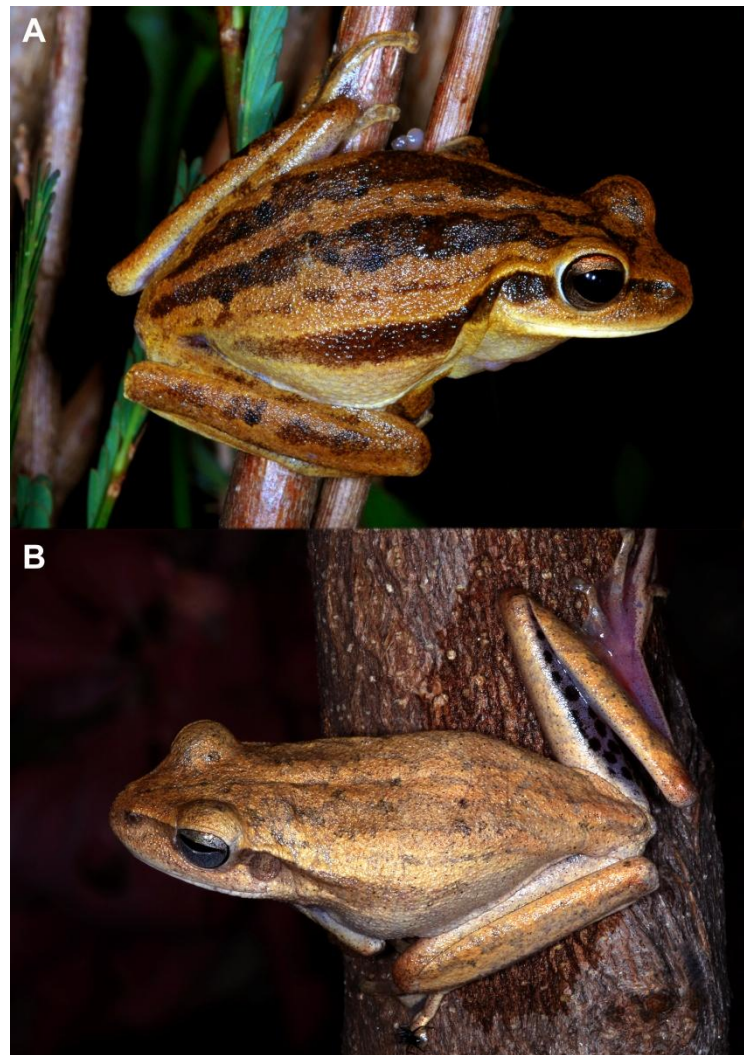
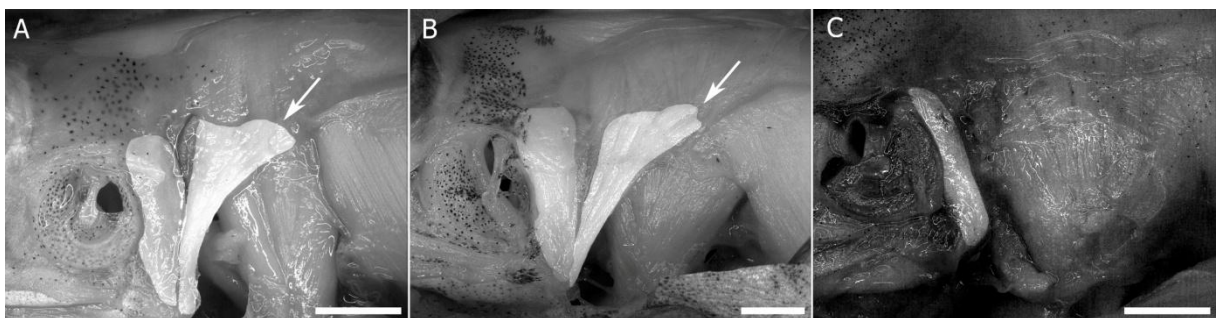
Figure 1**Figure 2**

Figure 3

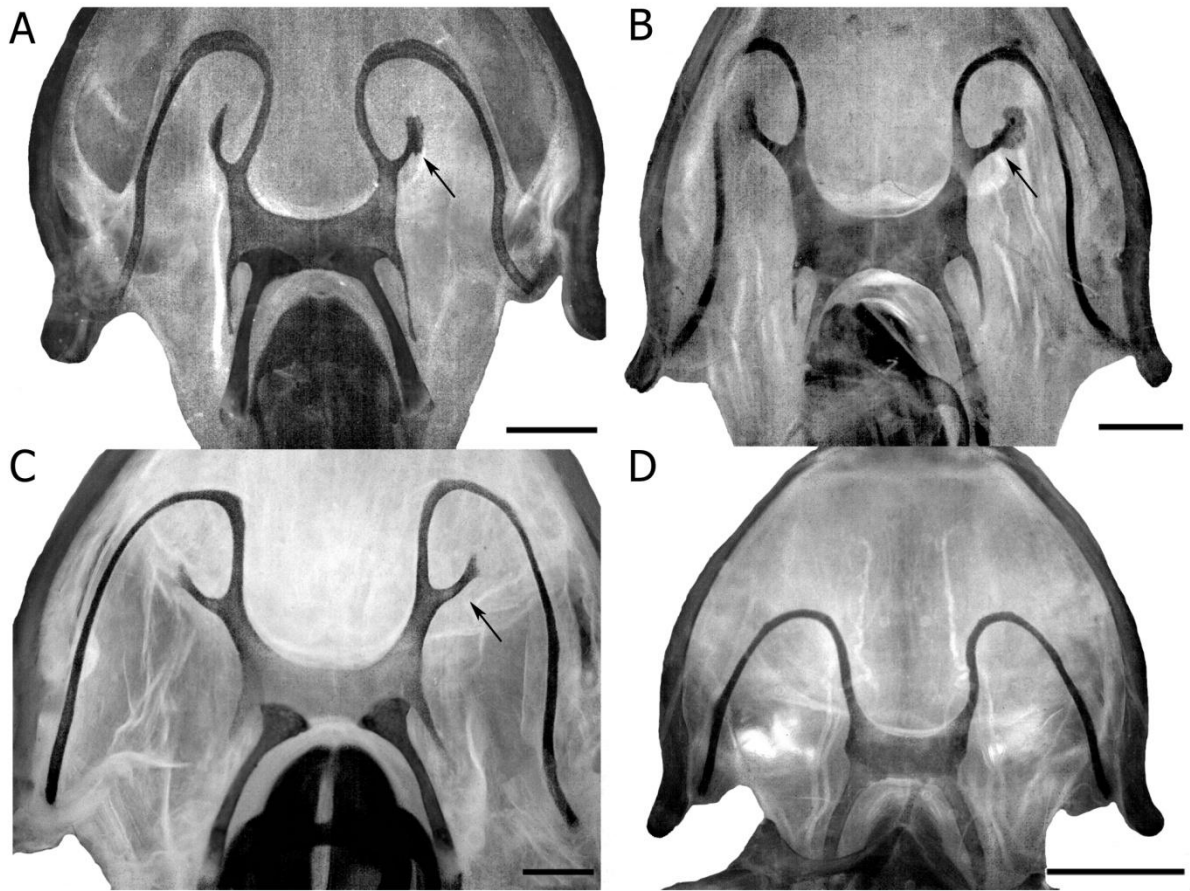


Figure 4

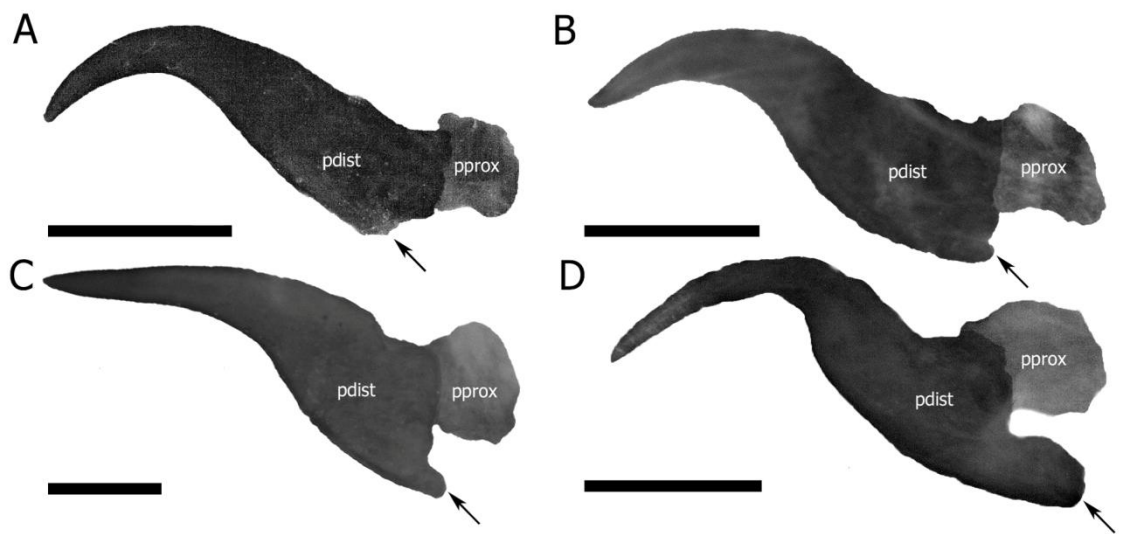


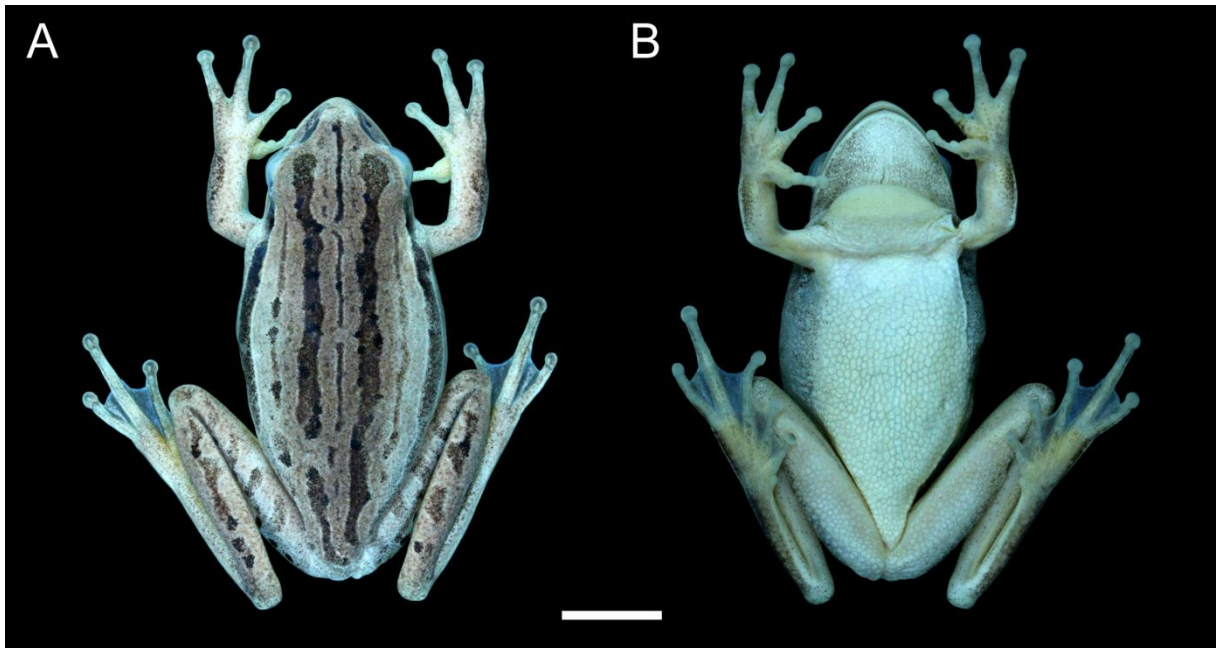
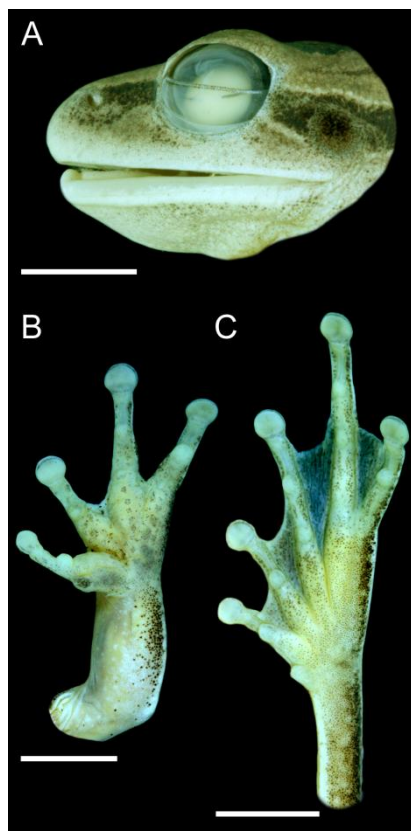
Figure 5**Figure 6**

Figure 7

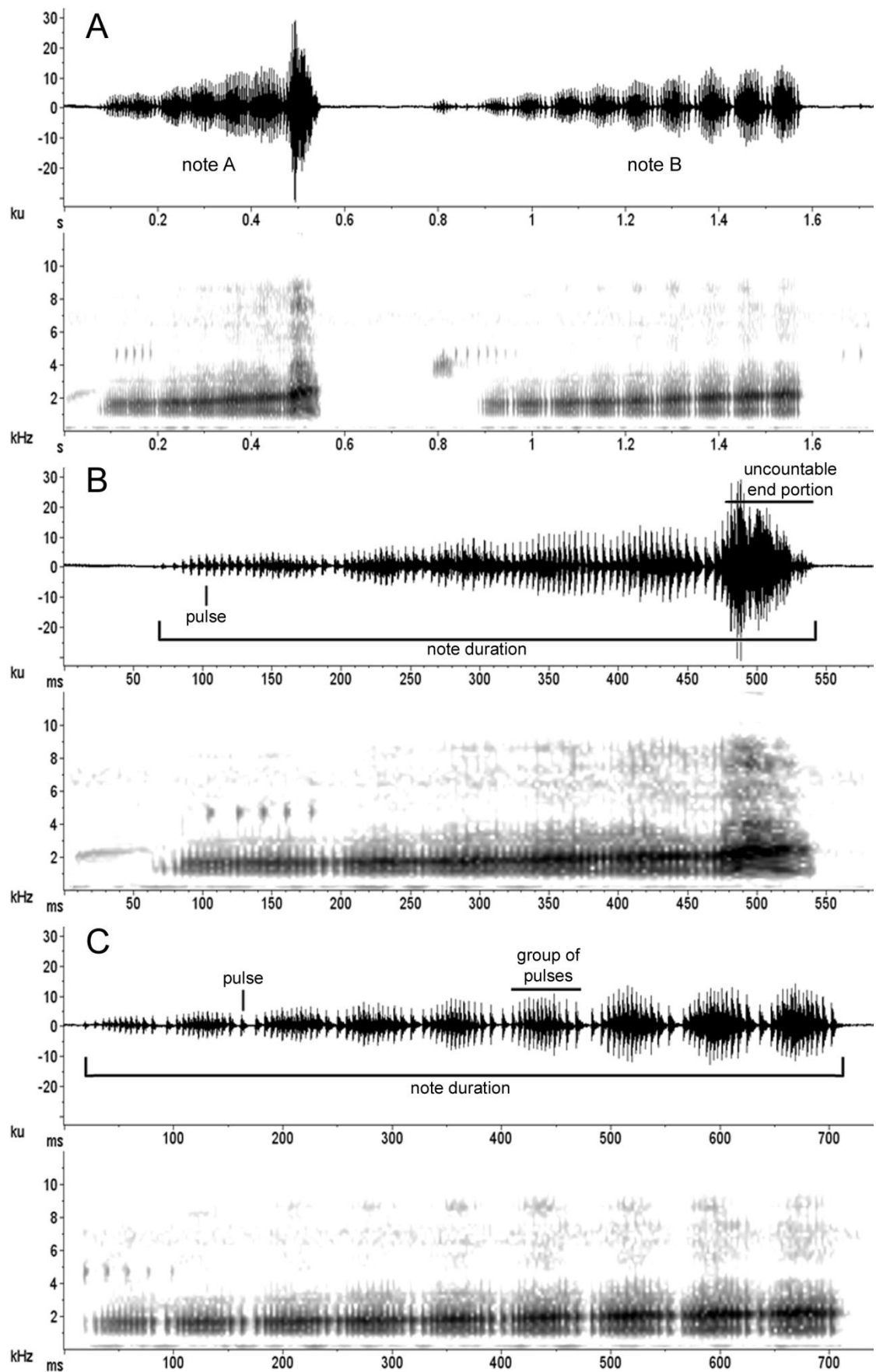
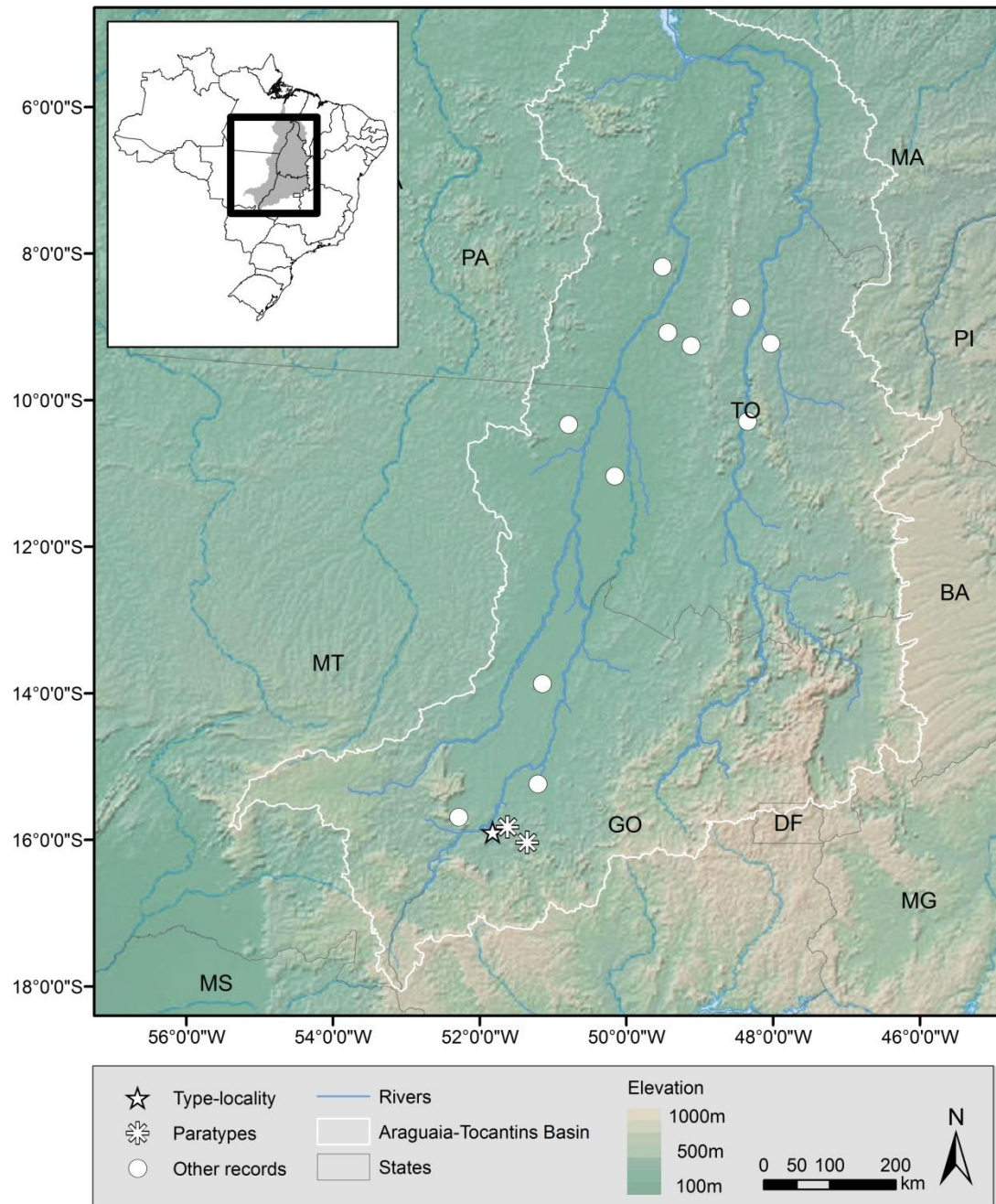


Figure 8



Seção 2

Estudos de sistemática e evolução de Cophomantini

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8 A new genus of Cophomantini, with comments on the taxonomic status of *Boana liliae*
9 (Anura, Hylidae)⁺

10 *Manuscrito preparado para ser submetido à Zoologica Scripta.

11 Paulo D. P. Pinheiro, Célio F. B. Haddad & Julián Faivovich

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13 New genus of Cophomantini

14 Pinheiro *et al.*

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27 ⁺Este trabalho foi realizado em colaboração com Phillipe J. R. Kok, Brice P. Noonan, D.
28 Bruce Means.

Abstract

Pinheiro, P. D. P., Kok, P. J. R., Noonan, B. P., Bruce Means, D. Haddad, C. F. B., Faivovich, J. (0000) A new genus of Cophomantini, with comments on the taxonomic status of *Boana liliae* (Anura, Hylidae). *Zoologica Scripta*, 00, 000-000.

The non-monophyly of the genus *Myersiohyla* and the *Boana punctata* group have been shown in distinct papers. The addition of sequence data for *Boana liliae*, a species tentatively assigned to the *B. punctata* group, to a DNA sequence dataset of Cophomantini, resulted in novel phylogenetic results for this hylid tribe. *Myersiohyla* is recovered paraphyletic, with *B. liliae* nested on it; *M. kanaima* is recovered as sister taxa to the other Cophomantini genera (except *Myersiohyla*), or poorly supported as the sister taxa to the remaining species of *Myersiohyla*. Those results led to two taxonomic changes, which are discussed in this paper. In order to avoid the paraphyly of *Myersiohyla*: (i) The new genus *Nesorohyla* is described to allocate *M. kanaima*; (ii) *B. liliae* is transferred to *Myersiohyla* and a new diagnosis for this species is provided.

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Introduction

The tribe Cophomantini was recognized by Faivovich *et al.* (2005), to include five genera of neotropical hylids: *Aplastodiscus* Lutz, 1950; *Boana* Gray, 1825 (as *Hypsiboas* Wagler, 1830); *Bokermannohyla* Faivovich, Haddad, Garcia, Frost, Campbell & Wheeler, 2005; *Hyloscirtus* Peters, 1882; and *Myersiohyla* Faivovich, Haddad, Garcia, Frost, Campbell & Wheeler, 2005. Subsequently, different studies which focused on the phylogenetic relationships of some of these genera, increased the taxonomic sampling, particularly of *Aplastodiscus* (Berneck *et al.* 2016), and *Hyloscirtus* (Coloma *et al.* 2012; Almendáriz *et al.* 2014; Guayasamin *et al.* 2015), and to a lesser extent *Boana* (Antunes *et al.* 2008; Lehr *et al.* 2010; Köhler *et al.* 2010; Caminer & Ron 2014; Fouquet *et al.* 2016; Orrico *et al.* 2017), and *Myersiohyla* (Faivovich *et al.* 2013). Higher level phylogenetic analyses (Wiens *et al.* 2010; Pyron & Wiens 2011; Duellman *et al.* 2016), mostly reanalyzed available sequences, obtaining results congruent with those of Faivovich *et al.* (2005) or differing in the position of poorly supported groups.

Myersiohyla was erected by Faivovich *et al.* (2005) for the two species of the former *Hyla aromatica* group (Ayarzagüena & Señaris 1994), *Hyla kanaima* Goin & Woodley, 1969, a species included in the former paraphyletic *Hyla geographica* group (Duellman & Hoogmoed, 1992), and, tentatively, *Hyla loveridgei* Rivero, 1961. Faivovich *et al.* (2013) described other two species, *M. chamaeleo* and *M. neblinaria*, provided comments on several aspects related to the genus, and a molecular phylogenetic analysis including the two new species and *M. kanaima*. Their analysis supports the monophyly of *Myersiohyla* with 91% jackknife resampling frequency, unlike previous analyses where it was only weakly supported or not monophyletic (Wiens *et al.* 2006, 2010). A subsequent reanalysis of hylid sequences in Genbank including only sequences of *M. kanaima* and *M. neblinaria* Faivovich, McDiarmid & Myers, 2013, did not recover *Myersiohyla* monophyletic (Duellman *et al.* 2016), as *M. kanaima* was recovered as the sister taxon of a weakly supported clade including *M. neblinaria* plus all other Cophomantini.

The results of Faivovich *et al.* (2013) indicated the non monophyly of the *Boana punctata* group as tentatively defined by Faivovich *et al.* (2005), due to the position of *B.*

ornatissima (Noble, 1923), nested in the *B. benitezi* group. Considering that the monophyly of the remaining exemplars, *B. cinerascens* (Spix, 1824), *B. picturata* (Boulenger, 1899), and *B. punctata* (Schneider, 1799), was only weakly supported, and that some species assigned to the group—*B. alemani* (Rivero, 1964), *B. hobbsi* (Cochran & Goin, 1970), *B. jimenezi* (Señaris & Ayarzagüena, 2006), and *B. liliae* (Kok, 2006) were still missing from the analysis, Faivovich et al. (2013) were explicit on the need for a stringent test of the monophyly of this species group. The availability of samples of one additional species of the *B. punctata* group, *B. liliae*, proved relevant both for testing the monophyly of the *B. punctata* group and *Myersiophyla*, and as a result, the description of a new genus of Cophomantini.

Material and methods

Taxon sampling

Our data set included the same taxonomic sampling employed by Faivovich *et al.* (2013), complemented with additional species of Cophomantini subsequently sequenced by Caminer & Ron (2014), Guayasamin *et al.* (2015), Fouquet *et al.* (2016), Berneck *et al.* (2016), and Orrico *et al.* (2017), and new sequences from four specimens of *B. liliae* and two specimens of *M. kanaima* produced for this study. See Supplementary material 1 for Genbank accession numbers.

Character sampling

We included up to 7486 bp per terminal from the same gene fragments employed by Faivovich *et al.* (2013): cytochrome b (CYTB), 12S, tRNA^{VAL}, and 16S (H1), intervening tRNA^{LEU}, NADH dehydrogenase subunit 1, and tRNA^{ILE} (ND1) mitochondrial genes; and also fragments of seven in absentia homolog 1 (SIA), exon 1 of rhodopsin (RHOD), tyrosinase (TYR), recombination activating gene 1 (RAG1), exon 2 of chemokine receptor 4 (CXCR4), and 28S nuclear genes. The primers are those used by Faivovich *et al.* (2013).

DNA isolation and sequencing

The DNA isolation, PCR, and sequencing protocols are those as described by Faivovich et al. (2013). Sequences were aligned using MAFFT (Katoh & Toh 2008). For the codifying genes (i.e., CYTB, ND1, SIA, RHOD, TYR, RAG1, CXCR4, and 28s) we used the G-INS-I strategy, and for the H1 we used the AUTO-FFT-NS-2 one. All the other parameters were set as default. Alignments were then edited using BioEdit (Hall 1999); sequence files were merged with SequenceMatrix (Vaidya *et al.* 2011).

Phylogenetic analysis

Phylogenetic analyses were done using parsimony as optimality criterion. The rationale for this is explained by Farris (1983) and discussed by others, like Goloboff (2003) and Goloboff & Pol (2005). The searches done with T.N.T Willi Hennig Society Edition (Goloboff *et al.* 2008), through New Technology Searches, combining Sectorial Search, Parsimony Ratchet, Tree Drift, and Tree Fusing, and requesting the driven search to hit the best length 100 times. Analyses were run alternatively with gaps treated as fifth state or as missing data. Parsimony Jackknife absolute frequencies (Farris *et al.* 1996) were calculated with the same parameters of the searches for the best score, although requesting the driven search to hit the best length ten times, for a total of 1000 replicates. To see the influences of *Boana liliae*, we performed parsimony analyses both with and without sequences of this taxa. Also, besides our explicit preference to parsimony, we know that many colleagues disagree with it. So, in order to provide pleasant information to the most colleagues as possible, we also run Bayesian analysis.

We run Bayesian analyses using MrBayes 3.2 (Ronquist *et al.* 2012). Models for each partition were selected with Partition Finder v2.1.1 (Lanfear *et al.* 2016). Branch lengths were treated as linked, and the analysis considered only models employed by MrBayes 3.2. The corrected Akaike Information Criterion (AICc) was used to select the best fitting model for each gene (Lanfear *et al.* 2016). First, second, and third codon

positions were treated as separate partitions for each protein-coding gene. The regions of [12S + tRNA^{VAL} + 16S(in part)], [16S(in part) + tRNA^{LEU}], [tRNA^{ILE} + tRNA^{GLN}], and 28S were treated as a single partitions for model selection. Partition Finder was run employing the greedy algorithm (Lanfear *et al.* 2012) and PhyML software (Guindon *et al.* 2010). As the software may result in a same model for the many different partitions, and Partition Finder may consider them as separate subsets, we joined all partitions having the same model in a single subset, in order to minimize the number of parameters during Bayesian analyses. Analyses were performed in the CIPRES web cluster (Miller *et al.* 2010). Analyses included two runs of 60 million generations and four Monte-Carlo Markov Chains each (with a burn-in fraction of 0.25). State Frequencies (statefreqpr) was set as fixed (equal); substitution rate (ratepr) was set as variable. The other priors were set as default. Stabilization of resulting parameters was evaluated using Tracer (Rambaut *et al.* 2014). Bayesian results are presented as Supplementary material 2.

Genetic distances among *Boana liliae* species were estimated by pairwise comparisons of the final ~500 bp sequences of the 16S mitochondrial rRNA gene (see Vences *et al.* 2005a, b; Fouquet *et al.* 2007) using PAUP* (Swofford 2002) through the command “dset distance=p”. This algorithm calculates the percentual of sites which differ between two sequences. Trees were edited with FigTree (Rambaut 2014).

Results

The parsimony phylogenetic analyses (gaps treated as a fifth state) resulted in 28 trees of 28869 steps. The conflict between these optimal hypotheses involves relationships between *Myersiohyla neblinaria specimens*, and also internal relationships of the *B. albopunctata* group, *B. faber*, and *B. pulchella* groups. The few topological differences between parsimony results, considering gaps as a fifth state or as missing data, and Bayesian hypotheses involve poorly supported clades in the parsimony analyses, including relationships among outgroups, the position of *M. kanaima*, internal relationships of a few taxa in *Aplastodiscus*, *Bokermannohyla*, and *Hyloscirtus*, the position of the *B. benitezi*, *B.*

punctata, and *B. semilineata* groups, *B. picturata* (Boulenger, 1899) and *B. sibleszi* (Rivero, 1972) with respect to other species groups of *Boana*.

The four specimens of *Boana liliae* are recovered nested within *Myersiohyla*, as the sister taxon of *Myersiohyla chamaeleo* (97% jackknife absolute frequency; gaps treated as a fifth state; 100% when treated as missing data), which makes *Myersiohyla* paraphyletic (Fig. 1).

When we exclude *B. liliae*, we obtain a monophyletic *Myersiohyla* with 85% support when gaps are treated as a fifth state, and 78% support with gaps as missing data. Considering gaps as a fifth state, the inclusion of *B. liliae* diminishes the support for the clade including *Myersiohyla kanaima*, *M. neblinaria*, *M. chamaeleo*, and *B. liliae* (<50%). When gaps are considered as missing data, alternative relationships are found. *Myersiohyla kanaima* is recovered as the sister taxon of the clade including *Hyloscirtus*, *Bokermannohyla*, *Aplastodiscus*, and *Boana*, with <50% of jackknife frequency.

Discussion

Our results revealed the non-monophyly of *Myersiohyla*, as *Boana liliae* is nested on it, as the sister taxon of *M. chamaeleo*. *Myersiohyla kanaima* is recovered as the poorly supported sister taxon of the remaining species of *Myersiohyla*—in the parsimony analysis considering gaps as a fifth state—, or as the sister taxon of the other genera of Cophomantini (*Aplastodiscus*, *Boana*, *Bokermannohyla*, *Hyloscirtus*), in the parsimony analysis considering gaps as missing data and in the bayesian analysis. Several reanalyses (Wiens *et al.* 2006, 2010; Pyron & Wiens 2011; Duellman *et al.* 2016) obtained a similar result to ours involving the possible non-monophyly of *Myersiohyla*. However, none of the reanalyses published subsequently to Faivovich *et al.* (2013)—where the monophyly of *Myersiohyla* was supported with 91% jackknife frequency—included the same three species of *Myersiohyla* employed by those authors.

On the basis of our results, it is necessary to remediate the non-monophyly of *Myersiohyla*. This requires the recognition of a new genus for *M. kanaima*, and the formal inclusion of *B. liliae* in *Myersiohyla*.

A new genus of Cophomantini

Nesorohyla, new genus

Type species. Hyla kanaima Goin and Woodley, 1969.

Diagnosis. Eggs entirely pigmented; iris entirely black; enlarged prepollex, not modified as a projecting spine; reduced fringes on fingers and toes; overall brownish coloration; nuptial pads present, light-colored, on inner margin of metacarpal II and inner metacarpal tubercle; two small calcar tubercles.

Comparison with other genera of Cophomantini. From the characters employed in the diagnosis, the only putative autapomorphies of *Nesorohyla* so far seems to be the entirely pigmented ovum (Duellman & Hoogmoed 1992; Faivovich *et al.* 2013) and the entirely black iris (MacCulloch & Latrop 2005). The value of the generic diagnoses that are not based on synapomorphies is extremely limited, as they are of actual use only for species already known to be included in those genera—and on which the generic diagnosis is made—but have no predictive value for new species that needs to be compared to a number of genera for which no synapomorphies are known. Having this in mind, we provide below a comparison of *Nesorohyla*, based on the diagnostic characters, with all other genera of Cophomantini.

The occurrence of entirely black ova and black iris differentiates *Nesorohyla* from all other genera of Cophomantini. The absence of a prepollical spine differentiates *Nesorohyla* from most species in the genera *Boana* and *Bokermannohyla* (Faivovich *et al.* 2005), and the three species of *Hyloscirtus* with a prepollical spine (Kizirian *et al.* 2003; Almendáriz *et al.* 2014; Rivera-Correa *et al.* 2016). The reduced fringes on fingers and toes differentiate *Nesorohyla* from all species of *Hyloscirtus* (Faivovich *et al.* 2005). The overall brownish coloration differentiates *Nesorohyla* from *Aplastodiscus* (overall green, with only

one brown species; Berneck *et al.* 2016). The small, light colored nuptial pad differentiates *Nesorohyla* from *Myersiohyla* (dark colored simple or double nuptial pads covering the medial margin of Finger II, including prepollex and Metacarpal II; Faivovich *et al.* 2013). The calcar composed of two small tubercles distinguishes *Nesorohyla* from *Myersiohyla* (calcar absent in *M. aromatica*, *M. chamaleo*, *M. inparquesi*, *M. liliae*—see below—, *M. neblinaria*; calcar as a transversal ridge on the heel in *M. loveridgei*; Rivero, 1961; Ayarsagüena & Señaris 1994; Kok 2006; Faivovich *et al.* 2013).

Etymology. The name *Nesorohyla* is derived from the combination of Greek roots *nesos* (island) and *oros* (mountain), and the classical genus *Hyla*, meaning *Hyla* from the mountain island. It is an allusion to the geologic formation where the species is found: the Tepuis in northern South America, which are usually referred to as altitude islands.

Content. *Nesorohyla kanaima* (Goin & Woodley, 1969) new combination.

Comments. Our study of some adult male specimens (vouchers ROM 39575–76, 43861, 43871, from Mount Ayanganna, western Guyana) did not indicate a mental gland, but this needs to be corroborated with histology. The polarity of most phenotypic diagnostic characters is unclear, with the exception of the iris entirely black and the entirely pigmented ova, which are likely autapomorphies of this new genus. The tadpoles described by MacCulloch & Lathrop (2005) were tentatively assigned to *Nesorohyla kanaima* due to the presence of both juveniles and recently metamorphosed individuals, associated to the species by the color pattern. However, the tadpoles described differ from other tadpoles of early diverging lineages of Cophomantini. The identification of these tadpoles was already discussed by Faivovich *et al.* (2013).

There are few observations about the biology of *N. kanaima*. Duellman & Hoogmoed (1992) reported the absence of ponds in Mt. Roraima (limits between southeastern Venezuela and northeastern state of Roraima, Brazil), and associated this to the large oviducal eggs of females to suggest that probably the species reproduces in rivers and

rivulets. MacCulloch & Lathrop (2005) collected tadpoles and juveniles in a lentic riverine pond on Mt. Ayanganna.

The two probably autapomorphies of *Nesorohyla kanaima*, black iris in life (MacCulloch & Latrop 2005), and mature oocytes entirely pigmented, without a noticeable external difference between animal and vegetal poles (Duellman & Hoogmoed 1992; Faivovich *et al.* 2013; voucher USNM 549311) are very infrequent in Hylidae. The iris in the other species of *Myersiohyla* has been described as dark brown in *M. aromatica* (Ayarzagüena & Señaris, 1994), black with metallic copper reticulation in *M. chamaeleo* and *M. neblinaria*, bronze in *M. inparquesi* (Ayarzagüena & Señaris, 1994), silver to bronze in *M. liliae*, and gray in *M. loveridgei* (Rivero 1972; Ayarzagüena & Señaris 1994; Kok 2006, Faivovich *et al.* 2013).

The entirely pigmented ovum is a rare character state. Normally, anuran eggs have an animal pole pigmented with melanin, and an unpigmented vegetatal pole; less frequently an unpigmented animal pole. Entirely pigmented eggs have also been described in *Bufo bufo* (Linnaeus, 1758) and *Leptophryne borbonica* (Tschudi, 1858) (Bufonidae); *Centrolene geckoideum* Jiménez de la Espada, 1872 (Centrolenidae; Rueda-Almonacid, 1994); *Crossodactylodes itambe* Barata, Santos, Leite & Garcia, 2013 (Leptodactylidae; M.T.T. Santos personal communication) and *Odorrana bacboensis* (Bain, Lathrop, Murphy, Orlov & Ho, 2003) (Ranidae; Boulenger 1898b; Berry 1972; Iskandar 1998; Bain *et al.* 2003), but overall remains a poorly studied character.

Whereas both Duellman & Hoogmoed (1992) and Faivovich *et al.* (2013) report large, mature, and entirely pigmented eggs for specimens of Mt. Kanaima and Mt. Roraima, MacCulloch & Latrop (2005) report 14 females with black and white oocytes, 1 mm in diameter—a size that may indicate that these oocytes were not mature yet—, and four females with just tiny completely white oocytes.

A sixth species of Myersiohyla

Our results indicate that *Boana liliae* should be transferred to *Myersiohyla*. The species is supported by a 97% Parsimony Jackknife absolute frequency as the sister taxon

of *M. chamaeleo*. Also, with its transference to *Myersiohyla* we present below a new diagnoses for the species. We therefore recognize it as:

Myersiohyla liliae (Kok, 2006) **New Combination.**

Hypsiboas liliae Kok, 2006. Original description

Hypsiboas liliae—Kok & Kalamandeen (2008). Characterization in a regional faunal study of Kaieteur National Park, Guyana.

Hypsiboas liliae—Faivovich *et al.* 2013. Comments in the context of dubious monophyly of the *Boana punctata* group.

Boana liliae—Dubois *et al.* 2017. First combination with *Boana* Gray, 1825.

Diagnosis. *Myersiohyla liliae* can be diagnosed by the following combination of characters: (1) small snout-vent length in males (SVL 32.5-37.1 mm; females unknown); (2) presence of a small and oval mental gland; (3) granular skin on dorsum; (4) presence of an ulnar fold on forearm; (5) presence a single, dark colored nuptial pad on Finger II; (6) overall coloration green to yellowish; (7) white parietal peritoneum; (8) advertisement call composed by a sequence of notes which increase in intensity and rate, as the interval between notes diminishes; (9) dominant frequency of the notes 3.24-3.94 kHz (Kok 2006).

Comparison with other species of *Myersiohyla*. The SVL of male in *M. liliae* (32.5-37.1 mm; Kok 2006;) promptly distinguishes it from all other species of the genus, which are larger (combined SVL of males of *M. aromatica*, *M. chamaeleo*, *M. inparquesi*, *M. loveridgei*, and *M. neblinaria* 42-52.3 mm; Rivero 1961, 1972; Ayarzagüena & Señaris 1994; Faivovich *et al.* 2013). The presence of an externally visible mental gland is shared by *M. liliae*, *M. chamaeleo*, and *M. loveridgei*; *M. neblinaria* has a mental gland that is evident only through dissection; the presence of this character in *M. aromatica* and *M. inparquesi* remains unknown (Kok 2006; Faivovich *et al.* 2013). The dorsal granular skin promptly distinguishes *M. liliae* from all the other species of *Myersiohyla* (dorsal skin smooth; Rivero 1961, 1971; Ayarzagüena & Señaris 1994; Kok 2006; Faivovich *et al.*

2013). The presence of an ulnar fold on the forearm distinguishes *M. liliae* from *M. chamaeleo* (ulnar fold absent in this species; Kok 2006; Faivovich *et al.* 2013). Whereas *M. liliae* has a single nuptial pad on Finger II, *M. aromatica*, *M. chamaeleo*, and *M. loveridgei* have two (Ayarzagüena & Señaris 1994; Kok 2006; Faivovich *et al.* 2013), and *M. inparquesi* and *M. neblinaria* have a single, larger nuptial pad which covers dorsally the prepollex and medially the first finger (Ayarzagüena & Señaris 1994; Faivovich *et al.* 2013). The only other species reported to present an overall greenish coloration, is *M. chamaeleo*. However it also has stellated melanophores, which seem to be absent in *M. liliae* (Kok 2006; Faivovich *et al.* 2013). The remaining *Myersiohyla* species present a brownish dorsum that can be marbled with cooper (*M. aromatica*), with thin black reticulations (*M. inparquesi*), marbled with darker colors (*M. loveridgei*), or present variable spots (*M. neblinaria*; Rivero 1961, 1971; Ayarzagüena & Señaris 1994; Faivovich *et al.* 2013). The white peritoneum is shared only with *M. chamaeleo*; *M. neblinaria* present a translucent peritoneum (Faivovich *et al.* 2013). The other species of the genus remain with this character unknown. Finally, species of *Myersiohyla* with described vocalizations (all but *M. loveridgei*) have calls as a long series of repeated notes; however, the call of *M. liliae* has an increase in both intensity and rate of the call, while *M. aromatica*, *M. chamaeleo*, *M. inparquesi* and *M. neblinaria* have a call with a constant interval between notes, and constant intensity (Ayarzagüena & Señaris 1994; Kok 2006; Faivovich *et al.* 2013). The notes dominant frequency of the advertisement call of *M. liliae* (3.24-3.94 kHz; Kok, 2006) is higher than in the other *Myersiohyla* species for which the advertisement call is known (combined values of note dominant frequency of *M. aromatica*, *M. chamaeleo*, *M. inparquesi*, and *M. neblinaria* 1.52–2.2 kHz; Ayarzagüena & Señaris 1994; Faivovich *et al.* 2013).

Comments. See Kok (2006) for a thorough description of the type series. In the original description of *Boana liliae*, Kok (2006) tentatively assigned the new species to *Boana* (as *Hypsiboas*), and to the *B. punctata* group, on the basis of its similarity with *B. cinerascens*, although stressing that there were no putative synapomorphies for this association. Our results, instead, recover a strongly supported sister taxon relationship with *Myersiohyla*

chamaeleo, indicating the association of that species with the genus *Myersiohyla*. This placement, based on our molecular data actually implies no incongruence with phenotypic evidence.

Kok (2006) characterized *Boana liliae* on the basis of the combination of 22 characters:

(1) medium size (SVL 32.5-37.1 mm in adult males; unknown females); (2) skin of dorsum and belly thickly granular; (3) body slender; (4) head slightly wider than long, wider than body; (5) snout truncate in dorsal view and slightly protruding in lateral view, with strongly protuberant nostrils; (6) large prominent eyes, palpebral membrane lacking reticulations; (7) tympanum large, round, approximately half the horizontal diameter of the eye; (8) supratympanic fold strongly visible, not or feebly obscuring the upper margin of the tympanum; (9) limbs long and slender; (10) axillary membrane absent; (11) subarticular tubercles on fingers single; (12) enlarged prepollex not modified as a projecting spine; (13) nuptial pads present in males; (14) small mental glands in males; (15) hands about one-fifth webbed, feet about four-fifths webbed; (16) distinct ulnar fold; (17) weak inner tarsal fold, tarsal tubercles absent; (18) heel tubercles and calcar absent; (19) cloacal sheath absent or very short; (20) in life, dorsal surfaces bright green to bright yellowish green during the day, greenish brown at night, ventral surfaces blue, translucent in the central portion of abdomen, iris silver with black periphery during the day, bronze at night; in preservative all surfaces become whitish; (21) peritoneum white; (22) breeding call consisting of a long series of loud percussive notes gradually increasing in speed and loudness (call length about 60 seconds, up to seven notes per second).

Most these characters would allow associations with many species in most genera of Cophomantini. A few of these, however, require comment. An enlarged prepollex not modified as a projecting spine (Ch. 12) is shared with *Nesorohyla*, *Myersiohyla*, *Hyloscirtus* (except *H. condor* Almendáriz, Brito, Batallas & Ron, 2014, *H. diabolus* Rivera-Correa, García-Burneo & Grant, 2016, and *H. tapichalaca* Kizirian, Coloma & Paredes-Recalde, 2003), *Aplastodiscus*, and some species of the *Boana semilineata* group (*B. diabolica* [Fouquet, Martinez, Zeidler, Courtois, Gaucher, Blanc, Lima, Souza, Rodrigues & Kok, 2016], *B. geographica* [Spix, 1824], *B. hutchinsi* [Pyburn & Hall, 1984],

and *B. semilineata* [Spix, 1824]; Faivovich *et al.* 2006; Fouquet *et al.* 2016). Nuptial pads (Ch. 13) occur in *Myersiohyla*, *Nesorohyla* (Ayarzagüena & Señaris 1994; Faivovich *et al.* 2013), and also in one species of *Aplastodiscus* (Lutz 1950), some species of *Bokermannohyla* (Leite *et al.* 2011), *Hyloscirtus* (Coloma *et al.* 2012; Rivera-Correa & Faivovich 2013), and the *Boana semilineata* species group (Faivovich *et al.* 2006). The presence of a mental gland in males (Ch. 14), is shared with several species of *Boana*, and also many species of *Aplastodiscus*, *Bokermannohyla*, *Hyloscirtus*, and *Myersiohyla* (see Brunetti *et al.* 2014). White peritonea (Ch. 21), the presence of iridophores on parietal or visceral peritonea is reported in *Aplastodiscus* (Berneck *et al.* 2016), some species of *Boana* of the *B. benitezi*, *B. faber*, *B. pellucens*, *B. pulchella*, and *B. punctata* groups (Duellman 1971; Lutz 1973; Hoogmoed 1979; Garcia 2003; Faivovich *et al.* 2005, 2006, 2013;), the *Hyloscirtus bogotensis* group (Ruiz-Carranza & Lynch 1991), and *Myersiohyla chamaeleo* (Faivovich *et al.* 2013). The call composed by a long series of notes (Ch. 22) as discussed above, is shared with all species of *Myersiohyla* with call described. In fact, to our knowledge, in *Boana* a similar call structure, in terms, is present only in *B. faber* (Wied-Neuvied, 1821), *B. pellucens* (Werner, 1901) and *B. boans* (Linnaeus, 1758) (*B. faber* and *B. semilineata* groups, respectively; Martins and Haddad, 1988; Duellman, 2005).

Specimens of *Myersiohyla liliae* were collected calling from water filled phytotelms of the bromeliad *Brocchinia micrantha*, but in a nearby locality males were heard calling from high elevation in trees close to a field of bromeliads of the same species (Kok 2006). Whether the species actually reproduces on the phytotelms remains unknown. Although it remains also unknown where the other species of *Myersiohyla* lay their eggs, tadpoles of four species have been collected in streams (Ayarzagüena & Señaris 1994; Faivovich *et al.* 2013); *M. aromatica* and *M. chamaeleo* have been reported to call from bromeliads, close to streams; and *M. neblinaria* at least uses bromeliads for day retreat (Ayarzagüena & Señaris 1994; Faivovich *et al.* 2013). Five species of *Myersiohyla* are known from vegetation around streams in the flat-topped Tepuis in southern Venezuela, at least at 900 m a.s.l. (Rivero 1961, 1971; Ayarzagüena & Señaris 1994; Faivovich *et al.* 2013). *M. liliae*, however, is an inhabitant of primary forests, known in lower areas at 400—550 m a.s.l. in

two localities (Kok 2006), but probably widespread in the Pakaraima Mountains of Guyana (Kok & Kalamandeen 2008). Our specimens of *M. liliae* from Kaieteur Plateau, Potaro-Siparuni district, Guyana (IRSNB 1965 and 1968) and from Imbaimadai, Guyana (BPN 1227 and 1234)—two localities 110 km distant each other—have *p*-distances in 16S of 2.2–2.3% (Table 1), indicating that more attention should be given to this species.

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- 668

669 Table 1. Uncorrected *p*-distances between 16S partial sequences of *Myersiohyla liliae*
 670 specimens. Percentage significant values are indicated by an asterisk.

	<i>M. liliae</i> BPN1227	<i>M. liliae</i> BPN1234	<i>M. liliae</i> IRSBN1968	<i>M. liliae</i> IRSBN1965
<i>M. liliae</i> BPN1227	-			
<i>M. liliae</i> BPN1234	0.00	-		
<i>M. liliae</i> IRSBN1968	2.16*	2.16*	-	
<i>M. liliae</i> IRSBN1965	2.35*	2.35*	0.54	-

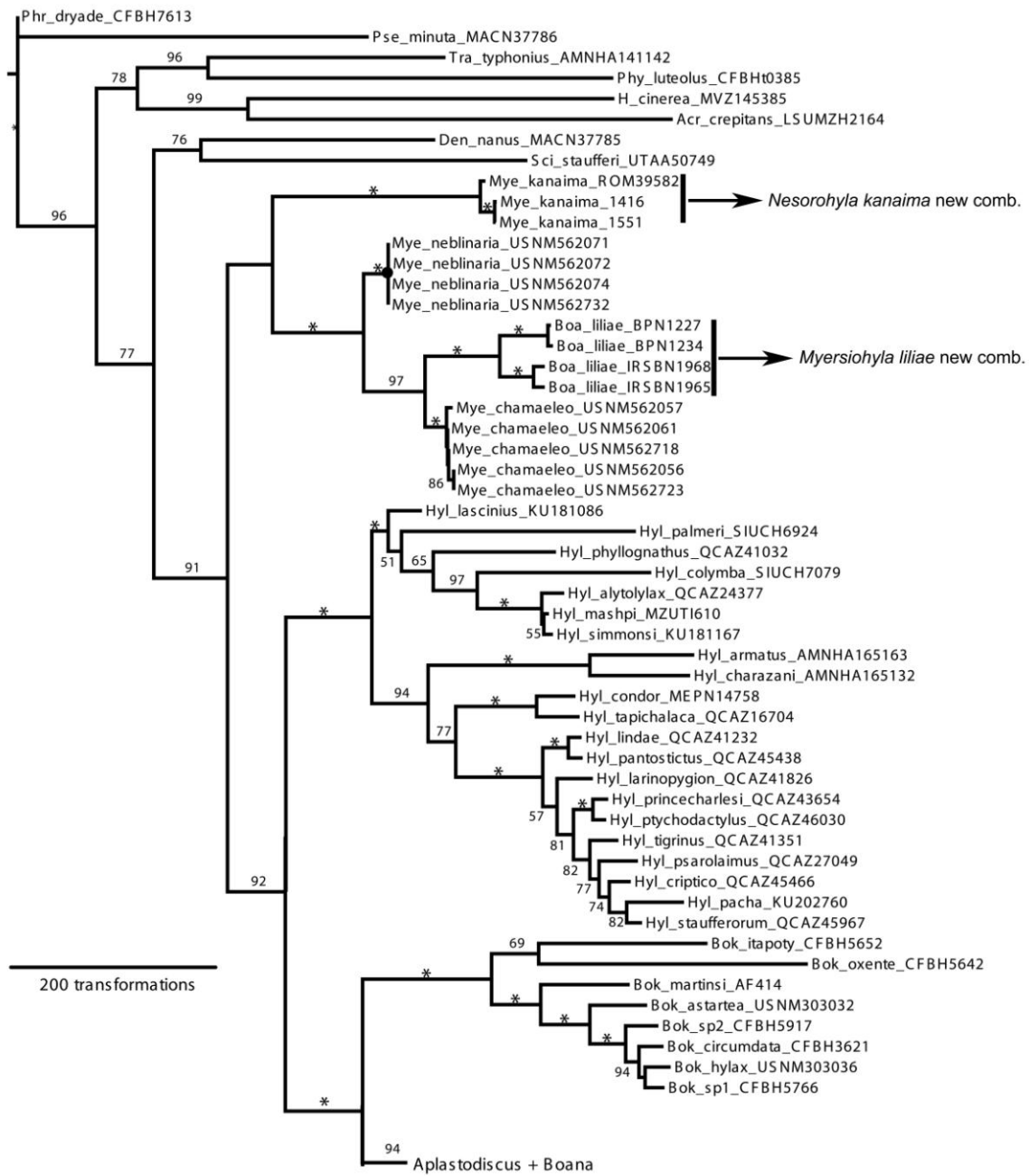
671

672

673 Figure Labels

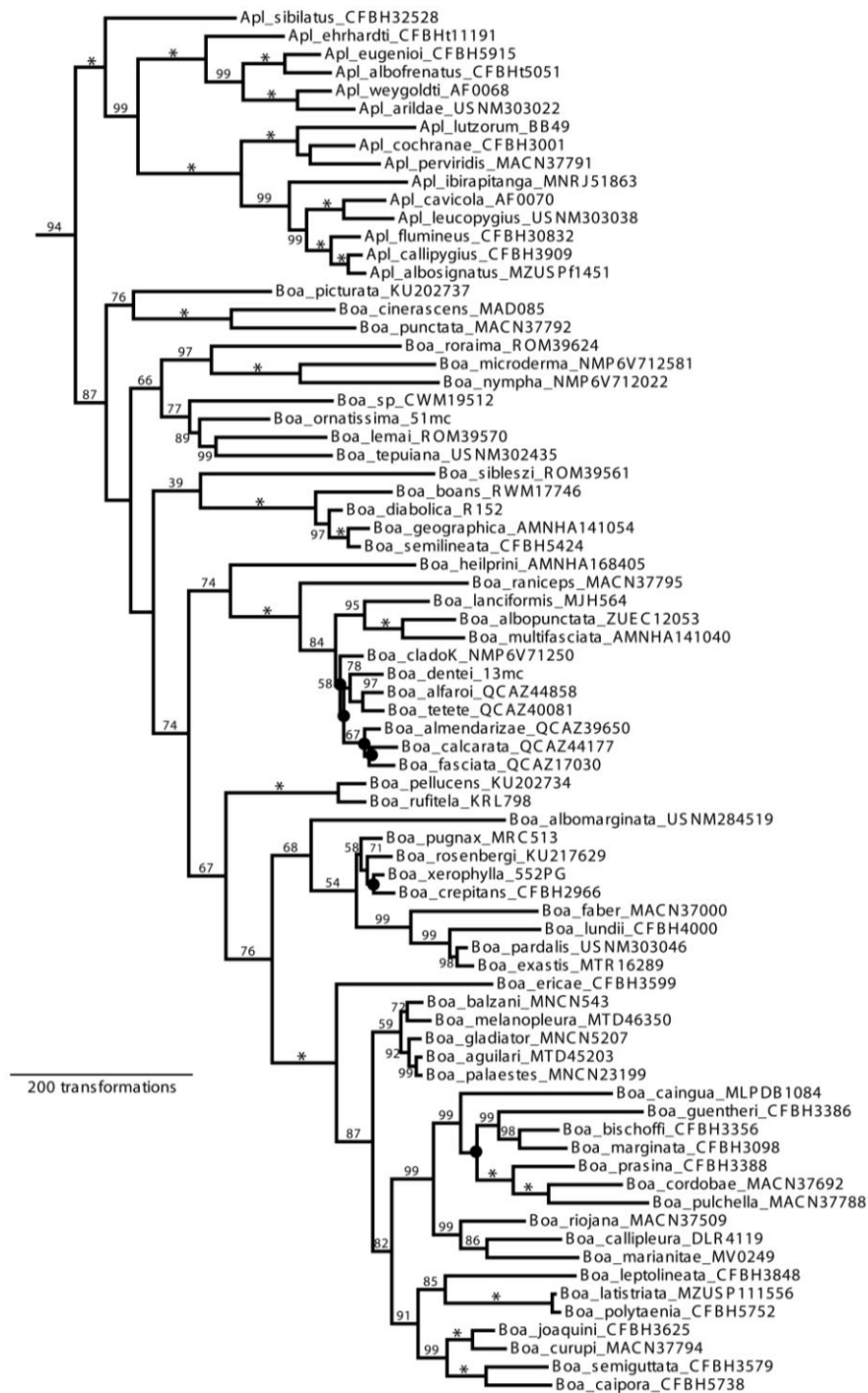
674 **Fig. 1.** One of the most parsimonious trees calculated treating gaps as a fifth state. Numbers
675 on nodes are Parsimony Jackknife Absolute Frequencies. An asterisk indicates 100%
676 jackknife values. Values below 50% are not shown. Black dots indicate nodes that collapse
677 under strict consensus. Numbers on terminals names are Vouchers numbers or sample
678 numbers.

679

680 **Figure 1.**

681

682

683 **Figure 1. Continued.**

684

685

686 Supplementary material 1

687 Genbank accession numbers for the sequences employed in the phylogenetic analyses and estimation of *p*-distances. Sequences
 688 were produced by Darst & Cannatella (2004), Faivovich *et al.* (2004, 2005, 2010, 2013), Salducci *et al.* (2005), Wiens *et al.*
 689 (2006), Antunes *et al.* (2008), Kohler *et al.* (2010), Lehr *et al.* (2010), Coloma *et al.* (2012), Almendáriz *et al.* (2014), Caminer
 690 & Ron (2014), Guayasamin *et al.* (2015), Berneck *et al.* (2016), Fouquet *et al.* (2016), Orrico *et al.* (2017). See those papers for
 691 locality data and other voucher information. Sequences produced for this project are in bold.

Taxon	Voucher	12s- tRNA ^{VAL} - 16s	16s- tRNA ^{LEU} - ND1- tRNA ^{ILE} - tRNA ^{GLN}	Cytochrome b	Rhodopsin Exon 1	Recombination Activating Gene 1	Tyrosinase	Seven in Absentia Homolog 1	Chemokine Receptor 4 Exon 2	28S
<i>Acris crepitans</i>	LSUMZ-H 2164	AY843559	GQ366290	AY843782	AY844533	AY844358	AY844019	AY844762	GQ365976	AY844194
<i>Aplastodiscus albofrenatus</i>	CFBH-t 5051	KU184021	-	-	KU184111	KU184083	KU184246	KU184149	-	-
<i>Aplastodiscus albosignatus</i>	MZUSP-field 1451	KU184037	-	-	KU184117	KU184086	KU184252	KU184155	-	-
<i>Aplastodiscus arildae</i>	USNM 303022	AY843604	-	AY843825	AY844578	AY844392	AY844049	AY844803	-	AY844223
<i>Aplastodiscus callipygius</i>	CFBH 3909	AY843614	-	AY843840	AY844592	AY844402	AY844058	AY844813	-	AY844236
<i>Aplastodiscus cavicola</i>	AF0070	AY843617	-	AY843843	AY844594	AY844405	-	AY844814	-	XXXXXXX
<i>Aplastodiscus cochranae</i>	CFBH 3001	AY843568	-	AY843790	AY844542	AY844365	AY844024	AY844770	-	AY844200
<i>Aplastodiscus ehrhardti</i>	CFBH-t 11191	KU184017	KU184225	-	KU184103	-	KU184239	KU184141	-	-
<i>Aplastodiscus eugenioi</i>	CFBH 5915	AY843669	-	AY843913	AY844660	AY844456	-	AY844875	KF751465	-
<i>Aplastodiscus flumineus</i>	CFBH 30832	KU184013	-	-	KU184127	KU184092	KU184260	KU184164	-	-
<i>Aplastodiscus ibirapitanga</i>	MNRJ 51863	KU184025	KU184228	-	KU184099	-	KU184236	KU184138	-	-
<i>Aplastodiscus leucopygius</i>	USNM 303038	AY843569	KF794106	AY843873	AY844622	AY844425	AY844084	AY844840	KF751466	AY844261
<i>Aplastodiscus lutzorum</i>	BB 49	KU184003	KU184217	-	KU184107	-	KU184242	KU184145	-	-
<i>Aplastodiscus perviridis</i>	MACN 37791	AY843569	KF794107	AY843791	AY844543	AY844366	AY844025	AY844771	KF751467	AY844201
<i>Aplastodiscus sibilatus</i>	CFBH 32528	KU184014	-	-	KU184133	KU184094	KU184264	KU184170	-	-

<i>Aplastodiscus weygoldti</i>	AF 0068	AY843685	-	AY843931	AY844678	AY844467	-	AY844887	-	-
<i>Boana aguilari</i>	MTD 45203	HM444785	KF794115	HM444762	-	-	-	-	KF751475	KF751464
<i>Boana albomarginata</i>	USNM 284519	AY549316	KF794116	AY549369	AY844568	AY844348	-	AY844794	KF751476	AY844218
<i>Boana albopunctata</i>	ZUEC 12053	AY549317	-	AY549370	AY844569	-	AY844041	AY844795	-	-
<i>Boana alfaroi</i>	QCAZ 44858	JN970469/ JN970605	-	-	-	-	-	-	-	-
<i>Boana almendarizae</i>	QCAZ 39650	JN970394/ JN970530	-	-	-	-	-	-	-	-
<i>Boana balzani</i>	MNCN 543	HM480432	-	HM535348	-	-	-	-	-	-
<i>Boana bischoffi</i>	CFBH 3356	AY549324	-	AY549377	AY844586	AY844398	-	-	-	-
<i>Boana boans</i>	RWM 17746	AY843610	KF794118	AY843835	AY844588	-	AY844055	AY844809	KF751478	AY844231
<i>Boana caingua</i>	MLP-DB 1084	AY549326	KF794119	AY549379	AY844591	-	AY844057	AY844812	KF751479	AY844234
<i>Boana caipora</i>	CFBH 5738	EU077268	KF794120	EU077267	EU077265	EU077266	-	EU077264	-	EU077263
<i>Boana calcarata</i>	QCAZ 44177	JN970417/ JN970553	-	-	-	-	-	-	-	-
<i>Boana callipleura</i>	DLR 4119	AY549323	KF794121	AY549376	AY844582	AY844395	-	AY844806	-	AY844226
<i>Boana cinerascens</i>	MAD 085	AY549336	-	AY843861	AY844610	-	-	AY844828	KF751480	-
<i>Boana clade K¹</i>	NMP6V 71250	AY843613	-	AY843839	-	-	-	-	-	AY844235
<i>Boana cordobae</i>	MACN 37692	AY549330	KF794122	AY549383	AY844600	AY844411	AY844066	AY844819	KF751481	AY844244
<i>Boana crepitans</i>	CFBH 2966	AY843621	-	AY843850	AY844601	AY844412	AY844067	-	KF751482	-
<i>Boana curupi</i>	MACN 37793	AY549359	-	AY549412	-	-	-	-	-	-
<i>Boana dentei</i>	13 mc	AF467270/ EF376018	-	-	-	-	EF376124	-	-	-
<i>Boana diabolica</i>	R 152	KU168869	-	-	-	-	-	-	-	-
<i>Boana ericae</i>	CFBH 3599	AY549332	KF794123	AY549385	AY844605	AY844416	AY844071	-	-	-
<i>Boana exastis</i>	MTR 16289	KX697973	-	-	-	-	-	-	-	-
<i>Boana faber</i>	MACN 37000	AY549334	KF794124	AY549387	AY844607	-	-	AY844825	-	-
<i>Boana fasciata</i>	QCAZ 17030	JN970399/ JN970535	-	-	-	-	-	-	-	-
<i>Boana geographica</i>	AMNH-A 141054	AY843628	-	-	-	-	-	-	-	-
<i>Boana gladiator</i>	MNCN 5207	HM480405	-	HM535327	-	-	-	-	-	-

<i>Boana guentheri</i>	CFBH 3386	AY843631	KF794125	AY549390	AY844612	-	-	AY844830	-	AY844253
<i>Boana heilprini</i>	AMNH-A 168405	AY843632	KF794126	AY843864	AY844613	-	-	AY844831	-	-
<i>Boana joaquina</i>	CFBH 3625	AY549339	KF794127	AY549392	AY844616	AY844421	-	AY844834	KF751484	AY844256
<i>Boana lanciformis</i>	MJH 564	AY843636	-	AY843870	AY844619	-	AY844081	AY844837	-	AY844258
<i>Boana latistriata</i>	MZUSP 111556	AY549360	KF794128	AY549413	AY844668	-	-	-	-	AY844293
<i>Boana lemai</i>	ROM 39570	AY843637	KF794129	AY843871	AY844620	AY844423	AY844082	AY844838	KF751485	AY844259
<i>Boana leptolineata</i>	CFBH 3848	AY549341	KF794130	AY549394	AY844621	AY844424	AY844083	AY844839	-	AY844260
<i>Boana lundii</i>	CFBH 4000	AY843639	-	AY843874	AY844623	-	AY844085	AY844841	-	AY844262
<i>Boana marginata</i>	CFBH 3098	AY549342	KF794131	AY549395	AY844624	AY844426	-	AY844842	KF751486	AY844623
<i>Boana marianitae</i>	MV 0249	AY549344	KF794132	AY549397	AY844625	AY844427	-	AY844843	-	-
<i>Boana melanopleura</i>	MTD 46350	HM444779/ HM444774	KF794133	HM444756	HM444766	-	-	HM444789	KF751487	-
<i>Boana microderma</i>	NMP6V 712581	AY843644	KF794134	AY843881	-	-	-	-	-	AY844267
<i>Boana multifasciata</i>	AMNH-A 141040	AY843648	GQ366299	AY843887	AY844633	AY844436	AY844093	AY844851	GQ365986	AY844270
<i>Boana nympha</i>	NMP6V 71202/2	AY843670	KF794135	AY843914	AY844661	AY844457	AY844112	-	KF751488	AY844289
<i>Boana ornatissima</i>	51 mc	EF376019/ EF376056	-	-	-	-	EF376125	-	-	-
<i>Boana palaestes</i>	MNCN 23199	HM480418	-	HM535351	-	-	-	-	-	-
<i>Boana pardalis</i>	USNM 303046	AY843651	KF794136	AY843891	AY844637	-	AY844096	AY844855	-	-
<i>Boana pellucens</i>	KU 202734	AY326058	-	-	-	-	-	-	-	-
<i>Boana picturata</i>	KU 202737	AY326055	-	-	-	-	-	-	-	-
<i>Boana polytaenia</i>	CFBH 5752	AY843655	AY794137 ²	AY843895	AY844641	AY844443	-	AY844859	-	-
<i>Boana prasina</i>	CFBH 3388	AY549347	-	AY549400	AY844642	-	AY844100	AY844860	-	-
<i>Boana pugnax</i>	MRC 513	KX697964	-	-	-	-	-	-	-	-
<i>Boana pulchella</i>	MACN 37788	AY549352	KF794138	AY549405	AY844644	AY844445	AY844102	AY844862	-	AY844278
<i>Boana punctata</i>	MACN 37792	AY549353	KF794139	AY549406	AY844645	-	-	-	-	-
<i>Boana raniceps</i>	MACN 37795	AY843657	KF794140	AY843900	AY844646	-	AY844103	AY844863	KF751489	-

<i>Boana riojana</i>	MACN 37509	AY549355	KF794141	AY549408	AY844648	AY844447	-	AY844865	-	AY844279
<i>Boana roraima</i>	ROM 39624	AY843660	KF794143	AY843903	AY844650	AY844448	AY844104	AY844866	KF751490	AY844280
<i>Boana rosenbergi</i>	KU 217629	AY819438	KF794142	-	-	-	-	-	-	-
<i>Boana rufitela</i>	KRL 798	AY843662	KF794144	AY843905	AY844652	-	AY844105	AY844867	-	AY844282
<i>Boana semiguttata</i>	CFBH 3579	AY549357	KF794145	AY549410	AY844655	AY844452	-	AY844870	-	AY844285
<i>Boana semilineata</i>	CFBH 5424	AY843778/ AY843779	-	AY843909	AY843656	AY844453	AY844108	AY844871	KF751491	AY844286
<i>Boana sibleszi</i>	ROM 39561	AY843667	KF794147	AY843911	AY844658	AY844455	AY844110	AY844873	KF751492	AY844288
<i>Boana sp.</i>	CWM 19512	AY843671	-	AY843915	AY844662	-	AY844113	-	KF751493	AY844290
<i>Boana tepuiana</i> ³	USNM 302435	AY843606	KF794117	AY843830	AY844583	AY844396	-	-	KF751477	AY844227
<i>Boana tetete</i>	QCAZ 40081	JN970404/ JN970540	-	-	-	-	-	-	-	-
<i>Boana xerophylla</i>	552 PG	KX697932	-	-	-	-	-	-	-	-
<i>Bokermannohyla astarteae</i>	USNM 303032	AY549322	-	AY549375	AY844580	-	-	-	-	AY844225
<i>Bokermannohyla circumdata</i>	CFBH 3621	AY549328	KF794108	AY549381	AY844598	AY844409	AY844064	AY844817	KF751468	AY844242
<i>Bokermannohyla hylax</i>	USNM 303036	AY549338	-	AY549391	AY844614	AY844419	AY844077	AY844832	-	AY844254
<i>Bokermannohyla itapoty</i>	CFBH 5652	AY843677	KF794109	AY843922	AY844669	AY844461	-	AY844881 ⁴	KF751469	AY844294
<i>Bokermannohyla martinsi</i>	AF 414	AY843641	-	AY843878	AY844626	-	AY844086	AY844844	-	AY844264
<i>Bokermannohyla oxente</i>	CFBH 5642	AY843676	-	AY843919	AY844667	AY844460	AY844118	AY844879	KF751470	AY844292
<i>Bokermannohyla sp.1</i>	CFBH 5766	AY843673	-	AY843916	AY844664	-	AY844115	-	-	-
<i>Bokermannohyla sp.2</i>	CFBH 5917	AY843674	-	AY843917	AY844665	AY844458	AY844116	AY844877	-	-
<i>Dendropsophus nanus</i>	MACN 37785	AY549346	-	AY843888	AY844634	AY844437	-	AY844852	-	AY844271
<i>Hyla cinerea</i>	MVZ 145385	AY549346	KF794110	AY549380	AY844597	AY844408	AY844063	AY844816	KF751471	AY844241
<i>Hyloscirtus alytolylax</i>	QCAZ 24377	JX155798/ JX155825	-	-	-	-	-	-	-	-
<i>Hyloscirtus armatus</i>	AMNH-A 165163	AY549321	KF794111	AY540374	AY844579	AY844393	AY844050	AY844804	-	AY844224
<i>Hyloscirtus charazani</i>	AMNH-A 165132	AY843618	KF794112	AY843844	AY844595	AY844406	AY844061	-	-	AY844239
<i>Hyloscirtus colymba</i>	SIUC-H 7079	AY843620	KF794113	AY843848	AY844599	AY844410	AY844065	AY844818	KF751472	AY844243

<i>Myersiohyla liliae</i>	BPN 1227	XXXXXX	-	XXXXXX	XXXXXX	XXXXXX	-	-	-	-
<i>Myersiohyla liliae</i>	BPN 1234	XXXXXX	-	XXXXXX	-	-	XXXXXX	-	-	-
<i>Myersiohyla liliae</i>	IRSBN 1968	XXXXXX	XXXXXX	XXXXXX	XXXXXX	-	-	-	XXXXXX	-
<i>Myersiohyla liliae</i>	IRSBN 1965	XXXXXX	XXXXXX	-	XXXXXX	-	XXXXXX	XXXXXX	XXXXXX	-
<i>Myersiohyla neblinaria</i>	USNM 562071	AY843672	KF794149	-	AY844663	-	AY844114	AY844876	KF751494	AY844291
<i>Myersiohyla neblinaria</i>	USNM 562072	KF751504	-	-	-	-	-	-	-	-
<i>Myersiohyla neblinaria</i>	USNM 562074	KF751502	-	-	-	-	-	-	-	-
<i>Myersiohyla neblinaria</i>	USNM 562732	KF751503	-	-	-	-	-	-	-	-
<i>Nesorohyla kanaima</i>	CPI 10249	XXXXXX	-	XXXXXX	XXXXXX	-	-	-	-	-
<i>Nesorohyla kanaima</i>	CPI 10314	XXXXXX	-	-	XXXXXX	-	-	XXXXXX	-	-
<i>Nesorohyla kanaima</i>	ROM 39582	AY843634	GQ366307	AY843868	AY844617	AY844422	AY844079	AY844835	GQ365994	-
<i>Phrynomedusa dryade</i> ⁶	CFBH 7613	GQ366234	GQ366313	-	-	GQ366078	GQ366199	GQ366167	-	-
<i>Phyllodytes luteolus</i>	CFBH-t 0385	AY843721	GQ366314	AY843966	AY844708	AY844494	AY844150	AY844913	-	AY844324
<i>Pseudis minuta</i>	MACN 37786	AY843739	GQ366339	AY843985 ⁵	-	AY844505	-	AY844929	GQ366028	AY844336
<i>Scinax staufferi</i>	UTA-A 50749	AY843761	GQ366340	AY844006	AY844748	AY844523	AY844183	-	GQ366029	-
<i>Trachycephalus typhonius</i>	AMNH-A 141142	AY549362	GQ366341	AY549415	AY844707	AY844493	AY844149	AY844912	GQ366030	AY844322

¹ These are the sequences were identified as *Boana calcarata* by Faivovich *et al.* (2005) and subsequent papers. Caminer and Ron (2014) redefined *Boana calcarata* and recovered sequences of Faivovich *et al.* (2005) as a distinct species (identifying it as Clade K), as the sister taxa to *B. maculateralis*. Due to *Boana clade K* have available sequences of more gene fragments than *B. maculateralis*, he decided to use *B. clade K* sequences instead of *B. maculateralis*.

² This sequence was wrongly typed in Faivovich *et al.* (2013) as KF894137.

³ Previously identified as *Boana benitezi* (Faivovich *et al.* 2005, 2013; Wiens *et al.* 2006, 2010; Pyron and Wiens, 2011; Duellman *et al.*, 2016).

⁴ Voucher number of this sequence is wrongly informed as CFBH 5642 on Genbank.

⁵ This sequence was wrongly typed in Faivovich *et al.* (2005, 2013) as AY843984

⁶ The voucher of these sequences was identified as *Phrynomedusa marginata* in previous works. Baêta *et al.* (2016) erected it as a paratype of *Phrynomedusa dryade* Baêta, Giasson, Pobal Jr. & Haddad, 2016...

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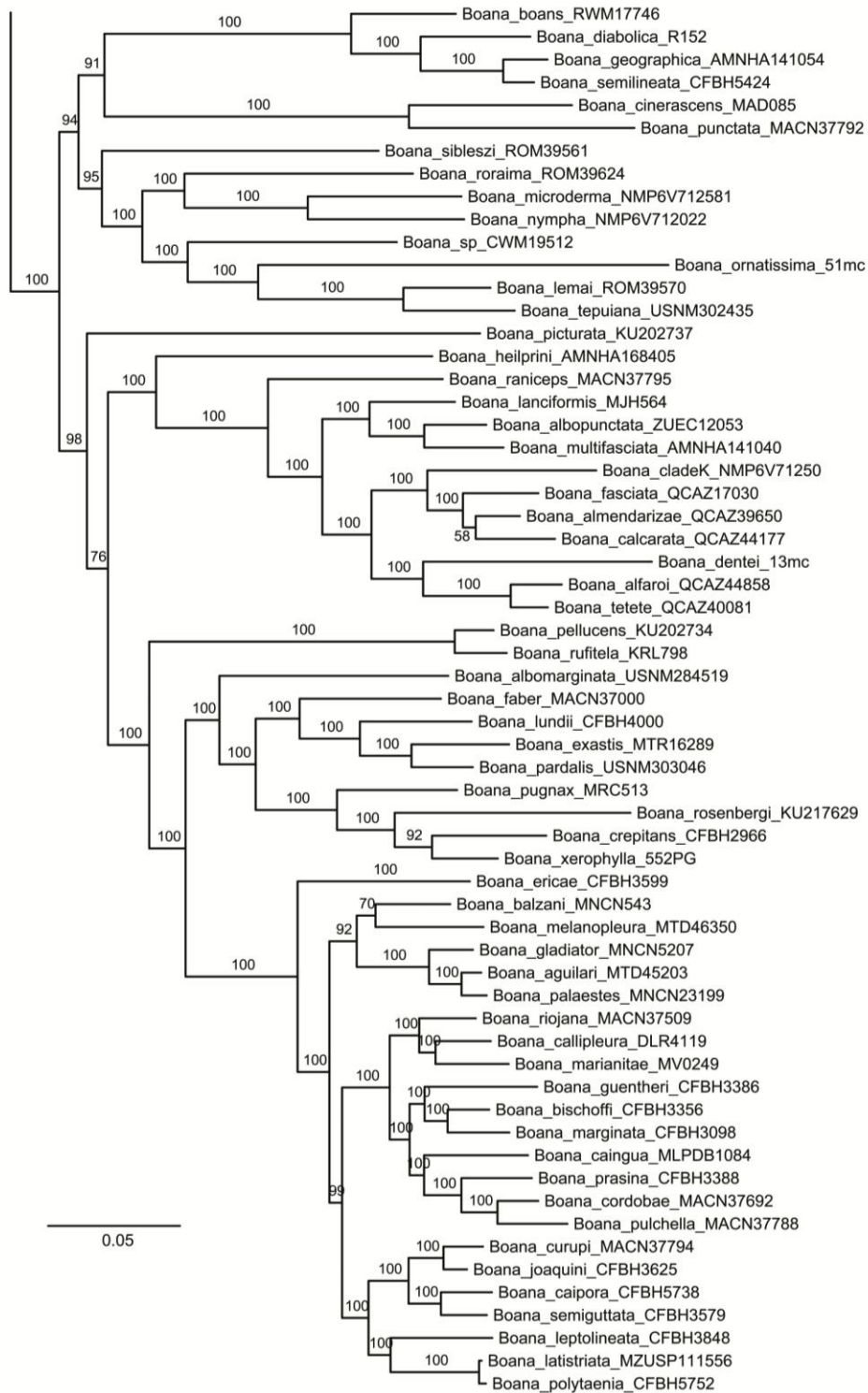
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762 Supplementary material 2

763 The 50% majority rule consensus tree from Bayesian analysis. Numbers on nodes are
 764 posterior probabilities. Numbers on terminals names are Vouchers numbers or sample
 765 numbers.



767 *Continued.*

768

PHYLOGENETIC ANALYSIS OF *BOANA* GRAY, 1825 (ANURA: HYLIDAE: HYLINAE)*

Paulo Durães Pereira Pinheiro; Célio Fernando Baptista Haddad; Julián Faivovich

ABSTRACT

The large genus *Boana* currently includes 92 species, most of them assigned to seven species groups. But only about 60% of its taxonomic diversity had already been included in analyses of more inclusive data sets. Some of its groups and other particular internal relationships of the *Boana* genus remain poorly supported. We constructed a molecular data set including terminals representing 83 species of *Boana* and DNA sequences of up to 10 gene fragments per terminal and present here the most inclusive analysis for the genus. The *Boana benitezi* and *B. punctata* group were recovered non-monophyletic. In some lineages, genetic divergence indicates that apparently more than one species are under a same name. We discuss the taxonomy of the seven species groups, their diversity, putative synapomorphies and present phenotypic characterization for each group. Our results improved the support of many internal relationships of *Boana*, although some other groups remain poorly supported, so as the taxonomic relationship of *Boana sibleszi*.

Key words. *Boana*; Cophomantini; Neotropical Frogs; Systematics; Taxonomy.

INTRODUCTION

The term Gladiator Frogs was first coined by Kluge (1979) referring to the frogs then placed in the *Hyla boans* group. Faivovich et al. (2005) expanded the usage of that name applying it to all Neotropical hylids which present a prepollical spine. Among the many taxonomic rearrangements, those authors resurrected *Hypsiboas* Wagler, 1830 from its

*Além do autor desta tese, de seu orientador e co-orientador, diversos outros co-autores vêm colaborando com o desenvolvimento do presente trabalho.

synonymy with *Hyla* Laurenti, 1768. As *Hyla* was recovered paraphyletic by Faivovich et al. (2005), the term “Gladiator Frogs”—which was currently attributed to several groups of *Hyla* (e.g., *Hyla boans*, *H. circumdata*, *H. pulchella*)—showed to designate a paraphyletic group. To avoid misinterpretations with the paraphyletic “Gladiator Frogs”, Faivovich et al. informally referred to *Hypsiboas* as the True Gladiator Frogs. Recently Dubois (2017) reinterpreted the confusing text of Gray (1825), inferring that *Boana* Gray, 1825 is an available name and has priority over *Hypsiboas* Wagler, 1830.

Boana, together with *Aplastodiscus* Lutz, 1950, *Bokermannohyla* Faivovich, Haddad, Garcia, Frost, Campbell, and Wheeler, 2005, *Hyloscirtus* Peters, 1882, *Myersiohyla* Faivovich, Haddad, Garcia, Frost, Campbell, and Wheeler, 2005; and *Nesorohyla*, Pinheiro, Kok, Noonan, Haddad, Faivovich, Unpublished results a, form the tribe Cophomantini (Faivovich et al., 2005; Pinheiro et al., unpublished results a).

Boana is the most species-rich genus of Cophomantini, with 92 recognized species (Frost 2017). Its species are included in seven species groups (Faivovich et al., 2005): the *B. albopunctata*, *B. benitezi*, *B. faber*, *B. pellucens*, *B. pulchella*, *B. punctata*, and *B. semilineata* groups. The species content of each group was defined according to the results recovered by Faivovich et al. (2005), and also to phenotypical evidences and previously taxonomic relationships of the taxa not included in their data set.

Besides those seven groups, *Boana fuentei* (Goin and Goin, 1968) and *B. varelae* (Carrizo, 1992) remained unassigned to any group (Faivovich et al., 2005). Recently Orrico et al. (2017) included *B. fuentei* (Goin and Goin, 1968) on the synonymy of *Boana xerophylla* (Duméril and Bibron, 1841). *Boana varelae*, however, stills needs to be evaluated.

While the sister taxa relationship between the *Boana faber* and the *B. pulchella* groups is well supported, the relationships among the other groups of *Boana* is unstable. The *B. pellucens* group varies in being the sister taxon to the *B. albopunctata* group or the sister taxon of the *B. faber* + *B. pulchella* groups (e.g., Faivovich et al., 2005; 2013). Also, the relationships between the *B. benitezi*, *B. punctata*, and *B. semilineata* groups are poorly supported (Duellman et al., 2016; Faivovich et al., 2005, 2013; Pyron and Wiens 2011; Wiens et al., 2010).

Until the year of 2006 the *Boana punctata* group included ten species: *B. alemani* (Rivero, 1964); *B. atlantica* (Caramaschi and Velosa, 1996); *B. cinerascens* (Spix, 1824); *B. hobbsi* (Cochran and Goin, 1970); *B. jimenezi* (Señaris and Ayarzagüena, 2006); *Boana liliae* (Kok, 2006), *B. ornatissima* (Noble, 1923a); *B. picturata* (Boulenger, 1899); *B. punctata* (Schneider, 1799); and *B. sibleszi* (Rivero, 1972). From these, *B. ornatissima* was transferred to the *B. benitezi* group (Faivovich et al., 2013) and *B. liliae* was transferred to the genus *Myersiohyla* (Pinheiro et al., unpublished results a). *Boana alemani*, *B. hobbsi*, and *B. jimenezi* remain without sequences available. The poor support of *B. sibleszi* and *B. picturata* as members of the *B. punctata* group makes the inclusion of the missing taxa necessary to understand the relationships of the *B. punctata* group with the remaining taxa of the genus *Boana* (Faivovich et al., 2013).

Many distinct hypotheses for the relationships between the groups of *Boana* had been published. Some of them resulted from analyses of more inclusive data sets (e.g., Duellman et al., 2016; Faivovich et al., 2013; Pyron and Wiens, 2011), and others with smaller taxonomic sampling, as they focused in specific groups. Antunes et al. (2008), Faivovich et al. (2004), Lehr et al. (2010), for example, explored the relationships within the *B. pulchella* group. Caminer and Ron (2014) contain the phylogenetic relationships for

the so called *B. calcarata*/*B. fasciata* species complex, and the paper of Fouquet et al. (2016) contain a tree for the cryptic lineages associated to *B. diabolica*, *B. geographica* (an internal clade of the *B. semilineata* group that we will refer to as *B. geographica*/*B. semilineata* species complex).

The study of Faivovich et al. (2005) included half of the species known today for *Boana*, and many species have been only tentatively assigned to their respective groups based on different sources of evidence pending to be tested in a phylogenetic framework. Our first goal in this paper is to present a more inclusive phylogenetic hypothesis for the genus *Boana*. With this broader taxonomic sampling, we discuss the species groups of *Boana*, their diversity, putative synapomorphies, and provide a phenotypic characterization.

MATERIAL AND METHODS

Taxon Sampling

From the 92 species currently assigned to *Boana*, we included DNA sequences from 83. Many of them were produced for this study and others, which were already published in previous papers, were downloaded from GenBank (Almendáriz et al., 2014; Antunes et al., 2008; Berneck et al., 2016; Caminer and Ron, 2014; Coloma et al., 2012; Crawford et al., 2010; Darst and Cannatella, 2004; Faivovich et al., 2004, 2005, 2010, 2013; Fouquet et al., 2007, 2016; Funk et al., 2012; Guayasamin et al., 2015; Jansen et al., 2011; Köhler et al., 2010; Lehr et al., 2010; Orrico et al., 2017; Pinheiro et al., unpublished results a; Prado et al., 2012; Salducci et al., 2005; Wiens et al., 2006). Sequences not assigned to named species were maintained with their original names (e.g., *Boana* Clade J [Caminer and Ron, 2014], *B. aff. semilineata* 1 [Fouquet et al., 2016]), in order to make comparisons with original publications easier.

We could not have access to samples of nine species of *Boana*, including one the *B. albopuncta* group, *B. steinbachi* (Boulenger, 1905); three from the *B. benitezi* group, *B. benitezi* (Rivero, 1961), *B. pulidoi* (Rivero, 1968), and *B. rhythmica* (Señaris and Ayarzagüena, 2002); two from the *B. punctata* group, *B. alemani* (Rivero, 1964) and *B. jimenezi* (Señaris and Ayarzagüena, 2006); one from the *B. pulchella* group, *B. cymbalum* (Bokermann, 1963a); one from the *B. semilineata* group, *B. hutchinsi* (Pyburn and Hall, 1984) (*B. semilineata* group); and one species unassigned to any group, *B. varelae* (Carrizo, 1992).

The outgroup sampling included species from Cophomantini, Dendropsophini, Hylini, and Lophiohylini. From Cophomantini we included 15 species of *Aplastodiscus*, representing its four groups of species (*sensu* Berneck et al. 2016); eight species of *Bokermannohyla* representing three of its four groups; 21 species of *Dendropsophus nanus* (Boulenger, 1889), *Pseudis minuta* Günther, 1858, and *Scinax staufferi* (Cope, 1865) (Dendropsophini); *Acris crepitans* Baird, 1854 and *Hyla cinerea* (Schneider, 1799) (Hylini); *Phyllodytes luteolus* (Wied-Neuwied, 1824), and *Trachycephalus typhonius* (Linnaeus, 1758) (Lophiohylini). The tree was rooted with *Phrynomedusa dryade* Baêta, Giasson, Pombal Jr., and Haddad, 2016 which is the sister taxon of all the other phyllomedusines, as the subfamilies Pelodryadinae and Phyllomedusinae together form the sister taxon of Hylinae (Faivovich et al., 2005, 2010). For a list of all taxa and GenBank accession numbers see Appendix 1.

Character Sampling

Our data set includes up to 7787 bp per terminal. It includes mitochondrial DNA fragments of the cytochrome oxidase I, cytochrome b, 12S, tRNA^{VAL}, 16S, intervening tRNA^{LEU}, NADH dehydrogenase subunit 1, tRNA^{ILE} and tRNA^{GLN}. Also, the data set

includes nuclear DNA fragments of seven in absentia (homolog 1), rhodopsin (exon 1), tyrosinase, recombination activating gene 1, proopiomelanocortin A, and chemokine receptor 4 (exon 2). The primers employed are listed in Table 1. To visualize employed sequences per terminal see the Appendix I.

DNA Isolation and Sequencing

Whole cellular DNA was extracted from ethanol preserved muscle or liver tissues, following an ammonium acetate precipitation protocol (adapted for microcentrifuge tubes from Maniatis et al., 1982, p. 54; Lyra et al., 2016). The amplification reactions were carried out in a 21–25 µl reaction using puRe Taq Ready-To-Go PCR beads (Amersham Biosciences, Piscataway, NJ) or Fermentas Master Mix, with the primers listed in Table 1.

Polymerase chain reaction (PCR) were conducted through the following programs: for mitochondrial genes: 3m00s of denaturation at 95°C, followed by 36 cycles of 0m20s of denaturation at 95°C plus 0m20s of annealing at 45–50°C plus 1m00s–1m20s of extension at 60–68°C, followed by 5m00s of final extension at 60–68°C, and stored at 12°C; for nuclear genes: 3m00s of denaturation at 95°C, followed by 40–45 cycles of 0m20s–0m45s of denaturation at 95°C plus 20s–45s of annealing at 45–56°C plus 45s–60s of extension at 60–72°C, followed by 5m00s–7m00s of final extension at 60–72°C, and stored at 12°C.

PCR products were purified using Exo I/SAP (Fermentas) and were sent to Macrogen inc., Seoul, South Korea, for sequencing. All samples were sequenced in both directions to check for potential errors. Chromatograms resulted from the sequencing reaction were read and contigs were made using Sequencher 3.0 software (Gene Codes, Ann Arbor, MI). The sequences were aligned using MAFFT v.7 (Katoh and Standley, 2013). We used the FFT-NS-2 strategy for the 12s + tRNA^{VAL} + 16s sequences, and G-INS-i strategy for the other

gene fragments. Alignments were then edited with BioEdit software (Hall, 1999). Sequence files were merged with SequenceMatrix (Vaidya et al., 2011).

Phylogenetic Analysis

We conducted our analysis choosing parsimony as optimality criterion. The rationale for this is explained by Farris (1983) and discussed by others, like Goloboff (2003) and Goloboff & Pol (2005).

The searches were conducted employing T.N.T Willi Hennig Society Edition (Goloboff et al., 2008), through New Technology Searches, combining Sectorial Searches, Tree Drift, Parsimony Ratchet and Tree Fusing strategies (using default parameters), requesting the driven search to hit the best length 100 times. Gaps were treated as a fifth state. The Parsimony Jackknife absolute frequencies (Farris et al., 1996) were calculated with the same parameters of the searches for the best score, although requesting the driven search to hit the best length ten times, for a total of 1000 replicates.

Genetic distances between specimens were estimated by pairwise comparisons of the final ~500 bp sequences of the 16S mitochondrial rRNA gene (see Fouquet et al., 2007; Vences et al., 2005a, b) using PAUP* (Swofford 2002) through the command “dset distance=p”. This algorithm calculates the percentual of sites which differ between two sequences. Trees were edited with FigTree (Rambaut, 2014).

RESULTS

We included up to ten gene fragments per terminal. 98% of the terminals of *Boana* have at least one fragment of the 12S-tRNA^{VAL}-16S mitochondrial gene sequenced. 82% have at least one nuclear gene fragment sequenced. Our data set have around 49% of

missing fragments for the genus *Boana*. The parsimony analyses resulted in 235 equally optimal trees, with 46040 steps. One of the best trees is shown in Figs. 1-4, and the strict consensus is presented on Fig. 5.

Among outgroups, Dendropsophini is not monophyletic because *Scinax staufferi* is the sister taxon of the clade that includes Cophomantini, Hylini, Lophiohylini, and the remaining Dendropsophini. Hylini and Lophiohylini are recovered monophyletic, both supported by 90% and 91% Jackknife support respectively. In Cophomantini, *Nesorohyla kanaima* is recovered as the sister taxon of (*Hyloscirtus* (*Bokermannohyla* (*Aplastodiscus* + *Boana*))) with 73% Jackknife support. The individual monophyly of *Myersiohyla*, *Hyloscirtus*, *Bokermannohyla* and *Aplastodiscus* is supported by 99–100% Jackknife support (Fig. 1).

The conflict in *Boana* is mostly among terminals within same species (e.g., *B. atlantica*, *B. raniceps*, *B. albopunctata*; see Figs. 1-5 for more), and also among some lineages of the *B. semilineata*/*B. geographica* and *B. calcarata*/*B. fasciata* species complexes (Caminer and Ron, 2014; Fouquet et al, 2016).

The genus *Boana* is recovered monophyletic with 98% Jackknife support. It is the sister taxon of *Aplastodiscus* (84% Jackknife support). Most species groups of *Boana* are recovered monophyletic and well supported (93–100% Jackknife support), with the exception of the *B. benitezi* and the *B. punctata* groups. The *Boana benitezi* group is recovered as the sister taxon to the remaining groups with 98% jackknife support. The *B. punctata* group is poorly supported (Jackknife support < 50%). It is recovered as the sister taxon of the *B. semilineata* group, but the monophyly of this clade is poorly supported (Jackknife support < 50%). *B. punctata* + *B. semilineata* groups are poorly supported as the sister taxon to the pectinated series that includes (Jackknife support < 50%): the *B.*

albopunctata group (86% Jackknife); the *B. pellucens* group (92% Jackknife support); and the clade that includes the *B. faber* + *B. pulchella* groups (95% Jackknife support; Figs. 2–3).

***Boana albopunctata* group.** The *B. albopunctata* group is recovered with 93% Jackknife support (Fig. 3). It is the sister taxon of the clade which includes the *B. pellucens*, *B. faber*, and *B. pulchella* groups supported by 86% Jackknife support. *Boana heilprini* is the sister taxon of the remaining species of the group, that are monophyletic and supported by 99% Jackknife support, and are recovered in three main clades. The early divergent includes *B. raniceps* and *B. caiapo*. Its sister taxon includes two other clades. One of these includes *B. albopunctata*, *B. lanciformis*, *B. leucocheila*, *B. multifasciata*, and *B. paranaiba*. Samples of *B. lanciformis* present high levels of genetic divergence on the 16S. The sample TG398, which is the sister taxa of the remaining terminals of this species, presents 3.91–4.19% of difference compared to the other terminals (Table 2). *Boana multifasciata* is paraphyletic in relation to *B. paranaiba* and to the sequences from Bolivia identified as *B. aff. albopunctata* by Jansen et al. (2011). Whereas sequences of *B. paranaiba* and *B. aff. albopunctata* diverge only 1.9–2.0% on 16S from topotypic sample of *B. multifasciata* (sample 5002), sample 102 (which is the sister taxa of the remaining) presents 4.22–5% of difference from the remaining terminals of this clade (Table 3). The other main clade of the *B. albopunctata* group includes the *B. calcarata*/*B. fasciata* species complex: *B. alfaroi*, *B. almendarizae*, *B. calcarata*, *B. dentei*, *B. fasciata*, *B. maculateralis*, *B. tetete*, the specimens from Clade G, Clade H, Clade I, and Clade J of Caminer and Ron (2014) and also other terminals that are being called here *Boana aff. calcarata* (samples 3744 and 3746) and *B. aff. fasciata* (sample 5004). Whereas *B. aff. fasciata* presents 4.39–10.60% of genetic

differences from all the other sequences of this clade (i.e., the *B. calcarata*/*B. fasciata* species complex), samples of *Boana* aff. *calcarata* are quite similar to the sequences of *B.* Clade J (2.57–2.75% of differences; Table 4).

***Boana benitezi* group.** We recovered a paraphyletic *Boana benitezi* group, with *B. hobbsi* (currently in the *B. punctata* group) nested on it as the sister taxon of *B. lemai* + *B. tepuiana* with 98% Jackknife support (Fig. 2). The monophyly of the clade of the *B. benitezi* group (including *B. hobbsi*) is poorly supported with 68% Jackknife support. This clade includes two well-supported major clades (Jackknife support $\geq 95\%$). One of them includes *Boana roraima* as the sister taxon of *B. nympa* + *B. microderma*. The other clade is a pectinated series with *Boana* sp., *B. ornatissima*, and *B. hobbsi* as the sister taxon of *B. lemai* + *B. tepuiana*. The two samples of *B. roraima* present high levels of genetic differences between them (4.93%).

***Boana faber* group.** The group was recovered monophyletic, with 96% Jackknife support (Fig. 3). *Boana albomarginata* is the earlier diverging lineage of this clade, and the sister taxon of two well supported main clades (100% Jackknife support). One of these includes *B. faber* as the sister taxon of a clade including *B. lundii*, and *B. exastis* + *B. pardalis*. The other clade includes *B. rosenbergi* as the sister taxon of a clade including *B. pugnax*, and *B. crepitans* + *B. xerophylla*.

***Boana pellucens* group.** The group was recovered monophyletic and well supported (100% Jackknife support). *Boana rubracyla* is the sister taxon of *B. pellucens* + *B. rufitela* (Fig. 3).

***Boana pulchella* group.** This group was recovered monophyletic, supported by 100% Jackknife support (Fig. 4). Its topology is the same as that of Faivovich, Pinheiro et al. (in prep).

1008 ***Boana punctata* group.** We recovered a polyphyletic *B. punctata* group, as *B. hobbsi* is
 1009 nested in the *B. benitezi* group (Fig. 2). All other included species compose a single clade,
 1010 with *Boana sibleszi* as the sister taxon of the remaining species, however with low support
 1011 (< 50% Jackknife support). The monophyly of the sister taxon to *B. sibleszi* is supported by
 1012 84% Jackknife support. *Boana picturata* is the sister taxon of a clade including *B.*
 1013 *cinerascens*, *B. punctata*, and *B. atlantica*. *Boana cinerascens* is recovered paraphyletic in
 1014 two well-supported distinct lineages. One of which is the poorly supported sister taxon of
 1015 the clade including *B. punctata* and *B. atlantica* (< 50% Jackknife support). Also, this clade
 1016 presents high level of genetic divergence between its terminals (0.36–5.09%; Table 5). We
 1017 recovered *B. punctata* into three main lineages, paraphyletic in relation to *B. atlantica*.
 1018 These four lineages (three of *B. punctata* and one of *B. atlantica*) present genetic distance
 1019 of 2.29–4.75% between them (Table 6).

1020 ***Boana semilineata* group.** We recovered a monophyletic *Boana semilineata* group
 1021 supported by 100% Jackknife support (Fig. 2). *Boana pombali* and *B. secedens* are
 1022 monophyletic, recovered supported with 100% Jackknife support, and as the sister taxon of
 1023 a clade including the remaining species of the group (100% Jackknife support). This clade
 1024 includes a pectinated series, composed of an undescribed species that we are referring to as
 1025 *Boana* sp. (from the state of Rondônia, Brasil), *B. boans* (100% Jackknife support), *B.*
 1026 *wavrini* (98% Jackknife support), and a clade (85% Jackknife support) including *B.*
 1027 *diabolica*, *B. geographica*, *B. semilineata*, and all the cryptic lineages reported by Fouquet
 1028 et al. (2016), which we called here *B. geographica/semilineata* species complex. Whereas
 1029 some samples that we added in our study are very similar genetically to the cryptic lineages
 1030 of Fouquet et al. (2016), the sample ML1269 presents high levels of genetic differences
 1031 from the other samples of this clade (3.44–8.07%; Table 7).

DISCUSSION

Outgroup

In our results Dendropsophini is not monophyletic. The non-monophyly of this tribe was already recovered by several other analyses (e.g., Duellman et al., 2016; Faivovich et al., 2013; Pyron and Wiens, 2011; Wiens et al., 2005, 2006). The sister relationship between *Pseudis* and *Dendropsophus*, so as their relationship with other Hylineae tribes, are poorly supported. Nevertheless the relationships outside Cophomantini are beyond the scope of this paper.

The monophyly of Cophomantini is supported by 86% Jackknife support. We recovered *Nesorohyla* as the sister taxon of a clade including *Hyloscirtus*, *Bokermannohyla*, *Aplastodiscus*, and *Boana*, a result with higher support than that obtained by Pinheiro et al. (unpublished results a). There are no incongruences in the internal relationships of *Bokermannohyla* and *Myersiohyla* (see Faivovich et al., 2013; Pinheiro et al., unpublished results a). Also, compared to published analyses, our results show little incongruences in the internal relationships of *Hyloscirtus* and *Aplastodiscus* (for comparisons see Berneck et al., 2016; Faivovich et al., 2013; Guayasamin et al., 2015).

Boana

Boana includes seven main clades corresponding to the currently recognized species groups in the genus (Faivovich et al., 2005), and which we discuss in more detail bellow. In our results, the genus *Boana* is recovered with higher jackknife support values than in the results of Faivovich et al. (2013). This may be due to our more inclusive taxonomic sampling for the genus. We recovered higher supports for the monophyly of the *B.*

albopunctata, *B. faber*, and *B. semilineata* groups and also for the relationships between the *Boana albopunctata*, *B. faber*, *B. pellucens*, and *B. pulchella* groups than in previous analyses. The monophyly of the *B. benitezi* and *B. punctata* groups remain poorly supported so as their relationships, and also the relationship of the *B. semilineata* group, with the remaining species of *Boana*. From the nine missing taxa on the present analysis, six are from these three groups.

Putative phenotypic synapomorphies of *Boana*.—Pinheiro et al. (unpublished results c) found an expanded medial process on the proximal epiphysis of the Metacarpal II, which articulates with the prepollex in several species of *Boana*. Among other Cophomantini, those authors only found this character state to be present in *Hyloscirtus larinopygion*, *H. lindae*, *H. princecharlesi*, *Bokermannohyla oxente*, *B. clepsydra*, and *B. lucianae*. This is the only putative phenotypic synapomorphy of *Boana*, with reversals in *Boana heilprini*, *B. microderma*, and *B. pellucens* (Pinheiro et al., unpublished results c). However, the taxonomic distribution of this character in Cophomantini should be better surveyed.

Characterization of *Boana*.—The species of *Boana* have a tympanum diameter/eye diameter (TD/ED) proportion varying from small (0.25%; *B. ornatissima*) to large (0.98%; *B. rosenbergi*; Hoogmoed, 1979; Duellman, 1970); snout rounded (*B. cambui*), acuminate (*B. semilineata*), or truncated (*B. nympha*) in dorsal profile (Faivovich et al., 2006; Pinheiro et al., 2016; Spix, 1824); a snout-vent length (SVL) of adult males that varies from 23.9 mm (*B. jaguariaivensis*) to 113 mm (*B. wavrini*; Hoogmoed, 1990; Caramaschi et al., 2010); males forearm slim (*B. microderma*) to robust (*B. riojana*; Barrio, 1965; Pyburn, 1977); skin on dorsum varying from smooth (*B. picturata*) to granulose (*B. lundii*; Burmeister, 1856; Boulenger, 1899); webbing on hands reduced (*B. almendarizae*) to very

developed (*B. boans*; Hoogmoed 1990; Caminer and Ron, 2014). Also all *Boana* species have an enlarged Distal Prepollex. It is spine-shaped in most species, but sickle-shaped in *Boana diabolica*, *B. geographica*, *B. hutchinsi*, and *B. semilineata* (Faivovich et al., 2006; Fouquet et al., 2016; Pinheiro et al., unpublished results c). The labial tooth row formulae (LTRF) of larvae varies from 2(2)/3(1), as in *B. leptolineata*, to 6(6)/9(1) in *B. heilprini* (Both et al., 2007; Díaz et al., 2015).

Content. The genus includes 92 species, most of which are assigned to the *Boana albopunctata*, *B. benitezi*, *B. faber*, *B. pellucens*, *B. pulchella*, *B. punctata*, and *B. semilineata* groups as defined below. Only three are not assigned to any group.

The *Boana albopunctata* group

Boana heilprini is recovered as the sister taxon of the remaining species of the *B. albopunctata* group in all analysis since Faivovich et al. (2005) (Duellman et al., 2016; Faivovich et al., 2013; Pinheiro et al., unpublished results a; Pyron and Wiens, 2011; Wiens et al., 2006, 2010). Besides its phenotypical differences with the remaining species of the group and in order to avoid the creation of a monotypic group, Faivovich et al. (2005) included *B. heilprini* in the *B. albopunctata* group. Our bigger taxa sampling effort resulted in a better support for this relationship than previous studies.

The relationships within the clade which includes the remaining species of the group however, are unstable. For *B. raniceps*, alternative relationships were presented by Wiens et al. (2005) and Pyron and Wiens (2005). In the analysis of Wiens et al. (2005), combining morphological and molecular data, *B. raniceps* was recovered with low support as the sister taxon of *B. calcarata* and *B. fasciata*. Pyron and Wiens (2011) recovered *B. raniceps* as the sister taxon to *B. dentei* and *B. fasciata*, but also without support. Our results for *B.*

1104 *raniceps* corroborate those of Duellman et al. (2016), Faivovich et al. (2005, 2013), and
 1105 Wiens et al. (2010).

1106 Considering *B. albopunctata*, *B. lanciformis*, and *B. multifasciata*, our results are
 1107 congruent with those of Duellman et al. (2016), Pyron and Wiens (2011), and Wiens et al.
 1108 (2005, 2006, 2010), but in our analyses we added sequences of *B. leucocheila* and *B.*
 1109 *paranaiba*. Faivovich et al. (2005, 2013), otherwise, recovered *B. lanciformis* as the sister
 1110 taxon of *B. fasciata* and *B. calcarata* with less than 50% Jackknife support (Faivovich et al.
 1111 2013). In our analysis we recovered *B. lanciformis* as the sister taxon to the clade which
 1112 includes *B. albopunctata* and *B. multifasciata* supported by 99% Jackknife support. This
 1113 may be due to the inclusion of sequences of *B. leucocheila*, which is nested within the
 1114 mentioned clade.

1115 *Boana calcarata* and *Boana fasciata* were recovered as sister taxa in many analyses
 1116 (Faivovich et al., 2005, 2013; Wiens et al., 2005, 2006, 2010). Pyron and Wiens (2011),
 1117 however, recovered *B. fasciata* and *B. dentei* as sister taxa, and these as the sister taxon of
 1118 *B. raniceps*. *Boana calcarata* was recovered by those authors as the sister taxon of the
 1119 clade including *B. lanciformis*, *B. albopunctata* and *B. multifasciata*. But the results
 1120 recovered for the relationships of both *B. calcarata* and *B. fasciata* were poorly supported.
 1121 All those papers used the same sequences as Faivovich et al. (2005) for *B. calcarata* and *B.*
 1122 *fasciata*. Subsequently, Caminer and Ron (2014) reviewed the so called *B. calcarata* and *B.*
 1123 *fasciata* species complexes. Those authors redefined both *B. calcarata* and *B. fasciata*, and
 1124 also found that the sequences employed by Faivovich et al. (2005) identified as *B.*
 1125 *calcarata* actually correspond to the candidate species they identified as ‘Clade K’, which
 1126 is the sister taxon of *B. maculateralis*. The sequences of *B. fasciata* from previous studies
 1127 correspond to the candidate species identified as ‘Clade H’ by Caminer and Ron (2014).

Duellman et al. (2016) found similar results to Caminer and Ron (2014); minor topological differences could be explained by the fact that those lineages considered as candidate species by Caminer and Ron (2014) were not included in Duellman et al.'s (2016) analysis. Our hypotheses recover the same relationships for *Boana* Clade K and *B.* Clade H as did Caminer and Ron (2014).

The clade which includes *Boana dentei* and the *B. calcarata/B. fasciata* species complex requires an exhaustive taxonomic revision including both phenotypic and molecular data. As our trees show, the clades of *B. alfaroi*, *B. tetete*, Clades G–K, and other undescribed taxa, collapse into a polytomy. Species in this clade have a broad geographic distribution, and morphologically similar populations. A large increase in sampling effort in terms of its geographic distribution is essential for a taxonomic revision.

Remarks. *Boana heilprini* is very distinct from the other members of the group. This includes overall coloration of adults (the only species of the group with greenish adults); unpigmented eggs (Nali et al., 2014), Landestoy (2013) suggested that probably it lay its eggs in small hidden crevices on creeks margins (confirmed by Marco-Rada, personal communication); larva with labial tooth row formula reaching 6(6)/9(1) (Noble, 1927; Díaz et al., 2015; Galvis et al., 2014); a large spine-shaped Distal Prepollex with a post-articular process present, but short (Pinheiro et al. unpublished results c). All of these likely being autapomorphies of this species. The reason of its inclusion in the group by Faivovich et al. (2005) is feasible. Also, the sister relationship with the remaining species is well supported (93% Jackknife Support). But at the same time, the biology and phenotypic characters of this species are very distinct from the other species of the group (see below).

Prado et al. (2012) reported that populations of *B. albopunctata* from Chapada dos Guimarães are isolated from other populations of this species, and probably could be a

different species. We included sequences of their study from Chapada dos Guimarães in our analysis. Those terminals are nested within *B. albopunctata*, and they collapse on the strict consensus. But we had access to only two gene fragments for those terminals (one mitochondrial and one nuclear). According to our results, the taxonomy of populations from Chapada dos Guimarães remains in need of more studies.

Boana multifasciata is recovered paraphyletic with respect to *B. paranaiba* and *B. aff. albopunctata* (Jansen et al. 2011). *Boana paranaiba* and *B. multifasciata* are morphologically similar (Carvalho et al., 2010). In the original description of *B. paranaiba*, the authors compare its type series (from Araguari, state of Minas Gerais, southeastern Brazil), only with topotypic specimens of *B. multifasciata* (from Belém, state of Pará, northern Brazil). The two type localities are distant 1895 km (air line). Carvalho et al. (2010) did not evaluate intermediate populations of *B. multifasciata* between type localities of the two species. The differences found between them are restricted to few measurements, proportions, some parameters of advertisement call—although authors state the resemblance between calls of both species (Carvalho et al., 2010)—, and absence of mid-dorsal line in *B. paranaiba* specimens (present in some specimens of *B. multifasciatus*; Carvalho et al., 2010). The dark mid-dorsal line is a character commonly variable among many species (e.g., *B. almendarizae*, *B. calcarata*, *B. fasciata*; Caminer and Ron, 2014). Also, the 16S sequences of *B. paranaiba* differ in 1.9% from sequences of topotypic specimen of *B. multifasciata* (sample 5002). Similarly, sequences of *B. aff. albopunctata* differ 1.9-2.0% from *B. multifasciata* (sample 5002). The 16S sequence of the sample 0120 (from Guiana), which is the sister taxon to the remaining terminals of *Boana multifasciata*, *B. paranaiba*, and *B. aff. albopunctata*, differ in 4.2-5% from all other terminals (Table 3). As there are no phenotypic characters differentiating those populations, the only argument

for considering them as distinct taxa is the differences found on 16S sequences. A larger sampling effort accross the geographic distribution of *B. multifasciata* is necessary to study their taxonomic status. However, the level of genetic divergences suggests that more than one species might be included under *B. multifasciata* Günther.

Another taxon which deserves attention within the *Boana albopunctata* group is *B. lanciformis*. The 16S sequence of the sample TG398 of *B. lanciformis*, which is the sister taxon to the remaining terminals of this species, differ in 3.9-4.2% from its conspecifics, suggesting that more than one species might be under the name *B. lanciformis* (Table 2). The sample TG398 is from São Gabriel da Cachoeira, northwestern state of Amazonas, Brazil. If these populations are shown to be a different species from *B. lanciformis* (Cope, 1871), there are three names available for the Western Amazon that should be investigated: *Hyla microcentra* Werner, 1921 (type locality: Colombia; described originally as “Kolumbien”); *Hyla hypocellata* Miranda-Ribeiro, 1926 (type locality: Eirunepé, Juruá River, Amazonas, Brazil; see Bokermann, 1966); and *Hyla lanciformis guerreroi* Rivero, 1971 (type locality: Guatapo, state of Miranda, Venezuela).

In the *Boana albopunctata* group, there is a reduction in chromosome number from $2n = 24$ to $2n = 22$ in *B. albopunctata* and *B. lanciformis* (Beçak, 1968; Bogart, 1973; Gruber et al., 2007, 2014; de Oliveira et al., 2010; Ferro et al., 2012; Mattos et al., 2014). Karyotypes are known from 29 of the 92 species of *Boana* (see Carvalho et al., 2014; Mattos et al., 2014). From these 29 species, 27 are $2n = 24$.

While *B. multifasciata* and *B. raniceps* are $2n = 24$ (de Oliveira et al., 2010; Gruber et al., 2007; Mattos et al., 2014; Rabello, 1970; Rabello et al., 1971), there is no data on karyotypes of *B. caiapo*, *B. heilprini*, *B. leucocheila* and species of the *B. calcarata/B. fasciata* species complex. The absence of karyotypic data for *B. leucocheila* makes the

1200 optimization of chromosome reduction ambiguous. The reduction to $2n = 22$ could have
 1201 happened at the node of *B. lanciformis*, *B. albopunctata*, *B. leucocheila* and *B.*
 1202 *multifasciata*, with a subsequent reversion to $2n = 24$ at the node of *B. multifasciata*, or it
 1203 would be equally parsimonious to interpret the reduction to $2n = 22$ as having occurred
 1204 independently in *B. lanciformis* and *B. albopunctata*.

1205 **Missing taxa.** The only species that is missing from our analysis is *Boana steinbachi*
 1206 (Boulenger, 1905), known only from its type series. It was resurrected from the synonymy
 1207 of *Boana fasciata* (Günther, 1858) by Caminer and Ron (2014), and no recently collected
 1208 specimen have been associated with it. However, these authors raised the possibility that
 1209 this name might apply to the specimens identified as Clade J in their study.

1210 **Putative phenotypic synapomorphies.** Pinheiro et al. (unpublished results c) reported that
 1211 the Distal Prepollex has a short post-articular process (in dorsal view it do not exceeds the
 1212 level of the articulation between Element Y, Proximal Prepollex, and Distal Carpal II) in *B.*
 1213 *heilprini* and it is reduced or absent on the remaining species of the *B. albopunctata* group,
 1214 which could be a synapomorphy of the sister taxon of *B. heilprini*, being homoplastic in the
 1215 *B. benitezi* and *B. punctata* groups. Taboada et al. (2017) summarized species of *Boana* that
 1216 have green coloration pattern only on juveniles: *B. albopunctata*, *B. lanciformis*, and *B.*
 1217 *raniceps*, all of them from the *B. albopunctata* group. *B. heilprini* have not only green
 1218 metamorphs, but also the adults (Díaz et al., 2015). The green pattern of juveniles could be
 1219 a synapomorphy of the group. But this character deserves further investigation on the other
 1220 species of the group. Also, it seems to be homoplastic in *B. pugnax*, *B. rosenbergi*, and *B.*
 1221 *xerophyla* (Höbel, 2008; Marco-Rada personal communication). Other two characters that
 1222 deserves special attention on future studies of *B. albopunctata* group are the

presence/absence of the *processus pre-nasalis medius*, and the reduction in chromosome number from $2n = 24$ to $2n = 22$.

Characterization. Besides the putative synapomorphies listed above, species in the *Boana albopunctata* group can be characterized as small to large treefrogs with snout-vent length (SVL) of males ranging from 27.6 mm in *B. calcarata* (Caminer and Ron, 2014) to 67 mm in *B. raniceps* (Lutz, 1973), and SVL of females ranging from 32.0 mm in *B. maculateralis* (Caminer and Ron, 2014) to 87 mm in *B. lanciformis* (Lutz, 1973); the head varies from wider than long, in *B. alfaroi* (Caminer and Ron, 2014) to longer than wide, in *B. leucocheila* (Caramaschi and Niemeyer, 2003); a snout, in dorsal view, rounded, as in *B. heilprini* (Noble, 1923b), acuminate, as in *B. albopunctata* (Lutz, 1973), or truncated, *B. tetete* (Caminer and Ron, 2014); a medium-size tympanum, with tympanum diameter/eye diameter proportion of males varying from 0.43-0.86 in *B. multifasciata* (Carvalho et al., 2010; Lutz, 1973, as *Hyla daudini*, but see Duellman, 1974b); body slender (*B. dentei*; Bokermann, 1967a) to robust (*B. heilprini*; Noble, 1923b); skin on dorsum smooth (*B. maculateralis*; Caminer and Ron, 2014) to finely granular (*B. lanciformis*; Cope 1871). Larvae of this group generally have a single row of marginal papillae with a few submarginal papillae, and LTRF 2/3, with P3 being much shorter than the other rows (Kolenc et al., 2008). The exception is *B. heilprini* that have double row of papillae, many lateral flaps with teeth, and LTRF 6/9 (Díaz et al., 2015; Galvis et al., 2014; Noble, 1927). *Boana albopunctata*, *B. fasciata*, and *B. raniceps* have a spiracular tube free from the body (de Sá, 1995; Kolenc et al., 2008; Rossa-Feres and Nomura, 2006; Spirandeli Cruz, 1991; Wild, 1992).

Content. 16 species: *Boana albopunctata* (Spix, 1824); *B. alfaroi* (Caminer and Ron, 2014); *B. almendarizae* (Caminer and Ron, 2014); *B. caiapo* Pinheiro et al. unpublished

results b; *B. calcarata* (Troschel, 1848); *B. dentei* (Bokermann, 1967a); *B. fasciata* (Günther, 1858); *B. heilprini* (Noble, 1923b); *B. lanciformis* (Cope, 1871); *B. leucocheila* (Caramaschi and Niemeyer, 2003); *B. maculateralis* (Caminer and Ron, 2014); *B. multifasciata* (Günther, 1859); *B. paranaiba* (Carvalho and Giaretta, 2010); *B. raniceps* (Cope, 1862); *Boana steinbachi* (Boulenger, 1905); and *B. tetete* (Caminer and Ron, 2014).

The *Boana benitezi* group

The relationships for this group obtained in our analyses are congruent with those of Duellman et al. (2016), Faivovich et al. (2005; 2013), Pyron and Wiens (2011), and Wiens et al. (2010), with the addition of *B. hobbsi* nested in the group. Wiens et al. (2006), however, recovered a paraphyletic *Boana benitezi* group, with the *B. semilineata* group nested on it, and they also recovered the undescribed *Boana* sp. (sequenced by Faivovich et al. [2005]) as the sister taxon of *B. roraima*, *B. nympa*, and *B. microderma*.

Remarks. *Boana hobbsi* (Cochran and Goin, 1970) was tentatively assigned to the *B. punctata* group by Faivovich et al. (2005) due to its earlier association with *B. punctata* (Duellman, 1974a; Pyburn, 1978). Our analyses recover it nested in the *B. benitezi* group, as the sister taxon of *B. lemai* and *B. tepuiana*, with 98% Jackknife support. To remediate the paraphyly of the *Boana benitezi* group, *B. hobbsi* is transferred to this group.

Originally this group was associated to higher altitudes environments due to the taxa composition of one of its clades (Faivovich et al., 2005). With advances acquired by subsequent papers (Faivovich et al., 2006, 2013) and with the present inclusion of *Boana hobbsi*, the *Boana benitezi* group now includes four lowland inhabitant species (*B. hobbsi*, *B. microderma*, *B. nympa*, and *B. ornatissima*), all riverine (Faivovich et al., 2006; Hoogmoed, 1979; Melo-Sampaio, 2012; Pyburn 1978). The highland species also inhabits

river environments, but generally rivulets with cascades or rapids (Barrio-Amorós et al., 2011; Donnelly and Myers, 1991; Duellman, 1997; Faivovich et al., 2006; Ouboter and Jairan, 2012; Pyburn, 1978; Rivero, 1961; Señaris and Ayarsagüena, 2002). The presence of lowland species (*B. hobbsi*, *B. microderma*, *B. nympha*, and *B. ornatissima*) and highland species (*B. lemai*, *Boana* sp., *B. roraima* and *B. tepuiana*) in the two clades of the *B. benitezi* group makes ambiguous the inference of the biogeographic origin of this group.

The uncorrected *p*-distance between 16S sequences of the two samples of *B. roraima* is 4.9%, which might indicate more than one species under this name. The two specimens are from two distinct Tepuis from Guyana: Mount Ayanganna and Mount Wokomung, Guyana. The Mount Ayanganna is the easternmost known distribution of *B. roraima*. However, this species is described for Mount Roraima (Duellman and Hoogmoed, 1992), which is western to Ayanganna and Wokomung, in the border between Guyana, Brazil and Venezuela. The species is also reported for the Sierra de Lema, Venezuela, NW to these three mountains, and have its westernmost distribution known for the Mount Ayuantepui, state of Bolívar, Venezuela. This latter population was originally described as *Hypsiboas angelicus* by Myers and Donnelly (2008) being subsequently considered a junior synonym of *B. roraima* (Barrio-Amorós et al., 2011). From these four mountains, the closest one to Ayanganna is Wokomung. The *p*-distance between samples from these two localities suggests the need to survey the other populations of *B. roraima*, and the need of a taxonomic revision.

Faivovich et al. (2005, 2006) considered the mental gland in males the only putative synapomorphy of the *Boana benitezi* group. However, Brunetti et al. (2015) showed this character state to have a broader distribution in Cophomantini, suggesting that it is likely plesiomorphic for the *B. benitezi* group.

Missing taxa. Three species currently assigned to the *Boana benitezi* group have no available samples: *B. benitezi* (Rivero, 1961), *B. pulidoi* (Rivero, 1968), and *B. rhythmica* (Señaris and Ayarzagüena, 2002). The sequences used by Faivovich et al. (2005), and many subsequent contributions (e.g., Duellman et al., 2016; Faivovich et al., 2013; Pyron and Wiens, 2011; Wiens et al., 2006, 2010), identified as *B. benitezi* are from a specimen collected at Vila Pacaraíma, state of Roraima, Brazil. Myers and Donnely (1997) had previously observed that populations from the east of the Maigualima-Parima Mountains (which cross the border between state of Roraima, Brazil, and departments of Amazonas and Bolívar, Venezuela) might belong to a distinct taxon from *B. benitezi*. Then, Barrio-Amorós and Brewer-Carias (2008) attributed those populations to *B. tepuiana*, restricting *B. benitezi* to the populations from the west of the Maigualima-Parima Mountains. However, as *B. benitezi* and *B. tepuiana* are quite similar, we do not see reason to doubt that *B. benitezi* will be recovered in the nominal group, and possibly, closely related with the clade including *B. lemai* and *B. tepuiana*.

Boana pulidoi and *B. rhythmica* are known only from their original descriptions and type localities (Rivero, 1968; Señaris and Ayarzagüena, 2002). They are also morphologically similar to *B. benitezi*, *B. lemai*, and *B. tepuiana* (Barrio-Amorós and Brewer-Carias, 2008; Rivero, 1985; Señaris and Ayarzagüena, 2002). Due to this, we also expect their association with the clade including *B. lemai* and *B. tepuiana* in future analyses. Faivovich et al. (2005) commented that the study of the holotype of *B. pulidoi* and comments of Rivero (1985) led them to tentatively include this species in the *B. benitezi* group. The only difference found by them between *B. pulidoi* and *B. benitezi* is that the former present a red iris in life, whereas the later was described as copper (Rivero 1961,

1968). Rivero (1985) even considered the possibility that *B. pulidoi* (Rivero, 1968) could be a junior synonym of *B. benitezi* (Rivero, 1961).

Putative phenotypic synapomorphies. We are not aware of any putative phenotypic synapomorphy for the *Boana benitezi* group.

Characterization. Species in the *Boana benitezi* group can be characterized as small treefrogs, with SVL in males ranging from 24.4 mm (*B. nympa*; Faivovich et al., 2006) to 42.5 mm (*B. benitezi*; Rivero, 1972), and in females from 23.2 mm (*B. pulidoi*; Rivero, 1968) to 51.5 mm (*B. benitezi*; Myers and Donnelly, 1997); head wider than long; truncate snout in dorsal view; moderately small tympanum diameter/eye diameter proportion (0.25 in *B. ornatissima*, to 0.51 in *B. nympa*; Hoogmoed, 1979; Faivovich et al., 2006); body slender; skin on dorsum smooth (*B. pulidoi*; Rivero, 1968) to finely shagreened (*B. nympa*; Faivovich et al., 2006). Larvae of *B. roraima* have a ventrolaterally emarginated oral disc, and LTRF 2(1,2)/3 (Myers and Donnelly, 2008), and larvae of *B. benitezi* have a not emarginated oral disc, completely surrounded by a double row of papillae, with few lateral submarginal papillae and a high number of tooth rows: 5/8 (Myers and Donnelly, 1997). However, those larvae were assigned to those species tentatively. Duellman (1997) reported a female of *B. lemai* laying its unpigmented eggs on a leaf, but inside a plastic bag. Reproductive biology of the other species remains unknown.

Content. Ten species: *B. benitezi* (Rivero, 1961); *B. hobbsi* (Cochran and Goin, 1970); *B. lemai* (Rivero, 1972); *B. microderma* (Pyburn, 1977); *B. nympa* (Faivovich, Moravec, Cisneros-Heredia, and Köhler, 2006); *B. ornatissima* (Noble, 1923a); *B. pulidoi* (Rivero, 1968); *B. roraima* (Duellman and Hoogmoed, 1992); *B. rhythmica* (Señaris and Ayarzagüena, 2002); and *B. tepuiana* (Barrio-Amorós and Brewer-Carias, 2008).

The *Boana faber* group

Our results for the *Boana faber* group are congruent with those of Duellman et al. (2016), Pyron and Wiens (2011), Faivovich et al. (2005, 2013), and Wiens et al. (2010). The trees recovered by Wiens et al. (2005, 2006) present alternative relationships for *B. albomarginata*. In the study of Wiens et al. (2005), *B. albomarginata* is recovered with low support as the sister taxon of the clade which includes both the *B. faber* and *B. pulchella* groups. Wiens et al. (2006) recovered *B. albomarginata* as the sister taxon of the *B. pellucens* group, also with low support. Orrico et al. (2017) recovered a tree on which the *B. faber* group is paraphyletic, with respect to *B. lanciformis* and *B. multifasciata* (*B. albopunctata* group). However, these authors had not designed their analysis to study globally the relationships of the *B. faber* group, but to test if *B. xerophylla* and *B. crepitans* were distinct species.

Remarks. The relationship of *Boana albomarginata* with the *B. faber* group, is as curious, as the sister relationship between *B. heilprini* and the remaining species of the *B. albopunctata* group. As in the case of *B. heilprini*, *B. albomarginata* is the only green species of its group.

Boana albomarginata is a species with a broad geographic distribution through the Atlantic Forest from the state of Rio Grande do Norte (Northeastern Brazil) to the state of Santa Catarina (South Brazil; Lutz, 1973; Haddad et al., 2013). Besides the green coloration shared with the *B. pellucens* group (see below), it shares with the *B. pellucens* and *B. faber* groups the presence of a short post-articular process of the Distal Prepollex of males (see Pinheiro et al., unpublished results c). *Boana albomarginata* is the only species of the *B. faber* group where males do not construct or use natural mud basins as nests, as other

species of the group do (Faivovich et al., 2005). Females of *B. albomarginata* lay their eggs at the margins of ponds and lakes (Giasson and Haddad, 2007).

The monophyletic *Boana lundii*, *B. exastis*, and *B. pardalis*, are the only species of the *B. faber* group having a granulose skin. This clade was also recovered by Orrico et al. (2017), and briefly discussed by them. The monophyletic *B. faber*, *B. lundii*, *B. pardalis* and *B. exastis* have an Atlantic Forest distribution, as so do *B. albomarginata* (Haddad et al., 2013). This clade is the sister taxon of a clade including *B. rosenbergi*, *B. pugnax*, *B. xerophylla*, and *B. crepitans*. All these but *B. crepitans* have a northern South America distribution (Kluge, 1979; Orrico et al., 2017). Faivovich et al. (2005) suggested that probably the *B. faber* group originated in the Atlantic Forest and one lineage dispersed to Amazon, giving rise to the clade of *B. rosenbergi*, *B. pugnax*, and *B. xerophylla*. Our results and those of by Orrico et al. (2017) corroborate this hypothesis, and also suggest a subsequent transition from Amazon to Atlantic Forest giving rise to *B. crepitans*.

Putative phenotypic synapomorphies. Faivovich et al. (2005) commented that the use or construction of mud basins by males could be a putative synapomorphy of the sister taxon of *B. albomarginata*. This character state is homoplastic in at least some species of the *B. semilineata* group (*B. boans* and *B. wavrini*), and in the *Bokermannohyla circumdata* group. An additional putative synapomorphy of the sister clade of *B. albomarginata* is the presence of vertical dark lines or bars on hidden surfaces of thighs, which can present anastomosis between them. Kolenc et al. (2008) reported the presence of a pair of long and ramified lingual papillae to *B. faber*, *B. lundii*, and *B. rosenbergi*. Those authors commented that this character state, among hyelines is only known to occur in these three species, and it is likely a putative synapomorphy of the *Boana faber* group or of a less inclusive clade, due to its possible absence in *B. albomarginata*. *Boana faber*, *B. lundii*, and

1389 *B. pardalis* share a short, posterior gap in the row of marginal papillae (Heyer et al., 1990;
 1390 Kolenc et al., 2008; Rossa-Feres and Nomura, 2006). This character state seems to be a
 1391 putative synapomorphy for this clade, showing homoplasy in *B. raniceps* (Kolenc et al.,
 1392 2008).

1393 **Characterization.** Besides the putative synapomorphies listed above, species of the *Boana*
 1394 *faber* group can be characterized as large treefrogs, with SVL ranging from 48 mm (*B.*
 1395 *pardalis*; Lutz, 1973) to 104 mm (*B. faber*; Heyer et al., 1990) in males; and 54.3 mm (*B.*
 1396 *lundii*; Caramaschi and Napoli, 2004) to 103.8 mm (*B. faber*; Heyer et al., 1990) in
 1397 females. The exception is *Boana albomarginata*, which is a medium-sized species, (SVL
 1398 39-55 mm in males, 50-62 mm in females; Lutz, 1973); head longer than wide (*B. exastis*;
 1399 Caramaschi and Rodrigues, 2003) to wider than long (*B. crepitans*; Lutz, 1973); snout
 1400 rounded in dorsal view; a medium to large tympanum diameter/eye diameter, which varies
 1401 from 0.5 in *B. faber* to 0.98 in *B. rosenbergi* (Duellman, 1970; Heyer et al., 1990); males
 1402 with a moderately robust bodies. The skin is smooth in all species except *B. exastis*, *B.*
 1403 *lundii*, *B. pardalis*, where it is granulose. Kolenc et al. (2008) diagnosed larvae of the *B.*
 1404 *faber* group as having LTRF 2/4 (sometimes 2/3 in *H. pardalis*; Bokermann, 1968; Heyer
 1405 et al., 1990). P4 is usually noticeably shorter than the other rows and fragmented. Lateral
 1406 submarginal papillae or flaps bearing teeth are reported for *B. albomarginata*, *B. faber*, *B.*
 1407 *xerophylla* (Kolenc et al., 2008; fig. 20 of Kenny, 1969; Peixoto and Cruz, 1983). A
 1408 spiracular tube free from the body is present in *B. albomarginata*, *B. faber* and *B.*
 1409 *xerophylla* (Kolenc et al., 1981, Peixoto and Cruz, 1983; fig. 7 of Rada de Martínez, 1981).
 1410 **Content.** Nine species: *B. albomarginata* (Spix, 1824); *B. crepitans* (Wied-Neuwied,
 1411 1824); *B. exastis* (Caramaschi and Rodrigues, 2003); *B. faber* (Wied-Neuwied, 1821); *B.*

1412 *lundii* (Burmeister, 1856); *B. pardalis* (Spix, 1824); *B. pugnax* (Schmidt, 1857); *B.*
 1413 *rosenbergi* (Boulenger, 1898a); and *B. xerophylla* (Duméril and Bibron, 1841).

1414

1415 **The *Boana pellucens* group**

1416 In previous analyses, *Boana pellucens* and *B. rufitela* were recovered as well supported
 1417 sister taxa (Duellman et al., 2016; Faivovich et al., 2005, 2013; Pyron and Wiens, 2011;
 1418 Wiens et al., 2005, 2006, 2010). However, the relationship of this group with other groups
 1419 of *Boana* is unstable. As in our results, the group has already been recovered as the sister
 1420 taxon of the *B. faber* and *B. pulchella* groups by Duellman et al. (2016), Faivovich et al.
 1421 (2013), Pyron and Wiens (2011), and Wiens et al. (2006, 2010). For alternative relationship
 1422 hypotheses see Faivovich et al. (2005) and Wiens et al. (2005, 2006).

1423 **Remarks.** The position of *Boana rubracyla* nested in this group is an interesting result, as
 1424 *B. rubracyla* and *B. pellucens* were already considered synonyms (Duellman, 1971). Our
 1425 results corroborate the validity of *B. rubracyla* and also support the originally tentative
 1426 assignment to the group by Faivovich et al. (2005).

1427 **Putative phenotypic synapomorphies.** We are not aware of any putative phenotypic
 1428 synapomorphy for the *B. pellucens* group.

1429 **Characterization.** Species of the *Boana pellucens* group can be characterized for being
 1430 small to medium-sized species, with SVL from 39 mm (*B. rufitela*; Fouquette, 1961) to
 1431 50.4 mm (*B. rubracyla*; Cochran and Goin, 1970) in males; and from 46.4 mm (*B. rufitela*;
 1432 Fouquette, 1961) to 58.4 mm (*B. rubracyla*; Cochran and Goin, 1970) in females; head as
 1433 wide as long; snout rounded in dorsal profile; tympanum diameter between one half to two
 1434 thirds of eye diameter (Fouquette, 1961; Cochran and Goin, 1970; Duellman 1971); males
 1435 with robust bodies; skin on dorsum smooth. Larvae have LTRF 2/4 (Kolenc et al., 2008).

Content. Three species: *B. pellucens* (Werner, 1901); *B. rubracyla* (Cochran and Goin, 1970); and *B. rufitela* (Fouquette, 1961).

The *Boana pulchella* group

Our results for this group are very similar to Faivovich et al. (unpublished results). This group was extensively discussed by these authors, and the sequences included here for this group are all present in their data set.

Putative phenotypic synapomorphies. Faivovich et al. (2005) mentioned the absence of the slip of *m. depressor mandibulae* with origin at the scapular level as a phenotypic synapomorphy for the *Boana pulchella* group. This character shows homoplasy in *B. atlantica*, *B. cinerascens*, and *B. punctata*, (P.D.P. Pinheiro, personal observation). Pinheiro et al. (unpublished results c) found two additional putative synapomorphies for the group, a large post-articular process on the Distal Prepollex (in dorsal view it reaches the articulation between the Element Y and the Radiale level), and the Distal Prepollex is ventral to the Metacarpus II. The absence of the antero-lateral process of the hyoid could also be a synapomorphy of this group (Garcia et al., 2001; Pinheiro et al., unpublished results b). The distribution of this character in *Boana* should be better explored.

Characterization. Besides the putative synapomorphies listed above, species of the *Boana pulchella* group can be characterized as small to medium-sized treefrogs, with SVL ranging from 24.2 mm (*B. beckeri*; Caramaschi and Cruz, 2004) to 57.6 mm (*B. andina*; Duellman et al., 1997) in adult males; from 29 mm (*B. leptolineata*; Braun and Braun, 1977) to 69 mm (*B. bischoffi*; Lutz, 1973) in adult females; head almost wider as long; snout rounded in dorsal view; medium-sized tympanum, with tympanum-diameter/eye-diameter proportion ranging from 0.38 in *B. cambui* to 0.68 in *B. joaquina* (Garcia et al., 2003; Pinheiro et al.,

2016); bodies varying from slim (e.g., *B. goiana*; Lutz, 1968a) to robust (e.g., *B. curupi*; Garcia et al., 2007); skin on dorsum smooth. Kolenc et al. (2008) diagnosed species of the *B. pulchella* group as presenting a LTRF 2/3 in most species, but in some species the LTRF is 2/4 (*B. andina*, *B. balzani*, *B. caipora*, *B. freicanecae*, *B. joaquini*, *B. marginata*, *B. marianitae*, *B. palaestes*, *B. riojana*, and *B. semiguttata*; Antunes et al., 2008; Carnaval and Peixoto, 2004; Duellman et al., 1997; Garcia et al., 2001, 2003, 2007; Kolenc et al., 2008; Lötters et al., 1999), in *B. poaju* is 2/5 (Garcia et al., 2008), and in *B. curupi* is 3/5 (Faivovich 1996). These species also have lateral flaps or submarginal papillae bearing labial teeth (same references; also present in *B. cambui*, *B. cordobae*, *B. pulchella*; Kolenc et al., 2008; Pinheiro et al., 2016). The last posterior row is usually much shorter than the other rows, and P4, when present, is usually fragmented. The oral cavities were described for *B. andina*, *B. caingua*, *B. cordobae*, *B. joaquini*, *B. leptolineata*, *B. pulchella*, *B. prasina*, and *B. riojanus* (Both et al., 2007; d’Heursel and Haddad, 2007; Kolenc et al., 2008; Lavilla and Fabrezi, 1987; Spirandeli Cruz, 1991). The absence of infralabial papillae laying on the infrarostral cartilages within the orobranchial chamber is known for *B. andina*, *B. caingua*, *B. cordobae*, *B. leptolineata*, *B. pulchella*, *B. prasina*, and *B. riojana*. Also, the presence of 8–40 long and conical papillae on the central area of the buccal roof arena, arranged forming a V in the posterior limit of the central arena is reported for all of those studied species (except *B. caingua*, *B. cordobae* and *B. joaquini*, where these are absent).

Content. 38 species: *B. aguilari* (Lehr, Faivovich, and Jungfer, 2010); *B. albonigra* (Nieden, 1923); *B. balzani* (Boulenger, 1898b); *B. bandeirantes* (Caramaschi and Cruz, 2013); *B. beckeri* (Caramaschi and Cruz, 2004); *B. bischoffi* (Boulenger, 1887); *B. botumirim* (Caramaschi, Cruz, and Nascimento, 2009); *B. buriti* (Caramaschi and Cruz,

1999); *B. caingua* (Carrizo, 1991); *B. caipora* (Antunes, Faivovich, and Haddad, 2008); *B. callipleura* (Boulenger, 1902); *B. cambui* (Pinheiro, Pezzuti, Leite, Garcia, Haddad, and Faivovich, 2016); *B. cipoensis* (Lutz, 1968a); *B. cordobae* (Barrio, 1965); *B. curupi* (Garcia, Faivovich, and Haddad, 2007); *B. cymbalum* (Bokermann, 1963); *B. ericae* (Caramaschi and Cruz, 2000); *B. freicanecae* (Carnaval and Peixoto, 2004); *B. gladiator* (Köhler, Koscinski, Padial, Chaparro, Handford, Loughheed, and De la Riva, 2010); *B. goiana* (Lutz, 1968a); *B. guentheri* (Boulenger, 1886); *B. jaguariaivensis* (Caramaschi, Cruz, and Segalla, 2010); *B. joaquini* (Lutz, 1968b); *B. latistriata* (Caramaschi and Cruz, 2004); *B. leptolineata* (Braun and Braun, 1977); *B. marginata* (Boulenger, 1887); *B. marianitae* (Carrizo, 1992); *B. melanopleura* (Boulenger, 1912); *B. palaestes* (Duellman, De la Riva, and Wild, 1997); *B. phaeopleura* (Caramaschi and Cruz, 2000); *B. poaju* (Garcia, Peixoto, and Haddad, 2008); *B. polytaenia* (Cope, 1870); *B. prasina* (Burmeister, 1856); *B. pulchella* (Duméril and Bibron, 1841); *B. riojana* (Koslowky, 1895); *B. semiguttata* (Lutz, 1925); *B. stellae* (Kwet, 2008); and *B. stenocephala* (Caramaschi and Cruz, 1999).

1499

1500 **The *Boana punctata* group**

1501 The *Boana punctata* group is recovered polyphyletic, with *B. hobbsi* nested in the *B.*
1502 *benitezi* group. To remediate the non-monophyly of the *B. punctata* group we transferred *B.*
1503 *hobbsi* to the *B. benitezi* group. The remaining included species of the group are recovered
1504 monophyletic.

1505 The phylogenetic position of *Boana sibleszi* has been unstable, always poorly
1506 supported. Faivovich et al. (2005) recovered it as the sister taxon of the remaining
1507 exemplars of the *B. punctata* group. Wiens et al. (2005) recovered *B. sibleszi* within the *B.*

punctata group, as the sister taxa to the *B. pellucens* group (nested within the *B. punctata* group). Wiens et al. (2006) recovered *B. sibleszi* as the sister taxon of the *B. albopunctata* and *B. punctata* groups. Duellman et al. (2016), Pyron and Wiens (2011), and Wiens et al. (2010) recovered it as the sister taxon of the *B. benitezi* group. Faivovich et al. (2013) recovered the species as the sister taxon of the *B. semilineata* group. In the present analysis, *B. sibleszi* is recovered as the sister taxon of the remaining species of the *B. punctata* group, also with low support (< 50 Jackknife support %). Due to the instability of the phylogenetic relationships of *B. sibleszi*, it is better to remove it from the *B. punctata* group, and maintain it unassigned to any group until the situation improves.

The phylogenetic position of *B. picturata* has also been unstable. It was recovered in the *B. punctata* group by Faivovich et al. (2005, 2013), and Wiens et al. (2005, 2006, 2010). Alternatively, it was recovered —also with low support— as the sister taxon of the *B. albopunctata* group (Pyron and Wiens, 2011), or as the sister taxon of the clade including the *B. albopunctata*, *B. pellucens*, *B. faber*, and *B. pulchella* groups (Duellman et al., 2016). In the present analysis, which has an improved taxonomic sampling, *B. picturata* is the sister taxon to the remaining species of the *B. punctata* group with 84% Jackknife support.

Boana cinerascens and *B. punctata* were recovered as sister taxa in all previous analyses (Duellman et al., 2016; Faivovich et al., 2005, 2013; Wiens et al., 2005, 2006, 2010). Here we recovered both species paraphyletic. *Boana cinerascens* is recovered as two distinct lineages, being one of them the sister taxon to the clade including *B. punctata* and *B. atlantica*. *Boana atlantica*, which was only tentatively assigned to the group (Faivovich et al., 2005), is recovered nested within *B. punctata*.

Remarks. As other species of the group, *Boana picturata* is a lowland inhabitant, but it occurs in forest rivulets whereas other species of *B. punctata* group occur in flooded areas and lentic waters (Brunetti et al., 2014; Caramaschi and Velosa, 1996; Hoogmoed, 1979; Ortega-Andrade et al., 2010). While *B. atlantica*, *B. cinerascens*, and *B. punctata* are green species, *B. picturata* present a marbled pattern of violet and cream (Boulenger, 1899; Caramaschi and Velosa, 1996; Hoogmoed, 1979).

Our results recover *Boana cinerascens* in two main lineages, one of which is more closely related to the clade including all terminals assigned to *B. punctata* and *B. atlantica*. This lineage includes specimens from localities South of the Amazonas River, from Anapu 5133, state of Pará, but also to the North of it, from Guyana 2245 and 189 BM, and 2370. Terminals in this lineage are highly divergent in terms of uncorrected *p*-distances of 16S sequences (Table 5). The other lineage assigned to *Boana cinerascens* includes only terminals distributed North of the Amazonas River, including samples from São Gabriel da Cachoeira, state of Amazonas, Brazil (TG393 and 405); and from Guyana (0416, 2247, and 2371). Terminals in this lineage are poorly divergent in terms of uncorrected *p*-distances of 16S sequences (Table 5).

The type of *Boana cinerascens* is from “flumen Teffé” (Teffé River), a southern tributary of the Amazonas River (Spix, 1824). Its junior synonyms are *Hyla granosa* Boulenger, 1882; *Hyla granosa gracilis* Melin, 1941; and *Hyla inornata* Lutz, 1973. The first, *H. granosa*, has a lectotype designated from Canelos, Ecuador (Duellman, 1974a). *Hyla granosa gracilis* is from Vaupés, Ipanoré, state of Amazonas, Brazil. And finally, *Hyla inornata*, which seems to be collected in the state of Pará, Brazil, was considered a *nomen nudum* by Duellman (1974a, b). These three last names are from localities North of the Amazonas River. It is evident that there are at least two species under the name *Boana*

1555 *cinerascens* (Spix, 1824). However, we did not have the opportunity to make an appropriate
 1556 study of specimens and types of the names in synonymy. A taxonomic review of this
 1557 species is badly needed.

1558 *Boana punctata* is paraphyletic with respect to *B. atlantica*. Our analysis recovers three
 1559 lineages under the name *Boana punctata* (Schneider, 1799). We identified four geographic
 1560 units for the lineages under the names *B. punctata* and *B. atlantica*. Those lineages are from
 1561 the eastern portion of the state of Bahia, Brazil; the Amazon Forest; Central-Western South
 1562 America; and from the Araguaia-Tocantins River Basin, at Central Brazil. The samples
 1563 from the Eastern state of Bahia are assigned to *B. atlantica*. This lineage is the sister taxon
 1564 of the clade including samples of both Central-Western South America and the Araguaia-
 1565 Tocantins River Basin, arranged in two distinct clades. The samples of Amazon Forest are
 1566 grouped into a clade, which is the sister taxon to the other three geographic units. Samples
 1567 from Eastern state of Bahia are from Uruçuca (2111), Jequié (3662), Aurelino Leal (3670),
 1568 and Camamu (3688). Samples from Amazon Forest are from Trinidad and Tobago (4630),
 1569 Serra do Divisor, state of Acre, Brazil (5132), Terra Vermelha, state of Amazonas (5128,
 1570 5129), and Porto Velho, state of Rondonia (5130). Samples from Central-Western South
 1571 America are from Santa Cruz, Ñuflo de Chavez, San Sebastián, Bolivia (MNKA9133);
 1572 Lambari D'Oeste, state of Mato Grosso, Brazil (3686); Porto Murtinho, state of Mato
 1573 Grosso do Sul (3690); Teodoro Sampaio, state of São Paulo, Brazil (3673); Resistencia,
 1574 Chaco, Argentina (0041); 2663 and 2685. Samples from Araguaia-Tocantins River Basin
 1575 are from the Estação Ecológica Serra Geral do Tocantins (5126 and 5127); the
 1576 municipalities of Araguaína (2116), and Caseara (1852), state of Tocantins, Brazil.
 1577 Terminals in those lineages are highly divergent in terms of uncorrected *p*-distances of 16S
 1578 sequences (Table 6). Napoli and Cruz (2005) found a similar geographic pattern analyzing

bioacoustic data. But as their dataset did not included material from Araguaia-Tocantins River Basin, they divided *B. punctata* and *B. atlantica* into only the other three geographic units.

The type of *Boana punctata* is from Surinam. Its junior synonyms are *Hyla papillaris* Spix, 1824 (type locality: Rio Solimões, state of Amazonas); *Hyla variolosa* Spix, 1824 (type locality: Rio Amazonas, Brazil); *Hyla rhodoporus* Günther, 1869 (type locality: restricted to “Upper Amazon”; see Hoogomied, 1979); *Hylella pearsei* Ruthven, 1922 (type locality: Fundación, Santa Marta Mountains, Magdalena, Colombia); *Hyla punctata rubro-lineata* Lutz, 1949 (type locality: Buena Vista, Santa Cruz, Bolivia); *Hyla rubeola* Cochran and Goin, 1970 (type locality: Serrania de la Macarena, Meta, Colombia). From these names, only *Hyla punctata rubro-lineata* is attributed to a locality outside the Amazon Domain. The region from where it is described is dominated by seasonally dry tropical forests (Neves et al., 2015). If the lineage from Central-Western Brazil reveals to be a distinct taxon, this name is available for them. However, as with *Boana cinerascens*, the only evidences we have until now are the variable genetic differences between the terminals. The study of multiple populations assigned to *B. punctata*, and an increase in sampling in order to comprehend the high level of genetic variation between those populations is necessary to understand the taxonomic status of the distinct geographic lineages.

Missing taxa. Two species currently assigned to the *Boana punctata* group were not available for this study: *B. alemani* (Rivero, 1964) and *B. jimenezi* (Señaris and Ayarzagüena, 2006). *Boana alemani* is a species known only from its type series (Rivero, 1964), from lowlands on northern Venezuela, and by one lot of tadpoles collected close to the type locality and tentatively assigned to it (Mijares-Urrutia, 1992). The only character

Rivero (1964) used to separate *B. alemani* from *B. cinerascens*, is the presence of spots on the dorsum of the former. However, Hoogmoed (1979) in his revision indicated the presence of spots on the dorsum of several specimens of *B. cinerascens* from northern South America, including Venezuelan populations. Rivero (1967) briefly commented the possibility of synonymy between *B. alemani* and *B. cinerascens*. If these similarities are corroborated through the study of specimens, it is plausible that *B. alemani* is closely related to one of the lineages currently identified as *B. cinerascens*.

Boana jimenezi is superficially similar to *B. sibleszi* (Señaris and Ayarzagüena, 2006). Whereas all the other species of the *B. punctata* group are lowland inhabitants (Caramaschi and Velosa, 1996; Hoogmoed, 1979; Ortega-Andrade et al., 2010; Rivero, 1964), *B. jimenezi* and *B. sibleszi* occur between 900–1850 m a.s.l. (Señaris and Ayarzagüena, 2006). Both *B. jimenezi* and *B. sibleszi* may have a white dorso-lateral stripe (Señaris and Ayarzagüena, 2006); while this variable character is absent in the remaining species of the *B. punctata* group, it might be present in specimens of *B. benitezi*, *B. lemai*, and *B. tepuiana* (Barrio-Amorós and Brewer-Carias, 2008; MacCulloch and Latrop, 2005; Rivero, 1972), all from the *B. benitezi* group. *Boana jimenezi* and *B. sibleszi* share a white peritoneum covering inner organs on the abdominal cavity with species of both the *B. benitezi* (*B. nympha* and *B. ornatissima*; Faivovich et al., 2006; Hoogmoed, 1979) and *B. punctata* groups (*B. atlantica*, *B. cinerascens*, and *B. punctata*; Hoogmoed, 1979; Señaris and Ayarzagüena, 2006; P.D.P. Pinheiro, personal observation). *Boana jimenezi* and *B. sibleszi* do not have an externally evident mental gland in males, unlike species in the *B. benitezi* group, *B. atlantica*, *B. cinerascens*, and *B. punctata*, (Faivovich et al., 2006; Hoogmoed, 1979; Señaris and Ayarzagüena, 2006; P.D.P. Pinheiro, personal observation). As *B. jimenezi* have character states which approximates it to species from both the *B. benitezi*

and *B. punctata* groups, and it is morphologically similar to *B. sibleszi*, we prefer to remove it from the *B. punctata* group and maintain it unassigned to any group, as we did with *B. sibleszi*, until sequence data becomes available.

Putative phenotypic synapomorphies. The absence of the slip of the *m. depressor mandibulae* with origin at the level of the scapula occurs homoplastically in *B. pulchella* group (see above), and in *B. atlantica*, *B. cinerascens*, and *B. punctata*. We are not aware of this character on *B. alemani*, and *B. picturata*, but it could be a synapomorphy of the *B. punctata* group with homoplasy in the *B. pulchella* group. The overall green coloration, and its fluorescent properties (Taboada et al., 2017), could be putative synapomorphies of the internal clade including *B. atlantica*, *B. cinerascens*, and *B. punctata*. *Boana cinerascens* and *B. punctata* are the only species of *Boana* known to have tadpoles with a high square-shaped median ridge with undulations only in the ends, with lateral borders free of serrations and one short papilla at each side of the base, on their oral cavities (d’Heursel and Haddad, 2007; Kolenc et al., 2008).

Characterization. Besides the putative synapomorphies listed above, species in the *Boana punctata* group can be characterized as small treefrogs, with SVL ranging from 30 mm (*B. punctata*; Cei, 1980) to 43 mm (*B. cinerascens*; Hoogmoed, 1979) in males; and 24 mm (*B. alemani*; Rivero, 1964) to 59 mm (*B. picturata*; Boulenger, 1899) in females; head longer than wide (*B. alemani*; Rivero, 1964) to wider than long (*B. atlantica*; Caramaschi and Velosa, 1996); snout pointed (*B. punctata*) to rounded (*B. cinerascens*) in dorsal view (Hoogmoed, 1979); tympanum diameter/eye diameter proportion from 0.5 (*B. punctata*; Hoogmoed, 1979) to 0.71 (*B. atlantica*; Caramaschi and Velosa, 1996); body slender (*B. punctata*; Hoogmoed, 1979) to moderately robust (*B. atlantica*; Caramaschi and Velosa, 1996); skin on dorsum smooth (*B. picturata*; Boulenger, 1899), to finely granular (*B.*

atlantica; Caramaschi and Velosa, 1996). Kolenc et al. (2008) characterized larvae of this group as having LTRF 2/3, 2/4, 2/5, 3/4 and 3/5.

Content. Five species: *B. alemani* (Rivero, 1964); *B. atlantica* (Caramaschi and Velosa, 1996); *B. cinerascens* (Spix, 1824); *B. picturata* (Boulenger, 1899); *B. punctata* (Schneider, 1799).

The *Boana semilineata* group

Several contributions recovered *B. boans* as the sister taxon of *B. semilineata* and *B. geographica* (Duellman et al., 2016; Faivovich et al., 2005, 2013; Pyron and Wiens, 2011; Wiens et al., 2006, 2010). Our results differ from those of Fouquet et al. (2016), in the relationships between *B. diabolica*, *B. geographica*, *B. semilineata* and the other cryptic lineages named by those authors. In both analyses, however, relationships among many of those lineages are poorly supported. The tentative assignment of *B. pombali* and *B. wavrini* to the *B. semilineata* group by Faivovich et al. (2005) is corroborated by our results.

Remarks. *Boana pombali* and *B. secedens* are morphologically similar (Caramaschi et al., 2004; Lutz, 1963). Both occur in the Atlantic Forest; *B. secedens* is distributed South of the Paraíba do Sul River, in the state of Rio de Janeiro (Southeastern Brazil; Weber et al., 2009), and *B. pombali* has a broader distribution, occurring from the states of Espírito Santo and northeastern Minas Gerais (Southeastern Brazil), to Sergipe (Northeastern Brazil; Caramaschi et al., 2004).

The major clade of this group includes mostly Amazonian species, with the exception of *Boana semilineata*, from the Atlantic Forest (Spix, 1824). *Boana boans* and *B. wavrini*, share many morphological similarities, and have a broad distribution through the Amazon

(Hoogmoed, 1990). They were considered synonyms by Cochran and Going (1970), and *B. wavrini* was subsequently resurrected by Hoogmoed (1990). Our results corroborate the validity of these two species.

Fouquet et al. (2016) described *Boana diabolica* and found many cryptic lineages related to *B. geographica* and *B. semilineata*. Some specimens sequenced by us were recovered related to some of these lineages: sample 3477 as *B. aff. semilineatus* 2; sample TG243 as *B. aff. semilineatus* 3; and sequences previously identified as “*Hypsiboas geographicus*” by Faivovich et al. (2005) and subsequent contributions (i.e., Duellman et al., 2016; Faivovich et al., 2013; Pyron and Wiens, 2011; Wiens et al., 2006, 2010) actually correspond to the lineage named as *B. aff. semilineatus* 1 (as the results of Fouquet, et al., 2016). Sample ML1269 instead, presents high levels of genetic divergence from the other specimens of this clade (Table 7). The uncorrected pairwise distances corroborates the results of Fouquet et al. (2016) about the cryptic diversity under *B. geographica* and *B. semilineata* (Table 7). The sample ML1269, from São Gabriel da Cachoeira, state of Amazonas, Brazil, indicates one more population that should be better investigated taxonomically. The *B. geographica/semilineata* species complex is one more group of *Boana* which must be reviewed carefully.

Missing taxa. The only species for which samples were not available is *B. hutchinsi* (Pyburn and Hall, 1984). However, the transference of *B. hutchinsi* to this group by Faivovich et al. (2006), due to the absence of a prepollical spine, presence of keratinized nuptial pads in males, and presence of reticulations on palpebrae of both *B. hutchinsi*, *B. geographica* and *B. semilineata* is reasonable. *Boana diabolica* also have these character states (Fouquet et al., 2016). The close relationship of *B. diabolica* with *B. geographica* and *B. semilineata*, and the combination of those character states lead us to expect *B.*

1699 *hutchinsi* to be closely related to these species. Additionally, *B. hutchinsi* is known from
 1700 Colombian Amazon, and probably adjacent Peru (Lynch, 2008; Pyburn and Hall, 1984).
 1701 Two of the lineages presented by Fouquet et al. (2016)—*B. cf. geographica* 1; *B. aff.*
 1702 *semilineata* 5—present their geographic distribution close to the range known for *B.*
 1703 *hutchinsi*. However, those authors do not present morphological data for those specimens,
 1704 but it is possible that one of those lineages could be related or even assigned to *B. hutchinsi*.
 1705 **Putative phenotypic synapomorphies.** Faivovich et al. (2005) when defining the *Boana*
 1706 *semilineata* group stated the presence of a reticulated palpebral membrane as putative
 1707 synapomorphy for it, noticing that this character is homoplastic in *B. microderma* and *B.*
 1708 *roraima* (Barrio-Amorós et al., 2011; Faivovich et al., 2005). Males of the *B. semilineata*
 1709 group are unique, among *Boana* species, in presenting a colored nuptial pad on the first
 1710 finger (Caramaschi et al., 2004; Faivovich et al., 2006; Fouquet et al., 2016; Lutz, 1963;
 1711 P.D.P. Pinheiro personal observation). The presence of this sexually dimorphic character is
 1712 a putative synapomorphy of the *B. semilineata* group. Faivovich et al. (2005) also
 1713 commented that the schooling behavior of tadpoles could be a synapomorphy of at least the
 1714 internal clade including *B. geographica* and *B. semilineata*. Fouquet et al. (2016) reported
 1715 the presence of this behavior in tadpoles of *B. diabolica* and in *B. aff. semilineata* 1, two
 1716 species included in the same clade as *B. geographica* and *B. semilineata*, corroborating the
 1717 hypothesis of Faivovich et al. (2005). Additionally, these species have recently
 1718 metamorphosed individuals with a dark coloration pattern in the entire body (see
 1719 Bokermann, 1963b; Duellman, 1973; Fouquet et al. 2016). Tadpoles of *B. hutchinsi* do not
 1720 form schools (Pyburn and Hall; 1984), but its recently metamorphosed specimens have a
 1721 lavender-gray dorsum, black sides, black thighs, and black webs on hands and feet.
 1722 Tadpoles of *B. boans*, *B. pombali*, and *B. wavrini* are not black (Duellman, 2005; Juncá et

al., 2012; Martins and Moreira, 1991), and for *B. wavrini* there is a report of recently metamorphosed individuals with coloration pattern very similar to those of adults (Martins and Moreira, 1991). Pinheiro et al. (unpublished results c) reported the sickle-shaped Distal Prepollex as a character exclusive of *B. diabolica*, *B. geographica*, *B. hutchinsi*, and *B. semilineata* within the genus. The finely granular skin on dorsum could be a putative synapomorphy at least of the internal clade including *B. boans*, *B. wavrini*, *B. diabolica*, *B. geographica*, and *B. semilineata*.

Characterization. Besides the putative synapomorphies listed above, the species of the *Boana semilineata* group can be characterized as medium to large treefrogs, with SVL ranging from 38.5 mm (*B. diabolica*; Fouquet et al., 2016) to 113 mm (*B. wavrini*; Hoogmoed, 1990) in adult males; and from 53.4 mm (*B. pombali*; Caramaschi et al., 2004) to 105 mm (*B. boans*; Rivero, 1961) in adult females; head as wide as long (*B. hutchinsi*; Pyburn and Hall, 1984) to longer than wide (*B. pombali*; Caramaschi et al., 2004); snout ovoid in dorsal view; tympanum diameter/eye diameter proportion from 0.48 (*B. wavrini*; Hoogmoed, 1990) to 0.72 (*B. pombali*; Caramaschi et al., 2004); body slender (*B. hutchinsi*; Pyburn and Hall, 1984) to robust (*B. pombali*; Caramaschi et al., 2004); skin on dorsum smooth (*B. secedens*; Lutz, 1963) to finely granular (*B. wavrini*; Hoogmoed, 1990). Males *Boana boans* and *B. wavrini* are known to construct or use mud basins as nests (Duellman, 2005; Martins and Moreira, 1991). Kolenc et al. (2008) discussed that the remarkable ontogenetic changes in LTRF (ranging from 2/3 to 3/5; d’Heursel and de Sá, 1999; Kenny, 1969) might explain the different LTRF attributed to species of this group (e.g., *B. boans*, *B. geographica*, *B. hutchinsi*; Duellman, 1970, 1978; Duellman and Lescure, 1973; Pyburn and Hall, 1984).

Content. Eight species: *B. boans* (Linnaeus, 1758); *B. diabolica* (Fouquet, Martinez, Zeidler, Courtois, Gaucher, Blanc, Lima, Souza, Rodrigues, and Kok, 2016); *B. geographica* (Spix, 1824); *B. hutchinsi* (Pyburn and Hall, 1984); *B. pombali* (Caramaschi, Pimenta, and Feio, 2004); *B. secedens* (Lutz, 1963) *B. semilineata* (Spix, 1824); and *B. wavrini* (Parker, 1936).

Species of *Boana* unassigned to any group. Three species: *B. jimenezi* (Señaris and Ayarzagüena, 2006); *B. sibleszi* (Rivero, 1972); *B. varelae* (Carrizo, 1992).

CONCLUSIONS

We presented the most inclusive phylogenetic analysis of *Boana*. From its 92 currently assigned species, our dataset includes 256 terminals representing 83 nominal taxa, besides terminals of undescribed lineages. In our results, the support of some groups raised considerably, as did the support for the relationships of particular taxa. However, some major groups remain poorly supported and their relationships with the other species groups of the genus are uncertain. Considering that we sampled almost the entire taxonomic diversity of *Boana*, these results may imply that we must change our data sampling strategies, possibly including massive NGS sequencing, and explore exhaustively phenotypic characters from multiple character systems. In the meantime, there are several taxa within the genus *Boana* that need taxonomic revision. Such studies may result in synonymy, names resurrection and/or species description.

On the Appendix 2 we provide a discussion on several aspects of the biology and diversity of *Boana* which could probably be pursued and studied in the context of our phylogenetic results.

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2445 APPENDIX 1

2446 Genbank accession numbers for the sequences employed in the phylogenetic analyses and estimation of *p*-distances. Sequences were
 2447 produced by Almendáriz et al. (2014), Antunes *et al.* (2008), Berneck et al. (2016), Caminer and Ron (2014), Coloma et al. (2012),
 2448 Crawford et al. (2010), Darst and Cannatella (2004), Faivovich et al. (2004, 2005, 2010, 2013), Fouquet et al. (2007, 2016), Funk et al.
 2449 (2012), Guayasamin et al. (2015), Jansen et al. (2011), Köhler et al. (2010), Lehr et al. (2010), Orrico et al. (2017), Pinheiro et al.,
 2450 unpublished results a, Prado et al. (2012), Salducci et al. (2005), Wiens et al. (2006). See those papers for locality data and other
 2451 voucher information. An asterisk (*) on voucher numbers indicates topotype specimens. Sequences produced for this project are in
 2452 bold.

Taxon	Voucher	12s- tRNA ^{Val} - 16s	16s- tRNA ^{Leu} - ND1- tRNA ^{Ile} - tRNA ^{Gln}	Cytochrome oxidase I	Cytochrome b	Proopio melanocortin A	Rhodopsin Exon 1	Recombination Activating Gene 1	Tyrosinase	Seven in Absentia Homolog 1	Chemokine Receptor 4 Exon 2
<i>Acris crepitans</i>	LSUMZ-H 2164	AY843559	GQ366290	-	AY843782	-	AY844533	AY844358	AY844019	AY844762	GQ365976
<i>Aplastodiscus albofrenatus</i>	*CFBH-t 5051	KU184021	-	KU184058	-	-	KU184111	KU184083	KU184246	KU184149	-
<i>Aplastodiscus albosignatus</i>	*MZUSP-field 1451	KU184037	-	KU184064	-	-	KU184117	KU184086	KU184252	KU184155	-
<i>Aplastodiscus arildae</i>	USNM 303022	AY843604	-	-	AY843825	-	AY844578	AY844392	AY844049	AY844803	-
<i>Aplastodiscus callipygius</i>	CFBH 3909	AY843614	-	-	AY843840	-	AY844592	AY844402	AY844058	AY844813	-
<i>Aplastodiscus cavicola</i>	AF 0070	AY843617	-	-	AY843843	-	AY844594	AY844405	-	AY844814	-
<i>Aplastodiscus cochranæ</i>	CFBH 3001	AY843568	-	-	AY843790	-	AY844542	AY844365	AY844024	AY844770	-
<i>Aplastodiscus ehrhardti</i>	CFBH-t 11191	KU184017	KU184225	KU184050	-	-	KU184103	-	KU184239	KU184141	-
<i>Aplastodiscus eugenioi</i>	CFBH 5915	AY843669	-	-	AY843913	-	AY844660	AY844456	-	AY844875	KF751465
<i>Aplastodiscus flumineus</i>	*CFBH 30832	KU184013	-	KU184072	-	-	KU184127	KU184092	KU184260	KU184164	-
<i>Aplastodiscus ibirapitanga</i>	MNRJ 51863	KU184025	KU184228	KU184046	-	-	KU184099	-	KU184236	KU184138	-
<i>Aplastodiscus leucopygius</i>	USNM 303038	AY843569	KF794106	XXXX	AY843873	-	AY844622	AY844425	AY844084	AY844840	KF751466
<i>Aplastodiscus lutzorum</i>	BB 49	KU184003	KU184217	KU184054	-	-	KU184107	-	KU184242	KU184145	-
<i>Aplastodiscus perviridis</i>	MACN 37791	AY843569	KF794107	KU184041	AY843791	-	AY844543	AY844366	AY844025	AY844771	KF751467

<i>Aplastodiscus sibilatus</i>	CFBH 32528	KU184014	-	-	-	-	KU184133	KU184094	KU184264	KU184170	-
<i>Aplastodiscus weygoldti</i>	AF 0068	AY843685	-	-	AY843931	-	AY844678	AY844467	-	AY844887	-
<i>Boana aguilari</i>	*1246	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-	-	XXXX
<i>Boana aguilari</i>	1446	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-	-	XXXX
<i>Boana albomarginata</i>	140	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	XXXX
<i>Boana albomarginata</i>	*5008	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	-	XXXX	-
<i>Boana albonigra</i>	1523	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX
<i>Boana albonigra</i>	1819	XXXX	-	XXXX	XXXX	-	XXXX	-	-	-	-
<i>Boana albopunctata</i>	5005	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana albopunctata</i>	CFBH 8078	-	JN898883	-	-	-	JQ023442	-	-	-	-
<i>Boana albopunctata</i>	CFBH 8086	-	JN898890	-	-	-	JQ023443	-	-	-	-
<i>Boana albopunctata</i>	F05	XXXX	-	-	XXXX	-	XXXX	-	XXXX	XXXX	-
<i>Boana aff. albopunctata</i>	MNK A9279	JF790116	-	-	-	-	-	-	-	-	-
<i>Boana aff. albopunctata</i>	MNK A9369	JF790117	-	-	-	-	-	-	-	-	-
<i>Boana alfaroi</i>	QCAZ 44858	JN970469/ JN970605	-	JN970737	-	JN970860	-	-	-	-	-
<i>Boana alfaroi</i>	QCAZ 50785	KF955303/ KF955305	-	KF955306	-	KF955307	-	-	-	-	-
<i>Boana almendarizae</i>	QCAZ 32645	JN970386/ JN970522	-	JN970658	-	JN970777	-	-	-	-	-
<i>Boana almendarizae</i>	QCAZ 39650	JN970394/ JN970530	-	JN970665	-	JN970785	-	-	-	-	-
<i>Boana andina</i>	*164	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	-
<i>Boana andina</i>	1657	XXXX	-	-	XXXX	-	XXXX	XXXX	-	-	XXXX
<i>Boana atlantica</i>	2111	XXXX	XXXX	-	XXXX	-	XXXX	-	XXXX	XXXX	-
<i>Boana atlantica</i>	3662	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	-	-	-
<i>Boana atlantica</i>	3670	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	-	XXXX	-
<i>Boana atlantica</i>	3688	XXXX	XXXX	-	-	-	-	XXXX	XXXX	-	-
<i>Boana balzani</i>	1258	XXXX	-	XXXX	XXXX	-	XXXX	-	-	-	XXXX
<i>Boana balzani</i>	*3127	XXXX	XXXX	-	-	-	-	-	-	-	-
<i>Boana bandeirantes</i>	*4810	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana bandeirantes</i>	*4811	XXXX	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	-
<i>Boana beckeri</i>	*2048	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX	-	-
<i>Boana beckeri</i>	*4629	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana bischoffi</i>	2046	XXXX	XXXX	-	XXXX	-	XXXX	-	XXXX	-	-
<i>Boana bischoffi</i>	F46	XXXX	-	XXXX	XXXX	-	XXXX	XXXX	-	-	-
<i>Boana boans</i>	96	XXXX	-	-	XXXX	-	XXXX	-	XXXX	XXXX	-
<i>Boana boans</i>	486	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX

<i>Boana cladoI</i>	118 MC	JN970501/ JN970637	-	-	-	JN970891	-	-	-	-	-
<i>Boana cladoI</i>	168 MC	JN970498/ JN970634	-	-	-	JN970889	-	-	-	-	-
<i>Boana cladoJ</i>	MNKA 9468	JF790136	-	-	-	-	-	-	-	-	-
<i>Boana cladoJ</i>	MNKA 9477	JF790138	-	-	-	-	-	-	-	-	-
<i>Boana cladoK</i>	816	XXXX	-	-	XXXX	-	-	-	-	-	-
<i>Boana cordobae</i>	167	XXXX	-	XXXX	XXXX	-	XXXX	-	-	-	-
<i>Boana cordobae</i>	285	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX
<i>Boana crepitans</i>	680	XXXX	-	-	XXXX	-	XXXX	XXXX	XXXX	-	XXXX
<i>Boana crepitans</i>	ML 0668	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana curupi</i>	*36	XXXX	-	XXXX	XXXX	-	XXXX	-	-	XXXX	XXXX
<i>Boana curupi</i>	1658	XXXX	-	-	XXXX	-	XXXX	XXXX	-	XXXX	XXXX
<i>Boana dentei</i>	13MC	AF467270/ EF376018	-	-	-	-	-	-	EF376124	-	-
<i>Boana diabolica</i>	R149	KU168871	-	-	-	-	-	-	-	-	-
<i>Boana diabolica</i>	*R157	KU168874	-	-	-	-	-	-	-	-	-
<i>Boana ericae</i>	*428	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	-	-
<i>Boana ericae</i>	*4559	XXXX	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	-	-
<i>Boana exastis</i>	2057	XXXX	XXXX	-	XXXX	-	XXXX	-	XXXX	XXXX	-
<i>Boana exastis</i>	4999	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana faber</i>	3	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-	XXXX	-
<i>Boana faber</i>	39	XXXX	-	-	XXXX	-	-	-	-	-	-
<i>Boana faber</i>	ML 0463	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana fasciata</i>	415	XXXX	-	-	XXXX	-	XXXX	-	-	-	-
<i>Boana fasciata</i>	*QCAZ 17030	JN970399/ JN970535	-	JN970669	-	JN970790	-	-	-	-	-
<i>Boana aff. fasciata</i>	5004	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana freicanecae</i>	*2241	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-	-	XXXX
<i>Boana freicanecae</i>	4954	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana geographica</i>	MNKA 9343	JF790118	-	-	-	-	-	-	-	-	-
<i>Boana geographica</i>	MNKA 9347	JF790119	-	-	-	-	-	-	-	-	-
<i>Boana geographica</i>	*MZUSP 157060	KU168903	-	-	-	-	-	-	-	-	-
<i>Boana geographica</i>	MZUSP 157090	KU168898	-	-	-	-	-	-	-	-	-
<i>Boana cf. geographica1</i>	MPEG 24822	KU168893	-	-	-	-	-	-	-	-	-
<i>Boana cf. geographica1</i>	MTR 36719	KU168901	-	-	-	-	-	-	-	-	-
<i>Boana gladiator</i>	3720	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	-	-	XXXX
<i>Boana gladiator</i>	*MNCN 5523	HM480413	-	-	HM535330	-	-	-	-	-	-

<i>Boana goiana</i>	2412	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	-
<i>Boana goiana</i>	*4487	XXXX	-	XXXX	-	-	-	-	-	-	-
<i>Boana guentheri</i>	420	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-	XXXX	-
<i>Boana guentheri</i>	*3174	XXXX	XXXX	-	-	-	XXXX	-	-	XXXX	XXXX
<i>Boana heilprini</i>	*811	XXXX	XXXX	-	XXXX	-	XXXX	-	-	XXXX	-
<i>Boana hobbsi</i>	2041	XXXX	-	-	385	-	XXXX	-	-	-	-
<i>Boana jaguariaivensis</i>	*3455	XXXX	XXXX	-	-	-	XXXX	-	XXXX	XXXX	XXXX
<i>Boana jaguariaivensis</i>	*3457	XXXX	XXXX	-	-	-	XXXX	-	XXXX	XXXX	XXXX
<i>Boana joaquina</i>	421	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	XXXX
<i>Boana joaquina</i>	3499	XXXX	-	-	-	-	-	-	-	-	-
<i>Boana lanciformis</i>	472	XXXX	-	-	XXXX	-	XXXX	-	XXXX	XXXX	-
<i>Boana lanciformis</i>	5001	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana lanciformis</i>	QCAZ 20641	JN970512/ JN970648	-	JN970767	-	JN970898	-	-	-	-	-
<i>Boana lanciformis</i>	QCAZ 30936	JN970510/ JN970646	-	JN970765	-	JN970896	-	-	-	-	-
<i>Boana lanciformis</i>	TG398	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	-	-
<i>Boana latistriata</i>	2109	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	-	-
<i>Boana latistriata</i>	*4694	XXXX	-	-	-	-	XXXX	XXXX	XXXX	-	-
<i>Boana lemai</i>	641	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX
<i>Boana lemai</i>	1419	XXXX	-	XXXX	XXXX	-	XXXX	-	-	-	XXXX
<i>Boana leptolineata</i>	561	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-
<i>Boana leptolineata</i>	3160	XXXX	XXXX	-	-	-	-	-	-	-	XXXX
<i>Boana leucocheila</i>	2316	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana leucocheila</i>	2330	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana leucocheila</i>	2409	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	-	-	-
<i>Boana lundii</i>	826	XXXX	-	-	XXXX	-	XXXX	-	XXXX	XXXX	-
<i>Boana lundii</i>	2667	-	-	XXXX	-	-	XXXX	XXXX	-	-	-
<i>Boana lundii</i>	ML 0672	XXXX	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	-
<i>Boana maculateralis</i>	*QCAZ 40082	JN970405/ JN970541	-	JN970675	-	JN970796	-	-	-	-	-
<i>Boana maculateralis</i>	QCAZ 44452	JN970416/ JN970552	-	JN970685	-	JN970807	-	-	-	-	-
<i>Boana marginata</i>	423	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	XXXX
<i>Boana marginata</i>	2167	XXXX	XXXX	-	XXXX	-	-	-	XXXX	-	-
<i>Boana marianitae</i>	*291	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	-
<i>Boana marianitae</i>	*460	XXXX	-	-	XXXX	-	XXXX	-	-	-	-
<i>Boana melanopleura</i>	*1244	XXXX	XXXX	-	XXXX	-	XXXX	-	-	-	-
<i>Boana melanopleura</i>	1396	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-	XXXX	XXXX

<i>Boana microderma</i>	813	XXXX	XXXX	-	XXXX	-	-	-	-	-	-
<i>Boana microderma</i>	TG 391	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana microderma</i>	3685	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana microderma</i>	3692	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana multifasciata</i>	102	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX
<i>Boana multifasciata</i>	5006	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana multifasciata</i>	*5002	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana multifasciata</i>	3749	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana multifasciata</i>	3752	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana nympha</i>	814	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX	-	XXXX
<i>Boana nympha</i>	2357	XXXX	-	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	-
<i>Boana ornatissima</i>	4433	XXXX	-	XXXX	-	-	-	-	XXXX	-	-
<i>Boana ornatissima</i>	51 MC	EF376019/ EF376056	-	-	-	-	-	-	EF376125	-	-
<i>Boana palaestes</i>	MNCN 23199	HM480418	-	-	HM535351	-	-	-	-	-	-
<i>Boana paranaiba</i>	5007	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	-	XXXX	-
<i>Boana pardalis</i>	147	XXXX	XXXX	-	XXXX	-	XXXX	-	XXXX	XXXX	-
<i>Boana pardalis</i>	ML 0655	XXXX	-	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana pellucens</i>	KU 202734	XXXX	-	-	-	-	-	-	-	-	-
<i>Boana pellucens</i>	QCAZ 23680	XXXX	-	XXXX	-	-	-	-	-	-	-
<i>Boana pellucens</i>	QCAZ 30594	XXXX	-	XXXX	-	XXXX	-	-	-	-	-
<i>Boana phaeopleura</i>	2356	XXXX	XXXX	XXXX	-	-	XXXX	-	XXXX	-	-
<i>Boana phaeopleura</i>	*4490	XXXX	-	XXXX	-	-	-	-	-	-	-
<i>Boana picturata</i>	2886	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-
<i>Boana picturata</i>	KU 202737	XXXX	-	-	-	-	-	-	-	-	-
<i>Boana poaju</i>	*2545	XXXX	-	XXXX	XXXX	-	XXXX	-	-	XXXX	-
<i>Boana poaju</i>	2557	XXXX	XXXX	XXXX	-	-	-	-	-	-	-
<i>Boana polytaenia</i>	2029	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-
<i>Boana polytaenia</i>	4603	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana polytaenia</i>	4690	XXXX	XXXX	-	-	-	XXXX	XXXX	XXXX	-	-
<i>Boana polytaenia</i>	4737	XXXX	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	-
<i>Boana polytaenia</i>	4950	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana aff. polytaenia1</i>	2628	XXXX	XXXX	XXXX	-	-	XXXX	XXXX	-	XXXX	-
<i>Boana aff. polytaenia1</i>	4958	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	-	XXXX	-
<i>Boana aff. polytaenia2</i>	2630	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-	XXXX	-
<i>Boana aff. polytaenia2</i>	4956	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	-	XXXX	-
<i>Boana pombali</i>	2025	XXXX	-	-	XXXX	-	XXXX	-	XXXX	XXXX	XXXX
<i>Boana pombali</i>	2034	XXXX	-	-	XXXX	-	XXXX	-	XXXX	-	XXXX
<i>Boana pombali</i>	4998	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-

<i>Boana aff. prasina</i>	V 07	XXXX	XXXX	-	-	-	-	-	-	-	-
<i>Boana aff. prasina</i>	V 43	XXXX	XXXX	-	-	-	-	-	-	-	-
<i>Boana prasina</i>	*4741	XXXX	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	-	-
<i>Boana prasina</i>	F 27	XXXX	-	-	XXXX	-	XXXX	-	XXXX	XXXX	-
<i>Boana pugnax</i>	3079	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
<i>Boana pugnax</i>	3089	XXXX	XXXX	-	-	XXXX	-	XXXX	XXXX	-	-
<i>Boana pugnax</i>	3093	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana pugnax</i>	4691	XXXX	XXXX	-	-	XXXX	-	-	XXXX	-	-
<i>Boana pugnax</i>	4692	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana pugnax</i>	5119	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana pulchella</i>	289	XXXX	XXXX	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	-
<i>Boana pulchella</i>	2637	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana punctata</i>	4630	XXXX	XXXX	XXXX	-	-	-	-	-	-	-
<i>Boana punctata</i>	5128	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	XXXX	-
<i>Boana punctata</i>	5129	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	XXXX	-
<i>Boana punctata</i>	5130	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	-	-	-
<i>Boana punctata</i>	5132	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	-	XXXX	-
<i>Boana punctata</i>	1852	XXXX	XXXX	-	XXXX	XXXX	-	-	XXXX	-	XXXX
<i>Boana punctata</i>	2116	XXXX	XXXX	-	XXXX	-	XXXX	-	XXXX	-	-
<i>Boana punctata</i>	5126	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	-	XXXX	-
<i>Boana punctata</i>	5127	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana punctata</i>	41	XXXX	XXXX	XXXX	XXXX	-	-	-	-	-	-
<i>Boana punctata</i>	2663	XXXX	-	-	-	XXXX	-	XXXX	-	-	-
<i>Boana punctata</i>	2685	XXXX	XXXX	XXXX	-	-	XXXX	XXXX	-	XXXX	-
<i>Boana punctata</i>	3673	-	-	XXXX	-	XXXX	XXXX	XXXX	-	XXXX	-
<i>Boana punctata</i>	3686	XXXX	XXXX	-	-	XXXX	-	XXXX	-	-	-
<i>Boana punctata</i>	3690	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	-	-	-
<i>Boana punctata</i>	MNKA 9133	JF790121	-	-	-	-	-	-	-	-	-
<i>Boana raniceps</i>	2	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX
<i>Boana raniceps</i>	1799	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-	-	-
<i>Boana raniceps</i>	ML 1242	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana riojana</i>	*283	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	-
<i>Boana riojana</i>	1376	XXXX	-	XXXX	XXXX	-	XXXX	XXXX	-	-	XXXX
<i>Boana roraima</i>	642	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX
<i>Boana roraima</i>	1417	XXXX	-	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX
<i>Boana rosenbergi</i>	3072	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana rosenbergi</i>	5120	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	XXXX	XXXX	-
<i>Boana rosenbergi</i>	KU 217629	AY819438	-	-	-	-	-	-	-	-	-
<i>Boana rubracyla</i>	3448	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	-	-

<i>Boana rufitela</i>	1005	XXXX	XXXX	-	XXXX	-	XXXX	-	XXXX	XXXX	-
<i>Boana rufitela</i>	3087	XXXX	XXXX	-	-	XXXX	-	XXXX	-	XXXX	XXXX
<i>Boana rufitela</i>	KLR 0798	FJ784372	-	-	-	-	-	-	-	-	-
<i>Boana secedens</i>	3068	XXXX	XXXX	-	-	-	-	-	-	XXXX	-
<i>Boana secedens</i>	3085	XXXX	XXXX	-	-	XXXX	XXXX	-	-	XXXX	XXXX
<i>Boana secedens</i>	3532	XXXX	XXXX	-	-	-	XXXX	XXXX	XXXX	-	-
<i>Boana semiguttata</i>	2392	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-
<i>Boana semiguttata</i>	4640	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana aff. semiguttata</i>	4638	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana aff. semiguttata</i>	4639	XXXX	-	-	-	XXXX	XXXX	XXXX	-	XXXX	-
<i>Boana semilineata</i>	696	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX
<i>Boana semilineata</i>	ML0456	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana aff. semilineata1</i>	815	XXXX	-	-	-	-	-	-	-	-	-
<i>Boana aff. semilineata1</i>	MPEG 30285	KU168894	-	-	-	-	-	-	-	-	-
<i>Boana aff. semilineata1</i>	R 140	KU168866	-	-	-	-	-	-	-	-	-
<i>Boana aff. semilineata2</i>	3747	XXXX	XXXX	-	-	XXXX	-	XXXX	XXXX	-	-
<i>Boana aff. semilineata2</i>	BM 334	KU168883	-	-	-	-	-	-	-	-	-
<i>Boana aff. semilineata2</i>	MTR 7584	KU168907	-	-	-	-	-	-	-	-	-
<i>Boana aff. semilineata3</i>	AF 252	KU168880	-	-	-	-	-	-	-	-	-
<i>Boana aff. semilineata3</i>	JOG 737	KU168890	-	-	-	-	-	-	-	-	-
<i>Boana aff. semilineata3</i>	TG 243	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana aff. semilineata4</i>	SMS 153	KU168909	-	-	-	-	-	-	-	-	-
<i>Boana aff. semilineata5</i>	MTR 36136	KU168899	-	-	-	-	-	-	-	-	-
<i>Boana aff. semilineata5</i>	MTR 36149	KU168900	-	-	-	-	-	-	-	-	-
<i>Boana sibleszi</i>	643	XXXX	XXXX	-	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX
<i>Boana sibleszi</i>	1418	XXXX	-	XXXX	XXXX	-	XXXX	-	-	XXXX	XXXX
<i>Boana stellae</i>	1386	XXXX	-	XXXX	XXXX	-	XXXX	XXXX	-	-	XXXX
<i>Boana stellae</i>	2118	XXXX	XXXX	-	XXXX	-	XXXX	-	XXXX	-	-
<i>Boana stenocephala</i>	4996	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	-	-
<i>Boana stenocephala</i>	*5166	XXXX	XXXX	XXXX	-	-	-	-	-	-	-
<i>Boana tepuiana</i>	*136	XXXX	XXXX	XXXX	XXXX	-	XXXX	XXXX	-	-	XXXX
<i>Boana tepuiana</i>	*3683	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana tepuiana</i>	*3693	XXXX	XXXX	XXXX	-	XXXX	XXXX	XXXX	XXXX	XXXX	-
<i>Boana tetete</i>	*QCAZ 40080	JN970403/ JN970539	-	JN970673	-	JN970794	-	-	-	-	-
<i>Boana tetete</i>	*QCAZ 40081	JN970404/ JN970540	-	JN970674	-	JN970795	-	-	-	-	-
<i>Boana wavrini</i>	3158	XXXX	XXXX	-	-	XXXX	XXXX	XXXX	XXXX	-	XXXX
<i>Boana xerophylla</i>	552 PG	KX697932	-	KX697979	-	-	-	-	-	-	-

<i>Hyloscirtus phyllognathus</i>	QCAZ 41032	JX155801/ JX155828	-	-	-	-	-	-	-	-	-	-
<i>Hyloscirtus princecharlesi</i>	*QCAZ 43654	JX155807/ JX155834	-	-	-	-	-	-	-	-	-	-
<i>Hyloscirtus psarolaimus</i>	QCAZ 27049	JX155808/ JX155835	-	-	-	-	-	-	-	-	-	-
<i>Hyloscirtus ptychodactylus</i>	*QCAZ 46030	JX155804/ JX155831	-	-	-	-	-	-	-	-	-	-
<i>Hyloscirtus simmonsii</i>	*KU 181167	DQ380376	-	-	-	-	-	-	-	-	-	-
<i>Hyloscirtus staufferorum</i>	QCAZ 45967	JX155815/ JX155842	-	-	-	-	-	-	-	-	-	-
<i>Hyloscirtus tapichalaca</i>	*QCAZ 16704	AY563625	KF794114	-	AY843925	-	AY844672	-	AY844121	-	KF751474	
<i>Hyloscirtus tigrinus</i>	QCAZ 41351	JX155810/ JX155837	-	-	-	-	-	-	-	-	-	-
<i>Myersiohyla chamaeleo</i>	*USNM 562057	KF751500	KF794148	-	KF751495	-	XXXX	KF751496	-	KF751505	-	
<i>Myersiohyla liliae</i>	1914	XXXX	-	-	XXXX	-	XXXX	XXXX	-	-	-	-
<i>Myersiohyla liliae</i>	1915	XXXX	-	-	XXXX	-	-	-	-	-	-	-
<i>Myersiohyla liliae</i>	*2249	XXXX	XXXX	XXXX	XXXX	-	XXXX	-	-	-	XXXX	
<i>Myersiohyla liliae</i>	*2251	XXXX	XXXX	XXXX	-	-	XXXX	-	XXXX	XXXX	XXXX	
<i>Myersiohyla neblinaria</i>	*USNM 562071	AY843672	KF794149	-	-	-	AY844663	-	AY844114	AY844876	KF751494	
<i>Nesorohyla kanaima</i>	ROM 39582	AY843634	GQ366307	-	AY843868	-	AY844617	AY844422	AY844079	AY844835	GQ365994	
<i>Phrynomedusa dryade</i>	*CFBH 7613	GQ366234	GQ366313	XXXX	-	-	-	GQ366078	GQ366199	GQ366167	-	
<i>Phyllodytes luteolus</i>	CFBH-t 0385	AY843721	GQ366314	-	AY843966	-	AY844708	AY844494	AY844150	AY844913	-	
<i>Pseudis minuta</i>	MACN 37786	AY843739	GQ366339	XXXX	AY843985	-	-	AY844505	-	AY844929	GQ366028	
<i>Scinax staufferi</i>	UTA-A 50749	AY843761	GQ366340	-	AY844006	-	AY844748	AY844523	AY844183	-	GQ366029	
<i>Trachycephalus typhonius</i>	AMNH-A 141142	AY549362	GQ366341	XXXX	AY549415	-	AY844707	AY844493	AY844149	AY844912	GQ366030	

APPENDIX 2

Aspects of the biology and diversity of *Boana*. Cited references are listed with the Literature Cited of the main text.

There are species of *Boana* from lowlands, highlands, forested and open areas, occurring on lentic and rapid water-bodies. They explored many distinct niches, calling partially submerged, perched on marginal vegetation, or even from higher leaflets of trees or bromeliads (e.g., Barrio, 1965; Barrio-Amorós et al., 2011; Garcia et al., 2003; Hoogmoed 1979; Kluge, 1981; Martins et al., 1998; Señaris and Ayarzagüena, 2006). As a consequence of this huge variation, there is a high phenotypic diversity on the genus, expressed as various coloration patterns, snout-vent length, vocalizations, and natural history, which we briefly discuss below.

Coloration pattern. Within Cophomantini there are several instances of green coloration among its taxa: (i) the clade of *Myersiophyla chamaeleo* and *M. liliae*; (ii) the *Hyloscirtus bogotensis* group; (iii) *Aplastodiscus*; (iv) *B. nympha*; (v) *B. ornatissima*; (vi) *B. hobbsi*; (vii) the clade of *B. cinerascens*, *B. punctata*, and *B. atlantica*; (viii) *B. heilprini*; (ix) *B. pellucens* group; (x) *B. albomarginata*; (xi) *B. balzani*; (xii) *B. marianitae*; (xiii) *B. guentheri*; (xiv) *B. marginata*; (xv) the clade of *B. prasina*, *B. pulchella* and *B. cordobae*; (xvi) *B. poaju*; being also possible to be present as a polymorphism of several other species of the *B. pulchella* group. However, understand the nature of the pigments on all those distinct lineages is necessary to the study of the green coloration evolution.

Also, probably the green coloration performs distinct functions. It could act as a camouflage, as many green species are found perched within green vegetation. Hoogmoed (1979) discuss the coloration pattern and its function as a camouflage for *Boana ornatissima*. Recently, Taboada et al. (2017) published a new research showing that the

green *B. punctata* and *B. atlantica* emit fluorescent light in proper night conditions. But until now, the function of this fluorescence as a visual displaying is merely speculative.

Within the genus *Boana*, the lichenous pattern also presents several instances among its taxa content. The lichenous pattern is present in: (i) the *B. benitezi* group; (ii) *B. semilineata* group; (iii) *B. picturata*; (iv) the internal clade of the *B. faber* group, which is the sister to *B. albomarginata*.

The dorsal longitudinal stripes, used to define the clade of *Boana polytaenia* (Cruz and Caramaschi, 1998; Faivovich et al., 2005), also is present in several instances within the genus *Boana*. (i) In the *B. albopunctata* group it may be present as a polymorphism in *B. alfaroi*, *B. almendarizae*, *B. maculateralis*, and *B. tetete*; (ii) as a polymorphism in *B. bischoffi*; (iii) in the clade of *B. goiana* and *B. phaeopleura*; (iv) in *B. caingua*; (v) in the *B. polytaenia* clade.

Variation in size. *Boana* species have an huge variation on the snout-vent length (SVL) within adults of its species. The smallest treefrogs of this genus are populations of *B. aff. polytaenia* 2 from the Quadrilátero Ferrífero region, in the center of the state of Minas Gerais, Southeast Brazil, within which adult males of 22.03 mm can be found (P.D.P. Pinheiro, personal observation). And also there are much larger species, such as *B. wavrini*, from Amazon Rainforest, which presents adult males of 113 mm (Hoogmoed, 1990). However, there is no study on size evolution in this genus. As the group is highly diverse has a large geographic and altitudinal range, occupying many distinct environments, correlates species size with latitude, altitude, or even with the environment they inhabit becomes a difficult task. However, there is one possible correlation which should be better studied. The largest male specimens are those from the *B. faber* group (except *B. albomarginata*), with SVL ranges between 48–104 mm (see above), and also males of both

2501 *B. boans* and *B. wavrini* (SVL 76.9–113 mm; Hoogmoed, 1990; Lynch and Suárez-
 2502 Mayorga, 2001). Curiously those species are the only ones of the genus known to use mud
 2503 basings as nests to reproduce. Males of other *Boana* species have SVL 22.03–67 mm.

2504 Like the SVL, the tympanum diameter also has a huge variation among species of
 2505 *Boana*. In most anurans, acoustic communication plays an important role in the interaction
 2506 between individuals (Wells, 1977, 1988). And to a communication event completes
 2507 successfully, the receptor needs to receive the signal of the emitter with quality. In the
 2508 acoustic communication of vertebrates the ear is the receptor organ. The varied niches
 2509 explored by *Boana* species expose them to different kinds of sounds, which lead us to
 2510 expect differences between the ear-apparatus of distinct species. These sounds can have
 2511 their origins at the water noise of cascades and rains, winds, and may be interfered by the
 2512 presence of trees or not, depending on the environment being opened or forested, or even
 2513 by the relief. The individuals may also be exposed to calls of co-specific individuals, of
 2514 other anuran species, and even to calls of other animal groups, such as insects and birds. All
 2515 of these acoustic environments diversity faced by *Boana* species probably selected a high
 2516 diversity of tympanum sizes. The tympanum diameter/eye diameter proportion varies from
 2517 0.21 in males of *B. jimenezi* (Señaris and Ayarzagüena, 2006) to 0.98 in males of *B.*
 2518 *rosenbergi* (Duellman, 1970). As the high amplitude values of tympanum diameter
 2519 indicates, the medium-ear of *Boana* seems to be an important organ to be surveyed in an
 2520 evolutionary context.

2521 **Secondary Sexual Characters.** Kluge (1979) found a larger tympanum diameter in
 2522 females of *B. rosenbergi* than in males. Besides the vocal sac, secondary sexual differences
 2523 (SSD) within *Boana* are known in SVL, forearm hypertrophy, prepollex development,
 2524 nuptial pads, and mental glands. Considering the SVL, Duellman (2005) stated that *Boana*

2525 *boans* is the unique hyliid from Amazonian Cusco region to present a male biased SSD.
 2526 Hoogmoed (1990) found the same trend in *B. wavrini*. However, Kluge (1979) mentioned
 2527 that if the geography of *B. boans* is discharged, there is no difference on SVL between
 2528 sexes on this species. Also, Lynch and Soárez-Mayorga (2001) found no sex differences on
 2529 SVL among Colombian populations of *B. boans*, *B. pugnax*, *B. rosenbergi*, and *B. wavrini*,
 2530 and a female-biased SVL in *B. xerophylla*. Within the *B. punctata* group, there is no
 2531 difference on SVL between sexes on *B. cinerascens* and *B. punctata* (Rivero 1964;
 2532 Hoogmoed, 1979; Brunetti et al., 2014), and there is male-biased SVL in males (Camurugi
 2533 and Junca 2013). In other species of *Boana*, the common pattern is for females attain larger
 2534 sizes than males (e.g., Kluge, 1979; Menin et al., 2004; Giasson and Haddad, 2007).

2535 Both Wells (1978) and Shine (1979) hypothesized that a larger SVL in males is an
 2536 adaptation for territoriality. The taxonomic sampling employed by Shine (1979) was too
 2537 small considering the diversity of anurans known nowadays (Giasson and Haddad, 2007).
 2538 Within the genus *Boana*, males of many species present scars on their dorsum, probably
 2539 resulting from injuries caused by the prepollical spine of opponent males during combats
 2540 (see Pinheiro et al., unpublished results c). Females of several species of *Boana* are larger
 2541 than males. This could be interpreted as implying that, at least in *Boana*, territoriality and
 2542 male-male combats, do not favor larger SVL in males than in females. Indeed, Kluge
 2543 (1981) concluded that females of *B. rosenbergi* prefer resident males capable to maintain its
 2544 territories, what would favor aggressivity (but not larger males), and Martins (1993)
 2545 showed that females of *Boana faber* present no preference for larger males.

2546 **Reproductive biology.** In *Boana*, the reprocutive biology and reproductive modes are
 2547 better known for species of the *B. faber* group, and for *B. boans* and *B. wavrini*. Males of
 2548 these species are known to build mud basins, or to use natural watter filled depressions as

2549 nests—except *B. albomarginata*, which do not lay eggs on nests (Giasson and Haddad,
 2550 2007). Males usually call from their nests or close to them to attract their mates, who might
 2551 inspect the nest before the amplexus (Bokermann, 1968; Breder, 1946; Caldwell, 1992;
 2552 Chacón-Ortiz et al., 2004; Duellman, 1970; Goeldi, 1895; Höbel, 1999; Kluge, 1981;
 2553 Lehtinen, 2014; Lutz, 1960; Lynch and Vargas-Ramirez, 2000; Martins, 1993; Martins and
 2554 Moreira, 1991). Males of *Boana faber* and *B. rosenbergi* might assist their clutches during
 2555 few days after coupling (Kluge, 1981; Martins et al., 1998). This facultative egg-attendance
 2556 was positively correlated to years with higher population densities for both species. There is
 2557 no other report of this parental care in other species of *Boana*. Although clutches of the
 2558 those species are laid in nests, they are similar to the ones of *Boana albomarginata* and also
 2559 to several of other species of *Boana* (e.g., Duellman, 1971, 1978; Fouquet et al., 2016;
 2560 Giasson and Haddad, 2007; Savage, 2002). The clutches of *Boana* generally consists in a
 2561 floating film on the water surface—following the terminology of Altig and McDiarmid
 2562 (2007) for ovipositional modes. However, the clutches of the *B. pulchella* group, *B.*
 2563 *hutchinsi*, and *B. raniceps*, are distinct. They consist in an eggs mass arranged three-
 2564 dimensionally, submerged and attached to the substract, which might be vegetation or rocks
 2565 vegetation and rocks (Faivovich et al., unpublished results). There is no report on the clutch
 2566 of the *Boana benitezi* group, excepting by *B. lemai*. An amplexant pair of this species was
 2567 reported by Duellman (1997) to lay a clutch of unpigmented eggs on a leaf, while
 2568 transported in a plastic bag. Due to such event, the author speculated that in natural
 2569 conditions probably the eggs are layed on leafs, and subsequently fall on water. Other two
 2570 species of the *B. benitezi* group are reported to present unpigmented eggs: *B. nympa* and
 2571 *B. roraima* (Faivovich et al., 2006). However their biology remains unknown.

2572 Besides *Boana lemai*, *B. nympha*, and *B. roraima*, only *B. heilprini* is reported to have
2573 unpigmented eggs. Altig and McDiarmid (2007) related the presence of melanine on the
2574 ova to clutches laid in open, exposed areas. Eggs laid in isolated sites (e.g., hidden among
2575 rocks, forest debris, phytotelmata and leaves [probably the case of *B. lemai*]) tend to be
2576 poorly pigmented to despigmented. Landestoy (2013) supposed that *B. heilprini* couples lay
2577 their clutches in small cavities on creeks margins. This would corroborate the premises of
2578 Altig and McDiarmid (2007) for the absence of melanin on *B. heilprini* eggs.

2579 The genus *Boana* have at least two oviposition modes: floating film of eggs and egg-
2580 masses. Altig and McDiarmid (2007) commented that the floating film can easily sink or
2581 carried out due to any perturbation. So, the egg masses attached underwater could be an
2582 evolutionary acquisition of species which reproduces in rivulets, and torrential streams, as a
2583 guarantee to the clutch be not carried out. Within the *B. pulchella* group there are several
2584 species known to reproduce into rivulets (Faivovich et al., unpublished results). Both *B.*
2585 *lemai* and *B. heilprini* also reproduce in rivulets, presenting alternative evolutionary
2586 solutions to the problem of the clutches being carried by water. The first laying outside the
2587 water, on leaves, the later, laying into hidden crevices.

2588 Table 1. Primers employed in the present study to obtain the sequences.

Primers	Forward (F) /Reverse (R)	Gene Fragment	Sequences 5'–3'	Type of DNA	References
MVZ59	F	partial 12s	ATAGCACGTAAAAYGCTDAGATG	Mitochondrial	Graybeal (1997)
12s-L48	F	partial 12s	ATGCAAGYMTCMGCRYCCCNGTGA	Mitochondrial	Designed by M.L. Lyra
12s-FH	R	partial 12s	CTTGGCTCGTAGTTCCTGGCG	Mitochondrial	Goebel et al. (1999)
12s-H978	R	partial 12s + partial tRNA ^{VAL}	CTTACCRTGTTACGACTTRCCT	Mitochondrial	Designed by M.L. Lyra
12s-AL	F	partial 12s	AAACTGGGATTAGATACCCCACTAT	Mitochondrial	Goebel et al. (1999)
tVAL	R	partial 12s + tRNA ^{VAL}	GGTGTAAGCGARAGGCTTTKGTTAAG	Mitochondrial	Goebel et al. (1999)
12s-L13	F	partial 12s + tRNA ^{VAL} + partial 16s	TTAGAAGAGGCAAGTCGTAACATGGTA	Mitochondrial	Feller and Hedges (1998)
12sM	F	partial 12s + tRNA ^{VAL} + partial 16s	GGCAAGTCGTAACATGGTAAG	Mitochondrial	Darst and Cannatella (2004)
16sTitus_1	R	partial 16s	GGTGGCTGCTTTTAGGCC	Mitochondrial	Titus and Larson (1996)
16s-L2a	F	partial 16s	CCAAACGAGCCTAGTGATAGCTGGTT	Mitochondrial	Hedges (1994)
16s-H10	R	partial 16s	TGCTTACGCTACCTTTGCACGGT	Mitochondrial	Hedges (1994)
16s-AR	F	partial 16s	CGCCTGTTTATCAAAAACAT	Mitochondrial	Palumbi et al. (1991)
16s-BR	R	partial 16s	CCGGTCTGAACCTCAGATCACGT	Mitochondrial	Palumbi et al. (1991)
16sWilk2	R	partial 16s	GACCTGGATTACTCCGGTCTGA	Mitochondrial	Wilkinson et al. (1996)
16s-Frog	F	partial 16s + tRNA ^{LEU} + partial NADH dehydrogenase subunit 1	TTACCCTRGGGATAACAGCGCAA	Mitochondrial	Wiens et al. (2005)
Tmet-Frog	R	partial NADH dehydrogenase subunit 1+tRNA ^{ILE} + tRNA ^{GLN} +partial	TTGGGGTATGGGCCCAAAAGCT	Mitochondrial	Wiens et al. (2005)

		tRNA ^{MET}			
An-F1	F	partial cytochrome oxidase I	ACHAAYCAYAAAAGAYATYGG	Mitochondrial	Lyra et al. (2016)
An-R1	R	partial cytochrome oxidase I	CCRAARAATCARAADARRTGTTG	Mitochondrial	Lyra et al. (2016)
Chm-F4	F	partial cytochrome oxidase I	TYTCWACWAAYCAYAAAAGAYATCGG	Mitochondrial	Che et al. (2012)
Chm-R4	R	partial cytochrome oxidase I	ACYTCRGGRTGRCCRAARAATCA	Mitochondrial	Che et al. (2012)
MVZ15	F	partial cytochrome b	GAACTAATGGCCACACWWTACGNAA	Mitochondrial	Moritz et al. (1992)
CytB2	R	partial cytochrome b	AAACTGCAGCCCCTCAGAAATGATATTTGTCCTCA	Mitochondrial	Kocher et al. (1989)
SIA1	F	partial seven in absentia homolog 1	TCGAGTGCCCCGTGTGYTTYGAYTA	Nuclear	Bonacum et al. (2001)
SIA2	R	partial seven in absentia homolog 1	GAAGTGGAAGCCGAAGCAGSWYTGCATCAT	Nuclear	Bonacum et al. (2001)
RHOD-1A	F	partial exon 1 of rhodopsin	ACCATGAACGGAACAGAAGGYCC	Nuclear	Bossuyt and Milinkovich (2000)
RHOD-1D	R	partial exon 1 of rhodopsin	GTAGCGAAGAARCCTTCAAMGTA	Nuclear	Bossuyt and Milinkovich (2000)
TYR-1C	F	partial tyrosinase	GGCAGAGGAWCRTGCCAAGATGT	Nuclear	Bossuyt and Milinkovich (2000)
TYR-1G	R	partial tyrosinase	TGCTGGGCRTCTCTCCARTCCCA	Nuclear	Bossuyt and Milinkovich (2000)
R1-TG1F	F	partial recombination activating gene 1	CCAGCTGGAAATAGGAGAAGTCTA	Nuclear	Grant et al. (2006)
R1-TG1R	R	partial recombination activating gene 1	CTGAACAGTTTATTACCGGACTCG	Nuclear	Grant et al. (2006)
R1-GFF	F	partial recombination activating gene 1	GAGAAGTCTACAAAAVGGCAAAG	Nuclear	Faivovich et al. (2005)

R1-GFR	R	partial recombination activating gene 1	GAAGCGCCTGAACAGTTTATTAC	Nuclear	Faivovich et al. (2005)
POMC-1	F	partial proopiomelanocortin A	GAATGTATYAAAGMMTGCAAGATGGWCCT	Nuclear	Wiens et al. (2005)
POMC-2	R	partial proopiomelanocortin A	TAYTGRCCTTYTTGTGGGCRTT	Nuclear	Wiens et al. (2005)
POMC-DRVF1	F	partial proopiomelanocortin A	ATATGTCATGASCCAYTTYCGCTGGAA	Nuclear	Vieites et al. (2007)
POMC-DRVR1	R	partial proopiomelanocortin A	GGCRTTYTTGAAWAGAGTCATTAGWGG	Nuclear	Vieites et al. (2007)
CXCR4-C	F	partial exon 2 of chemokine receptor 4	GTCATGGGCTAYCARAAGAA	Nuclear	Biju and Bossuyt (2003)
CXCR4-G	R	partial exon 2 of chemokine receptor 4	AGGCAACAGTGGAARAANGC	Nuclear	Biju and Bossuyt (2003)

2589

2590

2591 Table 2. Uncorrected *p*-distances between 16S partial sequences of *Boana lanciformis*
 2592 specimens. Values in percentage.

Taxon/Sample	1	2	3	4	5
<i>B. lanciformis</i> TG398	-				
<i>B. lanciformis</i> 5001	3.91	-			
<i>B. lanciformis</i> 0472	3.92	1.78	-		
<i>B. lanciformis</i> QCAZ20641	4.01	2.48	2.11	-	
<i>B. lanciformis</i> QCAZ30936	4.19	2.67	2.30	0.19	-

2593

2594 Table 3. Uncorrected *p*-distances between 16S partial sequences of *Boana multifasciata*; *B.*
 2595 *paranaiba*, and *B. aff. albopunctata* specimens. Values in percentage.

Taxon/Sample	1	2	3	4	5	6	7	8
1 <i>B. multifasciata</i> 0102	-							
2 <i>B. aff. albopunctata</i> MNKA9279	4.22	-						
3 <i>B. aff. albopunctata</i> MNKA9369	4.22	0.00	-					
4 <i>B. paranaiba</i> 5007	5.00	2.91	2.91	-				
5 <i>B. multifasciata</i> 5006	4.83	3.09	3.10	2.49	-			
6 <i>B. multifasciata</i> 5002	4.47	2.00	2.00	1.96	1.25	-		
7 <i>B. multifasciata</i> 3749	4.82	3.11	3.11	3.02	1.96	1.60	-	
8 <i>B. multifasciata</i> 3752	4.82	3.11	3.11	3.02	1.96	1.60	0.00	-

2596

2597 Table 4. Uncorrected *p*-distances between 16S partial sequences of *Boana calcarata* / *fasciata* species complex. Values in percentage.

Taxon/Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 <i>B. clado</i> K 0816	-																							
2 <i>B. maculateralis</i> QCAZ40082	4.48	-																						
3 <i>B. maculateralis</i> QCAZ44452	4.70	0.00	-																					
4 <i>B. calcarata</i> QCAZ43256	5.91	6.48	6.81	-																				
5 <i>B. calcarata</i> 5003	5.75	6.89	7.25	1.88	-																			
6 <i>B. fasciata</i> QCAZ17030	5.92	6.86	7.20	5.10	4.52	-																		
7 <i>B. almendarizae</i> QCAZ32645	5.72	5.73	6.00	3.38	3.76	3.21	-																	
8 <i>B. almendarizae</i> QCAZ39650	6.42	6.36	6.33	3.87	4.29	3.67	0.20	-																
9 <i>B. dentei</i> 13MC	11.87	12.09	12.10	13.23	12.74	12.20	11.69	11.77	-															
10 <i>B. clado</i> H 188BM	10.27	9.21	9.42	9.98	9.01	9.18	8.79	9.37	10.80	-														
11 <i>B. clado</i> H 0415	9.17	8.79	9.24	9.43	8.03	8.71	8.30	9.20	10.80	0.39	-													
12 <i>B. clado</i> I 118MC	12.36	11.65	11.69	12.22	11.43	10.78	9.58	9.69	12.39	3.90	3.90	-												
13 <i>B. clado</i> I 168MC	12.37	11.65	11.69	12.23	11.44	10.78	9.59	9.70	12.40	4.17	4.16	0.28	-											
14 <i>B. aff. fasciata</i> 5004	7.41	8.41	8.82	8.33	7.70	7.81	7.97	8.41	10.60	5.71	5.01	7.40	7.67	-										
15 <i>B. tetete</i> QCAZ40081	9.46	9.71	9.77	7.73	8.36	8.72	8.33	8.75	11.82	5.76	5.97	7.01	7.27	5.16	-									
16 <i>B. tetete</i> QCAZ40080	9.08	9.31	9.59	7.38	7.99	8.75	7.97	8.56	11.57	5.50	5.66	7.31	7.58	4.86	0.20	-								
17 <i>B. alfaroi</i> QCAZ50785	9.55	10.06	10.56	8.28	8.10	7.76	8.09	8.53	9.82	5.88	5.84	8.21	8.49	5.66	3.75	3.48	-							
18 <i>B. alfaroi</i> QCAZ44858	9.38	9.89	10.39	8.11	7.94	7.58	7.92	8.35	9.62	5.89	5.85	8.23	8.51	5.66	3.76	3.49	0.00	-						
19 <i>B. clado</i> G WED59350	8.59	8.35	8.76	7.16	7.17	7.39	7.15	7.52	9.81	5.67	5.45	7.07	6.79	5.28	4.94	4.64	4.12	4.13	-					
20 <i>B. clado</i> G WED57865	8.60	8.36	8.77	7.16	7.18	7.40	7.16	7.53	9.83	5.69	5.47	7.08	6.79	5.28	4.94	4.65	4.12	4.13	0.00	-				
21 <i>B. clado</i> J MNKA9477	7.83	8.87	9.31	7.64	7.39	7.51	7.46	8.08	10.42	4.28	3.51	6.14	5.84	4.39	5.52	5.20	5.25	5.26	3.50	3.51	-			
22 <i>B. clado</i> J MNKA9468	7.85	8.90	9.34	7.66	7.41	7.52	7.48	8.10	10.41	4.29	3.52	6.16	5.87	4.41	5.54	5.22	5.27	5.27	3.51	3.52	0.00	-		
23 <i>B. aff. calcarata</i> 3746	8.13	9.18	9.43	8.52	7.52	7.62	8.35	8.62	10.35	5.88	5.18	8.47	8.19	4.98	5.17	5.06	4.71	4.72	2.84	2.84	2.75	2.76	-	
24 <i>B. aff. calcarata</i> 3744	8.14	8.99	9.23	8.34	7.35	7.43	8.16	8.41	10.09	5.68	5.00	8.19	7.91	4.80	4.97	4.86	4.53	4.53	2.65	2.65	2.57	2.57	0.18	-

2599 Table 5. Uncorrected p -distances between 16S partial sequences of *Boana cinerascens* specimens. See text for localities of the
 2600 samples. Values in percentage.

	Taxon/Sample	1	2	3	4	5	6	7	8	9
1	<i>B. cinerascens</i> 0416	-								
2	<i>B. cinerascens</i> 2247	0.00	-							
3	<i>B. cinerascens</i> 2371	0.00	0.00	-						
4	<i>B. cinerascens</i> TG393	0.72	0.72	0.72	-					
5	<i>B. cinerascens</i> TG405	0.72	0.72	0.72	0.00	-				
6	<i>B. cinerascens</i> 2245	10.24	10.24	10.24	10.60	10.60	-			
7	<i>B. cinerascens</i> 189BM	12.91	12.91	12.91	13.49	13.49	4.04	-		
8	<i>B. cinerascens</i> 2370	10.08	10.08	10.08	10.07	10.07	3.94	5.09	-	
9	<i>B. cinerascens</i> 5133	10.08	10.08	10.08	10.07	10.07	3.94	4.83	0.36	-

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2602

2603 Table 6. Uncorrected p -distances between 16S partial sequences of *Boana punctata* and *B. atlantica* specimens. See text for localities
 2604 of the samples. Values in percentage.

Taxon/Sample		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	<i>B. punctata</i> 4630	-																		
2	<i>B. punctata</i> 5132	1.83	-																	
3	<i>B. punctata</i> 5128	1.63	1.09	-																
4	<i>B. punctata</i> 5129	1.63	1.09	0.00	-															
5	<i>B. punctata</i> 5130	1.63	1.09	0.00	0.00	-														
6	<i>B. atlantica</i> 3670	4.39	4.58	4.20	4.20	4.20	-													
7	<i>B. atlantica</i> 3662	4.39	4.58	4.20	4.20	4.20	0.00	-												
8	<i>B. atlantica</i> 2111	4.21	4.40	4.03	4.03	4.03	0.00	0.00	-											
9	<i>B. atlantica</i> 3688	4.57	4.75	4.38	4.38	4.38	0.18	0.18	0.18	-										
10	<i>B. punctata</i> 1852	4.40	4.40	4.02	4.02	4.02	3.48	3.48	3.49	3.48	-									
11	<i>B. punctata</i> 2116	4.03	4.04	3.65	3.65	3.65	3.49	3.49	3.49	3.50	0.55	-								
12	<i>B. punctata</i> 5126	4.38	4.58	4.01	4.01	4.01	3.86	3.86	3.85	4.05	2.76	2.57	-							
13	<i>B. punctata</i> 5127	4.39	4.40	4.01	4.01	4.01	4.23	4.23	4.22	4.23	2.02	1.84	0.73	-						
14	<i>B. punctata</i> MNKA9133	3.01	3.42	2.64	2.64	2.64	2.48	2.48	2.30	2.67	3.40	3.02	3.41	3.78	-					
15	<i>B. punctata</i> 3686	3.81	4.57	4.00	4.00	4.00	3.65	3.66	3.48	4.01	4.03	3.67	4.03	4.40	1.50	-				
16	<i>B. punctata</i> 0041	3.45	4.20	3.64	3.64	3.64	3.29	3.29	3.12	3.65	3.66	3.30	3.67	4.03	1.13	0.36	-			
17	<i>B. punctata</i> 3690	3.63	4.38	3.82	3.82	3.82	3.11	3.11	2.94	3.47	3.84	3.48	3.85	4.21	1.13	0.55	0.18	-		
18	<i>B. punctata</i> 2663	3.45	4.20	3.64	3.64	3.64	3.29	3.29	3.12	3.65	3.66	3.30	3.67	4.03	1.13	0.36	0.00	0.18	-	
19	<i>B. punctata</i> 2685	3.45	4.20	3.64	3.64	3.64	3.29	3.29	3.12	3.65	3.66	3.30	3.67	4.03	1.13	0.36	0.00	0.18	0.00	-

2607 Table 7. Uncorrected *p*-distances between 16S partial sequences of *Boana geographica* / *semilineata* species complex specimens.
 2608 Values in percentage.

Taxon/Sample		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	<i>B. diabolica</i> R149	-																						
2	<i>B. diabolica</i> R157	0.38	-																					
3	<i>B. cf. geographica</i> 1 MPEG24822	5.56	5.95	-																				
4	<i>B. cf. geographica</i> 1 MTR36719	5.89	6.32	1.96	-																			
5	<i>B. geographica</i> MZUSP157060	4.55	4.76	4.51	4.57	-																		
6	<i>B. geographica</i> MZUSP157090	5.05	5.05	5.49	5.32	0.23	-																	
7	<i>B. geographica</i> MNKA9343	4.09	4.29	4.05	4.64	0.64	0.50	-																
8	<i>B. geographica</i> MNKA9347	3.89	4.09	3.86	4.42	0.43	0.24	0.18	-															
9	<i>Boana</i> sp. ML1269	7.11	7.50	6.12	8.07	6.61	7.93	5.53	5.34	-														
10	<i>B. aff. semilineata</i> 4 SMS153	8.73	8.96	6.48	7.47	6.28	6.50	6.14	5.88	3.59	-													
11	<i>B. aff. semilineata</i> 1 0815	5.98	6.37	5.19	6.55	5.37	6.53	4.62	4.43	3.64	4.53	-												
12	<i>B. aff. semilineata</i> 1 MPEG30285	5.77	6.16	4.79	6.31	5.14	6.22	4.65	4.46	3.44	4.27	0.38	-											
13	<i>B. aff. semilineata</i> 1 R140	5.77	6.16	4.79	6.31	5.14	6.22	4.65	4.46	3.44	4.27	0.38	0.00	-										
14	<i>B. aff. semilineata</i> 2 BM334	6.53	6.92	5.56	6.11	5.35	6.53	5.25	5.06	5.39	5.56	3.31	3.09	3.09	-									
15	<i>B. aff. semilineata</i> 2 MTR7584	7.47	7.86	5.93	6.55	6.60	8.00	6.40	6.21	6.14	6.30	4.06	3.84	3.84	1.34	-								
16	<i>B. aff. semilineata</i> 2 3747	7.12	7.51	5.93	7.00	6.00	7.28	5.71	5.53	5.82	6.31	3.83	3.85	3.85	1.54	0.97	-							
17	<i>B. aff. semilineata</i> 3 JOG737	8.46	8.69	5.76	6.75	6.75	6.50	5.83	5.57	4.80	4.81	3.81	3.28	3.28	4.84	5.58	5.59	-						
18	<i>B. aff. semilineata</i> 3 AF252	6.73	7.11	4.41	5.94	5.59	6.29	4.64	4.45	4.03	5.07	3.27	2.87	2.87	4.04	4.61	4.62	0.23	-					
19	<i>B. cf. geographica</i> TG243	6.75	7.14	4.40	5.94	5.60	6.30	4.41	4.23	3.83	5.07	3.10	2.87	2.87	4.05	4.62	4.38	0.24	0.00	-				
20	<i>B. aff. semilineata</i> 5 MTR36136	7.46	7.87	7.04	8.05	6.37	7.44	6.51	6.30	5.43	5.30	4.63	4.62	4.62	5.24	5.84	5.43	4.79	4.44	4.44	-			
21	<i>B. aff. semilineata</i> 5 MTR36149	7.46	7.87	7.04	8.05	6.37	7.44	6.51	6.30	5.43	5.30	4.63	4.62	4.62	5.24	5.84	5.43	4.79	4.44	4.44	0.00	-		
22	<i>B. semilineata</i> 0696	6.17	6.56	4.79	6.35	5.17	6.26	4.42	4.23	3.27	3.81	1.82	1.91	1.91	2.70	3.26	3.09	2.37	2.12	2.00	3.41	3.41	-	
23	<i>B. semilineata</i> ML0456	6.17	6.56	4.79	6.35	5.17	6.26	4.42	4.23	3.27	3.81	1.82	1.91	1.91	2.70	3.26	3.09	2.37	2.12	2.00	3.41	3.41	0.00	-

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FIGURE LABELS.

Fig. 1. Partial view of one of the most parsimonious trees showing the relationships within the outgroup taxon of the genus *Boana* (highlighted in red on the inset). Numbers on nodes are Parsimony Jackknife absolute frequencies. Jackknife values below 50% are not shown. Asterisks indicate nodes with 100% Jackknife support. The tree continues on Figs. 2–4. Scale bar represent the number of transformations.

Fig. 2. Partial view of one of the most parsimonious trees showing the relationships of the *Boana benitezi*, *B. punctata* and *B. punctata* groups (highlighted in red on the inset). Numbers on nodes are Parsimony Jackknife absolute frequencies. Jackknife values below 50% are not shown. Asterisks indicate nodes with 100% Jackknife support. Black dots indicate nodes which collapse on the strict consensus. The tree continues on Figs. 3–4. Scale bar represent the number of transformations.

Fig. 3. Partial view of one of the most parsimonious trees showing the relationships of the *Boana albopunctata*, *B. pellucens* and *B. faber* groups (highlighted in red on the inset). Numbers on nodes are Parsimony Jackknife absolute frequencies. Jackknife values below 50% are not shown. Asterisks indicate nodes with 100% Jackknife support. Black dots indicate nodes which collapse on the strict consensus. The tree continues on Fig. 4. Scale bar represent the number of transformations.

Fig. 4. Partial view of one of the most parsimonious trees showing the relationships of the *Boana pulchella* group (highlighted in red on the inset). Numbers on nodes are Parsimony Jackknife absolute frequencies. Jackknife values below 50% are not shown.

2635 Asterisks indicate nodes with 100% Jackknife support. The tree continues on Fig. 4.

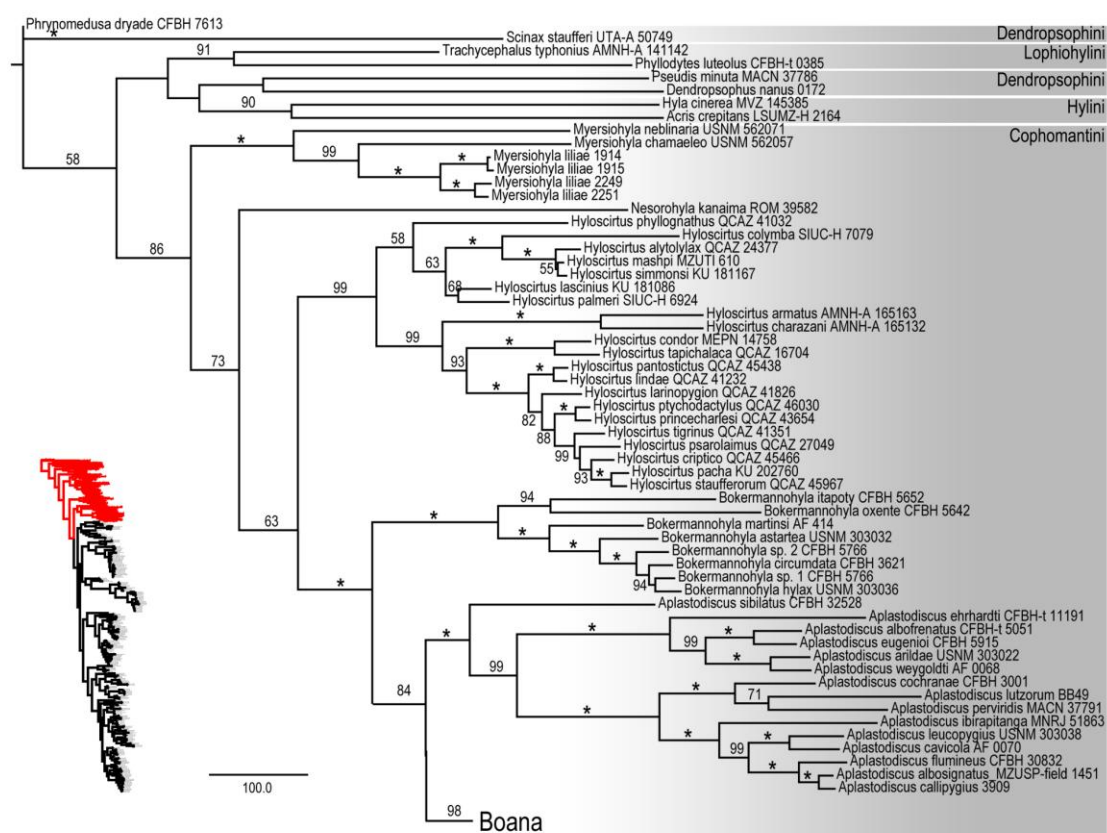
2636 Scale bar represent the number of transformations.

2637

2638 **Fig. 5.** Strict consensus of the 235 equally optimal trees recovered under static

2639 homology parsimony criterium with 46040 steps.

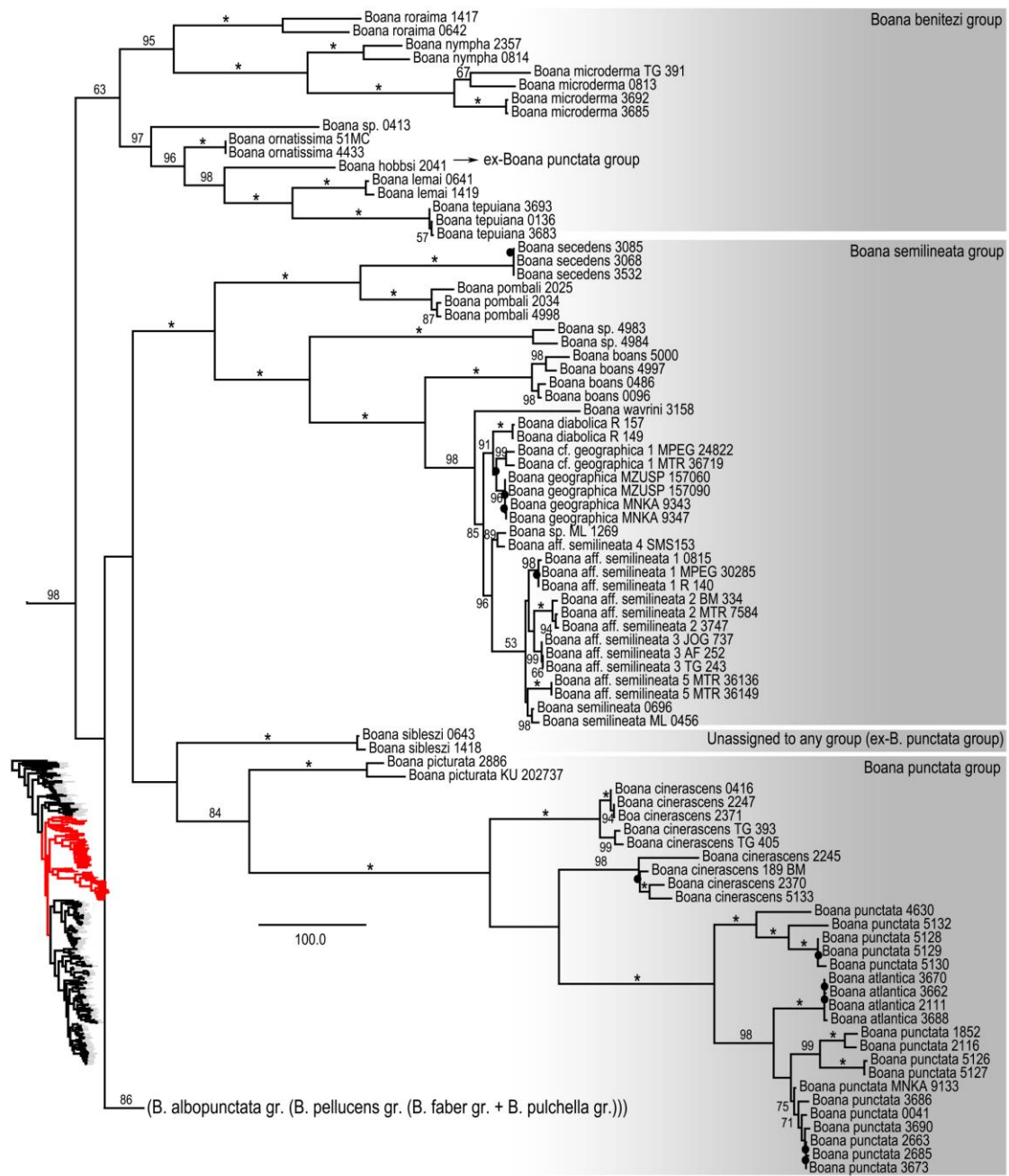
2640

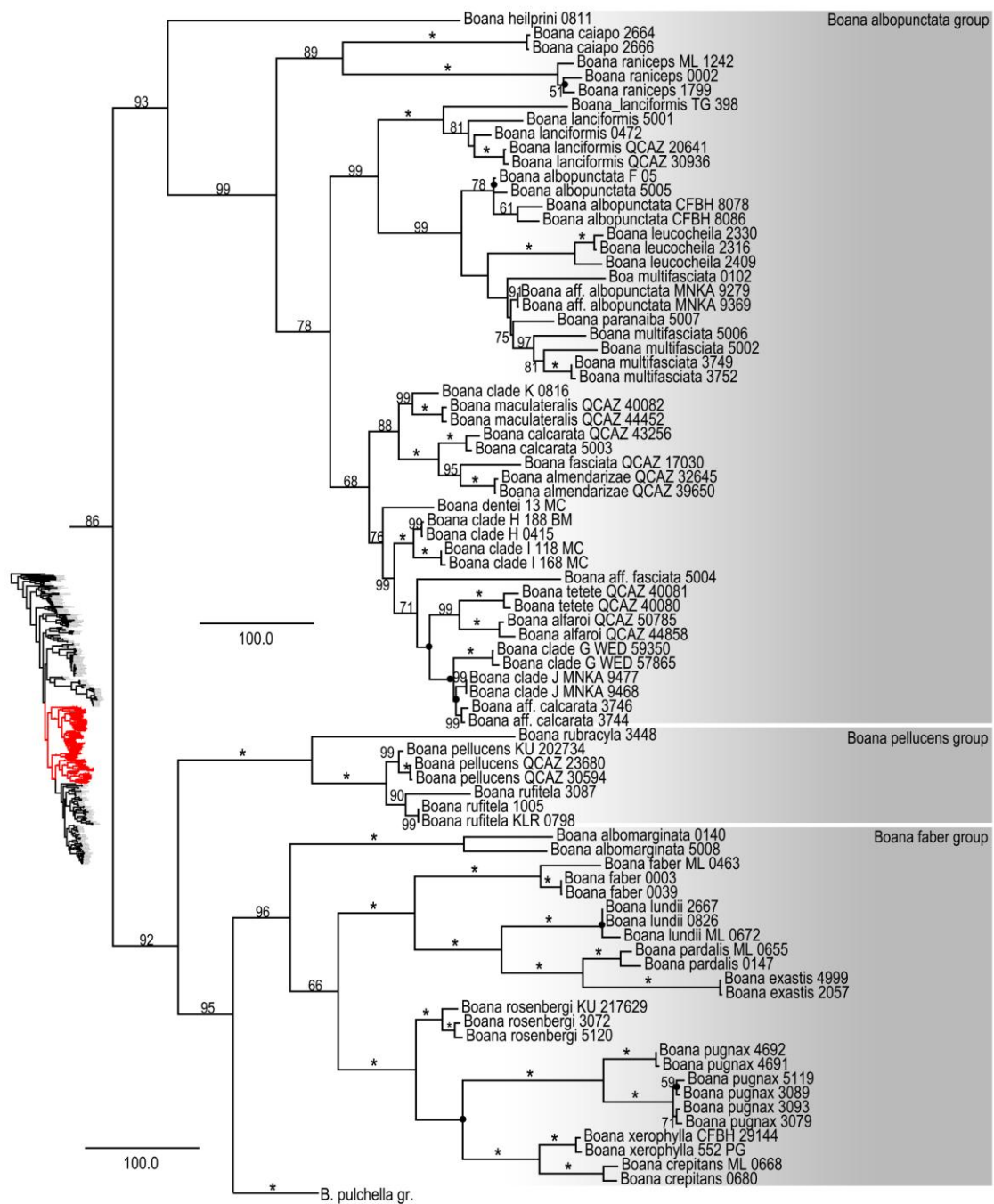
2641 **Figure 1.**

2642

2643

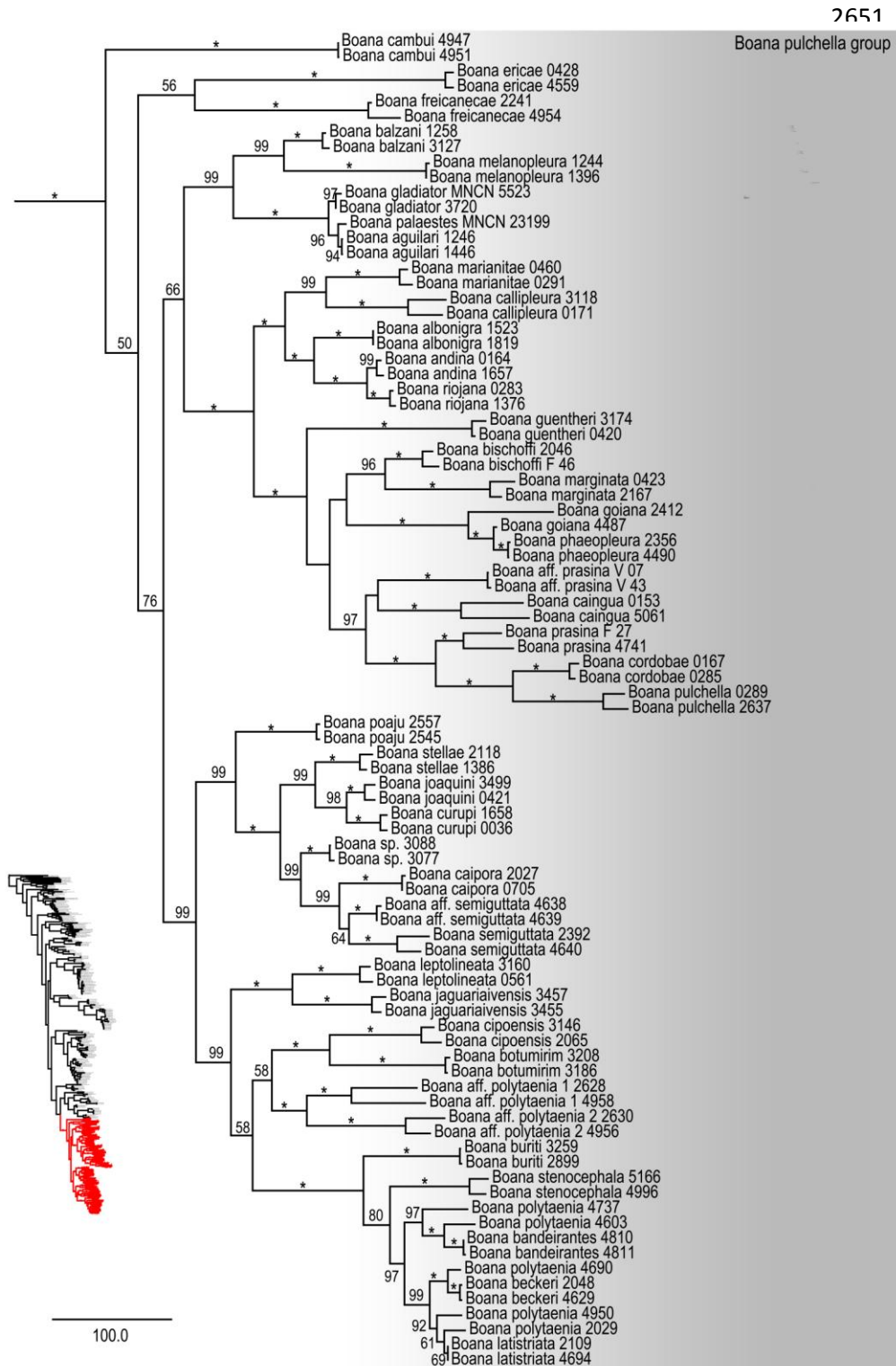
2644

2645 **Figure 2.**

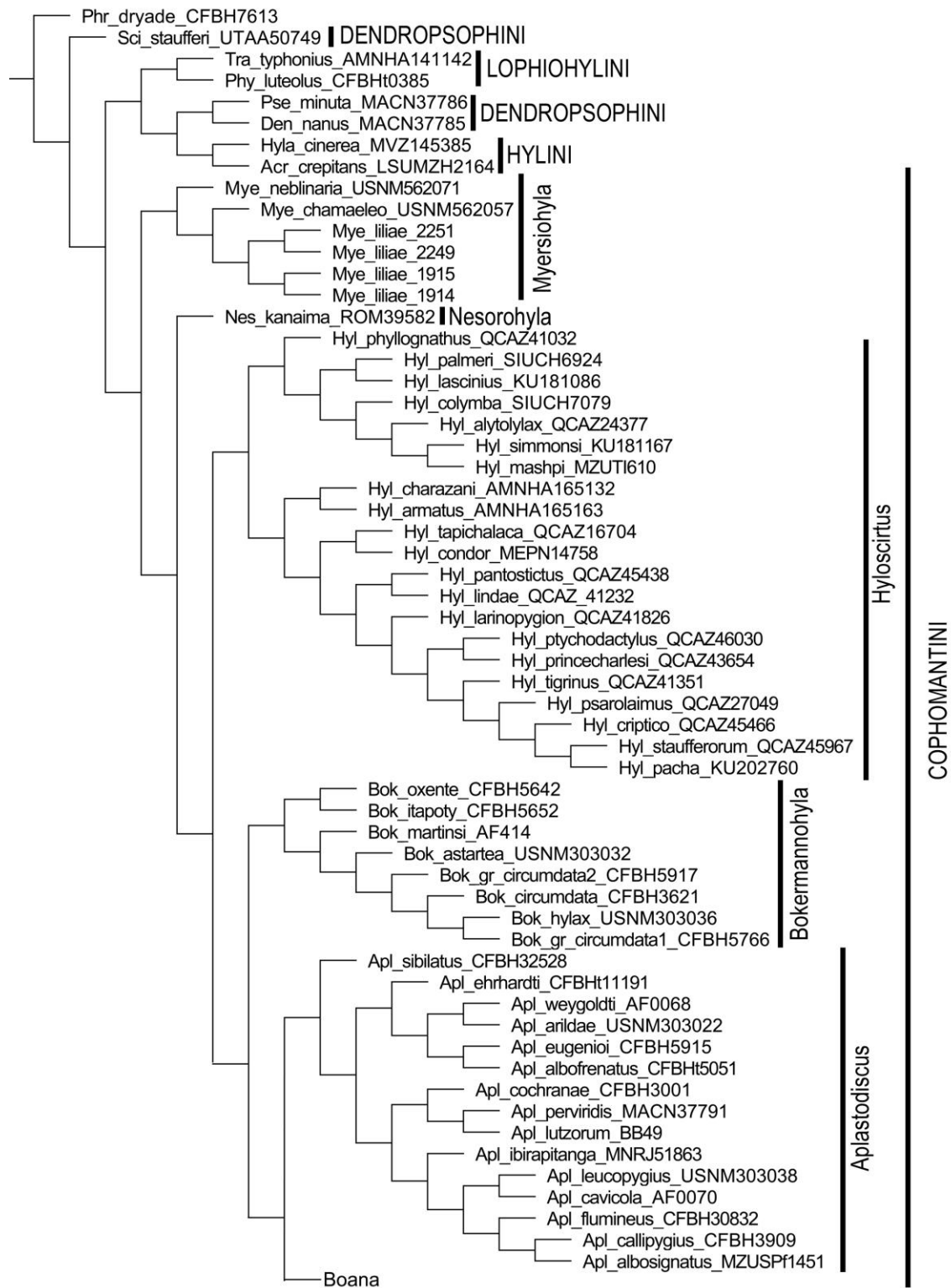
2647 **Figure 3.**

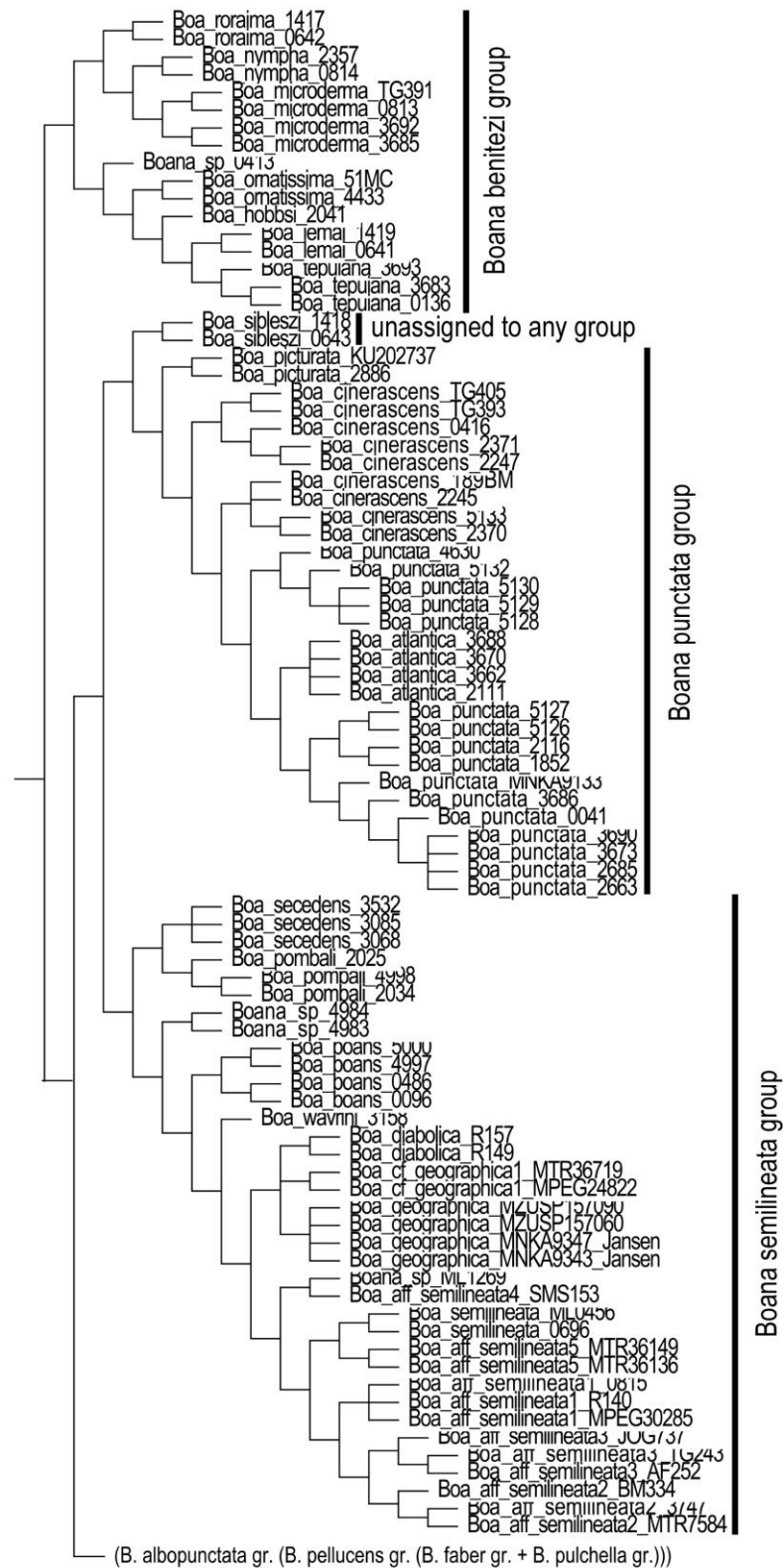
2648

2649

2650 **Figure 4.**

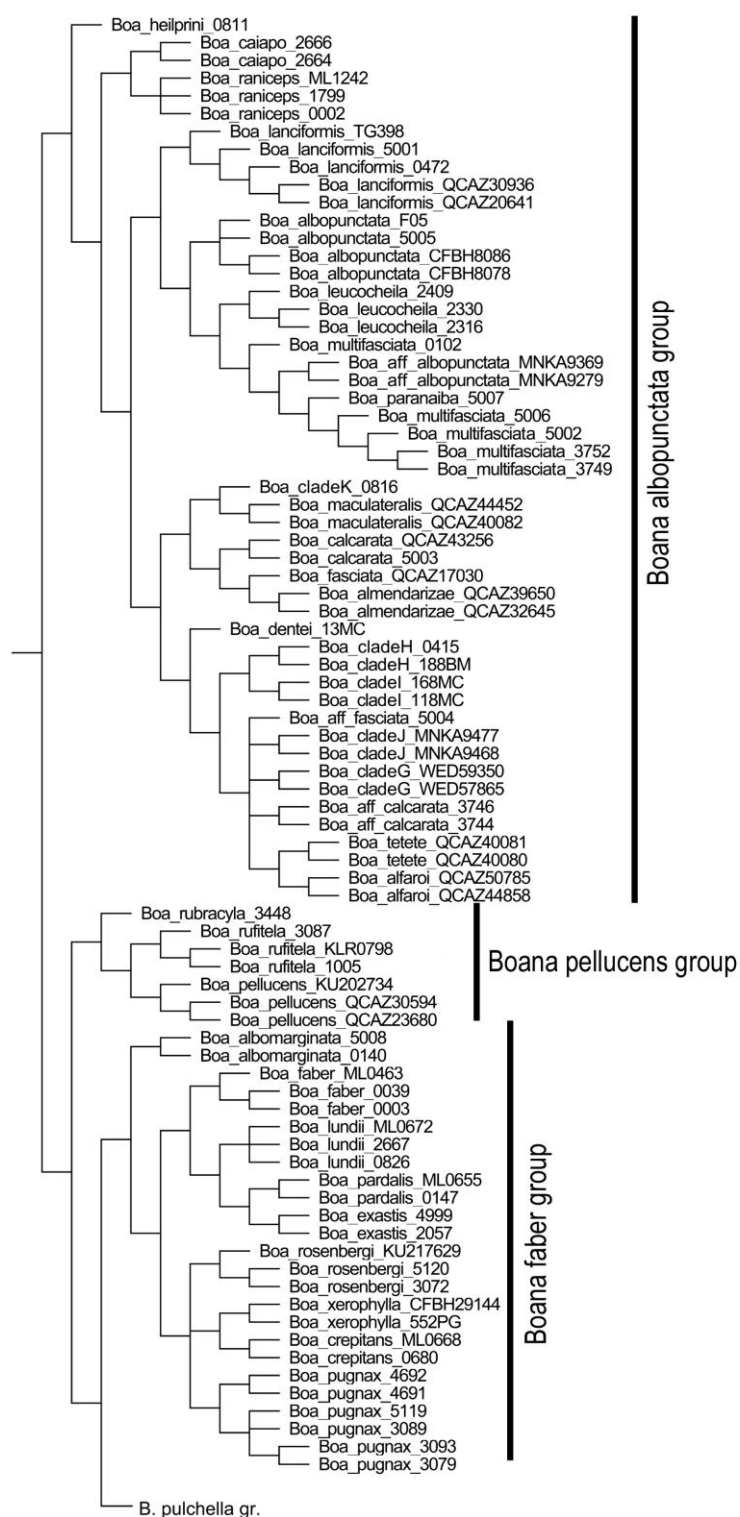
2652 **Figure 5.**



2655 **Figure 5. Continued.**

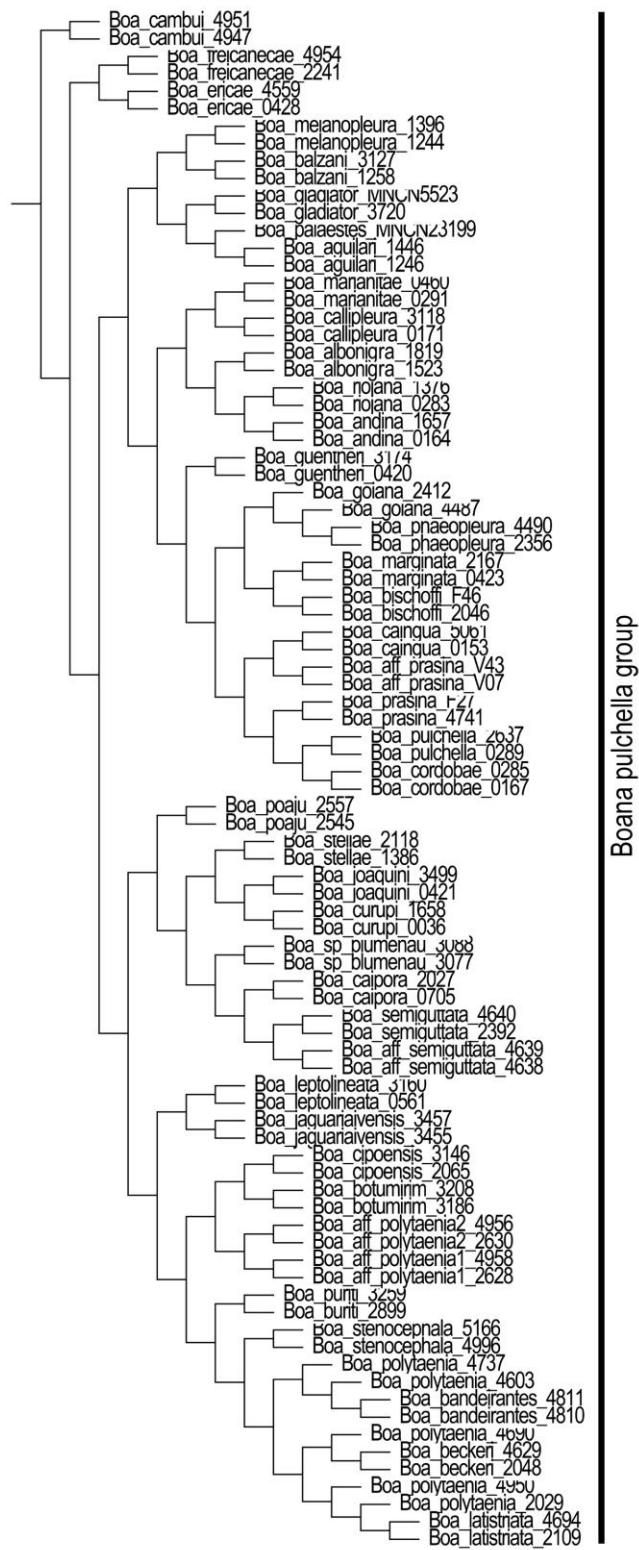
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2658 **Figure 5. Continued.**

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2661 **Figure 5. Continued.**

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2664 **Prepollex Diversity and Evolution in Cophomantini (Anura: Hylidae: Hylinae)⁺**

2665 *Manuscrito preparado para ser submetido ao Journal of Morphology.

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2676 Short title: Prepollex in Cophomantini

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2686 Christiano de Anchietta Garcia, Maurício Rivera-Correa, Edward L. Stanley,

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ABSTRACT Species of the tribe Cophomantini are known to have an enlarged prepollex. Many of those species are also referred to as presenting a prepollex modified into a protruding spine. We surveyed the osteology and myology of the prepollex and associated elements of 95 species of Cophomantini. Two distinct morphologies of the Distal Prepollex were found: a sickle-shaped and a spine-shaped prepollex. We established homology hypotheses for the informative variation in these character systems into 17 discrete characters. We optimized them on the most inclusive tree known for the tribe. The sickle-shaped and the spine-shaped prepollex appeared both more than once in Cophomantini evolution. The sickle-shaped prepollex of the *Hyloscirtus armatus* group have a medial dorso-ventral expansion which is unique among Cophomantini. The *m. abductor indicis longus* inserts on the Metacarpal II in the species which have a sickle-shaped prepollex, and have a second insertion on the Distal Prepollex on the species which have a spine-shaped prepollex. We discuss evolution, function, behavior, and sexual dimorphism related to the prepollical elements.

KEY WORDS: Comparative Morphology, Hylidae, Myology, Osteology, Prepollex,.

INTRODUCTION

The prepollex of anurans is a mesopodial structure positioned proximally with respect to the first finger, in the preaxial region, being the last element to form during hand development (almost during the metamorphosis; Fabrezi and Alberch, 1996). The Radius originates (by segmentation) the Radiale, the Element Y, and the prepollex (in this same sequence of development; Shubin and Alberch, 1986). In anurans, the

prepollex is usually composed by two elements (one proximal and the other distal), but also can be composed by three or more elements, or even be absent (Fabrezi, 2001).

Fabrezi (2001) surveyed the diversity in shape and number of elements of the prepollex in the different families of anurans. She also discussed the hypothesis of its homology with the first finger, concluding that these two structures are not homologous, and briefly discussed its evolution, involving the specialization in both morphology and function—like interaction with skin structures.

One specialization of the prepollex is a distal element modified as a protruding spine. This prepollical spine is used by males of many species during intraspecific fights for limited resources, i.e., vocalization or oviposition sites (e.g., Shine, 1979; Kluge, 1981; Martins and Haddad, 1988) or as a defensive structure against predators (Toledo et al., 2011). This modification into a protruding spine is present in some phylogenetically distant groups of anurans: ranids (*Babina subaspera* and *B. holsti*; Boulenger, 1892; Barbour, 1908; Van Denburgh, 1912); centrolenids (e.g., *Centrolene gemmatum*, *Cochranella duideana*, *Teratohyla spinosa*, *Vitreorana gorzulae*; Taylor, 1949; Flores, 1985; Señaris and Ayarzagüena, 2005); mantellids (*Boophis albilabris* group; Vences et al., 2010); and it is more common in hylids. Within this family, it is present in the tribe Hylini (the *Plectrohyla guatemalensis* group and in *Ecnomiohyla miliaria*; Duellman, 1961, 1968, 1970; Duellman and Campbell, 1992), and in several species of Cophomantini (all species of *Bokermannohyla*, most species of *Boana*, and some species of *Hyloscirtus* (Kizirian et al., 2003; Faivovich et al., 2005; Almendáriz et al., 2014; Rivera-Correa et al., 2016), a clade that has been characterized for having an enlarged prepollex (Faivovich et al., 2005).

The fact that 123 species in several genera of Cophomantini have a prepollical spine, that some variation had already been described (e.g., Bokermann, 1964; Garcia and Haddad, 2008), and that there is a reasonably stable hypothesis of phylogenetic relationships for this tribe makes this group an appropriate subject for the study of prepollical diversity and evolution. For this, we survey the diversity and taxonomic distribution of prepollical elements and associated metacarpal and carpal elements (Element Y, Distal Carpal II, and Metacarpal II), provide a description of the musculature related to those elements and its taxonomic variation, establish homology hypotheses for the informative variation in these character systems, and optimize it in a recent phylogenetic hypothesis. Finally we also discuss evolutionary aspects and the anatomy of the Prepollex and related structures.

MATERIALS 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 II, and Metacarpal II) of species pertaining to all taxonomic groups of the tribe Cophomantini. Studied specimens are listed in the Appendix. The abbreviations of collections follow Sabaj (2016): Célio F. B. Haddad (amphibians) Collection, Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista "Júlio de Mesquita Filho", Rio Claro, Brazil (CFBH); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina (MACN); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (UFMG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museu Paraense "Emílio

2758 Goeldi", Zoologia, Belém, BRAZIL (MPEG); Museo de Zoología, Pontificia
 2759 Universidad Católica del Ecuador, Quito, Ecuador (QCAZ); Museu de História Natural
 2760 da Universidade Federal de Alagoas, Maceió, Brazil (MUFAL); Museu de Ciências
 2761 Naturais, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil
 2762 (MCNAM); National Museum of Natural History, Smithsonian Institution, Department
 2763 of Vertebrate Zoology, Washington D.C., USA (USNM); Museo Nacional de Ciencias
 2764 Naturales, Madrid, Spain (MNCN); Instituto de Ciencias Naturales, Museo de Historia
 2765 Natural, Universidad Nacional de Colombia, Bogotá, Colombia (ICN); Museo de
 2766 Herpetología de la Universidad de Antioquia, Medellín, Colombia (MHUA). Other
 2767 abbreviations are from material that waits to be housed in a formal institution. They
 2768 correspond to field series numbers from the respective collectors: Andrés Brunneti
 2769 (AB); Miguel Trefault Rodrigues (MTR); Diego Baldo field (DB); Martin Pereyra
 2770 (MP); Boris Blotto (BB); Paulo C. A. Garcia (PCG); Fernanda Centeno (BA); José
 2771 Vicente Rueda-Almonacid (VR); Mauricio Rivera-Correa (MRC); Marco Rada (MAR);
 2772 María Cristina Ardila-Robayo (MC); Juan Manuel Rengifo (JMR); Eliana Muñoz
 2773 (EMM); Pedro Ruiz-Carranza (PR); Gustavo González (GGD). Most specimens are
 2774 cleared and stained males, prepared following the method of Taylor and Van Dike
 2775 (1985). Exceptions are *Bokermannohyla juiju*, *Bok. langei*, *Bok. martinsi*, *Boana*
 2776 *nympha*, *Boa. pellucens*, and *Boa. picturata*, for which we used X-ray images obtained
 2777 with a Faxitron X-ray equipment, and *Myersiohyla neblinaria* and *Hyloscirtus armatus*,
 2778 for which we used µct scanning microtomography images. The holotype of *Myersiohyla*
 2779 *neblinaria* was imaged by using a GE phoenix v|tome|x s equipment coupled to a micro-
 2780 focus X-ray tube of 240 kV/300 W at the Microscopy and Imaging Facility Lab of
 2781 American Museum of Natural History, New York, USA. Resulting images were

processed by GE phoenix datos|x v2.3 software. Finally, the production of 3-D renderings was done with Mimics v10.01 (Materialise, Leuven, Belgium). *Hyloscirtus armatus* was tomographed using a SkyScan 1176 X-ray Microtomograph (Antwerp, Belgium) equipment from the Departamento de Genética e Biologia Evolutiva, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil. Images were processed by the SkyScan NRecon software. Finally, the production of 3-D renderings was done with free-version of SkyScan, CTvox software (SkyScan, Kontich, Belgium).

The cleared and stained material was studied with a Nikon SMZ800 stereomicroscope coupled with a digital camera Micrometrics 391CU 3.2 M CCD. Measures and images were obtained with a Micrometrics® SE Premium 4 software.

The length of Metacarpal II is the distance between margins of its epiphyses, and the length of Distal Prepollex is the distance from the tip of the distal element to the articulation with the Proximal Prepollex. Terminology of forelimb bones follows Shubin and Alberch (1986) and Fabrezi and Alberch (1996); terminology of muscles follows Gaupp (1896), as modified by Burton (1996, 1998b).

Homology hypotheses were optimized in the most inclusive phylogenetic hypothesis available for Cophomantini (Pinheiro et al., in prep.) using Mesquite v3.04 software (Maddison and Maddison, 2017). From the taxa examined in the present study, we optimized just those that are included in the study of Pinheiro et al. (in prep.).

RESULTS

Osteology

We studied the carpal osteology of 85 Cophomantini formally recognized species and 10 undescribed taxa of the tribe, totalizing 95 species. The carpal morphology of all

studied species of Cophomantini corresponds to the Morphology C of Fabrezi (1992). It is formed by six carpal elements: one Distal Carpal V-IV-III, one Distal Carpal II, one Ulnare, one Radiale, one Element Y and the prepollex (which have two elements, Proximal Prepollex and Distal Prepollex). The Distal Carpal V-IV-III articulates with metacarpalia V, IV, and III distally; with the Distal Carpal II and Element Y pre-axially; and with the Ulnare and Radiale, proximally. Distal Carpal II articulates with the Metacarpal III distally; with Metacarpall II and Proximal Prepollex pre-axially; Distal Carpal V-IV-III post-axially; and with the Element Y. The Ulnare articulates with the Distal Carpal V-IV-III distally, and with the Ulna proximally. The Radiale articulates with the Distal Carpal V-IV-III distally, and with the Element Y distally and pre-axially, and with the Radius proximally. Element Y articulates with the Distal Carpal II distally; with the Proximal Prepollex pre-axially; with the Distal Carpal V-IV-III post-axially; and with the Radiale proximally and post-axially. The Proximal Prepollex articulates the Element Y proximally, with the Metacarpal II distally and post-axially, and with the Distal Prepollex distally. Distal Prepollex articulates with the Proximal Prepollex proximally, and with the Metacarpal II laterally.

Proximal Prepollex.—A cube-shaped element in all studied taxa.

Element Y.—This element does not present significant variation among the studied taxa.

Distal Prepollex.—In Cophomantini the Distal Prepollex may show two distinct morphologies: sickle-shaped and spine-shaped.

Sickle-shaped prepollex.—It is an enlarged Distal Prepollex, longer than wide, with its overall shape similar to a sickle, or blade. It is dorso-ventrally flattened, and its length in relation to Metacarpal II length varies between 0.53-0.97 times. Its medial

margin is convex, cartilaginous in many cases, and without a medial crest. The lateral margin is straight or concave. Its tip generally points to the Metacarpal II, and may include one or two small additional, small elements, mineralized or entirely cartilaginous.

The sickle-shaped prepollex is present in studied species of *Myersiohyla*, *Hyloscirtus* (except *H. tapichalaca*), *Aplastodiscus*, and in *Boana geographica* and *Boa semilineata* (both of the *Boa semilineata* group). In most *Aplastodiscus* and *Hyloscirtus* (except in *H. armatus* group and in *Aplastodiscus callipygius*), it has a cartilaginous medial margin (Fig. 1). In *Boana*, and *A. callipygius*, instead, the medial margin is entirely ossified (Fig. 2). In *Myersiohyla* there is a perforation in Distal Prepollex that we believe it to be filled with cartilage. However, micro-ct as employed in this study does not detect tissues with lower densities than bones. In *H. armatus* and *H. charazani*, the Distal Prepollex has a medial ossified surface expanded dorsally and ventrally. This supports the spine-shaped nuptial pad in males of these species (Fig. 3).

The lateral margin of the Distal Prepollex is straight in *Myersiohyla*, *Hyloscirtus* aff. *alytolylax*, *H. callipeza*, *H. colymba*, *H. denticulentus*, *H. lynchi*, *H. palmeri*, *H. aff. phyllognathus*, *H. piceigularis*, *H. aff. piceigularis*, *H. simmonsii*, *H. aff. simmonsii* sp. 1, and *H. aff. simmonsii* sp. 2 (*H. bogotensis* group), the *H. larinopygion* group, and *Aplastodiscus* (Figs. 1B–D and 2). The lateral margin is concave in *H. alytolylax*, *H. bogotensis*, *H. aff. palmeri*, *H. platydactylus*, *Aplastodiscus callipygius*, *Boana geographica*, and *Boa semilineata* (Fig. 1A, E–H). In *H. torrenticola* ($n = 2$), one specimen has a straight lateral margin and the other one have it concave.

A small, distal ossified distal element occurs in *Myersiohyla neblinaria* and in two specimens of *Boana semilineata* (Figs. 1G and 2). A small, distal unossified distal

element occurs in *Hyloscirtus alytolylax*, *H. bogotensis*, *H. colymba*, *H. palmeri*, *H. piceigularis*, and *H. aff. simmonsii* sp. 1 (*H. bogotensis* group); and *H. staufferorum* (*H. larinopygion* group; Fig. 1A). In *H. callipeza*, *H. lynchi*, *H. platydactylus*, and one of the specimens of *H. torrenticola* (*H. bogotensis* group) there are two small distal elements, pointing to the Metacarpal II (Fig. 1B and C)—in *H. platydactylus* the proximal additional element is partially mineralized.

In *Boana semilineata*, there are specimens with or without a small additional element distally, which might suggest that these structures fuse with the prepollex ontogenetically or vary intraspecifically (Fig. 1G and H).

The length of the sickle-shaped Distal Prepollex (including the distal elements) in relation to the Metacarpal II varies is 0.79 times in *Myersiohyla neblinaria*; 0.53–0.84 in *H. bogotensis* group; 0.7 in the *H. armatus* group; 0.59–0.85 in *H. larinopygion* group; 0.73–0.97 in *Aplastodiscus albofrenatus* group; 0.58–0.75 in *A. perviridis* group; 0.68 in *A. sibilatus*; 0.75 in *A. albosignatus*; and 0.63–0.72 in the *Boana semilineata* group.

Spine-shaped prepollex.—It is an enlarged Distal Prepollex that is wider proximally, and distally it ends in an acute tip, similar to a spine. This spine may vary in being straight or curved medially. The length of the spine-shaped Distal Prepollex in relation to Metacarpal II length varies between 0.72–1.48 times. Its position varies in being medial or ventral to Metacarpal II. Generally the spine-shaped prepollex has a medial crest dorsally. In a few species there is a smaller second spine, medially positioned, which seems to be a distal extension of this medial crest. In many species, the Distal Prepollex may also have a post-articular process proximally.

The spine-shaped prepollex occurs in *Hyloscirtus tapichalaca* (*H. larinopygion* group), all species of *Bokermannohyla*, and most species of *Boana* (except *Boa. semilineata* and *Boa. geographica*; of the *Boa. semilineata* group; Fig. 4). In most species with a spine-shaped prepollex, the spine is curved medially; however, in *Boana nympa* and *Boa. microderma* (*Boa. benitezi* group), the spine is almost straight (Fig. 4E). The spine is medial to Metacarpal II in most species. However, in members of the *Boana pulchella* group, the spine passes ventrally to Metacarpal II (Fig. 4K and L). In dorsal view, the inner margin of the Distal Prepollex contacts the medial margin of Metacarpal II in *Bokermannohyla clepsydra*, *Boana fasciata*, and *Boa. crepitans* (Fig. 4D and I). The medial crest occurs in most species with a spine-shaped prepollex (Fig. 4I), except in *Hyloscirtus tapichalaca*, *Bokermannohyla oxente*, and *Boana microderma*, in which the crest is absent (Fig. 4E). In *Bokermannohyla langei* and *Bok. martinsi* (*Bok. martinsi* group) and in *Boana ericae* there is a robust projection, which forms a second spine, distally to the medial crest (Fig. 4C, L).

In many groups there is a post-articular process in the Distal Prepollex that varies in size. We divided this process into three size classes: (i) Post-articular process absent, or a rudimentary tip. It occurs in *Hyloscirtus tapichalaca*, *Bokermannohyla*, and the *Boana albopunctata*, *B. benitezi*, and *B. punctata* groups, except those listed below (Fig. 4F). (ii) Post-articular process present, short; in dorsal view its proximal margin does not surpass the level of the articulation between Element Y, Proximal Prepollex, and Distal Carpal II. It occurs in *Bokermannohyla clepsydra* (*Bok. claresignata* group), *Boana boans*, *Boa. pombali*, and *Boa. wavrini* (*Boa. semilineata* group), *Boa. heilprini* (*Boa. albopunctata* group), *Boa. faber*, and *Boa. pellucens* (Fig. 4D). (iii) Post-articular process large; in dorsal view its proximal margin reaches or surpasses the level of the

2901 arm of Element Y that articulates with the Radiale. It occurs in *Bokermannohyla langei*,
 2902 *Bok. martinsi*, and in the *Boana pulchella* group (Fig. 4K).

2903 The length of the spine-shaped Distal Prepollex in relation to the length of
 2904 Metacarpal II is 0.73–1.16 times in *Boana albopunctata* group; 0.78–0.89 in the *Boa*.
 2905 *benitezi* group; 0.72–0.97 in the *Boa. faber* group; 0.99 in the *Boa. pellucens*; 0.8–1.22
 2906 in the *Boa. pulchella* group; 0.72–0.8 in the *Boa. punctata* group; 0.75–0.77 in the *Boa*.
 2907 *semilineata* group; 1.04–1.25 in the *Bokermannohyla circumdata* group; 0.84 in *Bok*.
 2908 *clepsydra*; 1.05–1.48 in the *Bok. martinsi* group; 0.86–1.20 in the *Bok. pseudopseudis*
 2909 group; 1.13 in *Hyloscirtus tapichalaca*.

2910 We were able to study females only of *Bokermannohyla alvarengai* and *Bok. hylax*.
 2911 The Distal Prepollex is entirely cartilaginous in *Bok. hylax* (Fig. 5). In *Bokermannohyla*
 2912 *alvarengai* it has its proximal portion and its distal tip mineralized, being the mid
 2913 portion cartilaginous.

2914 **Distal Carpal II.**—In dorsal view, the distal and proximal margins varies from
 2915 rounded to truncate. The post-axial margin, which articulates with Distal Carpal V-IV-
 2916 III, is concave. The pre-axial margin is straight or convex (Figs. 1E–H; 2–5). In some
 2917 species of *Hyloscirtus*, however, the pre-axial margin is concave: *H. alytolylax*, *H. aff.*
 2918 *alytolylax*, *H. bogotensis*, *H. callipeza*, *H. colymba*, *H. palmeri*, *H. aff. palmeri*, *H.*
 2919 *piceigularis*, *H. aff. piceigularis*, *H. platydactylus*, *H. simmonsii*, *H. aff. simmonsii* sp. 1,
 2920 *H. aff. simmonsii* sp. 2, *H. torrenticola* (*H. bogotensis* group); *H. antioquia*, *H.*
 2921 *caucanus*, *H. princecharlesi*, and *H. tapichalaca* (*H. larinopygion* group)—Fig. 1A–D.
 2922 Intraspecific variation was found in *H. aff. phyllognathus* (*H. bogotensis* group) and *H.*
 2923 *sarampiona* (*H. larinopygion* group).

Metacarpal II.—The Metacarpal II articulates with the prepollex through the medial surface of its proximal epiphysis. In all studied species of *Boana* (except *Boa. heilprini*, *Boa. microderma*, and *Boa. pellucens*—*Boa. albopunctata*, *Boa. benitezi*, and *Boa. pellucens* groups, respectively) and also in *Hyloscirtus larinopygion*, *H. lindae*, *H. princecharlesi* (*H. larinopygion* group), *Bokermannohyla oxente* (*Bok. pseudopseudis* group), *Bok. clepsydra* (*Bok. claresignata* group), and *Bok. lucianae* (*Bok. circumdata* group), there is a medial process which articulates with the prepollex. In *Myersiohyla*, the remaining species of *Hyloscirtus*, *Bokermannohyla*, *Aplastodiscus*, and *Boana*, the articulation is not enlarged (Figs 1–4). The distal epiphysis of the Metacarpal II bears a medial sesamoid in *Hyloscirtus armatus* and *H. charazani* (*H. armatus* group). This sesamoid supports the spine shaped nuptial pad in males of these species (Fig. 3).

Musculature

The musculature associated to the prepollex and related carpal elements, was studied in 25 species of Cophomantini.

Dorsal musculature.—The *m. abductor indicis longus* (ABL) arises through the longitudinal axis of the Ulna, and the point and nature of its insertion is variable. In the studied species of *Hyloscirtus* and *Aplastodiscus*, this muscle possesses a single insertion on Metacarpal II by a tendon. In *Bokermannohyla* and *Boana*, it inserts on the Metacarpal II, by a tendon, and in the Distal Prepollex, by a flat aponeurosis. The only exception is *Boana semilineata*, which has two insertions on the Metacarpal II: one distally to the other (Fig. 6).

The *m. extensor indicis brevis superficialis* (EBS) and *m. extensor indicis brevis medius* (EBM) arise from the Radiale. Their origins are separated by one tendon of the

2948 *m. extensor carpi radialis* (ECR) which inserts on the Element Y (this tendon passes
 2949 dorsally to the Radiale between EBS and EBM origins, and curves ventrally to insert in
 2950 the Element Y). The ECR has another insertion, through an aponeurosis, on the Ulna,
 2951 Ulnare and Radiale. The EBS has two insertions, one fleshy on Metacarpal II and
 2952 another by a tendon on Proximal Phalanx. The EBM has a fleshy insertion over the
 2953 Metacarpal II, contiguous to the insertion of the EBS.

2954 The *m. extensor indicis brevis profundi* (EBP) is formed by two slips originated
 2955 from the Metacarpal II, one latero-dorsal and one medio-dorsal. The first one arises on
 2956 the latero-dorsal portion of the proximal epiphysis of the Metacarpal II and inserts on
 2957 the basis of the terminal phalanx through a thin tendon that passes laterally to Finger II.
 2958 The second one arises just medially to this first muscle, it crosses the dorsum of
 2959 Metacarpal II obliquely and inserts on the base of the terminal phalanx, through a thin
 2960 tendon that passes medially to Finger II. Additionally the EBP has two supplementary
 2961 slips. The first, which we called *m. extensor brevis profundi extra metacarpus*
 2962 (EBPem), arises on the medial portion of the proximal epiphysis of the Metacarpal II,
 2963 and inserts by a common tendon with the dorsomedial slip of the EBP. This
 2964 supplementary slip is present in all the species of Cophomantini studied. The second
 2965 supplementary slip, which we called *m. extensor brevis profundi extra prepollex*
 2966 (EBPepp), was found only in the studied species of *Bokermannohyla* and *Boana* (except
 2967 *Boa. semilineata*). It arises from the Distal Prepollex and inserts by a common tendon
 2968 with both the EBPem and medio-dorsal slip of EBP (Fig. 7).

2969 The *m. abductor indicis brevis dorsalis* (ABD) arises from the Element Y and
 2970 inserts on the dorsal surface of the Distal Prepollex. In *Bokermannohyla*, *Boana*

tepuiana, and *Boa. microderma*, the ABD has a second slim, fleshy insertion on the proximal and medial region of the Metacarpal II (Fig. 8).

No studied specimen has the *mm. extensores breves distales* on finger II.

Palmar musculature.—The ventral muscles associated to the second finger and the prepollex show minimal variation, and are arranged according to the following description.

The *m. adductor pollicis* (ADP) arises medially on the ventral handle of the Distal Carpal V-IV-III and inserts on the ventral surface of the Distal Prepollex. The *m. flexor indicis superficialis proprius* (TS), *m. lumbricalis brevis indicis* (LBB), *m. flexor teres indicis* (FT), and *m. opponens indicis* (OPP), also arise on the Distal Carpal V-IV-III medially. The TS inserts through a broad flat tendon on the terminal phalanx; the LBB inserts on the basis of the Proximal Phalanx, medially to TS; the FT inserts on the basis of the Proximal Phalanx, laterally to TS; and the OPP, which is deeper than the other three muscles, inserts penniform on the Metacarpal II (see fig. 1 of Burton, 1996).

The *m. abductor pollicis* (ABPO) has double origin: one from the tip of Ulna and the other from the Ulnare. It inserts on the post-axial surfaces of prepollical elements. In the species which present a post-articular process on the Distal Prepollex, the insertion of the ABPO on this process is enhanced by an aponeurosis.

Homology hypotheses

On the basis of the informative variation described above, we defined the following characters related to the Distal Prepollex and Finger II. For the taxonomic distribution of each character state, see the Supplementary Material I.

1) Distal Prepollex. (0) Sickle-shaped. (1) Spine-shaped.

- 2995 2) Medial dorso-ventral expansion of the Distal Prepollex. (0) Absent. (1) Present.
- 2996 3) Medial crest on the Distal Prepollex. (0) Absent. (1) Present.
- 2997 4) Medial margin of Distal Prepollex. (0) Ossified (1) Cartilaginous.
- 2998 5) Number of additional elements distally on the sickle-shaped Distal Prepollex.
- 2999 (0) Zero elements. (1) One distal element. (2) Two distal elements.
- 3000 6) Lateral margin of the sickle-shaped Distal Prepollex. (0) Straight. (1) Concave.
- 3001 7) Post-articular process of the Distal Prepollex. (0) Post-articular process absent,
- 3002 or a rudimentary tip. (1) Post-articular process present, short; in dorsal view its
- 3003 proximal margin does not surpass the level of the articulation between Element
- 3004 Y, Proximal Prepollex, and Distal Carpal II. (2) Post-articular process present,
- 3005 large; in dorsal view its proximal margin reaches or surpass the level of the arm
- 3006 of Element Y that articulates with the Radiale.
- 3007 8) Curvature of the spine-shaped Distal Prepollex. (0) Spine curved medially. (1)
- 3008 Spine straight.
- 3009 9) Position of the spine-shaped Distal Prepollex in relation to the Metacarpal II.
- 3010 (0) Distal Prepollex medial to the Metacarpal II. (1) Distal Prepollex ventral to
- 3011 Metacarpal II.
- 3012 10) Distal projection forming a second spine. (0) Absent. (1) Present.
- 3013 11) Articulation of the Metacarpal II with the prepollical elements. (0) Metacarpal
- 3014 II articulates with the prepollex without an expanded process. (1) Metacarpal II
- 3015 articulates with the prepollex through a medial expanded process.
- 3016 12) Medial sesamoid on the distal epiphysis of the Metacarpal II. (0) Absent. (1)
- 3017 Present.

- 3018 13) Insertion of the *m. abductor indicis longus* (ABL) on the Metacarpal II. (0)
 3019 Single insertion through a tendon. (1) Two insertions over the Metacarpal II,
 3020 through two tendons.
- 3021 14) Insertion of the *m. abductor indicis longus* (ABL) on the Distal Prepollex. (0)
 3022 Absent. (1) Present, through an aponeurosis.
- 3023 15) *M. extensor brevis profundus extra metacarpus* (EBPem). (0) Absent. (1)
 3024 Present.
- 3025 16) *M. extensor brevis profundus extra prepollex* (EBPepp). (0) Absent. (1) Present.
- 3026 17) Additional insertion of the *m. abductor indicis brevis dorsalis* (ABD) on the
 3027 Metacarpal II. (0) Absent. (1) Present.

3028

3029 **Remarks.**—The ABD is commonly inserted on the Metacarpal II in several anurans
 3030 (see below). We found this muscle inserted on the prepollex of all Cophomantini
 3031 studied. Additionally we found a second small insertion of the ABD on the Metacarpal
 3032 II in a few species (ch. 17, st. 1). The condition of this character is unknown in
 3033 *Myersiohyla*, *Nesorohyla*, and other tribes of Hyalinae. An alternative possibility would
 3034 be to consider two distinct characters: (i) Absence/Presence of the insertion of ABD on
 3035 the Distal Prepollex; (ii) Absence/Presence of the insertion of ABD on the Metacarpal
 3036 II.

3037

3038 **Ancestral character reconstruction**

3039 The sickle-shaped prepollex optimizes at the node of Cophomantini (ch. 1, st. 0)
 3040 with an ambiguity given by the missing entries in *Myersiohyla chamaeleo*, *M. liliae*,
 3041 and *Nesorohyla kanaima*. However, we know these species lack a spine-shaped

prepollex and have an externally enlarged prepollex, suggesting that they also have a sickle shaped prepollex. The optimization of the spine-shaped prepollex (ch. 1, st. 1) is ambiguous, as it could have appeared independently in *Bokermannohyla* and *Boana*, or it could have evolved once in the common ancestor of *Bokermannohyla*, *Boana* and *Aplastodiscus*, with a subsequent reversal to sickle-shaped prepollex in *Aplastodiscus*. Additionally the spine-shaped prepollex appeared independently from a sickle-shaped prepollex in *Hyloscirtus tapichalaca*, and a reversal from the spine-shaped prepollex to the sickle-shaped prepollex occurred at the common ancestor of *Boana diabolica*, *Boa. geographica*, and *Boa. semilineata*.

The cartilaginous medial margin of the prepollex (ch. 4, st. 1) optimizes like the sickle-shaped prepollex. But besides the sickled shaped prepollex be present in *Boana semilineata* and *Boa. geographica*, the cartilaginous medial margin is absent in these species.

The presence of a medial crest (ch. 3, st. 1) optimizes very similar to the spine-shaped prepollex. From the species with a spine-shaped prepollex, only *Hyloscirtus tapichala*, *Bokermannohyla oxente*, and *Boana microderma* lack a medial crest. However, the presence of the medial crest in *Bok. alvarengai*, *Bok. ibitiguara*, *Bok. pseudopseudis*, and *Bok. saxicola* (members of the *Bok. pseudopseudis* group, so as *Bok. oxente*) might change the ch. 3 optimization for *Bokermannohyla*. Similarly, both the insertion of ABL on the Distal Prepollex (ch. 14, st. 1) and the presence of EBPepp (ch. 16, st. 1) optimize at the same nodes of the spine-shaped prepollex. Although we were not able to study muscle characters of *Hyloscirtus tapichalaca*.

The presence of a medial dorso-ventral expansion of the Distal Prepollex (ch. 2, st. 1) and the medial seasamoid on the distal epiphysis of the Metacarpal II (ch. 12, st. 1) originated in the common ancestor of the *Hyloscirtus armatus* group.

The presence of a well-developed post-articular process of the Distal Prepollex (ch. 7, st. 2) and a spine-shaped prepollex ventral to the Metacarpal II (ch. 9, st. 1) originated in an internal clade of the *Boana pulchella* group (this character is unknown in *Boa. cambui*). Character 7 (st. 2) is also present in the *Bokermannohyla martinsi* group. The short post-articular process (cf. 7, st. 1) evolved independently in the *B. semilineata* group (with a reversal to st. 0 on the node of *Boana diabolica*, *Boa. geographica*, and *Boa. semilineata*) and in the common ancestor of the *Boa. faber*, *Boa. pellucens*, and *Boa. pulchella* group (although with a possible ambiguity given by the unknown character state in *Boa. cambui*). The straight prepollical spine (ch. 8, st. 1) originated in the common ancestor of *Boana microderma* and *Boa. nympa*. However, ch. 8 (st. 1) could have evolved earlier, if it is also present in *Boa. roraima*.

The articulation of the Metacarpal II with the prepollex through a medial process on its proximal epiphysis (ch. 11, st. 1) originated in *Boana* (with reversals on *Boa. heilprini*, *Boa. microderma*, and *Boa. pellucens*), and independently in *Bokermannohyla oxente* and at an internal node of the *H. larinopygion* group. However, the study of other species of the *H. larinopygion* group might change this optimization, as *H. antioquia*, *H. caucanus*, and *H. sarampiona* have ch.11, st. 0.

The EBPem (ch. 15, st. 1) occurs in all studied Cophomantini, however we need to study the distribution of this character in *Myersiohyla* and *Nesorohyla*, and among other Hylineae, to understand if it could be an evolutionary acquisition of Cophomantini, or even a more inclusive character. The EBPepp (ch. 16, st. 1) optimizes like the the spine-

shaped prepollex (ch. 1, st. 1). However we were not able to study muscle characters on species of *Hyloscirtus* with spine-shaped prepollex.

DISCUSSION

Prepollex evolution.—Faivovich et al. (2005) notice the need of osteological studies on the enlarged prepollex, and associated characters in Cophomantini. Our results show notable evolutionary plasticity of these traits within the tribe. The two distinct morphologies found, sickled-shaped and spine-shaped prepollex, evolved more than once each, within Cophomantini. This involved changes in related musculature. The two morphologies have different characters related to them, which probably have distinct biological functions that we discuss below. Knowledge of the prepollical structure in the groups closely related to Cophomantini surely will allow to better understand the evolution of this character system.

A spine-shaped prepollex evolved independently several times in anurans. Among Ranoides, two species of *Babina* (Ranidae) are known to have a spine-shaped prepollex. As in Cophomantini, the prepollex of those species includes a small Proximal Prepollex and a large spine-shaped Distal Prepollex (Tokita and Iwai, 2010; Iwai, 2012). Also, the four species of the *Boophis albilabris* group (Mantellidae) have a spine-shaped prepollex (Cadle, 1995; Andreone, et al., 2002; Vences et al., 2010), but its osteology remains undescribed.

Among Hyloides, the spine-shaped prepollex is known to occur also in *Centrolene gemmatum* and *Cen. lynchi*; *Cochranella duideana* and *Coc. riveroi*; *Teratohyla spinosa*; *Vitreorana castroviejoi*, *V. gorzulae*, *V. helenae*, and *V. ritae* (Centrolenidae;

3112 Taylor, 1949; Flores, 1985; Señaris and Ayarzagüena, 2005). However, differently from
 3113 the spine-shaped prepollex of *Cophomantini*, where a proximal element is present, in
 3114 these centrolenids the prepollex is formed by a single element. In *Hylidae*, besides
 3115 *Cophomantini*, a spine-shaped prepollex occurs in some species of the *Plectrohyla*
 3116 *guatemalensis* group and in *Economiohyla miliaria* (Duellman, 1970; Duellman and
 3117 Campbell, 1992).

3118 Other sharp structures are known to occur in the hands of other anuran species. In
 3119 all species of *Petropedetes* (except *Pet. cameronensis*) and *Arthroleptides matiensseni*
 3120 (*Ranoides*: *Petropedetidae*) breeding males have a sharp osseous structure on Finger II
 3121 (Scott, 2005; Barej et al., 2010). However, in this group this sharp structure is a
 3122 prolongation of the Metacarpal II. Scott (2005), in her character 111, considered this
 3123 spine as a prepollex fused to the Metacarpal II. However, as evidenced from figure 15
 3124 of Barej et al. (2010) and the figure A15 of the supplementary material of Barej et al.
 3125 (2014), the spine of petropedetids is part of the Metacarpal II.

3126 In the genus *Leptodactylus*, males of several species of the *L. latrans*, *L.*
 3127 *melanonotus*, and *L. pentadactylus* groups have a robust spine distally on Metacarpal II,
 3128 and sometimes a robust and conical one on the prepollex (see fig. 46 of Lynch, 1971;
 3129 Heyer, 1970, 1979, 1994; Shine, 1979). However, in those species the spines are the
 3130 internal support of external black keratinous spines (Lynch, 1971; de Sá et al., 2014).
 3131 These do not occur in anuran species having a spine-shaped prepollex.

3132 Shine (1979) correlated the presence of all those sharp structures on the hands to
 3133 territoriality and male-male combat. The diversity and similarity in function of these
 3134 structures suggest that similar selective pressures could be acting in those various
 3135 distinct lineages.

Prepollical anatomy and behavior.—In Cophomantini there are reports of scars

on males (see Supplementary Material II), or aggressive behavior against the collector on many species that have a spine-shaped prepollex (e.g., Pombal and Haddad, 1993; Kizirian et al., 2003; Garcia et al., 2008; Toledo et al., 2011). Nevertheless, direct observations are less common in the literature, and scars serve as indirect evidence of fights among males (see Supplementary Material II for reports on wrestling behavior). This aggressive behavior has been associated to territoriality and/or defense of resources, such as vocalization or oviposition sites (Wells, 2007). However, there is no report of scars or fights on males of *Boana pulchella*, a well studied species with a well developed spine-shaped prepollex, and ABL insertion over it (J. Faivovich, pers.obs.). On the other hand, there are no reports of scars or fights in Cophomantini species with sickle-shaped prepollex, i.e, *Myersiohyla*, *Nesorohyla*, *Hyloscirtus* (except *H. condor*, *H. diabolus*, and *H. tapichalaca*), *Aplastodiscus*, and *Boana diabolica*, *B. geographica*, *B. hutchinsi*, and *B. semilineata*.

The spine-shaped prepollex is commonly referred to as a protruding spine, however its functional mechanism remains to be understood. We found many muscles associated to it, but we do not know how their integrated functionality is. It is unknown if there is a channel in the skin through which the spine is protruded, or if it simply pierces the skin during fights, and the skin subsequently heals. In the particular case of the ranid *Babina subaspera*, Iwai (2012) reported some male specimens with the tip of the prepollex wounded (see his fig. 3).

In many Cophomantini species with a spine-shaped prepollex, males also have hypertrophied forearms. While the former is positively correlated with aggressive behavior (Shine, 1979) the latter is not. Wells (2007) hypothesized that a wider arm

could increase chances of fighting success. He also commented the possibility of forearm hypertrophy be positively correlated to wrestling behavior at least in some Cophomantini. However, it seems that in this group the forearms hypertrophy is more related to the habitat than to the fight behavior. From 50 Cophomantini species with male-male combat reported, only 20 have forearm hypertrophy. But from those 20 species, 19 inhabit streams, creeks or rocky streams. From the other 30 species without forearm hypertrophy, only eight inhabit streams and the other 22 are known to live in lentic environments (see Supplementary Material II).

As our results show, the insertion of the *m. abductor indicis longus* (ABL) in the Distal Prepollex optimizes at the same nodes as the spine-shaped prepollex. This muscle inserted in the Distal Prepollex might protrude this element when contracted. It may also tense the structure for more resistance during fights. Unfortunately, we could not examine musculature of species of *Hyloscirtus* with spine-shaped prepollex, i.e., *H. condor*, *H. diabolus*, and *H. tapichalaca* (Kizirian et al., 2003; Almendáriz et al., 2014; Rivera-Correa et al., 2016) to study if the ABL insertion in these species is similar to *Bokermannohyla* and *Boana*. The species with a sickle-shaped prepollex, instead, have a unique ABL insertion on the Metacarpal II. The exception is *Boana semilineata*, which has a sickle-shaped prepollex, but has two insertions of the ABL on the Metacarpal II.

According to our results, all species with a spine-shaped prepollex have the second insertion of the ABL on the distal prepollex—but we were not able to study the musculature of *Hyloscirtus tapichalaca*. And all the species with a sickle-shaped prepollex (except *Boana semilineata*) have the ABL with a single insertion, on the Metacarpal II. *Boana semilineata* is nested among species with a spine-shaped prepollex. The ABL with two insertions of the former, both on the Metacarpal II,

suggests that one of these insertions could be homologous to the insertion on the Distal Prepollex of other species of *Boana*.

Fabrezi (2001) considered the internal support with skin structures a possible primary function of the prepollex in anurans. In the *Hyloscirtus armatus* group, the sickle-shaped prepollex have a medial dorso-ventral expansion that supports the spine-shaped nuptial pads (Duellman et al., 1997). A large prepollex could also be associated with nest construction behavior. Garcia et al. (2001) hypothesized the association of the enlarged inner carpal tubercles with the construction of subterranean nests in *Aplastodiscus*. Haddad et al. (2005) discuss the specialized reproductive mode of *A. perviridis*, on which males construct subterranean nests (see fig. 2 of Haddad et al., 2005). The inner carpal tubercle is internally supported by the sickle-shaped prepollex. In some species of the *Boana faber* group, males also use their hands to build nests (Goeldi, 1895; Lutz, 1960; Kluge, 1981).

In Cophomantini, the *m. abductor indicis brevis dorsalis* (ABD) inserts on the Distal Prepollex, with the primary function to abduct this bone. However, throughout Anura, the ABD inserts on the Metacarpal II, to abduct the Finger II (Gaupp, 1896; Burton, 1996, 1998a). The abduction of the prepollex could be important for distinct behaviors that occur in Cophomantini: (i) being abducted, the distal prepollex could act as a shovel, helping in digging; (ii) in species with nuptial pads, the abduction of the prepollex could help in steadying the pads against the female body; (iii) in species with a spine-shaped prepollex, the abduction of the bone could help in protruding it through the skin.

Gaupp (1896) and Burton (1996, 1998a, b) described the *mm. extensors indicis breves profundi* (EBP) as two slips with origin from the dorsum of the Metacarpal II.

One inserts medially and the other inserts laterally on the terminal phalanx. Besides those two slips, there are two supplementary medial slips in Cophomantini (EBPem and EBPepp). These seem to be a novelty at least for Cophomantini, although we are unaware about the distribution of these characters among other hylids. Whereas the EBPem is present in all studied species of Cophomantini, the EBPepp was found only in species with a spine-shaped prepollex. We could not study these characters in the species of *Hyloscirtus* with a spine-shaped prepollex.

Sexual dimorphism.—In the species with a spine-shaped prepollex, this element is smaller in females than on males, although still being evident externally (e.g., see Taucce et al., 2015: fig. 3). We studied sexual dimorphism of the spine shaped-prepollex in only two species. Whereas in males it is entirely ossified and proportionally larger (Distal Prepollex length/Metacarpal II length ratio 1.1 in *Bokermannohyla hylax*; 1.20 in *Bok. alvarengai*), in females it is entirely or partially cartilaginous and smaller (Distal Prepollex length/Metacarpal II length ratio 0.74 in *Bok. hylax*; 0.96 in *Bok. alvarengai*).

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 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 *Boo. occidentalis* (also from the *Boo. albilabris* group), presumably meaning that it is cartilaginous.

In the centrolenids with a spine-shaped prepollex (see above), it is large and ossified in both males and females (Hayes and Starret, 1980; Flores, 1985). Also, in the

3231 *Plectrohyla guatemalensis* group, both sexes have a large and ossified prepollex
3232 (Duellman, 1970).

3233

3234 **CONCLUSIONS**

3235 The prepollex shows an evolutionary plasticity within the tribe Cophomantini. The
3236 enlarged element could be an adaptation to digging nests with hands. The two distinct
3237 morphologies of the Distal Prepollex, the sickle-shaped and the spine-shaped prepollex,
3238 evolved more than once in the tribe Cophomantini, as did many associated characters.
3239 Two associated muscles that commonly insert on the Metacarpal II among anurans,
3240 insert on the Distal Prepollex of species of Cophomantini which present a spine-shaped
3241 prepollex. These modifications on muscles insertions probably are adaptations to protrude
3242 the spine, and consequently to fighting. But the mechanism of protruding, still waits to
3243 be understood. These prepollical morphologies have differences in osteological and
3244 myological characters, which presumably play distinct biological functions. However
3245 their functionality is still poorly understood. Natural history data, such as detailed
3246 observations of nest building, courtship behavior, territoriality, and amplexus probably
3247 would help in understanding more functions of the prepollex. We need to study the
3248 characters associated to the prepollex in the other taxa of hylids in order to understand
3249 how they evolved in the family and to try to solve some of the ambiguities found.

3250

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3397

3398 **APPENDIX**3399 ***Material examined***

3400 An asterisk (*) indicates cleared and double stained specimens; a numeral (#) indicates
 3401 specimens with X-ray images; two asterisk (**) indicate specimens with µct-scan
 3402 images; the supernumeral (+) indicates specimens dissected for the study of hand
 3403 muscles.

3404 ***APLASTODISCUS: Aplastodiscus albofrenatus* group.—*A. arildae*, CFBH**
 3405 **1242*, 30829+; *A. ehrhardti*, CFBH 3183*; *A. eugenioi*, CFBH 3181*. *Aplastodiscus***
 3406 ***albosignatus* group.—*A. albosignatus*, CFBH 3910*; *A. callipygius*, CFBH 4941+,**
 3407 **4944*. *Aplastodiscus perviridis* group.—*A. cochranæ*, CFBH 2193*, 2987+; *A.***
 3408 ***perviridis*, PCG 1061* MACN 35170+, CFBH 11206+. *Aplastodiscus sibilatus***
 3409 **group.—*A. sibilatus*, MNRJ 36946*. *BOANA: Boana albopunctata* group.—*Boa.***
 3410 ***albopunctata*, CFBH 739*, 4434*, 6051*, 7456+, 22086*, 22087*, 22089, UFMG**
 3411 **1174*, AB 497+; *Boa. caiapo*, MZUSP 139009*; *Boa. calcarata*, MPEG 25035*; *Boa.***
 3412 ***fasciata*, MPEG 14101*; *Boa. heilprini*, UFMG 8641*; *Boa. lanciformis*, MZUSP**
 3413 **121577*; *Boa. multifasciata*, UFMG 5279*; *Boa. raniceps*, UFMG 1547*, MACN**
 3414 **45053+. *Boana benitezi* group.—*Boa. microderma*, MTR 28289*+; *Boa. nympa*,**
 3415 **QCAZ 2145*, 28184*; *Boa. ornatissima*, MPEG 20361*; *Boa. tepuiana*, MTR**
 3416 **20735*+. *Boana faber* group.—*Boa. albomarginata*, UFMG 8231*, CFBH 10596*,**
 3417 **10597*, 10599*, 10602*, 17639*, 34999*; *Boa. crepitans*, UFMG 6937*; *Boa. exastis*,**
 3418 **UFMG 11059*; *Boa. faber*, UFMG 3318*; *Boa. lundii*, CFBH 34316+, UFMG 1637*;**
 3419 ***Boa. pardalis*, UFMG 7730*. *Boana pellucens* group.—*Boa. pellucens*, QCAZ 7267#,**
 3420 **11596#, 40273(female)#. *Boana pulchella* group.—*Boa. bandeirantes*, UFMG 1419*;**
 3421 ***Boa. bischoffi*, CFBH 1009*; *Boa. botumirim*, UFMG 3793*; *Boa. cipoensis*, UFMG**

- 3422 1218*; *Boa. cordobae*, MP 231*+, 233*+, BB 1320+; *Boa. curupi*, MACN 42589+;
- 3423 *Boa. ericae*, UFMG 11583*; *Boa. freicanecae*, MUFAL 9472*; *Boa. goiana*, UFMG
- 3424 8452*; *Boa. aff. joaquina*, UFMG 10037*; *Boa. cf. joaquina*, CFBH3592*, 3594*,
- 3425 3595*, UFMG 10005*; *Boa. latistriata*, UFMG 2991*; *Boa. phaeopleura*, UFMG
- 3426 10346*; *Boa. aff. polytaenia*, UFMG1480*; *Boa. pulchella*, AB 223*+, 240*+, MACN
- 3427 40485+; *Boa. riojana*, AB 45*+, 46*+, MACN 43664+; *Boa. cf. stellae*, DB 5095*+;
- 3428 *Boa. stenocephala*, UFMG 11205*. *Boana punctata* group.—*Boa. atlantica*, CFBH
- 3429 13257+, CFBH 18725+, UFMG 5744*; *Boa. cinerascens*, MPEG 10001*; *Boa.*
- 3430 *picturata*, QCAZ 4055#, 4058#, 7233*; *Boa. punctata*, CFBH 9161*, MACN 40114+,
- 3431 MZUSP 53667*, 140455*. *Boana semilineata* group.—*Boa. boans*, MPEG 8863*;
- 3432 *Boa. geographica*, MPEG 17822*; *Boa. pombali*, CFBH 36791+; *Boa. semilineata*,
- 3433 CFBH 2389*, 10524*, 10528*, 10530*, 10533*, 13013+; *Boa. wavrini*, MPEG
- 3434 15315*. **BOKERMANNOHYLA: Bokermannohyla claresignata** group.—*Bok.*
- 3435 *clepsydra*, MZUSP 112612*. *Bokermannohyla circumdata* group.—*Bok. hylax*,
- 3436 CFBH 3620*(female), 11545*+; *Bok. lucianae*, MNRJ 40483*; *Bok. luctuosa*, AMC
- 3437 077*; *Bok. nanuzae*, UFMG 10940*. *Bokermannohyla martinsi* group.—*Bok. langei*,
- 3438 MZUSP 74275#; *Bok. juiju*, MZUEFS 1900#; *Bok. martinsi*, MNRJ 49675*, MZUSP
- 3439 73667#, UFMG 745*. *Bokermannohyla pseudopseudis* group.—*Bok. alvarengai*,
- 3440 MCNAM 3165*, BA 170*, 206*(female); *Bok. ibitiguara*, CFBH 17323*+, CFBH
- 3441 40583+; *Bok. oxente*, CFBH 30145*+; *Bok. pseudopseudis*, CFBH 6800*+; *Bok.*
- 3442 *saxicola*, CFBH 30901*+. **HYLOSCIRTUS: Hyloscirtus armatus** group.—*H.*
- 3443 *armatus*, USNM 346062+(female), 206715***(male), MNCN 43516*; *H. charazani*,
- 3444 MNCN 44823*. *Hyloscirtus bogotensis* group.—*H. alytolylax*, QCAZ 16411*; *H. aff.*
- 3445 *alytolylax*, PR 16277*; *H. bogotensis*, ICN 4420*; *H. callipeza*, VR 5150*, 5152*; *H.*

- 3446 *colymba*, MAR 1471*, 1628*(female); *H. denticulentus*, MRC 591*, 610*; *H. lynchi*,
 3447 PR 16302*; *H. palmeri*, ICN 20087+, MAR 1082*, 1196*, GGD 073*; *H. aff. palmeri*,
 3448 EMM 263*; *H. aff. phyllognathus*, MRC 701*, 702*; *H. piceigularis*, ICN 5307*; *H.*
 3449 *aff. piceigularis*, MC 9748*(female), 9749*; *H. platydactylus*, ICN 10471*, 10472*; *H.*
 3450 *simmonsii*, ICN 25906*, 41305*; *H. aff. simmonsii* sp. 1, MHUA 4098*, 5017*; *H. aff.*
 3451 *simmonsii* sp. 2, VR 3293*; *H. torrenticola*, ICN 23614*, MAR 1974*. *Hyloscirtus*
 3452 *larinopygion* group.—*H. antioquia*, ICN 9384*, 9392*; *H. caucanus*, ICN 7074*; *H.*
 3453 *larinopygion*, MRC 575*, 576*, ICN 36138+, ICN 31190+(female); *H. lindae*, ICN
 3454 49662*, QCAZ 10483*; *H. princecharlesi*, QCAZ 48075*; *H. sarampiona*, JMR 2434,
 3455 2888*; *H. staufferorum*, QCAZ 50381*; *H. tapichalaca*, QCAZ 16706*.
 3456 **MYERSIOHYLA**: *M. neblinaria*, USNM 562071**.
 3457

Figure Labels

Figure 1. Dorsal view of clear and double stained right hands of adult males of species with sickle-shaped prepollex. **(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; and **(G, H)** *Boana semilineata* CFBH 10524 and 10530, respectively. Medial cartilaginous margin (ch. 4, st. 1) in **(A)**, **(C)**, **(D)**, and **(E)**, and is barely present in **(B)**. Medial margin ossified (ch. 4, st. 0) in **(F–H)**. One additional distal element (ch. 5, st. 1) cartilaginous in **(A)**, and mineralized in **(G)**. Two additional distal elements (ch. 5, st. 2) patially mineralized in **(B)**; cartilaginous in **(C)**. **(H)** same species as **(G)** but without additional distal elements (ch. 5, st. 0). Lateral margin of the Distal Prepollex straight (ch. 6, st. 1) in **(C–D)**; concave (ch. 6; st. 0) in the remaining. Metacarpal II articulates with the prepollex without an expanded process (ch. 11, st. 0) in **(A–F)**; and with an expanded process (ch. 11, st. 1) in **(G–H)**. **CII** = Distal Carpal II; **DPrep** = Distal Prepollex; **CIII–IV–V** = Distal Carpal III–IV–V; **MII–V** = Metacarpal II to V; **R** = Radius; **r** = Radiale; **U** = Ulna; **u** = Ulnare; **Y** = Element Y (fractured in **A**); * = Proximal Prepollex. Scale bars: 1 mm.

Figure 2. Micro-ct reconstruction of the right hand of the *Myersiohyala neblinaria* USNM USNM 562071 (male), with sickle-shaped Distal Prepollex; dorsal view. Black arrow points the additional distal element on the Distal Prepollex (ch. 5, st. 1). **CII** = Distal Carpal II; **DPrep** = Distal Prepollex; **MII** = Metacarpal II (which is fractured); **Y** = Element Y; * = Proximal Prepollex. Scale bar = 2mm.

3482

3483 **Figure 3.** Micro-ct reconstruction of the right hand of the *Hyloscirtus armatus*
 3484 USNM 206715 (male), with sickle-shaped Prepollex with a medial dorso-ventral
 3485 expansion (ch. 2, st. 1); dorsal view. The inset shows in detail a distal view of the
 3486 prepollex showing the profile of the medial dorso-ventral expansion. **CII** = Distal
 3487 Carpal II; **DPrep** = Distal Prepollex; **MII** = Metacarpal II; **S** = sesamoid of Metacarpal
 3488 II; **Y** = Element Y; * = Proximal Prepollex. Scale bar = 5 mm.

3489

3490 **Figure 4.** Cleared and double stained whole-mounts (A-B, D-L) and X-ray (C) of
 3491 the hand of adult males with spine-shaped Distal Prepollex; dorsal view. (A) left hand;
 3492 (B–L) right hand. (A) *Hyloscirtus tapichalaca* QCAZ 16706; (B) *Bokermannohyla*
 3493 *ibitiguara* CFBH 17323; (C) *B. langei* 74275; (D) *B. clepsydra* MNRJ 112612; (E)
 3494 *Boana microderma* MTR 28289; (F) *B. tepuiana* MTR 20735; (G) *B. heilprini* UFMG
 3495 8641; (H) *B. raniceps* UFMG 1547; (I) *B. crepitans* UFMG 6937; (J) *B. pombali* CFBH
 3496 14917; (K) *B. pulchella* AB 223; (L) *B. ericae* CFBH 3604. Medial crest on the Distal
 3497 Prepollex absent (ch. 3, st. 0) in (E); present (ch. 3, st. 1) in (I). Post-articular process
 3498 absent in (F) or a rudiment tip in (H) (ch. 7, st. 0); present but short (ch. 7, st. 1) in (D);
 3499 present and large (ch. 7, st. 2) in (K). Distal projection forming a second spine present
 3500 (ch. 10, st. 1) in (C) and (L). Metacarpal II articulates with the prepollex without an
 3501 expanded process (ch. 11, st. 0) in (E); and with an expanded process (ch. 11, st. 1) in
 3502 (I). **CII** = Distal Carpal II; **DPrep** = Distal Prepollex (fractured in A); **CIII-IV-V** =
 3503 Distal Carpal V-IV-III; **MII-V** = Metacarpals II to V respectively; **R** = Radius; **r** =
 3504 Radiale; **U** = Ulna; **u** = Ulnare; **Y** = Element Y; * = Proximal Prepollex. Scale bars: 1
 3505 mm.

3506

3507 **Figure 5.** Sexual dimorphism of the prepollex in *Bokermannohyla hylax*. (A) Male
 3508 (CFBH 11545) with ossified distal prepollex; (B) female (CFBH 3620) with
 3509 cartilaginous distal prepollex. Scale bars: 1 mm.

3510

3511 **Figure 6.** Dorsal musculature of the right hand of males, showing the *m. abductor*
 3512 *indicis longus* (**ABL**, highlighted in orange), with *m. extensor digitorum communis*
 3513 *longus* removed. (A) *Hyloscirtus palmeri* ICN 20087; (B) *Bokermannohyla oxente*
 3514 CFBH 30145; (C) *Aplastodiscus cochranae* CFBH 2987; (D) *Boana pombali* CFBH
 3515 36791; (E and F) *B. semilineata* CFBH 13013. In (F), the **ABL** had its origin cut (also
 3516 highlighted in orange), and was deflected to show its two insertions (ch. 13, st. 1). An
 3517 asterisk indicates the same insertion showed in (E) Insertion of the (ABL) on the
 3518 Metacarpal II single (ch. 13, st. 1) in (A–D). Insertion of the (ABL) on the Distal
 3519 Prepollex (ch. 14, st. 1) in (B) and (D). Scale bars: 1 mm.

3520

3521 **Figure 7.** Dorsal view of the right hand of *Boana lundii* CFBH 34316, with the
 3522 superficial musculature removed (*m. abductor indicis longus*, *m. extensor brevis*
 3523 *superficialis* and *m. extensor brevis medius digiti II*) to expose the *m. extensor indicis*
 3524 *brevis profundus* (highlighted in orange). The common trend of this muscle in Anura is to
 3525 have two slips (**EBP**): one arises dorsolaterally, and the other mid-dorsally on the
 3526 Metacarpus II (**MII**), and they insert through respective lateral and medial thin tendons
 3527 on the terminal phalanx. In all studied Cophomantini it has an additional slip, the *m.*
 3528 *extensor brevis profundus extra metacarpus* (**EBPem**), which arises medially on **MII** and
 3529 inserts on the medial thin tendon of **EBP**. Another additional slip, occurring only in

3530 Cophomantini with a spine-shaped prepollex, is the *m. extensor brevis profundus extra*
 3531 *prepollex (EBPepp)* that arises on the Distal Prepollex (**DPrep**) and also inserts on the
 3532 medial thin tendon of **EBP**. Dashed white lines indicate Metacarpal II and Distal
 3533 Prepollex. Scale bar: 1 mm.

3534

3535 **Figure 8.** Dorsal view of the right hand of *Bokermannohyla ibitiguara* CFBH
 3536 17323, with the superficial musculature removed to show the *m. abductor indicis brevis*
 3537 *dorsalis (ABD)*, highlighted in orange. In most species this muscle originates on
 3538 Element Y and inserts in the dorsal surface of the Distal Prepollex (**DPrep**). In some
 3539 species, like *B. ibitiguara*, it has a second slim, fleshy insertion on the proximal and
 3540 medial region of the Metacarpal II (**MII**). Dashed white lines indicate Metacarpal II and
 3541 Distal Prepollex. Scale bar: 1 mm.

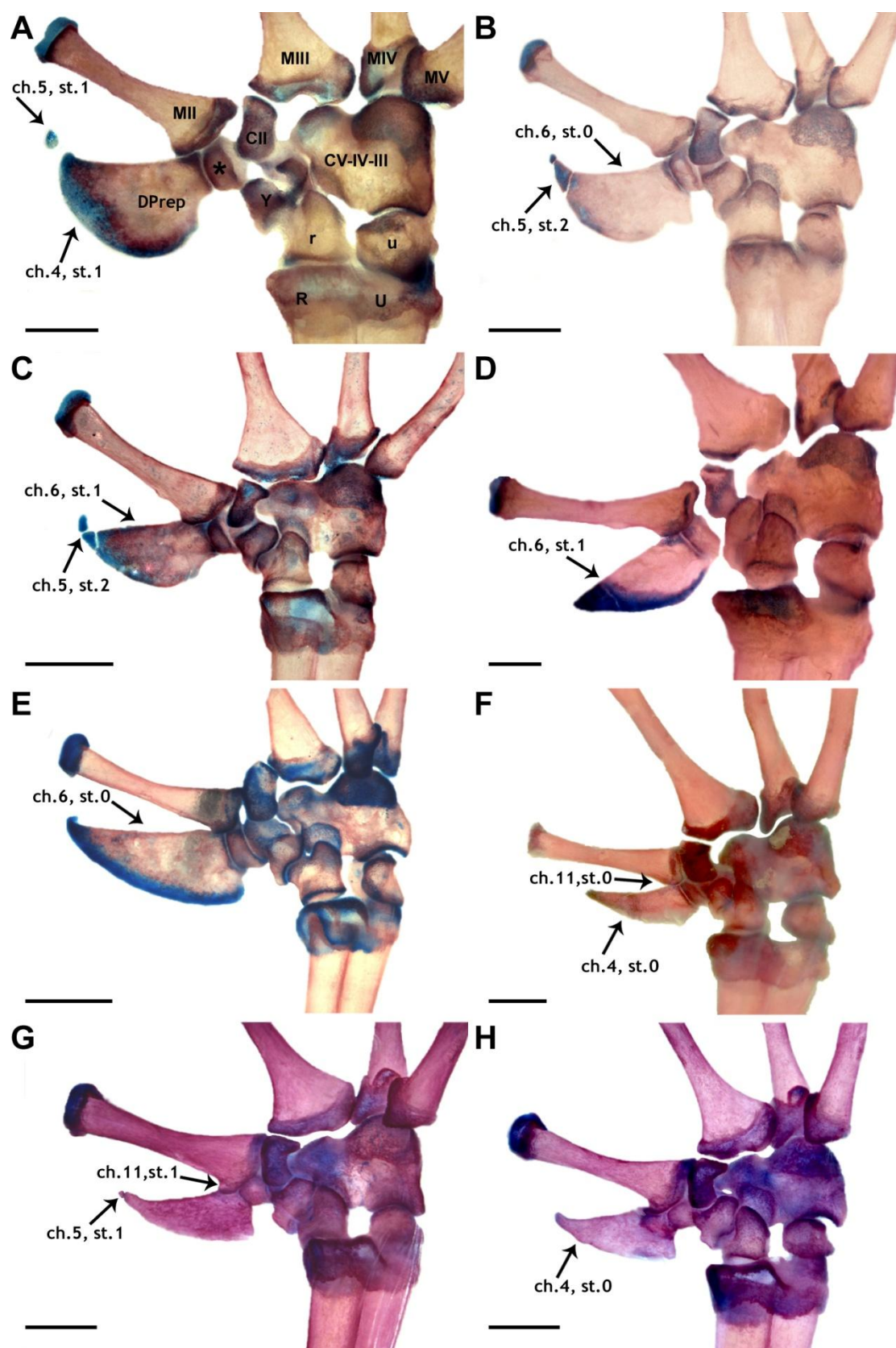
3542

3543 **Figure 9.** Optimization of characters of the prepollex on the most recently
 3544 phylogenetic hypothesis of the tribe Cophomantini (Pinheiro et al., in prep.). Characters
 3545 definitions are in the text. Red dots are homoplastic characters; white squares are
 3546 synapomorphies. One question mark means that only myological characters have
 3547 missing entries; two question marks mean that both myological and osteological
 3548 characters have missing entries. Orange drawings represent the presence of the sickle-
 3549 shaped prepollex in the group; purple drawings represent the presence of the spine-
 3550 shaped prepollex in the group; green drawn represent the acquisition of both the medial
 3551 dorso-ventral expansion on the sickle-shaped prepollex, and the sesamoid medial to the
 3552 Metacarpal II.

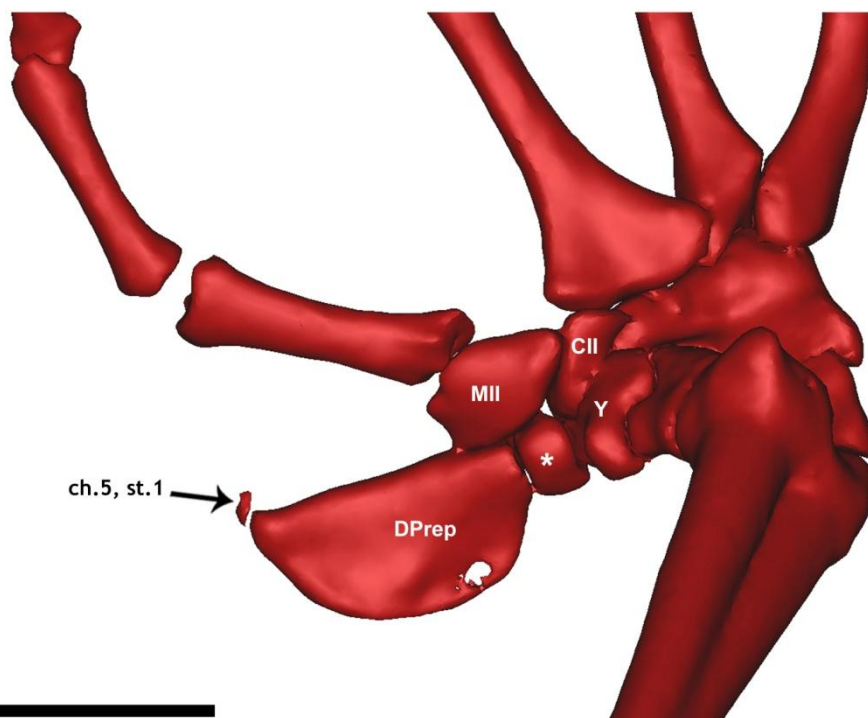
3553

3554

Figure 1.



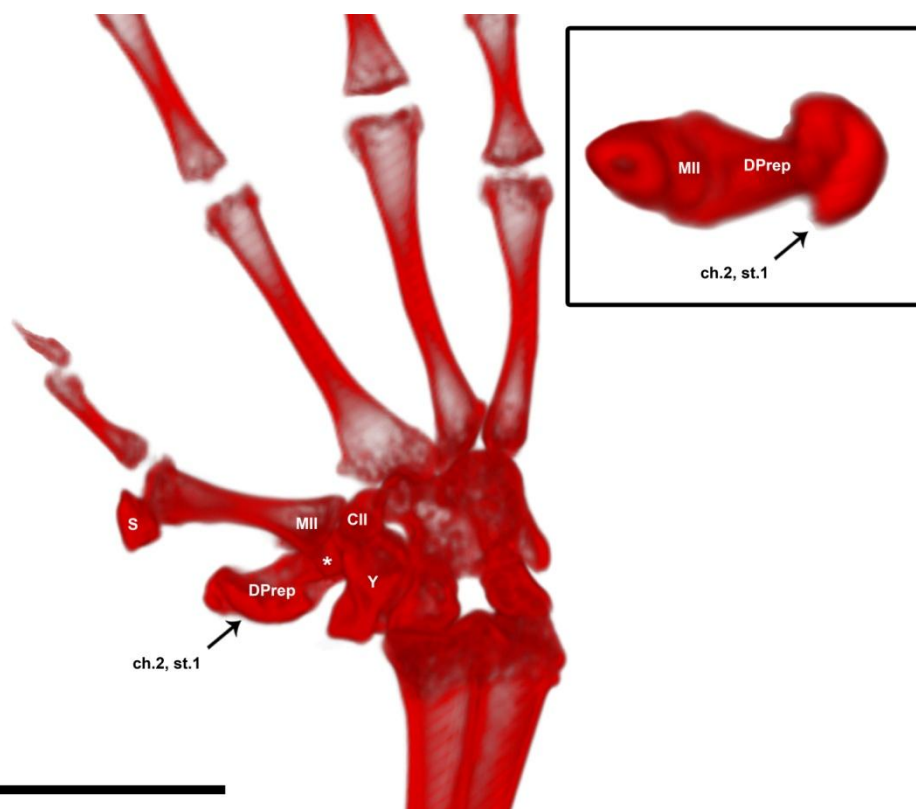
3555 **Figure 2.**



3556

3557

3558 **Figure 3.**



3559

Figure 4.

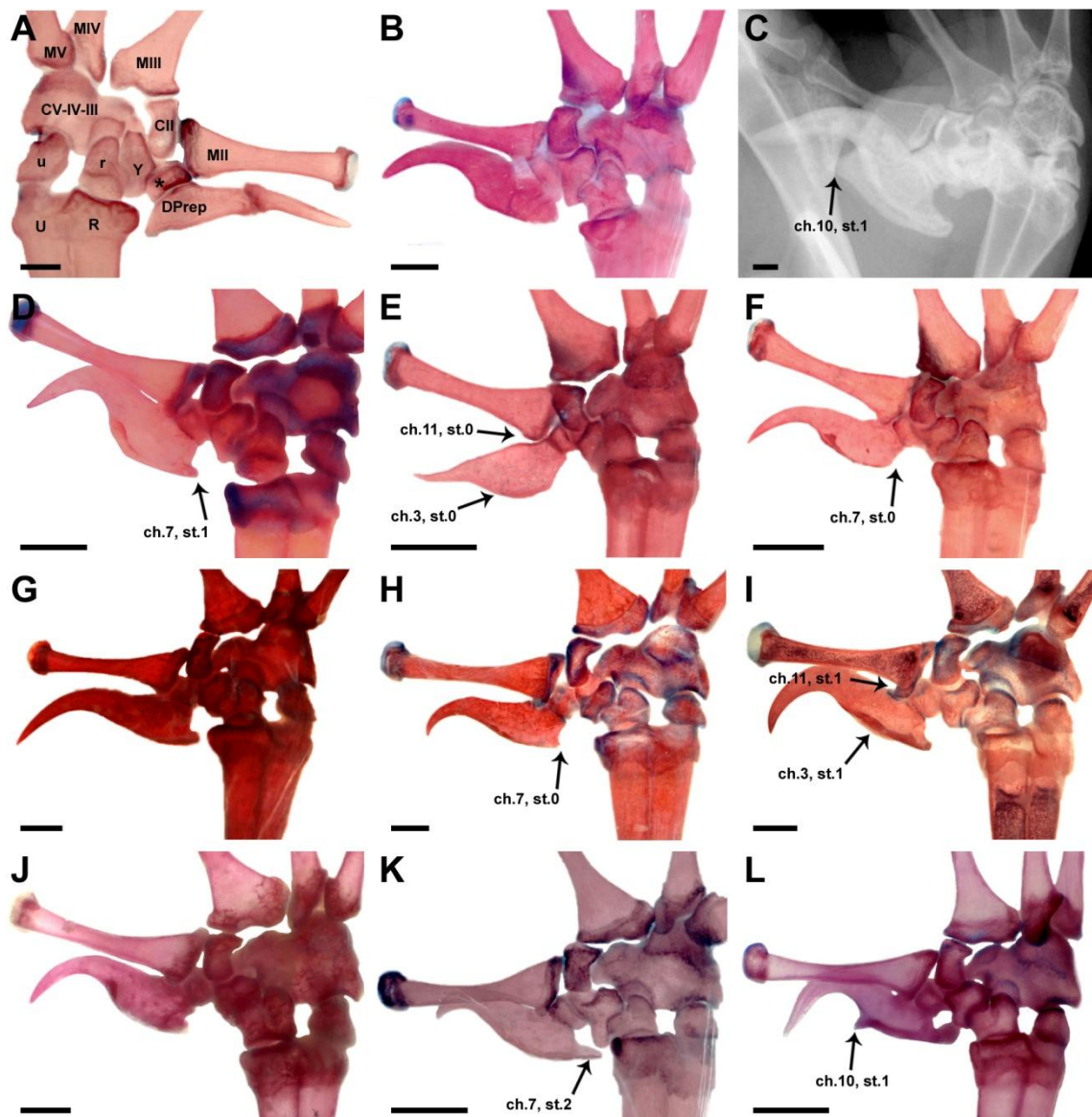
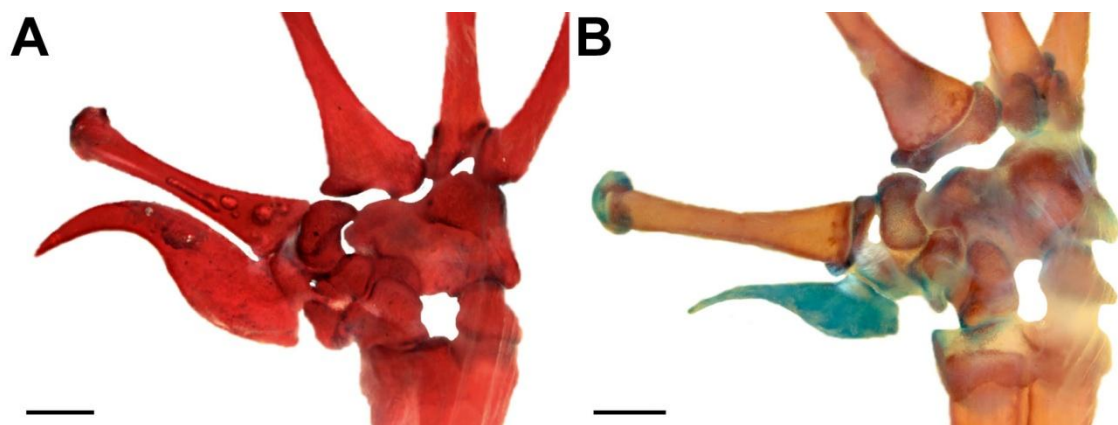
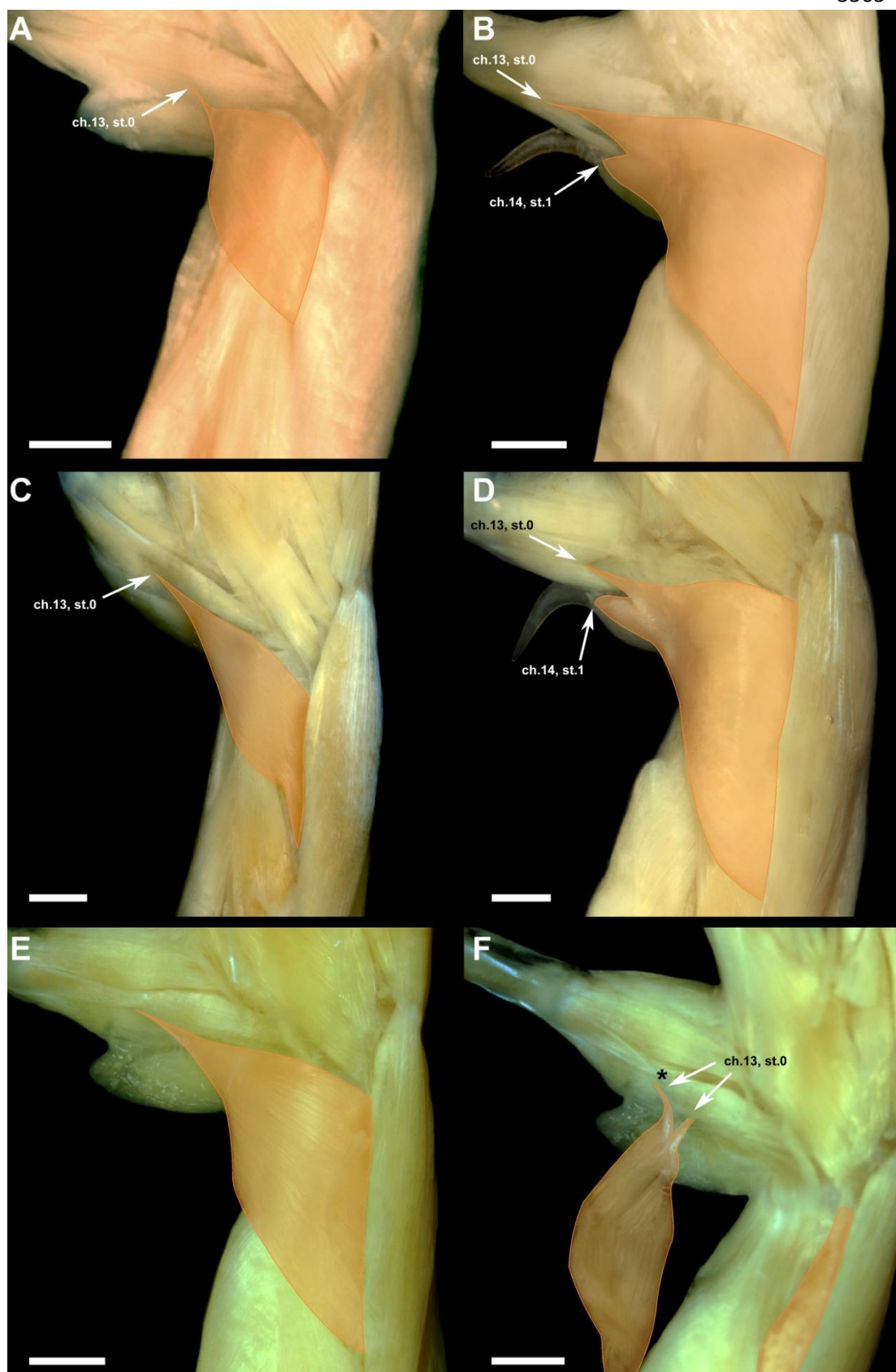


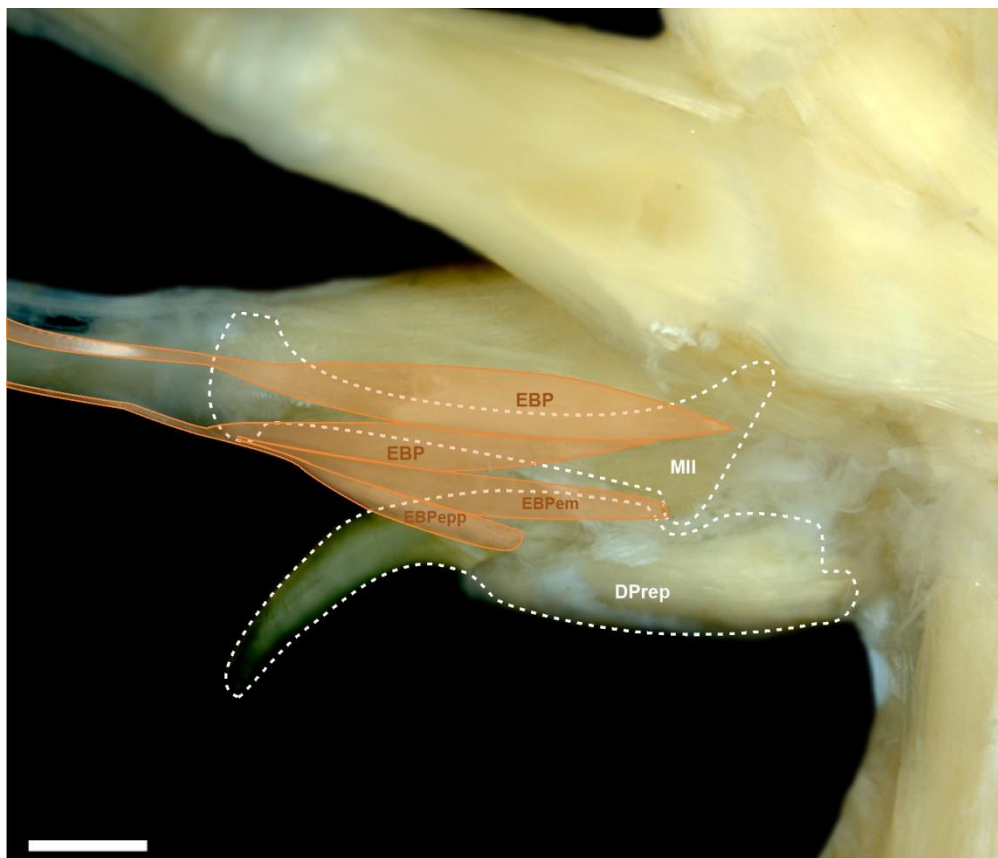
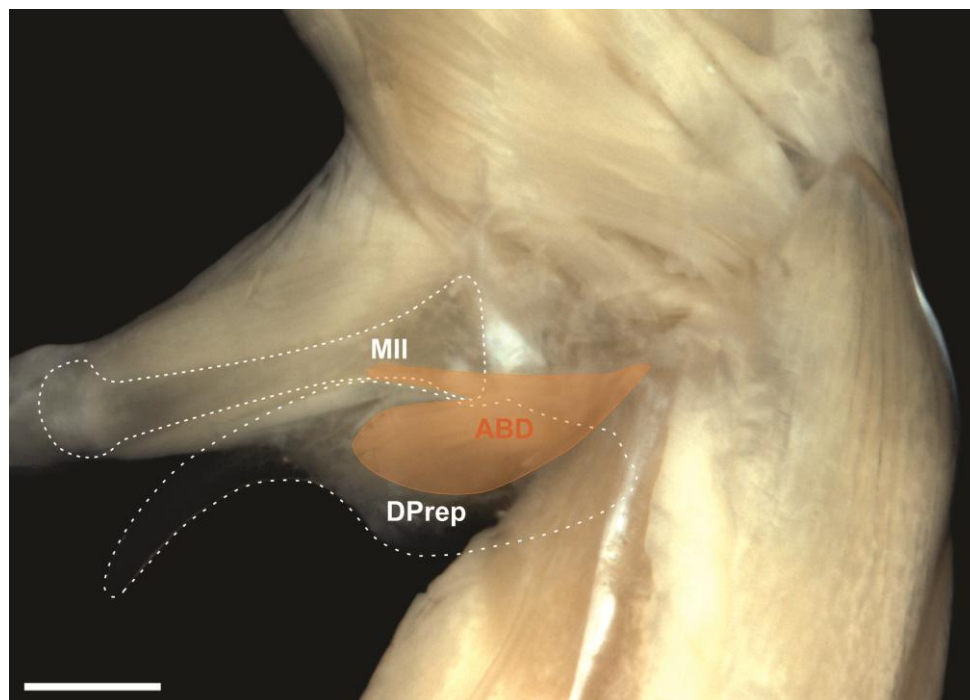
Figure 5.



3564 **Figure 6.**

3565



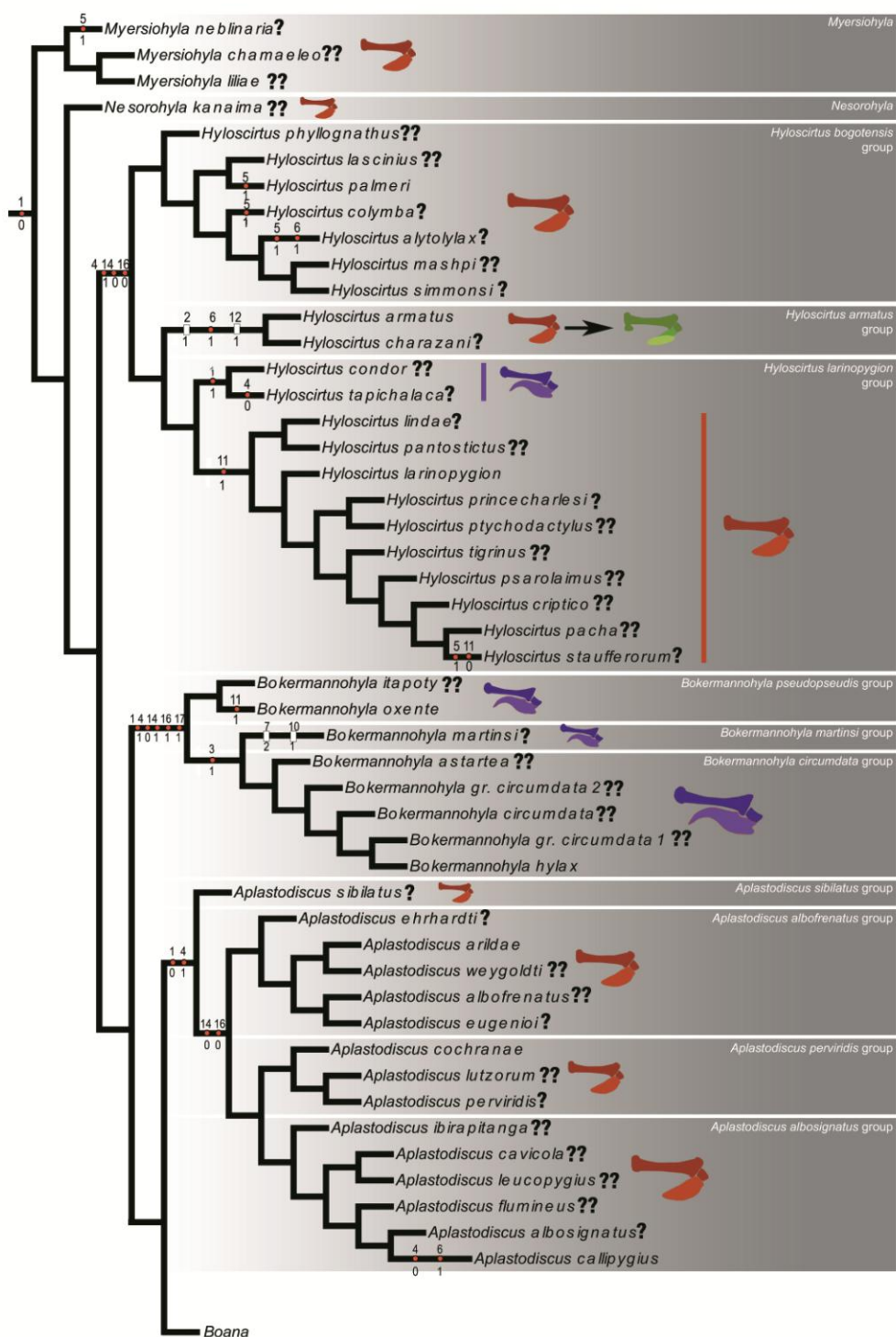
3566 **Figure 7.**3579 **Figure 8.**

3580

3581

3582

Figure 9.



3583

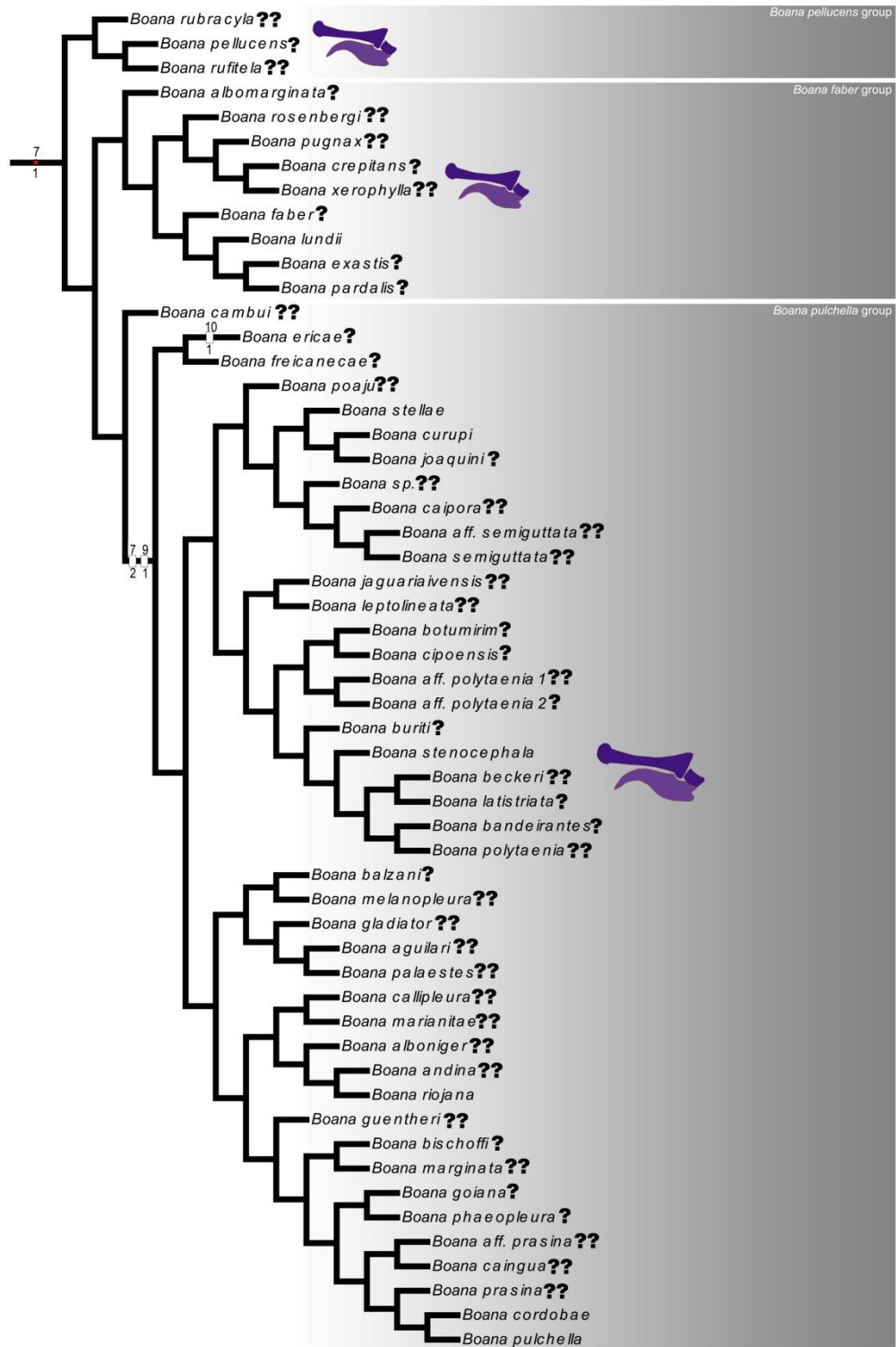
3584

3585



3587

Figure 9. Continued.



3588

3589 **SUPPLEMENTARY MATERIAL I**3590 Character Matrix showing states for the listed characters on the Results section. **(n/a)**

3591 character not applicable; (?) missing data; two numbers with a “/” indicate a

3592 polymorphism.

Taxa	Character States																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Aplastodiscus albosignatus</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Aplastodiscus arildae</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	0	0	1	0	0
<i>Aplastodiscus callipygius</i>	0	0	0	0	0	1	0	n/a	n/a	n/a	0	0	0	0	1	0	0
<i>Aplastodiscus cochranae</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	0	0	1	0	0
<i>Aplastodiscus ehrhardti</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Aplastodiscus eugenioi</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Aplastodiscus perviridis</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Aplastodiscus sibilatus</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Boana albomarginata</i>	1	0	1	0	n/a	n/a	1	0	0	0	1	0	?	?	?	?	?
<i>Boana albopunctata</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	0	1	1	0	0
<i>Boana atlantica</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Boana bandeirantes</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana bischoffi</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana boans</i>	1	0	1	0	n/a	n/a	1	0	0	0	1	0	?	?	?	?	?
<i>Boana botumirim</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana caiapo</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Boana calcarata</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Boana cf. stellae</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	0	1	1	1	0
<i>Boana cinerascens</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Boana cipoensis</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana cordobae</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	0	1	1	1	0
<i>Boana crepitans</i>	1	0	1	0	n/a	n/a	1	0	0	0	1	0	?	?	?	?	?
<i>Boana curupi</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	0	1	1	1	0
<i>Boana ericae</i>	1	0	1	0	n/a	n/a	2	0	1	1	1	0	?	?	?	?	?
<i>Boana exastis</i>	1	0	1	0	n/a	n/a	1	0	0	0	1	0	?	?	?	?	?
<i>Boana faber</i>	1	0	1	0	n/a	n/a	1	0	0	0	1	0	?	?	?	?	?
<i>Boana fasciata</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Boana freicanecae</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana geographica</i>	0	0	1	0	0	1	0	n/a	n/a	n/a	1	0	?	?	?	?	?
<i>Boana goiana</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana heilprini</i>	1	0	1	0	n/a	n/a	1	0	0	0	0	0	?	?	?	?	?
<i>Boana cf. joaquina</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana aff. joaquina</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?

<i>Boana lanciformis</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Boana latistriata</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana lundii</i>	1	0	1	0	n/a	n/a	1	0	0	0	1	0	0	1	1	1	0
<i>Boana microderma</i>	1	0	0	0	n/a	n/a	0	1	0	0	0	0	0	1	1	1	1
<i>Boana multifasciata</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Boana nympha</i>	1	0	1	0	n/a	n/a	0	1	0	0	1	0	?	?	?	?	?
<i>Boana ornatissima</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Boana pardalis</i>	1	0	1	0	n/a	n/a	1	0	0	0	1	0	?	?	?	?	?
<i>Boana pellucens</i>	1	0	1	0	n/a	n/a	1	0	0	0	0	0	?	?	?	?	?
<i>Boana phaeopleura</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana picturata</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Boana aff. polytaenia</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	?	?	?	?	?
<i>Boana pombali</i>	1	0	1	0	n/a	n/a	1	0	0	0	1	0	0	1	1	1	0
<i>Boana pulchella</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	0	1	1	1	0
<i>Boana punctata</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	0	1	1	1	0
<i>Boana raniceps</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	0	1	1	1	0
<i>Boana riojana</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	0	1	1	1	0
<i>Boana semilineata</i>	0	0	1	0	0/1	1	0	n/a	n/a	n/a	1	0	1	0	1	0	0
<i>Boana stenocephala</i>	1	0	1	0	n/a	n/a	2	0	1	0	1	0	0	1	1	1	0
<i>Boana tepuiana</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	0	1	1	1	1
<i>Boana wavrini</i>	1	0	1	0	n/a	n/a	1	0	0	0	0	0	?	?	?	?	?
<i>Bokermannohyla alvarengai</i>	1	0	1	0	n/a	n/a	0	0	0	0	0	0	?	?	?	?	?
<i>Bokermannohyla clepsydra</i>	1	0	1	0	n/a	n/a	1	0	0	0	1	0	?	?	?	?	?
<i>Bokermannohyla hylax</i>	1	0	1	0	n/a	n/a	0	0	0	0	0	0	0	1	1	1	1
<i>Bokermannohyla ibitiguara</i>	1	0	1	0	n/a	n/a	0	0	0	0	0	0	0	1	1	1	1
<i>Bokermannohyla juiju</i>	1	0	1	0	n/a	n/a	0	0	0	0	0	0	?	?	?	?	?
<i>Bokermannohyla langei</i>	1	0	1	0	n/a	n/a	2	0	0	1	0	0	?	?	?	?	?
<i>Bokermannohyla lucianae</i>	1	0	1	0	n/a	n/a	0	0	0	0	1	0	?	?	?	?	?
<i>Bokermannohyla luctuosa</i>	1	0	1	0	n/a	n/a	0	0	0	0	0	0	?	?	?	?	?
<i>Bokermannohyla martinsi</i>	1	0	1	0	n/a	n/a	2	0	0	1	0	0	?	?	?	?	?
<i>Bokermannohyla nanuzae</i>	1	0	1	0	n/a	n/a	0	0	0	0	0	0	?	?	?	?	?
<i>Bokermannohyla oxente</i>	1	0	0	0	n/a	n/a	0	0	0	0	1	0	0	1	1	1	1
<i>Bokermannohyla pseudopseudis</i>	1	0	1	0	n/a	n/a	0	0	0	0	0	0	0	1	1	1	1
<i>Bokermannohyla saxicola</i>	1	0	1	0	n/a	n/a	0	0	0	0	0	0	0	1	1	1	1
<i>Hyloscirtus alytolylax</i>	0	0	0	1	1	1	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus aff. alytolylax</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus antioquia</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus armatus</i>	0	1	n/a	1	0	1	0	n/a	n/a	n/a	0	1	0	0	1	0	0
<i>Hyloscirtus bogotensis</i>	0	0	0	1	1	1	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus callipeza</i>	0	0	0	1	2	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus caucanus</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus charazani</i>	0	1	n/a	1	0	1	0	n/a	n/a	n/a	0	1	?	?	?	?	?

<i>Hyloscirtus colymba</i>	0	0	0	1	1	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus denticulentus</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus larinopygion</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	1	0	0	0	1	0	0
<i>Hyloscirtus lindae</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	1	0	?	?	?	?	?
<i>Hyloscirtus lynchi</i>	0	0	0	1	2	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus palmeri</i>	0	0	0	1	1	0	0	n/a	n/a	n/a	0	0	0	0	1	0	0
<i>Hyloscirtus aff. palmeri</i>	0	0	0	1	0	1	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus aff. phyllognathus</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus piceigularis</i>	0	0	0	1	1	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus aff. piceigularis</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus platydactylus</i>	0	0	0	1	2	1	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus princecharlesi</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	1	0	?	?	?	?	?
<i>Hyloscirtus sarampiona</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus simmonsii</i>	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus aff. simmonsii</i> sp.1	0	0	0	1	1	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus aff. simmonsii</i> sp.2	0	0	0	1	0	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus staufferorum</i>	0	0	0	1	1	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Hyloscirtus tapichalaca</i>	1	0	0	0	n/a	n/a	0	0	0	0	0	0	?	?	?	?	?
<i>Hyloscirtus torrenticola</i>	0	0	0	1	0/2	0/1	0	n/a	n/a	n/a	0	0	?	?	?	?	?
<i>Myersiophyla neblinaria</i>	0	0	0	?	1	0	0	n/a	n/a	n/a	0	0	?	?	?	?	?

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SUPPLEMENTARY MATERIAL II

Table 1. Reports of fights and scars; male forearm hypertrophy; and habitats of species of Cophomantini which present a spine prepollux.

Species	Reports of Fights or Scars	Forearm hypertrophy in males	Habitat	References
<i>Hyloscirtus diabolus</i>	Scars	Greatly hypertrophied	Rocky streams	Rivera-Correa et al. (2016)
<i>H. tapichalaca</i>	Scars	Greatly hypertrophied	Rocky streams	Kizirian et al. (2003)
<i>Bokermannohyla alvarengai</i>	Scars*	Greatly hypertrophied*	Rocky streams*	Pers. Obs.
<i>Bok. astartea</i>	Scars (L. Malagoli, per. comm.)	Hyperthrophied	Bromeliads in small streams	Bokermann (1967)
<i>Bok. caramaschii</i>	Scars (on photo)	Hyperthrophied	Rocky streams	Napoli (2005)
<i>Bok. ibitiguara</i>	Scars	Hyperthrophied	Rocky streams	Nali et al. (2012)
<i>Bok. itapoty</i>	Fight	Hyperthrophied	Rocky streams	Lugli and Haddad (2006)
<i>Bok. martinsi</i>	Scars*	Greatly hypertrophied*	Rocky streams*	Pers. Obs.
<i>Bok. nanuzae</i>	Scars (on photo)	?	Rocky streams	Bokermann and Sazima (1973)
<i>Bok. napolii</i>	Scars	Hyperthrophied	Streams	Carvalho et al. (2012)
<i>Bok. pseudopseudis</i>	Scars	Hyperthrophied	Streams	Magalhães et al. (2016)
<i>Bok. ravida</i>	Scars (on photo)	Hyperthrophied	Rocky streams	Caramaschi et al. (2001)
<i>Boana aguilari</i>	Scars	Not hypertrophied	Shallow waters	Lehr et al. (2010)
<i>Boa. albomarginata</i>	Fight	Not hypertrophied	Lentic water bodies	Giasson and Haddad (2007)
<i>Boa. albopunctata</i>	Fight	Not hypertrophied	Lentic water bodies	Toledo et al. (2007)
<i>Boa. bandeirantes</i>	Scars*	Not hypertrophied*	Swampy*	Pers. Obs.
<i>Boa. beckeri</i>	Scars*	Not hypertrophied*	Swampy*	Pers. Obs.
<i>Boa. bischoffi</i>	Fight	Not hypertrophied	Lentic water bodies	Toledo et al. (2007)
<i>Boa. boans</i>	Fight	?	Streams	Duellman (2005)

<i>Boa. caipora</i>	Scars	Hyperthrophied	Forest streams	Antunes et al. (2008)
<i>Boa. cambui</i>	Scars	Not hypertrophied	Inundated areas in forests	Pinheiro et al. (2016)
<i>Boa. cipoensis</i>	Scars*	Not hypertrophied*	Lentic water bodies*	Pers. Obs.
<i>Boa. curupi</i>	Scars	Hyperthrophied	Lentic water bodies	Garcia et al. (2007)
<i>Boa. ericae</i>	Scars	Not hypertrophied	Lentic water bodies*	Garcia and Haddad (2008)
<i>Boa. exastis</i>	Scars	Not hypertrophied	?	Caramaschi and Rodrigues (2003)
<i>Boa. faber</i>	Scars	Not hypertrophied	Ponds and wet areas	Martins et al. (1988)
<i>Boa. gladiator</i>	Scars	Hyperthrophied	Rocky streams	Köhler et al. (2010)
<i>Boa. goiana</i>	Scars	Not hypertrophied	Lentic water bodies*	Menin et al. (2004)
<i>Boa. joaquini</i>	Scars	Hyperthrophied	Streams	Garcia et al. (2007)
<i>Boa. latistriata</i>	Scars*	Not hypertrophied	Stream and ponds in highlands	Orrico et al. (2007)
<i>Boa. leptolineata</i>	Scars*	Not hypertrophied*	Swampy*	Pers. Obs.
<i>Boa. leucocheila</i>	Scars (photo on Caramaschi and Niemeyer, 2003)	Not hypertrophied	Streams	Pansonato et al. (2011)
<i>Boa. lundii</i>	Fight	Not hypertrophied	Lentic water bodies	Pimenta et al. (2014)
<i>Boa. marginata</i>	Scars	Hyperthrophied	Streams	Garcia et al. (2001)
<i>Boa. marianitae</i>	Scars	Not hypertrophied	Rocky streams	Duellman et al. (1997)
<i>Boa. melanopleura</i>	Scars	Not hypertrophied	?	Lehr et al. (2010)
<i>Boa. paranaiba</i>	Scars	Not hypertrophied	Streams	Carvalho et al. (2010)
<i>Boa. pardalis</i>	Scars	?	Ponds and wet areas	Lutz (1973)
<i>Boa. phaeopleura</i>	Scars (on photo)	Not hypertrophied	Lentic water bodies*	Caramaschi and Cruz (2000)
<i>Boa. poaju</i>	Scars	Hyperthrophied	Rocky streams	Garcia et al. (2008)
<i>Boa. polytaenia</i>	Scars*	Not hypertrophied	Swampy*	Pers. Obs.
<i>Boa. pugnax</i>	Fight	Not hypertrophied	Drainages of rivurine	Kluge (1979)

			environments	
<i>Boa. punctata</i>	Fight	Not hypertrophied	Lakes and inundated areas	Brunetti et al. (2014)
<i>Boa. riojana</i>	Scars (photo on fig. 3P of Köhler et al 2010)	Hyperthrophied	Rocky streams	Barrio (1965)
<i>Boa. rosenbergi</i>	Fight	Not hypertrophied	Streams	Kluge (1981)
<i>Boa. secedens</i>	Scars (on photo)	Not hypertrophied	Forest streams	Weber et al. (2009)
<i>Boa. semiguttata</i>	Scars	Hyperthrophied	Forest streams	Garcia et al. (2007)
<i>Boa. stellae</i>	Scars	Hyperthrophied	Forest streams	Kwet (2008)
<i>Boa. wavrini</i>	Scars	Not hypertrophied	Inundated areas in forests	Hoogmoed (1990)
<i>Boa. xerophylla</i>	Fight	Not hypertrophied	Temporary ponds	Kluge (1979)

*P.D.P. Pinheiro pers. observ.

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CONCLUSÕES GERAIS

- O nome *Hyla leucotaenia* Burmeister, 1860, que vinha sendo tratado como sinônimo júnior de *Hyla pulchella* Duméril & Bibrón, 1841, na verdade é um sinônimo de *Hyla squalirostris* Lutz, 1925. Caso esta espécie (atualmente alocada no gênero *Scinax*) se mostre na verdade constituir um complexo de espécies, e, as populações do Sul do Brasil, Uruguai e norte da Argentina se mostrem uma unidade taxonômica distinta, o nome *Hyla leucotaenia* se mostra disponível e perfeitamente aplicável para estas.
- *Boana cambui* (nova combinação entre a descrição original e a taxonomia vigente) corroborou-se pertencente ao grupo de *B. pulchella* nas análises moleculares. Apesar da morfologia extremamente similar à congênica *B. freicanecae*, as duas não são espécies irmãs, de acordo com nossas inferências moleculares. Mas por ser a espécie irmã de todas as demais espécies do grupo de *B. pulchella*, *B. cambui* dá suporte à hipótese de este grupo ter sido originado de uma linhagem evolutiva ocorrente na Mata Atlântica, no sudeste do Brasil.
- *Boana caiapo* corroborou-se pertencente ao grupo de *B. albopunctata* nas análises moleculares, como irmã de *B. raniceps*. Este resultado ajuda a demonstrar a importância do Cerrado no processo de radiação evolutiva do grupo de *B. albopunctata*.
- *Boana liliae* (Kok, 2006) trata-se na realidade de uma espécie de *Myersiohyla*, irmã de *M. chamaeleo*.
- Nós provemos aqui o maior data set molecular de *Boana* construído até o momento. Incluindo quase a total diversidade taxonômica do gênero (83 das 92 espécies descritas) com até 10 fragmentos genéticos por terminal. O suporte de muitos relacionamentos filogenéticos dentro do gênero melhorou em relação a publicações passadas. Porém, mesmo com tal data set, o suporte do grupo de *B. benitezi* permanece baixo, e o relacionamento deste grupo, e também dos grupos de *Boana punctata* e *B. semilineata*

com os demais grupos de *Boana* permanece incerto. O que é bastante curioso. Isso nos faz pensar que uma amostragem massiva de caracteres moleculares (NGS) e fenotípicos é crucial para entender as relações evolutivas de *Boana*.

- O pré-polex das espécies de Cophomantini apresenta uma plasticidade evolutiva extremamente interessante. Suas duas formas gerais, laminar e espinho, surgiram mais de uma vez ao longo da evolução da tribo. No caso do grupo de *Hyloscirtus armatus* o pré-polex laminar sofreu uma modificação única na tribo. As espécies de *Boana* apresentam um processo articular na região proximal do Metacarpo II que articula com o pré-polex. Esta estrutura aparenta ser sinapomórfica para o gênero. Junto à estrutura esquelética foram descobertas diversas modificações de musculatura que provavelmente desempenham diferentes funções de acordo com a morfologia do pré-polex. Apesar de o pré-polex em forma de espinho ser correntemente considerado como uma estrutura protrusível, tal mecanismo permanece desconhecido.