



## Phylogenetic relationships of the poorly known treefrog *Boana hobbsi* (Cochran & Goin, 1970) (Anura: Hylidae), systematic implications and remarks on morphological variations and geographic distribution

ALEXANDRE P. DE ALMEIDA<sup>1,2\*</sup>, LEANDRO J.C.L. MORAES<sup>3,7</sup>, ROMMEL R. ROJAS<sup>2,8</sup>,  
IGOR J. ROBERTO<sup>2,9</sup>, VINICIUS TADEU DE CARVALHO<sup>2,4,10</sup>, ROBSON W. ÁVILA<sup>5,11</sup>,  
LUCIANA FRAZÃO<sup>2,12</sup>, ARIANE A.A. SILVA<sup>3,13</sup>, MARCELO MENIN<sup>1,6,14</sup>, FERNANDA P. WERNECK<sup>3,15</sup>,  
TOMAS HRBEK<sup>1,2,16</sup>, IZENI P. FARIAS<sup>1,2,17</sup> & MARCELO GORDO<sup>1,6,18</sup>

<sup>1</sup>Universidade Federal do Amazonas, Instituto de Ciências Biológicas, Programa de Pós-Graduação em Zoologia, Avenida General Rodrigo Otávio J. Ramos 6200, 69080-900, Manaus, Amazonas, Brazil.

<sup>2</sup>Universidade Federal do Amazonas, Laboratório de Evolução e Genética Animal, Departamento de Genética, Avenida General Rodrigo Otávio J. Ramos 6200, Japim, 69080-900, Manaus, Amazonas, Brazil.

<sup>3</sup>Instituto Nacional de Pesquisas da Amazônia (INPA), Coordenação de Biodiversidade, Programa de Coleções Científicas Biológicas, Avenida André Araújo, 69067-375, Petrópolis, Manaus, Amazonas, Brazil.

<sup>4</sup>Universidade Regional do Cariri, Programa de Pós-Graduação em Diversidade Biológica e Recursos Naturais, Campus do Pimenta, Rua Cel. Antônio Luiz, 1161, 63105-000, Crato, Ceará, Brazil.

<sup>5</sup>Universidade Federal do Ceará, Departamento de Biologia, Centro de Ciências, Campus do Pici, Fortaleza, Ceará, Brazil

<sup>6</sup>Universidade Federal do Amazonas, Departamento de Biologia, Avenida General Rodrigo Otávio J. Ramos, 6200, Coroado, 69080-900, Manaus, Amazonas, Brazil.

<sup>7</sup>✉ [leandro.jclm@gmail.com](mailto:leandro.jclm@gmail.com); <https://orcid.org/0000-0001-6704-898X>

<sup>8</sup>✉ [rrojaszamora@gmail.com](mailto:rrojaszamora@gmail.com); <https://orcid.org/0000-0003-3154-8549>

<sup>9</sup>✉ [igorjoventino@yahoo.com.br](mailto:igorjoventino@yahoo.com.br); <https://orcid.org/0000-0003-3268-9597>

<sup>10</sup>✉ [anfibilios.repteis@gmail.com](mailto:anfibilios.repteis@gmail.com); <https://orcid.org/0000-0001-7644-6090>

<sup>11</sup>✉ [robsonavila@gmail.com](mailto:robsonavila@gmail.com); <https://orcid.org/0000-0003-3641-8321>

<sup>12</sup>✉ [luca.frazao@gmail.com](mailto:luca.frazao@gmail.com); <https://orcid.org/0000-0002-4715-2728>

<sup>13</sup>✉ [ariane.silva@inpa.gov.br](mailto:ariane.silva@inpa.gov.br); <https://orcid.org/0000-0002-3172-8446>

<sup>14</sup>✉ [menin.m@gmail.com](mailto:menin.m@gmail.com); <https://orcid.org/0000-0002-7209-5083>

<sup>15</sup>✉ [fewerneck@gmail.com](mailto:fewerneck@gmail.com); <https://orcid.org/0000-0002-1335-0822>

<sup>16</sup>✉ [tomas@evoamazon.net](mailto:tomas@evoamazon.net); <https://orcid.org/0000-0003-3239-7068>

<sup>17</sup>✉ [izeni@evoamazon.net](mailto:izeni@evoamazon.net); <https://orcid.org/0000-0002-1416-4351>

<sup>18</sup>✉ [mgordo@ufam.edu.br](mailto:mgordo@ufam.edu.br); <https://orcid.org/0000-0001-5230-9091>

\*Corresponding author. ✉ [alexandre.dealmeida@hotmail.com](mailto:alexandre.dealmeida@hotmail.com); <https://orcid.org/0000-0003-3938-4198>

### Abstract

*Boana hobbsi* is a poorly known hylid frog currently placed within the *Boana punctata* group. Yet, morphological, ecological and bioacoustic traits do not support this placement, with no molecular data being available to date to test this hypothesis. Based on newly collected mitochondrial DNA sequences, morphological data review and field observations, we provide new insight into the phylogenetic relationships, morphological variations and geographic distribution of *B. hobbsi*. Our findings reveal that *B. hobbsi* is nested (with strong support) within the *Boana benitezi* group, recovering once more a polyphyletic *Boana punctata* group. Supported by this new genetic, morphological and ecological evidence, we propose a new taxonomic arrangement which includes *B. hobbsi* as a member of the *Boana benitezi* group. Furthermore, we emphasize the importance of conducting biological inventories in remote Amazonian areas, where many taxonomic and geographic knowledge gaps persist with regards to Amphibian diversity.

**Key words:** Amazonia, Cophomantini, *B. benitezi* group, *B. punctata* group, Darwinian shortfall, Phylogeny, Wallacean shortfall

### Introduction

Biodiversity research in the Neotropics is a scientific priority across many knowledge areas (Antonelli *et al.* 2018a).

However, conducting studies in this region can be particularly challenging due its high species-richness (Moritz *et al.* 2000; Field *et al.* 2009) and vast area covering many biomes (Morrone, 2014; Antonelli *et al.* 2018b). Such a complex system generates knowledge bias of species diversity and of their respective geographic distributions limits, resulting in the so-called Linnean and Wallacean shortfalls (Whittaker *et al.* 2005; Cardoso *et al.* 2011). Among Neotropical fauna, knowledge involving anurans is particularly affected by these shortfalls. In addition to that, the high levels of cryptic species with morphological conservativeness within this group (Funk *et al.* 2012; Castroviejo-Fisher *et al.* 2017; Rojas *et al.* 2018; Ramos *et al.* 2019; Carvalho *et al.* 2020) and the many gaps on species geographic distributions (Mayer *et al.* 2019) result in a lack of fully resolved phylogenies known as the Darwinian shortfall (Diniz-Filho *et al.* 2013). Those issues persist even in common and widespread anuran taxa, such as the species of *Boana punctata* group.

The *Boana punctata* group (formerly named *Hypsiboas punctatus* group; see Dubois 2017 for nomenclatural changes), originally included eight species (Faivovich *et al.* 2005): *B. alemani* (Rivero, 1964), *B. atlantica* (Caramaschi & Velosa, 1996), *B. punctata* (Schneider, 1799), *B. cinerascens* (Spix, 1824), *B. hobbsi* (Cochran & Goin, 1970), *B. ornatissima* (Noble, 1923), *B. picturata* (Boulenger, 1899), and *B. siblezi* (Rivero, 1972). Two additional species were later included in this group, based on their overall morphological similarities with *B. cinerascens* (Kok 2006; Señaris & Ayarzagüena 2006): *B. liliae* (Kok, 2006) and *B. jimenezi* (Señaris & Ayarzagüena, 2006). However, subsequent studies evidenced this arrangement as non-monophyletic (Pyron & Wiens 2011; Faivovich *et al.* 2013; Duellman *et al.* 2016; Pinheiro *et al.* 2019; Sturaro *et al.* 2020), resulting in the transfer of *B. ornatissima* to the *Boana benitezi* group (Faivovich *et al.* 2013), and of *B. liliae* to the genus *Myersiohyala* Faivovich *et al.* 2005 (Pinheiro *et al.* 2019). These taxonomic uncertainties are also consequences of the uncertain phylogenetic relationships of *B. siblezi*, *B. picturata* and *B. jimenezi*; and of the absence of genetic and refined phenotypic data for some nominal taxa (*B. alemani* and *B. hobbsi*—Wiens *et al.* 2005; Faivovich *et al.* 2013; Duellman *et al.* 2016; Pinheiro *et al.* 2019; Sturaro *et al.* 2020).

*Boana hobbsi* (Cochran & Goin 1970) is a treefrog with a complex taxonomic history, described for forested habitats of northwestern lowland Amazonia (Cochran & Goin 1970). Authors describe the presence of dorsolateral folds over the shoulders as a diagnostic character for the species (Cochran & Goin 1970). This apomorphic character, unknown for any other South American hylid frog, precluded the authors from hypothesizing the phylogenetic relationships of *B. hobbsi*. Duellman (1974) reviewed the taxonomic status of some Neotropical frogs and concluded that this unique diagnostic feature was, in fact, an artifact that resulted from the shrinkage of the preserved holotype caused by the high alcohol concentration during storage. As a result, Duellman (1974) synonymized *B. hobbsi* with the widely distributed *B. punctata*. Nevertheless, Pyburn (1978) noticed that divergences in external morphology of living specimens, habitat preferences and advertisement calls did not support this synonymization and restored the full species status of *B. hobbsi* after examining new specimens and the type series. Furthermore, Pyburn (1978) argued based on the evidence at hand that *B. hobbsi* and *B. punctata* may not even be closely related.

In the phylogenetic revision of Hylidae, Faivovich *et al.* (2005) tentatively placed *B. hobbsi* within the *B. punctata* group using this historical taxonomic assessment as support, given the lack of hard data at hand. To date, the phylogenetic placement of *B. hobbsi* within *Boana* remains to be formally tested. After the study of Pyburn (1978), no additional taxonomic or phylogenetic studies included this species. Knowledge advances associated with this species are mostly based only on new distributional records in the rainforests of Colombia (Ruiz-Carranza *et al.* 1996; Acosta-Galvis 2000, 2018; Lynch 2005, 2007; Suárez-Mayorga & Lynch 2017), Venezuela (McDiarmid *et al.* 1988; Barrio-Amorós *et al.* 2019) and Brazil (Simões *et al.* 2019). The latter also presents descriptions of the species advertisement calls (Simões *et al.* 2019).

Based on a new record series of *B. hobbsi* specimens collected in field expeditions at the extreme northwest of Brazil, we assess here, for the first time, the species phylogenetic position based on molecular data, testing the assignment of *B. hobbsi* to the *Boana punctata* group. We also provide data on the external morphology of these specimens and compare it with known variations of closely related taxa. In addition, we provide new data on the species geographic distribution in the Brazilian Amazon forest.

## Material and methods

We recorded individuals of *B. hobbsi* during night surveys by visual encounter, following Crump & Scott Jr. (1994).

Fieldwork was conducted at the forest margins of small streams from two distinct localities in the northwest region of the state of Amazonas, Brazil. Six specimens were collected on the right bank of the Japurá River (1.845994° S, 69.029466° W), located about 50 km southeast of Vila Bittencourt, at the end of rainy season on September 8<sup>th</sup>, 2014. Five specimens were collected in the vicinity of the city of São Gabriel da Cachoeira, on November 15<sup>th</sup>, 2016 (0.130547°S, 67.038947°W). Collected specimens were euthanized with a topical solution of 10% xylocaine, and their femoral muscle or liver tissues were collected and stored in 95% ethanol. Specimens were then fixed with 10% formalin, afterwards preserved in 70% ethanol and deposited at the amphibian section of the Paulo Bührnheim Zoological Collection of the Federal University of Amazonas (CZPB-AA), and at the Amphibians and Reptiles Collection of the National Institute of Amazonian Research (INPA-H), both located in the city of Manaus, Brazil (see voucher numbers at Appendix I). Collecting permits were issued by the Chico Mendes Institute of Biodiversity Conservation (ICMBio/SISBio #11323 and ICMBio/SISBio #44832).

**Molecular data collection and phylogenetic analysis.** We extracted total DNA using standard phenol/chloroform technique (Sambrook *et al.* 1989) and the Wizard® commercial kit (Promega, Wisconsin, USA). We selected the mitochondrial 16S ribosomal RNA gene (16S) as a molecular marker due to its recognized relevance as the amphibian DNA barcode (Vences *et al.* 2005; Fouquet *et al.* 2007; Padial & De la Riva, 2009; Padial *et al.* 2012), and to its efficiency in revealing phylogenetic relationships (e.g., Fouquet *et al.* 2011; Avila *et al.* 2018). The 16S gene was amplified with primers 16Sar and 16Sbr (Palumbi 1996) via Polymerase Chain Reactions (PCR) in 15 µL reaction volumes containing 5.8 µL of ddH<sub>2</sub>O, 1.5 µL of 25mM MgCl<sub>2</sub>, 1.5 µL of 10X amplification buffer (75mM of Tris HCl, 50 mM of KCl and 20 mM of (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>), 1.5 µL of a 2 µM solution of each primer, 1.5 µL of 10 mM dNTPs (2.5mM of each dNTP), 0.7 µL of Taq DNA polymerase 1 U/µL (Fermentas, Lithuania) and 1 µL of template DNA (about 40 ng/µL). The temperature profile consisted of (a) preheating at 90 °C for 60 s, (b) denaturation at 92 °C for 60 s, (c) primer annealing at 50 °C for 50 s, (d) extension at 72 °C for 90 s, and (e) final extension at 72 °C for 5 min. Steps 2–4 were repeated in 35 cycles. PCR products were purified with exonuclease and alkaline phosphatase (Fermentas, Lithuania), and sequenced using standard protocols of ABI BigDye Terminator Cycle Sequencing Kit (ThermoFisher, USA). The resulting single-stranded products were resolved on an ABI 3130xl automatic capillary sequencer and edited using Geneious v.6.1.8. (Kearse *et al.* 2012). Laboratory procedures were conducted at the Laboratory of Animal Genetics and Evolution (LEGAL)—UFAM, and the Thematic Laboratory of Molecular Biology (LTBM)—INPA, both in the city of Manaus, Brazil.

We compiled a dataset containing the new 16S gene sequences of eight specimens of *B. hobbsi*, together with additional 75 homologous sequences downloaded from GenBank (Benson *et al.* 2013); these included 73 sequences of 53 congeneric species, and two sequences of the closely related genus *Aplastodiscus* Lutz, 1950, which were used as outgroup. To embrace the historical knowledge of hyloid frog phylogenies, as well as the most recent taxonomic and systematic changes in its groups, our dataset included sequences from: broader phylogenetic studies (e.g. Salducci *et al.* 2002; Darst & Cannatella, 2004; Faivovich *et al.* 2004; 2005; Köhler *et al.* 2010; Berneck *et al.* 2016; Lyra *et al.* 2017), studies on cryptic diversity and new species descriptions (e.g. Fouquet *et al.* 2007, 2015, 2016; Antunes *et al.* 2008; Lehr *et al.* 2010; Jansen *et al.* 2011; Funk *et al.* 2012; Caminer & Ron, 2014, 2020; Guarnizo *et al.* 2015; Peloso *et al.* 2018; Motta *et al.* 2018) and recent studies focused in the *B. punctata* group (Lima *et al.* 2019; Sturaro *et al.* 2020). Our dataset (Appendix I) contains representatives of all groups within *Boana* proposed by Faivovich *et al.* (2005). We aligned the dataset using the MAFFT online service, applying the L-INS-i strategy (Katoh *et al.* 2019), and selected the molecular substitution model GTR+I+G based on Akaike Information Criterion, as implemented in PartitionFinder 2.1.1 (Lanfear *et al.* 2017). The phylogenetic tree was inferred under a Bayesian framework, using the software MrBayes 3.2.6 (Ronquist *et al.* 2012), with two independent runs of 30<sup>6</sup> generations. We assessed parameter convergence through stability and convergence between independent and combined runs, and effective sample size (ESS) > 200 using the software Tracer 1.7 (Rambaut *et al.* 2018). We discarded a 10% burn-in of samples and extracted the maximum clade credibility (MCC) tree. Phylogenetic analysis was performed using CIPRES Science Gateway version 3.3 (Miller *et al.* 2010). We additionally estimated uncorrected pairwise distances (p-distances) between the sequences of our newly collected *B. hobbsi* specimens and of closely related congeners (newly evidenced and formerly considered). We estimated uncorrected p-distances using gamma rates and default parameters in MEGA X (Kumar *et al.* 2018).

**Morphological data.** We obtained the following morphometric measurements of 11 adult specimens: snout-vent length (SVL), head length (HL), head width (HW), interorbital distance (IOD), eye-nostril distance (EN), snout length (SL), eye diameter (ED), tympanum diameter (TD), tibia length (TL), thigh length (THL), tarsus length (TSL), foot length (FL), forearm length (FAL), and hand length (HAL). Measurements were taken with a digital caliper with a precision of 0.01 mm, and the terminology followed Kok & Kalamandeen (2008) and Watters *et al.* (2016). Webbing formula notation followed Savage & Heyer (1967), as modified by Myers & Duellman (1982). Fingers and toes were numbered pre-axially to post-axially, from I–IV and I–V, respectively. Sex was determined by the presence of vocal slits, prepollical spines and body size (Pyburn 1978). Color pattern in life was described based on field notes and photographs of living individuals.

## Results

### Phylogenetic analysis

Our alignment resulted in a dataset with 558 base pairs (bp) and 81 terminals from the genus *Boana*. Bayesian phylogenetic inferences based on two combined runs (LnL = -6907.7745, ESS = 5334) recovered a tree topology with high support values (posterior probability = 0.95–1.0) for major clades that can be directly associated with previously recognized groups, with the exception of the *Boana pulchella* and *Boana albopunctata* groups, which were recovered with low support values (Fig. 1). Even so, phylogenetic relationships among these major clades were poorly supported (posterior probability < 0.5) most likely due to the limited phylogenetic signal of the 16S gene in deeper nodes.

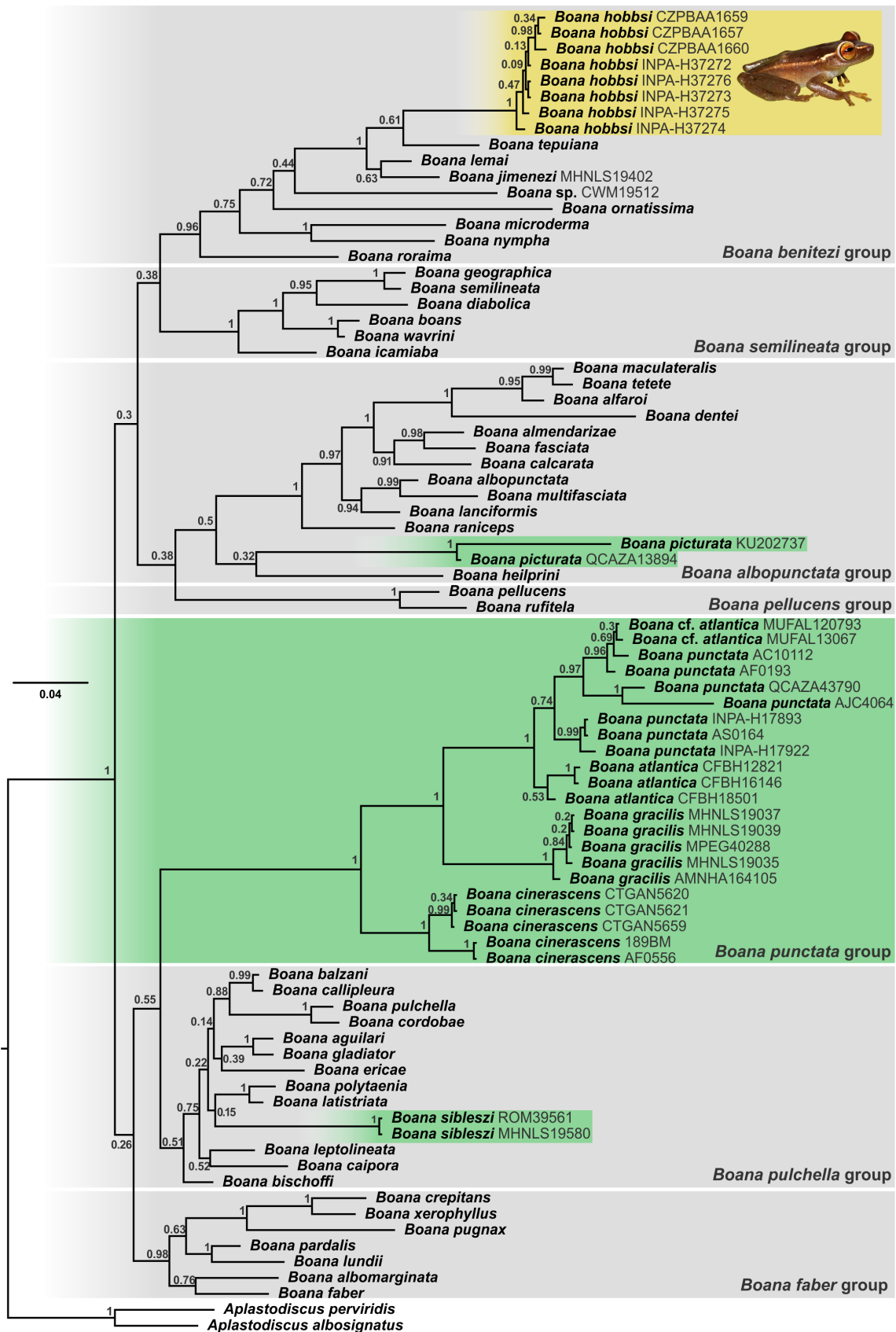
Our analysis did not recover the *B. punctata* group as monophyletic. Instead, *Boana sibleszi* was recovered with low support as the sister-taxon of a subclade composed by *B. polytaenia* (Cope, 1870) and *B. latistriata* (Caramaschi & Cruz, 2004), therefore nested in the *B. pulchella* group. *Boana picturata* was recovered with low support as the sister-taxon of *Boana heilprini* (Noble, 1923b), therefore nested in the *Boana albopunctata* group. *Boana jimenezi* and *B. hobbsi* were recovered nested in a highly supported clade corresponding to the *Boana benitezi* group (Fig. 1). The other green-colored species *B. atlantica*, *B. punctata*, *B. cinerascens* and *B. gracilis* formed a highly supported clade that comprised the former group of “green *Hylas* from Amazonian Hylaea” (Lutz, 1948), herein treated as the *Boana punctata* group *sensu stricto* (Fig. 1). *Boana hobbsi* was recovered as monophyletic and the sister-taxon of *Boana tepuiana* (Barrio-Amorós & Brewer-Carias, 2008), although with low support (pp = 0.61). This clade is sister to a clade composed of *B. lemai* (Rivero, 1972) and *B. jimenezi* that also is poorly supported (pp = 0.63). These four species comprise a highly supported clade (pp = 1) within the *B. benitezi* group (Fig. 1). Genetic distances (p-distances) between specimens of *B. hobbsi* from the two sampled localities are low, ranging from 0.1% to 1.2% (Table 1). When comparing specimens of *B. hobbsi* to other species of the *B. benitezi* group, the genetic distances ranged from 7% to 15% (Table 2), representing lower values in comparison to that of members of the *B. punctata* group (range 12–16%) (Table 3). Based on this molecular evidence, we propose to include *B. hobbsi* and *B. jimenezi* in the *B. benitezi* group, maintaining the monophyly of this non-morphologically diagnosable group. Our proposal regarding *B. jimenezi* is supported by the systematic review of the *B. punctata* group (Sturaro *et al.* 2020), who found the same result for its phylogenetic position nested in the *B. benitezi* group. To support this new arrangement, we also compare the morphological variations of *B. hobbsi*—which includes the new collected data here presented—with morphological variations of other members of this group.

### Systematic account and new data on morphology and distribution of *B. hobbsi*

#### Family Hylidae Rafinesque, 1815

#### Tribe Cophomantini (Faivovich, 2005)

#### Genus *Boana* Gray, 1825



**FIGURE 1.** Bayesian phylogenetic tree of the genus *Boana*, based on a fragment of the 16S mitochondrial rRNA, highlighting the position of *Boana hobbsi* (in yellow) in comparison to major clades representing known species groups, and indicating the phylogenetic position of remaining species included in the *B. punctata* group (in green). Support values are indicated close to the nodes. Branch scale is indicated as number of substitutions per site.

### *Boana benitezi* species group (Faivovich, 2005)

**Diagnosis.** No known morphological synapomorphy (see Faivovich, 2005). Faivovich *et al.* (2005; 2006) proposed the presence of a flat mental gland as a putative synapomorphy for this group. However, this character is widely shared among hylid species (Brunetti *et al.* 2012; 2015; Faivovich *et al.* 2013) and its consideration as a synapomorphic character for this group remains dubious (Barrio-Amorós & Brewer-Cárias 2008).

**Species content.** Ten species. *Boana benitezi* (Rivero, 1961); *Boana hobbsi* (Cochran & Goin, 1970) *Boana jimenezi* (Señaris & Ayarzagüena, 2006); *Boana lemai* (Rivero, 1971); *Boana microderma* (Pyburn, 1977); *Boana nympa* (Faivovich, Moravec, Cisneros-Heredia, & Köhler, 2006); *Boana ornatissima* (Noble, 1923a); *Boana rhythmica* (Señaris & Ayarzagüena, 2002); *Boana roraima* (Duellman & Hoogmoed, 1992); *Boana tepuiana* (Barrio-Amorós & Brewer-Cárias, 2008).

### *Boana hobbsi* (Cochran & Goin, 1970)

**Holotype.** MCZ 28052, from Caño Guacayá, a tributary of the Rio Apaporis, Amazonas, Colombia.

**TABLE 1.** Uncorrected pairwise distances between samples of *Boana hobbsi* (Cochran & Goin, 1970) from the two new localities of occurrence, showing low genetic distances. Specimens from the Japurá River (vicinity of Vila Bittencourt, Amazonas, Brazil) are represented with CZPB-AA vouchers, while the ones from São Gabriel da Cachoeira, Amazonas, Brazil are represented with INPA-H vouchers.

Specimens	1	2	3	4	5	6	7	8
1 <i>B. hobbsi</i> CZPB-AA 1657								
2 <i>B. hobbsi</i> CZPB-AA 1659	0.002							
3 <i>B. hobbsi</i> CZPB-AA 1660	0.005	0.007						
4 <i>B. hobbsi</i> INPA-H 37272	0.002	0.005	0.007					
5 <i>B. hobbsi</i> INPA-H 37273	0.002	0.005	0.007	0.001				
6 <i>B. hobbsi</i> INPA-H 37274	0.007	0.010	0.012	0.004	0.004			
7 <i>B. hobbsi</i> INPA-H 37275	0.005	0.007	0.010	0.002	0.002	0.006		
8 <i>B. hobbsi</i> INPA-H 37276	0.002	0.005	0.007	0.001	0.001	0.004	0.002	

**TABLE 2.** Uncorrected pairwise distances between samples of *Boana hobbsi* (Cochran & Goin, 1970) and congeneric species of the *Boana benitezi* group (highlighted in bold).

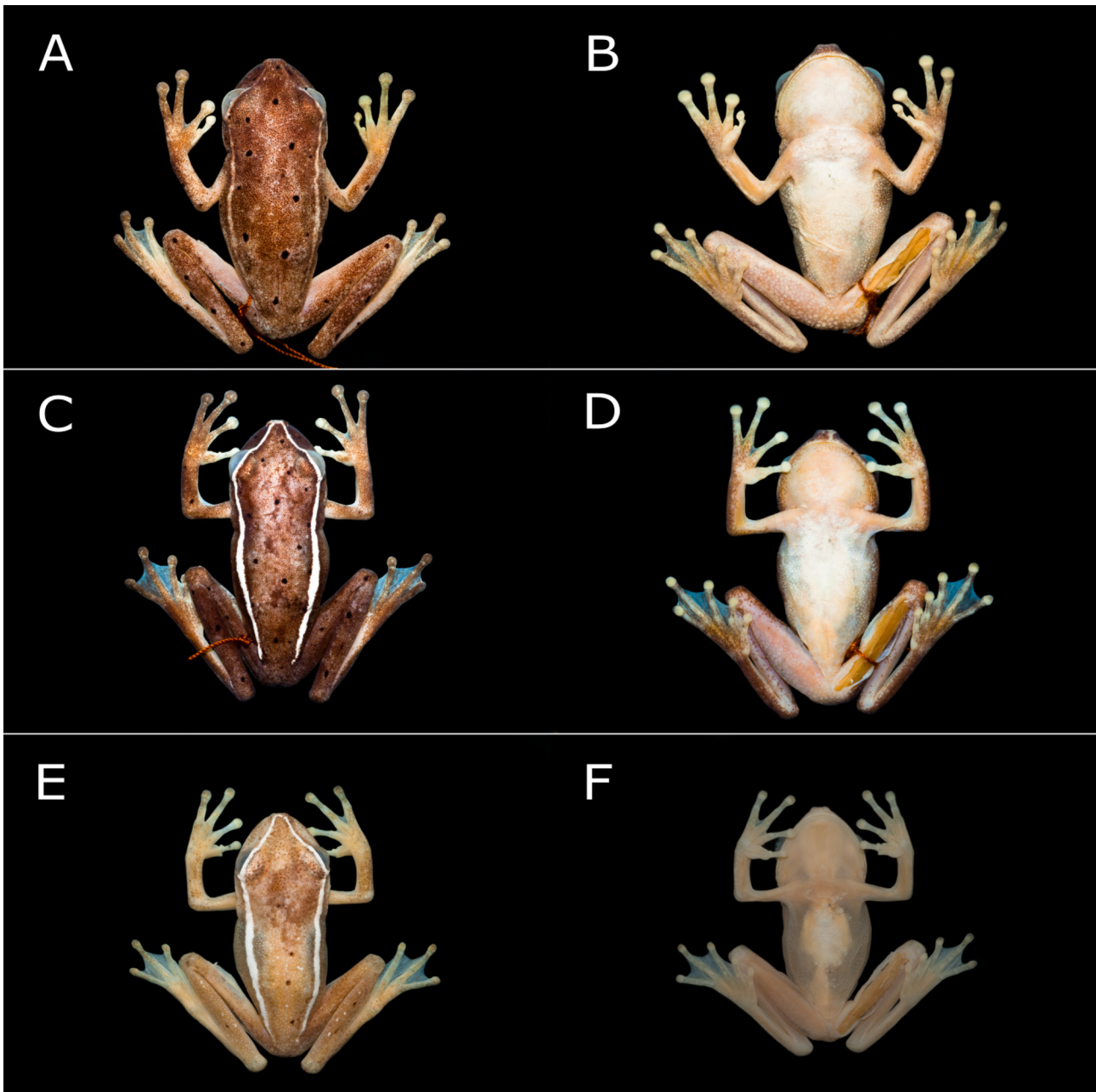
Taxon	1	2	3	4	5	6	7	8	9
1 <i>Boana hobbsi</i>									
2 <i>Boana jimenezi</i>	<b>0.07</b>								
3 <i>Boana lemai</i>	<b>0.07</b>	0.04							
4 <i>Boana microderma</i>	<b>0.11</b>	0.11	0.12						
5 <i>Boana nympa</i>	<b>0.12</b>	0.12	0.11	0.09					
6 <i>Boana ornatissima</i>	<b>0.15</b>	0.13	0.14	0.18	0.17				
7 <i>Boana roraima</i>	<b>0.12</b>	0.11	0.10	0.10	0.10	0.16			
8 <i>Boana</i> sp.	<b>0.13</b>	0.10	0.10	0.12	0.12	0.18	0.10		
9 <i>Boana tepuiana</i>	<b>0.07</b>	0.06	0.05	0.11	0.12	0.17	0.11	0.11	

**TABLE 3.** Uncorrected pairwise distances between samples of *Boana hobbsi* (Cochran & Goin, 1970) and congeneric species of the *Boana punctata* group *sensu lato* (highlighted in bold).

Taxon	1	2	3	4	5	6	7	8
1 <i>Boana hobbsi</i>								
2 <i>Boana atlantica</i>	<b>0.16</b>							
3 <i>Boana cf. atlantica</i>	<b>0.16</b>	0.04						
4 <i>Boana cinerascens</i>	<b>0.16</b>	0.10	0.10					
5 <i>Boana gracilis</i>	<b>0.15</b>	0.08	0.09	0.11				
6 <i>Boana picturata</i>	<b>0.14</b>	0.17	0.17	0.15	0.16			
7 <i>Boana punctata</i>	<b>0.16</b>	0.04	0.03	0.11	0.09	0.17		
8 <i>Boana sibleszi</i>	<b>0.12</b>	0.13	0.13	0.13	0.14	0.13	0.14	

**Morphological variation.** Morphometric data analysis of the newly collected *B. hobbsi* series showed measurements contained within the described variation of the species (Table 3). Other morphological data observed in preserved specimens include: (1) slender body with smooth to weakly shagreened dorsum skin fully covered by melanophores, and a finely granular ventral surface skin; (2) dark brown to pale yellowish dorsum with scattered black spots throughout the dorsal surfaces of body, arms, and shank (Figs. 2A, 2C, 2E); (3) white to cream dorsolateral stripe varying in evidence, beginning at the tip of the snout, crossing the upper eyelid, reaching the sacrum and ending just anterior to the groin (Figs. 2A, 2C, 2E); (4) greenish white to cream belly, with concentration of melanophores on the ventral surfaces of hands, forearms, and feet (Figs. 2B, 2D, 2F); (5) head truncate in lateral view and round in dorsal view, snout truncate in lateral and dorsal views (Figs. 3A, 3B), with an evident mental gland (Fig. 3C); (6) evident prepollex with no spine protruding out of the skin; (7) palmar tubercle rounded; (8) relative length of fingers I < II < IV < III, almost unwebbed (I–II 2–3· III 3–3·IV) (Fig. 3D); (9) subarticular tubercle rounded in fingers I and II, bifid in fingers III and IV (Fig. 3D); (10) supernumerary tubercles absent; (11) relative length of toes I < II < III < V < IV, fully webbed (I<sup>+</sup>–1·II 1<sup>+</sup>–3· III 1<sup>+</sup>–1<sup>1/2</sup>·IV 2<sup>+</sup>–0 V) (Fig. 3E). Coloration patterns of *B. hobbsi* in life (Fig. 4) include: (1) dark brown to pale green dorsum, with scattered blackish spots; light yellow flanks, fingers, toes and ventral surfaces of forearm and shank; (2) a cream stripe varying in evidence across the dorsolateral regions of head and body; (3) iris golden-yellow, bordered by an intense black ring, with black thin reticulation near the border of the eyelid and a reddish-brown pigmentation around the pupil (Fig. 4). Although analyzed specimens were collected from geographically distant localities (nearly 300 km apart), we did not notice any significant difference in morphological characteristics associated with the distinct sampling localities. Our morphological results indicate that despite its relatively wide geographic distribution, the species overall morphology is conserved throughout its range of occurrence.

**Comparisons.** Data from all other species of the *B. benitezi* group are provided in parenthesis except *Boana pulidoi*, which was recently synonymized. In living and in preserved specimens, *B. hobbsi* differs from all other species of the *B. benitezi* group by the presence of scattered black spots on the dorsal surfaces of body, arms and thighs (absent in all other species), and by a larger body size with mean SVL 41.14 mm (mean SVL < 40.0 mm). By exhibiting a brown dorsal color pattern with a cream dorsolateral stripe, *B. hobbsi* differs from *B. benitezi* (brown, with brown transverse bars varying in width and dorsolateral stripes absent), *B. jimenezi* (green, with large spots in limbs and forearms), *B. lemai* (light yellow to reddish-brown, with dark transversal stripes and eventually with white dorsolateral stripes), *B. microderma* (light yellow to orange-brown, with light brown transversal bars), *B. nympha* (bright yellowish green to reddish brown), *B. ornatissima* (green, with an elaborated ornamentation in the center of the dorsal surface), *B. rhythmica* (reddish brown, with fine black reticulation or black transverse lines, eventually with white dorsolateral stripes), *B. roraima* (light brown with irregular dark brown markings and eventually with middorsal dark stripes), and *B. tepuiana* (in life varying from bright yellow with brown marks, to brown with gray markings, and to dark brown with cream dorsolateral stripes; in preserved specimens a reticulated pattern can also be observed). By its greenish cream-colored ventral surface in living specimens, *B. hobbsi* also differs from *B. benitezi* (bright orange or white) and *B. ornatissima* (varying from greenish yellow to translucent blue). Male specimens of *B. hobbsi* also have an evident mental gland that differs from the condition observed in *B. jimenezi* (absent). In life, *B. hobbsi* can also be distinguished by a unique iris color, with its golden-yellow background, black reticulation and reddish-brown pigmentation around the pupil, from

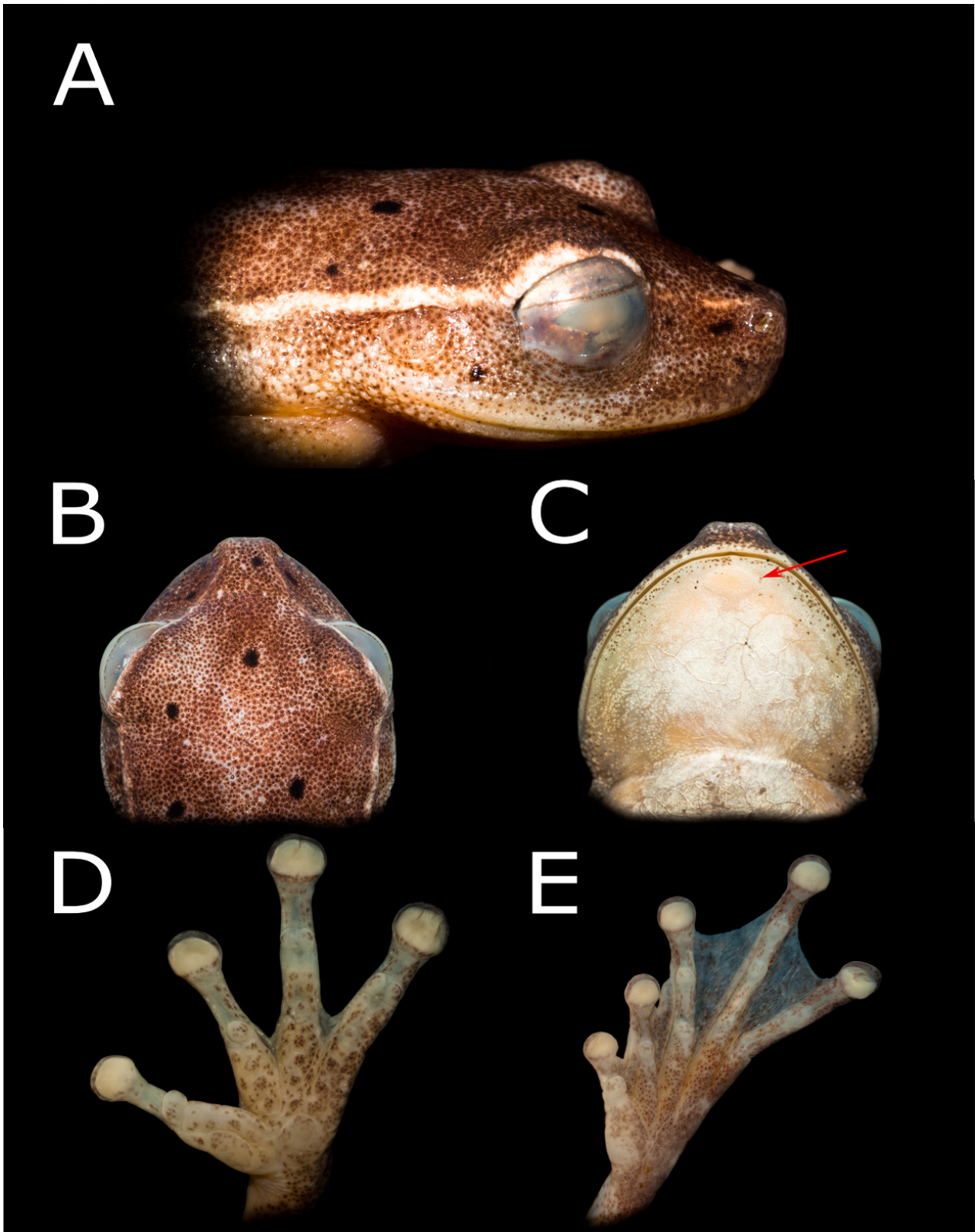


**FIGURE 2.** Dorsal and ventral views of newly collected preserved specimens of *Boana hobbsi* (Cochran & Goïn, 1970). (A, B) adult male, with dark brown dorsum and little evident dorsolateral stripe (CZPB-AA 1658, SVL= 46.2 mm); (C, D) adult female, with dark brown dorsum and evident dorsolateral stripe (CZPB-AA 1660, SVL= 43.5 mm); (E, F) adult male, with yellowish dorsum and evident dorsolateral stripe (CZPB-AA 1657, SVL= 33.7 mm). All specimens were collected on the right bank of the Japurá River, near to the city of Japurá, state of Amazonas, Brazil.

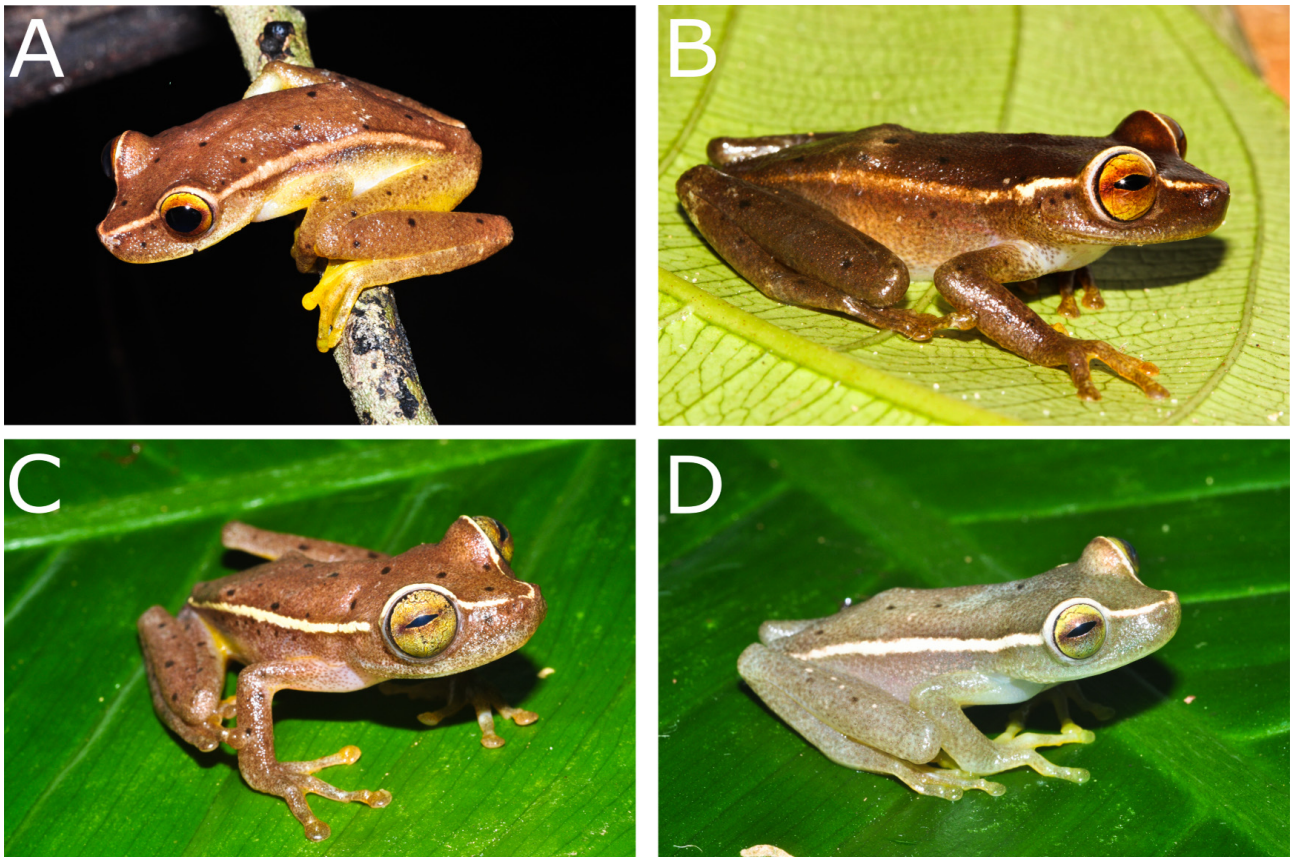
*B. benitezi* (varying from light brown to dark brown), *B. jimenezi* (silvery with a dark brown rim around the pupil and a fine dark reticulation), *B. lemai* (pale green to gray), *B. microderma* (cream to pale yellow with a black peripheric mark), *B. nympa* (varying from cream to creamy-golden with a black peripheric mark), *B. ornatissima* (varying from silver to gray-green background with a reddish-brown area around pupil), *B. rhythmica* (golden without reticulation), *B. roraima* (varying from pale green to yellow without reticulation and a black peripheric mark), and *B. tepuiana* (silvery-gray to dark brown).

Although aforementioned comparisons show that *B. hobbsi* is easily distinguished from congeneric species of the *B. benitezi* group, this species shares greater morphological affinity with this group than when compared to congeneric species of the *B. punctata* group. These morphological similarities include a brown dorsal surface of the body,





**FIGURE 3.** Morphological details of newly collected preserved specimens of *Boana hobbsi* (Cochran & Goin, 1970). (A–C) lateral, dorsal and ventral views of the head of an adult male (CZPB-AA 1658, SVL= 46.2 mm), highlighting the presence of an evident mental gland (red arrow). (D, E) ventral surfaces of the hands and feet of an adult female of *B. hobbsi* (CZPB-AA 1659; SVL = 45.8 mm).



**FIGURE 4.** Dorsolateral views of newly recorded living specimens of *Boana hobbsi* (Cochran & Goin, 1970): (A) adult female from the right bank of the Japurá River, near to Vila Bittencourt, Amazonas, Brazil (Photo: APA); (B) adult male from the municipality of São Gabriel da Cachoeira, Amazonas, Brazil (Photo: LJCLM); (C, D) adult and juvenile males from Japurá River, showing variations in dorsal coloration, from tan, to dark brown, to a pale green-grayish, respectively (Photo: VTC).

**TABLE 4.** Morphometric measurements (mm) of *Boana hobbsi* (Cochran & Goin, 1970), based on the newly collected specimens examined in our study (INPA-H and CZPB vouchers) and on information available in the literature. See text for measurement acronyms.

Voucher Number	Sex	SVL	HL	HW	SL	EN	IOD	ED
INPA-H 37272	Female	45.55	15.96	15.85	6.46	4.49	5.66	5.15
INPA-H 37273	Male	39.20	15.5	14.19	5.86	3.99	4.85	4.25
INPA-H 37274	Male	38.42	15.15	13.52	5.50	3.79	5.30	4.80
INPA-H 37275	Female	42.73	14.89	14.70	5.98	4.20	4.85	5.54
INPA-H 37276	Male	44.40	15.56	15.58	6.34	4.10	5.24	4.72
CZPB-AA 1655	Male	38.03	12.59	14.38	6.02	4.56	5.72	5.12
CZPB-AA 1656	Male	42.85	13.74	14.84	6.12	4.21	4.89	5.20
CZPB-AA 1657	Male	33.67	12.03	11.90	5.91	4.20	4.59	4.07
CZPB-AA 1658	Male	46.22	16.33	15.96	7.53	4.82	5.59	5.38
CZPB-AA 1659	Female	45.87	15.74	16.14	7.48	5.26	5.57	5.66
CZPB-AA 1660	Female	43.48	14.88	15.32	7.04	5.19	5.65	5.27
Pyburn (1978)	Male	38.70	14.30	13.70	-	-	-	4.80
Cochran & Goin (1970)	Female	42.50	17.20	14.70	-	-	-	-
	Male	38.00	-	-	-	-	-	-

continued.

Voucher Number	Sex	TD	HAL	FAL	THL	TSL	TL	FL
INPA-H 37272	Female	2.47	12.98	8.44	21.85	13.53	22.66	16.76
INPA-H 37273	Male	2.41	12.54	7.13	20.00	11.55	20.67	15.66
INPA-H 37274	Male	2.70	12.25	7.64	19.09	12.43	19.90	14.98
INPA-H 37275	Female	2.26	13.02	9.20	21.06	13.95	22.50	16.51
INPA-H 37276	Male	2.44	12.64	8.50	22.36	13.89	22.86	16.80
CZPB-AA 1655	Male	1.83	11.91	7.98	20.67	11.26	20.01	15.93
CZPB-AA 1656	Male	2.05	13.62	8.40	21.72	12.50	21.69	17.60
CZPB-AA 1657	Male	1.50	10.65	6.60	18.75	10.30	18.60	14.02
CZPB-AA 1658	Male	1.96	13.59	10.02	24.72	14.09	23.78	17.08
CZPB-AA 1659	Female	1.73	14.44	9.54	24.15	13.39	23.99	17.65
CZPB-AA 1660	Female	1.88	13.35	9.15	23.78	13.63	23.21	17.56
Pyburn (1978)	Male	2.10	-	-	20.10	-	-	-
Cochran & Goin (1970)	Female	-	11.20	-	21.60	-	21.30	-
	Male	-	-	-	-	-	-	-

eventually with highly contrasting white or cream dorsolateral stripes, as observed in *B. lemai*, *B. tepuiana* and *B. benitezi*; and the dense matrix of chromatophores in the dorsal surface and eventual presence of highly contrasting whitish-cream dorsolateral stripes shared with the greenish colored *B. jimenezi*. These similarities clearly reflect the closer phylogenetic relationships among species found in our molecular analysis (i.e. the highly supported clade containing *B. hobbsi*, *B. tepuiana*, *B. lemai* and *B. jimenezi*). With remaining members of *B. benitezi* group, *Boana hobbsi* shares a slender body and limbs, eyes bordered by an intense dark ring, and the presence of a mental gland (also present in *B. lemai* and *B. benitezi*).

**Geographic distribution.** New sampling localities filled relevant knowledge gaps in the geographic range of *B. hobbsi* (Fig. 5). One of these localities is a small stream inside the forest on the right bank of the Japurá River, near to Vila Bittencourt (1.845994° S, 69.029466° W), located 117 km east of the nearest record on the Caquetá River, and 185 km from the type locality (Caño Guacayá, a tributary of the Río Apoporis, in Amazonas, Colombia—Cochran & Goin [1970]). The second locality is a stream at the road to Cucuí village in the vicinity of São Gabriel da Cachoeira (0.130547°S, 67.038947°W), located 160 km south of the nearest record at Cerro de la Neblina base camp, Venezuela, and 390 km from the type locality (Fig. 5). Our record at São Gabriel da Cachoeira, along with the Cerro de la Neblina Venezuelan record, and the first Brazilian record at Japurá River, all represent the easternmost known limits of geographic range of *B. hobbsi*.

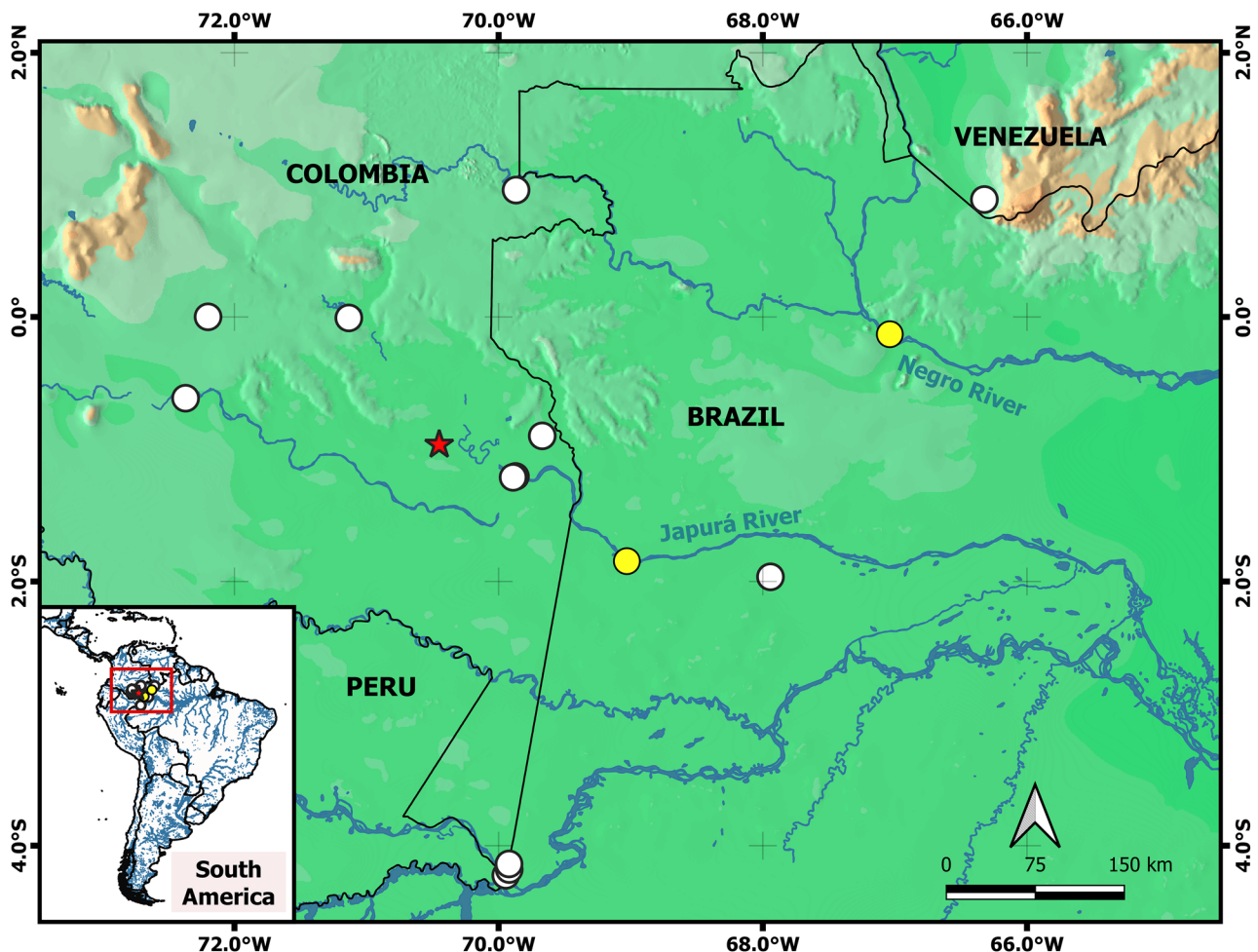
## Discussion

The 16S rRNA gene is widely used for reliable species identification (Vences *et al.* 2005; Fouquet *et al.* 2007), for evaluating the monophyly of species, and for discovering divergent lineages (Padial & De la Riva 2009; Padial *et al.* 2010; Padial *et al.* 2012; Motta *et al.* 2018). Our study supports that the variation at the 16S gene, combined with phenotypic data, can be useful to discuss phylogenetic relationships of poorly known anuran species (Fouquet *et al.* 2011; Ávila *et al.* 2018). Moreover, differences in optimality criteria and in number of terminals (Padial *et al.* 2014; Grant 2019) may also explain the divergence of our results from previously multi-locus phylogenetic studies (Faivovich *et al.* 2005; Wiens *et al.* 2005, 2010; Pyron & Wiens 2011; Duellman *et al.* 2016; Pinheiro *et al.* 2019).

The tree topology reported here recovered well-supported major clades representing four of the species groups currently considered within *Boana*: *Boana semilineata* group, *B. pellucens* group, *B. faber* group and *B. benitezi* group (as presently defined). The *Boana punctata* group was recovered here as polyphyletic, due to the phylogenetic position of *B. picturata* within the *B. albopunctata* group, and of *B. sibleszi* within the *B. pulchella* group. However, these relationships were not strongly supported, and in the light of our results, the relationships of *B. picturata* and

*B. sibleszi* remain uncertain. Nevertheless, a closer affinity of *B. picturata* with the *B. punctata* group is unlikely given the recent phylogenetic results of Caminer & Ron (2020) and the lack of morphological similarities. Thus, we suggest that phylogenetic approaches focused on the inclusion of unsampled species of the Cophomantini may help reveal the relationships of these taxa.

The monophyly of the *B. punctata* group as reported in the literature (e.g. Faivovich *et al.* 2005; Duellman *et al.* 2016; Pinheiro *et al.* 2019; Sturaro *et al.* 2020) has been mostly based on poorly supported phylogenetic relationships of *B. picturata* and *B. sibleszi*, and disregards *B. jimenezii* as part of this group. The lack of molecular affinities of *B. picturata*, *B. sibleszi* and *B. jimenezii* with other species in *B. punctata* group *sensu stricto* seen in our results confirms previous phylogenetic studies (Pyron & Wiens 2011; Pinheiro *et al.* 2019; Caminer & Ron 2020; Sturaro *et al.* 2020). Therefore, green-colored morphological patterns shared between this species is quite common in hyliid



**FIGURE 5.** Known geographic distribution of *Boana hobbsi* (Cochran & Goin, 1970) in the northwestern Amazonia. White circles indicate the historical localities of occurrence in Colombia, Venezuela and Brazil (Cochran & Goin 1970; Pyburn 1978; McDiarmid *et al.* 1988; Ruiz-Carranza *et al.* 1996; Acosta-Galvis 2000; Lynch 2005, 2007; Suárez-Mayorga & Lynch 2017; Acosta-Galvis 2018; Barrio-Amorós *et al.* 2019; Simões *et al.* 2019). Yellow circles on the Brazilian territory indicate new distribution records reported at Japurá and Negro river basins. The red star indicates type locality at Caño Guacaya, Apaporis River, Colombia (Cochran & Goin 1970).

frogs and constitute cases of evolutionary convergence (Taboada *et al.* 2020). Other studies also reported the non-monophyly of the *B. punctata* group, and even the nominal taxa *B. punctata*, *B. atlantica*, and *B. cinerascens* are paraphyletic and represent species complexes (Jansen *et al.* 2011; Guarnizo *et al.* 2015; Lima *et al.* 2019; Caminer & Ron, 2020; Sturaro *et al.* 2020). After our phylogenetic positioning of *B. hobbsi*, *B. alemani* remains the only nominal species historically attributed to the *B. punctata* group without a formal phylogenetic test (based on any kind of data). Furthermore, the taxonomic status of this species is uncertain and seems to be based on a mixed type

series, with the holotype being conspecific with *B. punctata* (La Marca, 1992; Camargo *et al.* 2014; Barrio-Amorós *et al.* 2019) and the paratypes likely being juveniles of *Boana xerophylla* (Duméril & Bibron, 1841) (Barrio-Amorós *et al.* 2019). This combination of new evidence points to a stability of the *B. punctata* group as an evolutionary unit, when comprising only the species related to the former *Hyla punctata* and *Hyla granosa* groups (the “green *Hylas* from Amazonian Hylaea” *sensu* Lutz [1948]). Nevertheless, a delimitation of the *B. punctata* group is beyond the scope of our study and requires denser taxonomic and molecular sampling.

Phylogenetic affinities of *B. hobbsi* were, until now, hypothesized only based on morphological comparisons (Duellman 1974; Pyburn 1978). Given the historical associations with *B. punctata*, Faivovich *et al.* (2005) provisionally allocated the species in the *B. punctata* group. However, such decision overlooked the divergences already pointed out by Pyburn (1978), who had questioned the phylogenetic affinities of these species due to their remarkable divergences in overall morphology, habitat use and vocalization. After 50 years of being originally described, our study presents the first evidence of the phylogenetic relationships of *B. hobbsi*, based on integrative molecular and morphological approaches, corroborating the statements of Pyburn (1978). In fact, despite advances in our understanding of phylogenetic relationships within the genus *Boana*, a number of issues still remain unclear, particularly regarding the *B. benitezi* group. With the recent taxonomic update of the “*B. benitezi*” sequence available at Genbank to *B. tepuiana* (Pinheiro *et al.* 2019), the nominal *B. benitezi* was never included in any molecular phylogenetic analysis. In a similar way, molecular information supporting the placement of *B. rhythmica* within this group is also missing. Furthermore, in a recent revision of Venezuelan anurans, Barrio-Amorós *et al.* (2019) recognized *Boana pulidoi* (Rivero, 1968) as a junior synonym of *B. benitezi*. Our results also unraveled an intriguing issue concerning the phylogenetic positioning of a sequence referred as *Boana* sp., from Cerro Guanay, Venezuela (Appendix I). This sequence likely represents a non-described species of the *B. benitezi* group, as already noted by Gorzula & Señaris (1998) and Myers & Donnelly (2008).

Morphologically, some issues involving the *B. benitezi* group also remain unresolved, such as diagnosable synapomorphies for the group. Based on current knowledge and on our results, we cannot point to any unambiguous synapomorphy. Still, morphological comparisons within the *B. benitezi* group evidence two groups of similarities: (1) characters shared by *B. hobbsi*, *B. benitezi* (Rivero 1961; Donnelly & Myers 1991; Heyer 1994), *B. lemai* (Rivero 1972; MacCulloch & Lathrop 2005; Señaris *et al.* 2014), *B. rhythmica*, *B. jimenezi* (Señaris & Ayarzagüena, 2006; Señaris *et al.* 2014), *B. ornatissima* and *B. tepuiana* (Barrio-Amorós & Brewer Cárias 2008; Señaris *et al.* 2014), as described above; and (2) characters shared by *B. nympha*, *B. microderma* and *B. roraima*, such as distinctive head, broader than the body, iris creamy golden without reticulation and with a black periphery, and tan to brownish dorsum with dark transversal markings. Studies of the internal morphology of the adults, as well as a refined assessment of tadpole morphology should shed some light into defining morphological synapomorphies for this group.

*Boana hobbsi* was known only from records reported in the Colombian and Venezuelan Amazon forest (Cochran & Goin 1970; Pyburn 1978; McDiarmid *et al.* 1988; Ruiz-Carranza *et al.* 1996; Acosta-Galvis 2000; Lynch 2005, 2007; Barrio-Amorós *et al.* 2019) until 2019, when the first record in the Brazilian territory was registered (Simões *et al.* 2019). Our results support the hypothesis that *B. hobbsi* is widely distributed in the northwest Brazilian Amazonia. This region is known to harbor a unique and endemic amphibian fauna (Azevedo-Ramos & Galatti 2002; Lynch 2005; Menin *et al.* 2017) and has been proposed to be a biogeographic unit (Godinho & Da Silva 2018). Highly restricted geographic distributions are a common pattern for the *B. benitezi* group, as most of its species apparently have small or fragmented ranges within the uplands and highlands of the northern Amazonia (Pantepui region) (Frost 2020). Still, the region is relatively poorly sampled due to the great difficulty of access. The only exceptions to this distribution pattern are *B. nympha*, *B. microderma* and *B. hobbsi*, which occupy the lowlands of western Amazonia (Frost 2020). In fact, we also recorded *B. microderma* syntopically with *B. hobbsi* in the two new localities reported in this study. Based on literature (Pyburn 1978; Simões *et al.* 2019) and on our new records, *B. hobbsi* is associated with small sandy riverbed streams in upland *terra-firme* (non-periodically flooded) forests. Increased fieldwork in these habitats and in this biogeographic region should reveal additional localities of occurrence for *B. hobbsi*, as well for other species from this group, clarifying their geographic ranges. Our results highlight the importance of conducting new biodiversity surveys in remote regions, like the northern and western Amazonia (Azevedo-Ramos & Gallati 2002; Mayer *et al.* 2019), to overcome the biodiversity shortfalls widespread in this mega diverse ecosystem (Bini *et al.* 2006; Brito 2010; Assis 2018).

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**APPENDIX I.** List of species included in our phylogenetic analysis, along with the associated voucher and GenBank accession numbers, locality of occurrence, and sequence references. Newly generated sequences are highlighted in bold.

Species	Voucher/Field Number	GenBank (Accession number)	Locality	References
<i>Aplastodiscus albosignatus</i>	CFBHT 14205	KU184018	Brazil: São Paulo, São Luis do Paraitinga	Berneck <i>et al.</i> (2016)
<i>Aplastodiscus perivividis</i>	AAG 1259	KY213874	Brazil: São Paulo, Atibaia	Berneck <i>et al.</i> (2016)
<i>Boana aguilari</i>	MUSM 19804	HM444783	Peru: Junin, Pampa Hermosa	Lehr <i>et al.</i> (2010)
<i>Boana albopunctata</i>	ZUEC 12053	AY549317	Brazil: São Paulo, Campinas	Faivovich <i>et al.</i> (2004)
<i>Boana albomarginata</i>	USNM 284519	AY549316	Brazil: Pernambuco, near Caraurucu, on the way to Serra dos Cavalos	Faivovich <i>et al.</i> (2004)
<i>Boana alfaroi</i>	QCAZ A50785	KF955305	Ecuador: Provincia de Sucumbios, Panacocha	Caminer & Ron (2014)
<i>Boana almendarizae</i>	QCAZ A31452	JN970618	Ecuador: Tungurahua, Rio Pastaza	Funk <i>et al.</i> (2012)
<i>Boana atlantica</i>	CFBH 12821	MK348482	Brazil: Bahia, Camumu	Lima <i>et al.</i> (2019)
<i>Boana atlantica</i>	CFBH 16146	MK348487	Brazil: Bahia, Uruçuca	Lima <i>et al.</i> (2019)
<i>Boana atlantica</i>	CFBH 18501	MK348492	Brazil: Bahia, Uruçuca	Lima <i>et al.</i> (2019)
<i>Boana cf. atlantica</i>	MUFAL 12079_3	MK348503	Brazil: Alagoas, Maceió	Lima <i>et al.</i> (2019)
<i>Boana cf. atlantica</i>	MUFAL 13067	MK348506	Brazil: Pernambuco, Paulista	Lima <i>et al.</i> (2019)
<i>Boana balzani</i>	DLR 41193	AY549323	Bolivia: Departamento La Paz, Provincia Noryungas, Serrania Bellavista	Faivovich <i>et al.</i> (2004)
<i>Boana bischoffi</i>	CFBH 3356	AY549324	Brazil: Santa Catarina, Rancho Queimado	Faivovich <i>et al.</i> (2004)
<i>Boana boans</i>	RWM 17746	AY843610	Venezuela: Amazonas, Caño Agua Blanca, 3.5 km SE to Neblina Base Camp on Rio Mawarinuma	Faivovich <i>et al.</i> (2005)
<i>Boana caipora</i>	CFBH 5738	EU077268	Brazil: São Paulo, Serra do Mar, Serra de Paranapiacaba, Município de Pilar do Sul	Antunes <i>et al.</i> (2008)
<i>Boana calcarata</i>	NMP6V 71250	AY843613	Peru: Anguilla 50 km of Iquitos	Faivovich <i>et al.</i> (2005)
<i>Boana callipleura</i>	MNCN 4112	HM480426	Bolivia: Cochabamba, between Los Guácharos and El Palmar	Kohler <i>et al.</i> (2010)
<i>Boana cinerascens</i>	AF 0556	KR811175	French Guiana: Savane Virginie	Fouquet <i>et al.</i> (2015)
<i>Boana cinerascens</i>	189bm	EU201113	French Guiana: Trinité	Fouquet <i>et al.</i> (2007)
<i>Boana cinerascens</i>	CTGA_N5620	MG806013	Brazil: Amazonas, FEX-CAMPUS, Manaus	Motta <i>et al.</i> (2018)

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APPENDIX 1. (Continued)

Species	Voucher/Field Number	GenBank (Accession number)	Locality	References
<i>Boana cinerascens</i>	CTGA_N5621	MG806016	Brazil: Amazonas, FEX-CAMPUS, Manaus	Motta <i>et al.</i> (2018)
<i>Boana cinerascens</i>	CTGA_N5659	MG806018	Brazil: Amazonas, FEX-CAMPUS, Manaus	Motta <i>et al.</i> (2018)
<i>Boana cordobae</i>	MLP 2139	AY549329	Argentina: Cordoba, Tanti	Faivovich <i>et al.</i> (2004)
<i>Boana crepitans</i>	CFBHT 12841	KU495262	Brazil: Bahia, Camumu	Lyra <i>et al.</i> (2016)
<i>Boana dentei</i>	l3mc	AF467270	French Guiana: Guiana Mountain of Kaw (3)	Salducci <i>et al.</i> (2002)
<i>Boana diabolica</i>	MTB 136	KU168891	French Guiana: Gaa Kaba	Fouquet <i>et al.</i> (2016)
<i>Boana ericae</i>	CFBH 3599	AY549332	Brazil: Goiás, Alto Paraíso de Goiás	Faivovich <i>et al.</i> (2004)
<i>Boana faber</i>	CFBHT 279995	KU495264	Brazil: São Paulo, Nazaré Paulista	Lyra <i>et al.</i> (2016)
<i>Boana fasciata</i>	QCAZ 17030	JN970535	Ecuador: Morona Santiago, Tiink, Rio Zamora	Funk <i>et al.</i> (2012)
<i>Boana geographica</i>	AMNH A141054	AY843628	Guyana: Warniabo Creek, 4 mi SW Dubulay Ranch house	Faivovich <i>et al.</i> (2005)
<i>Boana gladiator</i>	MNCN 5523	HM480413	Peru: Cusco, Valle de Marcapata	Kohler <i>et al.</i> (2010)
<i>Boana gracilis</i>	AMNH A164105	AY549336	Guyana: Iwokrama, Muri Serub camp, 80m	Faivovich <i>et al.</i> (2004)
<i>Boana gracilis</i>	MHNLS 19035	MN781658	Venezuela: Amazonas: San José de Chipiro, boca del rio Ventuari, municipio Atapabo, alto Orinoco	Sturaro <i>et al.</i> (2020)
<i>Boana gracilis</i>	MHNLS 19037	MN781659	Venezuela: Amazonas: San José de Chipiro, boca del rio Ventuari, municipio Atapabo, alto Orinoco	Sturaro <i>et al.</i> (2020)
<i>Boana gracilis</i>	MHNLS 19039	MN781660	Venezuela: Amazonas: San José de Chipiro, boca del rio Ventuari, municipio Atapabo, alto Orinoco	Sturaro <i>et al.</i> (2020)
<i>Boana gracilis</i>	MPEG 40288	MN781661	Brazil: Amazonas: Novo Airão: Parque Nacional do Jaú	Sturaro <i>et al.</i> (2020)
<i>Boana heilprini</i>	AMNH A168405	AY843632	Pet trade	Faivovich <i>et al.</i> (2005)
<b><i>Boana hobbsi</i></b>	<b>CZPB-AA1657</b>	<b>MW423779</b>	<b>Brazil: Amazonas, rio Japurá, Japurá, near Villa Bittencourt</b>	<b>This study</b>
<b><i>Boana hobbsi</i></b>	<b>CZPB-AA1659</b>	<b>MW423778</b>	<b>Brazil: Amazonas, rio Japurá, Japurá, near Villa Bittencourt</b>	<b>This study</b>
<b><i>Boana hobbsi</i></b>	<b>CZPB-AA1660</b>	<b>MW423777</b>	<b>Brazil: Amazonas, rio Japurá, Japurá, near Villa Bittencourt</b>	<b>This study</b>
<b><i>Boana hobbsi</i></b>	<b>INPA-H37272</b>	<b>MW423781</b>	<b>Brazil: Amazonas, São Gabriel da Cachoeira</b>	<b>This study</b>
<b><i>Boana hobbsi</i></b>	<b>INPA-H37273</b>	<b>MW423783</b>	<b>Brazil: Amazonas, São Gabriel da Cachoeira</b>	<b>This study</b>

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APPENDIX 1. (Continued)

Species	Voucher/Field Number	GenBank (Accession number)	Locality	References
<i>Boana hobbsi</i>	INPA-H 37274	MW423784	Brazil: Amazonas, São Gabriel da Cachoeira	This study
<i>Boana hobbsi</i>	INPA-H 37275	MW423780	Brazil: Amazonas, São Gabriel da Cachoeira	This study
<i>Boana hobbsi</i>	INPA-H 37276	MW423782	Brazil: Amazonas, São Gabriel da Cachoeira	This study
<i>Boana icamiaba</i>	MPEG 27245	MG840873	Brazil: Para, Juruti, Capiranga	Peloso <i>et al.</i> (2018)
<i>Boana jimenezi</i>	MHNLS 19402	MN688742	Venezuela: Bolívar: Gran Sabana, Campamento Guayaraca, Sabana de Guayaraca, P.N. Canaima	Sturaro <i>et al.</i> (2020)
<i>Boana lanciformis</i>	AJC 3973	KP149465	Colombia: Casañare, Sabanalarga, Sabanalarga	Guarnizo <i>et al.</i> (2015)
<i>Boana latistriata</i>	MZUSP 111556	AY549360	Brazil: Minas Gerais: Município Itamontes	Faivovich <i>et al.</i> (2004)
<i>Boana lemai</i>	ROM 39570	AY843637	Guyana: Mount Ayanganna	Faivovich <i>et al.</i> (2005)
<i>Boana leptolineata</i>	CFBH 3848	AY549341	Brazil: Santa Catarina: Município de São Domingos	Faivovich <i>et al.</i> (2004)
<i>Boana lundii</i>	CFBHT 01902	KU495270	Brazil: Minas Gerais: São Roque de Minas	Lyra <i>et al.</i> (2016)
<i>Boana maculateralis</i>	WED 60015	JN970627	Peru: Loreto: San Jacinto	Funk <i>et al.</i> (2012)
<i>Boana microderma</i>	NMP6V 71258/1	AY843644	Peru: Anguilla, 50 km of Iquitos	Faivovich <i>et al.</i> (2005)
<i>Boana multifasciata</i>	ROM 22756	JN970642	Guyana: Baramitã	Funk <i>et al.</i> (2012)
<i>Boana nympha</i>	NMP6V 71202/2	AY843670	Peru: 50 km W of Iquitos	Faivovich <i>et al.</i> (2005)
<i>Boana ornatissima</i>	51mc	EF376056	French Guiana: Chutes Voltaires	Salducci <i>et al.</i> (2002)
<i>Boana pardalis</i>	CFBHT 04366	KU495275	Brazil: Rio de Janeiro: Petrópolis	Lyra <i>et al.</i> (2016)
<i>Boana pellucens</i>	248804	JN970652	Ecuador: El Oro Avanzada-Playón road, km 8	Funk <i>et al.</i> (2012)
<i>Boana picturata</i>	KU 202737	AY326055	Pichincha, Tinalandia, Santo Domingo de Colorados, Ecuador	Darst & Cannatella (2004)
<i>Boana picturata</i>	QCAZ A13894	MN921776	Pichincha, Amanecer Campesino, Rio Santiago, Ecuador	Caminer & Ron (2020)
<i>Boana polytaenia</i>	CFBHT 06606	KU495277	Brazil: São Paulo, São Luis do Paraitinga, Santa Virginia	Lyra <i>et al.</i> (2016)
<i>Boana pugnax</i>	AJC 3529	KP149296	Colombia: Santander: San Vicente de Chucuri, Vereda las Margaritas, Reserva el arboretum, Quebrada los Cauchos	Guarnizo <i>et al.</i> (2015)
<i>Boana pulchella</i>	MNCN 37790	AY549350	Argentina: Buenos Aires, Escobar, El Cazador	Faivovich <i>et al.</i> (2004)

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APPENDIX 1. (Continued)

Species	Voucher/Field Number	GenBank (Accession number)	Locality	References
<i>Boana punctata</i>	AC_101_12	MN172521	Pilcopata, Distrito Kosnipata, Provincia Paucartambo, Cusco, Peru	von May <i>et al.</i> (2019)
<i>Boana punctata</i>	AF193	EU201112	French Guiana: Mana	Fouquet <i>et al.</i> (2007)
<i>Boana punctata</i>	AJC 4064	KP149397	Colombia: Casañare, Sabanalarga, Sabanalarga	Guarnizo <i>et al.</i> (2015)
<i>Boana punctata</i>	AS0164	JF790122	Bolivia: Santa Cruz: Ñuflo de Chavez, San Sebastian	Jansen <i>et al.</i> (2011)
<i>Boana punctata</i>	APL17893	MK348507	Brazil: Rondônia	Lima <i>et al.</i> (2019)
<i>Boana punctata</i>	APL17922	MK348508	Brazil: Rondônia	Lima <i>et al.</i> (2019)
<i>Boana punctata</i>	QCAZ A43790	MN921797	Ecuador: Orellana, Rio Napo, La Primavera	Camner & Ron (2020)
<i>Boana raniceps</i>	N/A	AF467269	Guyane: Yi-Yi's Creek	Salducci <i>et al.</i> (2002)
<i>Boana roraima</i>	ROM 39624	AY843660	Guyana: Mount Ayanganna	Faivovich <i>et al.</i> (2005)
<i>Boana rufiela</i>	KRL 798	AY843662	Panama: Cocle, El Cope, Parque Nacional 'Omar Torrijos'	Faivovich <i>et al.</i> (2005)
<i>Boana semilineata</i>	CFBH 5424	AY843779	Brazil: Rio de Janeiro, Duque de Caxias	Faivovich <i>et al.</i> (2005)
<i>Boana sibleszi</i>	MHNLS 19580	MN688743	Venezuela: Bolívar: Gran Sabana, Sierra Lema, Troncal 10.6 km al S de la alcabala	Sturaro <i>et al.</i> (2020)
<i>Boana sibleszi</i>	ROM 39561	AY843667	Guyana: Mount Ayanganna	Faivovich <i>et al.</i> (2005)
<i>Boana</i> sp.	CWM 19512	AY843671	Venezuela: Bolívar, Cerro Guanay	Faivovich <i>et al.</i> (2005)
<i>Boana teputiana</i>	USNM 302435	AY843606	Venezuela: Brazil, Roraima, Villa Pacaraima, border marker BV (Brazil) 8	Faivovich <i>et al.</i> (2005)
<i>Boana tetete</i>	QCAZ A40080	JN970539	Ecuador: Napo, Comunidad Santa Rosa	Funk <i>et al.</i> (2012)
<i>Boana wavrini</i>	MTR_ACLX120P8	KU495289	Brazil: Mato Grosso, Guaranta do Norte	Lyra <i>et al.</i> (2016)
<i>Boana xerophylla</i>	AJC 4116	KP149478	Colombia: Casañare, Sabanalarga, Sabanalarga	Guarnizo <i>et al.</i> (2015)