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► To cite this version:

Moisés Escalona, Enrique La Marca, Michelle Castellanos, Antoine Fouquet, Andrew Crawford, et al.. Integrative taxonomy reveals a new but common Neotropical treefrog, hidden under the name *Boana xerophylla*. *Zootaxa*, 2021, 4981 (3), pp.401-448. <10.11646/zootaxa.4981.3.1>. <hal-03410766>

HAL Id: hal-03410766

<https://hal.science/hal-03410766v1>

Submitted on 18 Nov 2021

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Integrative taxonomy reveals a new but common Neotropical treefrog, hidden under the name *Boana xerophylla*

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Abstract

Boana xerophylla is a common treefrog widely distributed in northern Brazil, Colombia, French Guiana, Guyana, Panama, Suriname, Trinidad and Tobago, and Venezuela. A recent study found molecular, acoustic, and morphometric differences between the populations located on opposite sides of the Orinoco River. Here, we carry out an updated molecular phylogenetic analysis, including new samples from all the countries along the distribution area, and analyzed additional call recordings from Brazil, Colombia, French Guiana, Panama, Trinidad and Tobago, and Venezuela. Our phylogenetic inference reveals three geographically restricted lineages: one in the eastern Guiana Shield (corresponding to *B. xerophylla* sensu stricto), another in the western Guiana Shield, and a third one north of the Orinoco River. Morphological and acoustic data agree with the differentiation between the populations north of the Orinoco River and the eastern Guiana Shield despite the low genetic p-distances observed (16S rRNA: 0.7–2.2 %). We argue that the populations north of the Orinoco River correspond to a new species, sister of *B. xerophylla*. We name and describe *Boana platanera* **sp. nov.** from the southern versant of the Cordillera de Mérida (08°48'26" N, 70°30'46" W, WGS 84; 947 m asl) Venezuela, and refer all the populations north of the Orinoco River currently identified as *B. xerophylla* to this species. The new species can be readily diagnosed from *B. xerophylla* (characters of the latter in parentheses) by a pale orange-yellow or light brown dorsal coloration (dark brown to green), palpebral membrane with dark pigments (pigments absent); pericloacal region dark brown (cream), advertisement call with shorter first note length than *B. xerophylla*. This study represents an empirical example regarding false negatives behind genetic thresholds for species discovery, appraising the use of integrative taxonomic approaches.

Key words: Bioacoustics, Cordillera de Mérida, cryptic species, Hylidae, molecular phylogenetics, morphology, Venezuela

Introduction

Hylidae Rafinesque, 1815 is among the most species-rich anuran families in the world (Frost 2020). Within this family, the treefrog species of the genus *Boana* Gray, 1825 form a conspicuous component of the Neotropical anurofauna, occurring in open and forested environments from Nicaragua to Argentina, and the islands of Trinidad and Tobago (Frost 2020). The species of *Boana* vary widely in a number of phenotypic traits such as size, shape, color, bony spines, integument structures (folds, spicules, warts, toe webbing, etc.), and behaviors (e.g., vocalizations, parental care) (Duellman 2001). *Boana* currently includes 95 described species (Frost 2020) arranged in seven species groups (Pinheiro *et al.* 2019). One of these species groups, the *Boana faber* group (Faivovich *et al.* 2005), contains nine species: *B. faber* (Wied-Neuwied, 1821), *B. albomarginata* (Spix, 1824), *B. crepitans* (Wied-Neuwied, 1824), *B. exastis* (Caramaschi & Rodrigues, 2003), *B. lundii* (Burmeister, 1856), *B. pardalis* (Spix, 1824), *B. pugnax* (Schmidt, 1857), *B. rosenbergi* (Boulenger, 1898), and *B. xerophylla* (Duméril and Bibron, 1841). The monophyly of this species group is well supported by molecular synapomorphies, and the behavior of nest-building by males was suggested as a putative phenotypic synapomorphy (Faivovich *et al.* 2005).

Boana xerophylla was described from “Cayenne”, French Guiana. Guibé (1948) considered it a junior synonym of *B. crepitans*, a name that has been widely used during more than 70 years. Orrico *et al.* (2017) performed an integrative taxonomic assessment of *B. crepitans* using northern South American and Brazilian Atlantic Forest specimens and resurrected *B. xerophylla* from its synonymy with *B. crepitans*. As currently understood, *B. xerophylla* is known from Brazil, Colombia, French Guiana, Guyana, Panama, Suriname, Trinidad and Tobago, and Venezuela (Orrico *et al.* 2017). This species is colloquially called *rana platanera* (banana tree dwelling frog) in Colombia and Venezuela (La Marca 1996, Lynch & Suárez-Mayorga 2001) and it is considered one of the most common and widespread anuran species in Venezuela (Donoso-Barros & Leon 1972). Paradoxically, the systematics of this geographically widespread, abundant, and popularly known species is still debated.

During decades, several authors have suggested that *Boana xerophylla* (referred to as *B. crepitans*) represented multiple species (Duellman 1970, 1997, 2001; Donoso-Barros & Leon 1972; Kluge 1979; La Marca 1992; Lynch & Suárez-Mayorga 2001; Faivovich *et al.* 2005; Vanzolini & Myers 2015). In Venezuela, Barrio-Amorós *et al.* (2019) suggested that there are at least three different taxa under the name *Boana xerophylla*, although without supporting this contention. Escalona *et al.* (2019a) revealed genetic, acoustic, and morphometric differentiation between populations across the Orinoco River, further supporting the idea of the existence of cryptic species under this name.

Aiming at evaluating the species level systematics of *Boana xerophylla*, we collected new molecular, morphological, and acoustic data. A detailed comparison of phenotypic and genotypic variation indicates that there are three independently evolving lineages within *B. xerophylla*, two of them corresponding to phenotypically differentiated populations: *Boana xerophylla* sensu stricto and an unnamed taxon. Accordingly, we name and describe this new species following the rules of the International Code of Zoological Nomenclature (Anonymous 1999).

Materials and methods

Sampling. We compiled and obtained new molecular, acoustic, and morphological data from specimens of *Boana xerophylla* from Brazil, Colombia, French Guiana, Guyana, Panama, Suriname, Trinidad & Tobago, and Venezuela. More specifically, we updated the molecular dataset of Escalona *et al.* (2019a) with newly acquired and recently deposited GenBank sequences from all the countries along the species distribution area (Appendix 1); we updated the acoustic dataset with calls from Brazil, Colombia, French Guiana, Panama, Trinidad and Tobago, and Venezuela (Appendix 2); and we also updated the morphometric dataset with additional female specimens from other Venezuelan localities (Appendix 3). We complemented the three datasets with data from the *Boana faber* species group (Appendices 1–3).

Molecular methods. We extracted genomic DNA from samples preserved in 95 % ethanol (Appendix 1). Muscle samples were digested using proteinase K (10 mg/mL) and DNA was extracted following a standard salt protocol (Bruford *et al.* 1992). Amplification by polymerase chain reaction (PCR) was conducted to obtain one fragment from each of the mitochondrial genes 16S rRNA (16S) and cytochrome oxidase I (COI). The primers used were 16sar-L and 16sar-H (Kessing *et al.* 1989) for 16S, and dgLCO and dgHCO (Meyer 2003) for COI.

The PCR reactions were carried out as described in Escalona *et al.* (2019a). Successfully amplified products

were purified using Exonuclease I and Shrimp Alkaline Phosphatase (Werle *et al.* 1994), and then sequenced in an Applied Biosystems® 3130 automated Sanger DNA sequencer using the forward and reverse primers. Resulting chromatograms were assembled and edited using the CodonCode aligner software (v. 4.0.4, Codon Code Corporation). BLAST searches were performed to validate the taxonomic identity of sequences and the corresponding sequences were submitted to GenBank (Appendix 1).

Taxon and character sampling. The ingroup is composed by *Boana xerophylla* and additional species of the *B. faber* group: *B. albomarginata*, *B. crepitans*, *B. exastis*, *B. faber*, *B. lundii*, *B. pardalis*, *B. pugnax*, and *B. rosenbergi*. Our outgroup, following Faivovich *et al.* (2005), included *Aplastodiscus leucopygius*, *B. albopunctata*, *B. boans*, *B. cinerascens*, *B. ericae*, *B. lanciformis*, *B. melanopleura*, *B. multifasciata*, *B. nympa*, *B. pellucens*, *B. pulchella*, *B. punctata*, *B. roraima*, *B. rufitela*, and *Bokermannohyla alvarengai*. We included homologous sequences from GenBank of 12S, 16S, and COI for the phylogenetic analyses. In order to reduce the amount of missing entries per terminal and search space during phylogenetic analyses (Wilkinson 1995; Kearney 2002; Brower 2018), we combined sequences from two conspecific specimens in a single composite terminal (only in the outgroup; see Campbell & Lapointe 2009). Taxon and character sampling, as well as composite terminals, are listed in Appendix 1.

Phylogenetic analyses. Sequences of each locus were individually aligned using the MAFFT online service (Katoh *et al.* 2019). We used the alignment strategies E-INS-i for 12S and 16S and FFT-NS-i for COI, both under default parameters. We visualized and checked all alignments in AliView (Larsson 2014), and combined them into a single matrix using SequenceMatrix 1.8 (Vaidya *et al.* 2011). The dataset is available from MES upon request. We used the greedy algorithm of PartitionFinder v2 (Lanfear *et al.* 2016) and the Bayesian information criterion to select the optimal combination of partition schemes and DNA substitution models for the concatenated matrix. We defined 12S and 16S as potential character sets as well as each codon position of COI.

The best-fitting partition scheme and DNA substitution models were applied to maximum likelihood (ML) optimization and tree searches, with indels coded as unknown nucleotides, and performed in Garli v2.01 (Zwickl 2006). We did 500 independent searches using a fast ML stepwise-addition algorithm (“streefname = stepwise”), with stepwise-addition set to 379 (“attachmentspertaxon”), 60,000 generations without topology improvement required for termination (“genthreshfortopoterm”), tree rejection threshold at 50 (“treerejectionthreshold”), and the maximum number of branches away from original location that a branch may be reattached during a limited SPR move was 6 (“limsprange”). Bootstrap frequencies were calculated with 1,000 pseudoreplicates under the same tree search parameters outlined above. Phylogenetic analyses were run in the cluster of the Laboratório de Alto Desempenho (LAD) at PUCRS. Bootstrap frequencies were assigned to the corresponding clades of the optimal tree using SumTrees 4.3.0 of the DendroPy 4.3.0 package (Sukumaran & Holder 2010).

We considered an optimal phylogenetic hypothesis as supported if not contradicted by other, equally optimal hypotheses (Jaramillo *et al.* 2020). We interpreted Bootstrap values, when $\geq 50\%$, as a proxy of the relative amount of favorable and contradictory evidence for each clade present in the optimal topology (Goloboff *et al.* 2003; Ramírez 2005).

Mean, minimum, and maximum genetic p-distance of the 16S between members of the major clades of *Boana xerophylla* sensu lato (s.l.) were calculated in MEGA 7.0 (Kumar *et al.* 2016) using the default parameters. We used only this molecular marker because it is the most common in our dataset (Appendix 1).

Bioacoustics. We used the advertisement calls analyzed by Escalona *et al.* (2019a), new recordings from northern Brazil, French Guiana, and Venezuela and additional recordings from northern Brazil, Colombia, Panama, and Trinidad and Tobago obtained from Fonoteca Zoológica at Museo Nacional de Ciencias Naturales, Macaulay Library at Cornell Lab, and other published sources (Ibáñez *et al.* 1999; Loebmann *et al.* 2008; Appendix 2). Furthermore, we analyzed advertisement calls of all the species from the *Boana faber* species group, with the purpose of acoustically diagnosing the new species, using sound recordings obtained from Fonoteca Zoológica, Macaulay Library, and Museo de Zoología de la Pontificia Universidad Católica del Ecuador via Anfibios del Ecuador site (Ron *et al.* 2019) (Appendix 2).

We obtained spectrograms, power spectra (Hamming window, 256 samples, FFT size = 1024, and overlap = 85%), and oscillograms using Raven Pro 1.3 (Cornell Lab of Ornithology). Illustrations of oscillograms and spectrograms were generated with the R (R Core Team 2017) packages *tuneR* version 1.3.3 (Ligges *et al.* 2017) and *Seewave* version 1.7.3 (Sueur *et al.* 2008). The following call variables were obtained by ME from power spectra and oscillograms (the spectral and temporal traits, respectively): (1) NN, number of notes (following the note centered approach of Köhler *et al.* 2017); (2) 1st NL, first note length; (3) CL, call length, following Crocoft & Ryan

(1995); (4) PI, pulse interval, measured as the distance between higher amplitude peaks of two pulses (this value was obtained by calculating the mean of the PI values at the beginning, middle, and end of call); (5) FF, fundamental frequency, determined according to Duellman & Trueb (1986); (6) DF, dominant frequency, determined according to Duellman & Trueb (1986); (7) SFB, second frequency band; (8) NT, note type (*i.e.*, simple or complex), following Köhler *et al.* (2017). Additionally, we measured the length of the second phase (2nd PL), following Littlejohn (2001), for calls of *B. xerophylla* s.l. This second phase is the time between the beginning of the second note and the end of the call. Whenever possible, five calls per specimen (sparsely chosen along the recording) were quantified and the mean of each parameter for each frog was used to calculate the average, minimum, and maximum values for each group of interest. We collected and summarized acoustic data from different call types independently (see Results).

We performed a principal component analysis (PCA) with the call variables quantified for *Boana xerophylla* s.l. in order to evaluate graphically the existence of different groups. Mean values per individual were used for the PCA. We included the two call types found in the populations south of the Orinoco River. Because the advertisement call DF varies inconsistently between the upper and lower frequency bands (see Results), we included the DF of each band as independent variables in the PCA—second frequency band (SFB) and fundamental frequency (FF), respectively). We assessed the correlation between call length (CL) and number of notes (NN), as well as between FF and SFB through ordinary least square models. Since, CL and NN, and FF and SFB are correlated ($r^2 = 0.85$, $p = 0.0001$ [CL~NN]; $r^2 = 0.71$, $p = 0.0001$ [FF~SFB]), we carried out a second PCA excluding NN and SFB. We tested for statistically significant differences between the calls of *B. xerophylla* from the eastern Guiana Shield (call type I: $n = 8$; call type II: $n = 6$) and north of the Orinoco River ($n = 31$) using the first two principal components, as well as the acoustic variables. We used the exact Wilcoxon Mann-Whitney Rank Sum test in PAST version 3.19 (Hammer *et al.* 2001).

Morphological data. We examined adult specimens of the *Boana faber* group from the following museums: CVULA, Colección de Vertebrados de la Universidad de Los Andes, Mérida, Venezuela; MCNG, Museo de Ciencias Naturales de Guanare, Guanare, Venezuela; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MHNLS, Museo de Historia Natural La Salle, Caracas, Venezuela; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MTR, Miguel Trefaut Rodrigues' collection, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; and ULABG, Colección de Anfibios y Reptiles del Laboratorio de Biogeografía de la Universidad de Los Andes, Mérida, Venezuela. Species, voucher numbers, and localities are provided in Appendix 3. We identified males as specimens possessing prominent prepollex (with roughly 20 % of specimens corroborated by direct observation of gonads) and confirmed female specimens as those possessing convoluted oviducts or mature ovarian eggs. We included data from the material examined in Escalona *et al.* (2019a).

For morphological discrete and qualitative characters, we followed Duellman (1970) except for snout shape, anal plate, and thenar tubercle, for which we followed Caramaschi & Rodrigues (2003). We changed the adjective “anal” for “cloacal” because it is the appropriate term in anuran anatomy. We coded webbing extension using La Marca (1994). We used a Famex® digital calliper with precision to the nearest 0.01 mm to measure 17 external morphometric variables as described in Escalona *et al.* (2019a). Specimens of *B. rosenbergi* were kindly measured by Paulo Pinheiro following the same protocol (Appendix 3).

Integrative taxonomy and species concept. We based our taxonomic decision on the integration by congruence of different kinds of data (*e.g.*, Padial *et al.* 2010) and using the evolutionary species concept of Wiley (1978; see Frost & Hillis 1990). Thus, species are considered as separately evolving metapopulation lineages that are operationally identifiable from their sister species by fixed differences in phenotypic data (see de Queiroz 2007; Padial *et al.* 2010)—including data indicative of reproductive isolation (*i.e.*, advertisement call)—and reciprocal monophyly (Castroviejo-Fisher *et al.* 2017).

Results

Molecular analysis. We generated 107 new sequences from 87 specimens and obtained 256 sequences from GenBank, totalizing 363 sequences (Appendix 1). Our complete molecular dataset consisted of 53 DNA sequences of 12S (940 aligned bp), 167 DNA sequences of 16S (590 bp), and 143 DNA sequences of COI (657 bp). Partition-

Finder selected four partitions with the following best-fit models of nucleotide substitution for each one: 1) 12S plus 16S with a GTR+I+ Γ model; 2) COI first codon position with TRNEF+I+ Γ model; 3) COI second position, F81 model; 4) COI third position, TRN+ Γ model.

The ML tree included a monophyletic *Boana faber* species group as originally defined, but with BS < 50 % (Fig. 1). Within the *B. faber* species group, *B. albomarginata* was recovered as the most external species. Its sister clade was divided into two subgroups: a south of Amazonia clade, comprising *B. exastis*, *B. faber*, *B. lundii*, and *B. pardalis*, and a widespread group comprising *B. crepitans*, *B. pugnax*, *B. rosenbergi*, and *B. xerophylla* s.l. Within *B. xerophylla* s.l., the most external clade (BS = 100) is composed by specimens from the Venezuelan Amazonas state in the western Guiana Shield. We consider it as a candidate species requiring the acquisition of more data to be formally described (Fig. 1). This clade is sister to a large clade that is divided into two main groups, one (BS = 61) containing only specimens from the eastern Guiana Shield (northern Brazil, French Guiana, Guyana, Suriname, and Venezuela), and another (BS = 60) with specimens north of the Orinoco River (*i.e.*, Colombia, Panama, Trinidad and Tobago, Venezuela). Within each of the two aforementioned clades, branch lengths are short (≤ 0.01 expected substitutions/nucleotide), with abundant polytomies and BS values typically below 50 % (Fig. 1).

Uncorrected genetic distances for 16S among specimens of *Boana xerophylla* s.l. are summarized in Table 1. Average pairwise genetic distances are 0.1 % (0–0.7 %) within the eastern Guiana Shield clade, 0 % within the western Guiana Shield clade, and 0.5 % (0–1.4 %) within north of the Orinoco River clade. Distances among these three clades are relatively moderate compared to intraspecific distance usually observed between currently recognized species of *Boana* (Vacher *et al.* 2020), especially between the eastern Guiana Shield and north of the Orinoco River clades: 1.3 % (0.7–2.2 %).

TABLE 1. Uncorrected genetic (16S rRNA) p-distances within and between the clades of *Boana xerophylla* sensu lato found in this study: *B. platanera* sp. nov. north of the Orinoco River, *B. xerophylla* from the eastern Guiana Shield (E-GS), and *B. sp.* from the western Guiana Shield (W-GS). Values are shown as percentages (%) and represent the average followed by the minimum and maximum values.

Clade	<i>B. platanera</i> sp. nov.	<i>B. xerophylla</i> E-GS	<i>B. sp.</i> W-GS
<i>B. platanera</i> sp. nov. (n = 73)	0.5 (0.0–1.4)	-	-
<i>B. xerophylla</i> E-GS (n = 50)	1.3 (0.7–2.2)	0.1 (0.0–0.7)	-
<i>B. sp.</i> W-GS (n = 5)	2.0 (1.6–2.6)	2.5 (2.5–2.8)	0.0

Bioacoustics. We analyzed 193 calls from 42 individuals of *Boana xerophylla* s.l., and 187 calls from 41 individuals from *B. albomarginata*, *B. exastis*, *B. faber*, *B. lundii*, *B. pardalis*, and *B. rosenbergi*. Descriptive statistics of acoustic variables of all currently recognized species of the *Boana faber* group are in Table 2. Within *B. xerophylla* s.l., we found four distinct types of calls: two are unique to the populations north of the Orinoco River, while the other two are unique to the populations from the eastern Guiana Shield (Fig. 2). One of the call types of the populations north of the Orinoco River was found in 31 recordings, while the other was found predominantly in three recordings. We also identified this call type in some recordings as part of the background calls of a chorus. We considered that the most frequent type of vocalization is the advertisement call. We did not include in our analysis the three recordings with the uncommon call—MES_LC1 (ULABG 7770), MES_CA6 (unvouchered) and MES_CA7 (unvouchered)—since it could be a different kind of vocalization (*e.g.*, territorial call). Eighteen percent of recordings from the eastern Guiana Shield contain just one type of call, while 82 % recordings include two types of calls, emitted without any evident pattern and apparently by the same individual. We did not observe different behavioral contexts between recordings from the eastern Guiana Shield (*i.e.*, individuals were usually vocalizing with at least two conspecifics and often with a heterospecific).

The first three components of the PCA with all the acoustic measurements (Fig. 3A) explain 51.8 %, 20.6 % and 9.6 % of the acoustic variance, respectively. The summary and loadings of the PCA are shown in Table 3. The variables with the highest loadings in the first principal component are: number of notes (NN) and call length (CL). The variables with the highest loading in the second component are second frequency band (SFB) and fundamental frequency (FF), while the variable with the highest loading in the third component is second phase length (2nd PL). The first three components of the PCA obtained without including NN and SBF (Fig. 3B) explain 52.14 %, 16.01 % and 12.26 % of the acoustic variance. Call length is the variable with the highest loading in the first principal component and FF is the variable with the highest loading in the second principal component. There is not overlapping in

the acoustic space between the populations north of the Orinoco River versus the eastern Guiana Shield (Fig. 3). We found significant differences ($p \leq 0.05$) between the populations north of the Orinoco River versus the eastern Guiana Shield (using the two call types independently, see below) in the first and third principal components, pulse interval (PI), and first note length (1st NL)—calls north of the Orinoco River populations have longest PI and shortest 1st NL. Additionally, comparing with the call type I of the eastern Guiana Shield populations, we found significant differences with the populations north of the Orinoco River in the second principal component, number of notes and call length—calls north of the Orinoco River populations are longer and with a higher number of notes. Comparing with the call type II of the eastern Guiana Shield populations, the second phase of calls north of the Orinoco River populations are significantly longer. Below, we describe in detail the calls of each group of interest.

TABLE 2. Advertisement call data of species of the *Boana faber* group obtained in this study (see Appendix 2 for details of sound records). Values are given as average followed by minimum and maximum values when there is variation. NT = Note type; ST = structure; NN = number of notes; CL = call length (ms); FF = fundamental frequency (Hz); DF = dominant frequency (Hz). The data of *B. exastis* and *B. crepitans* is from Loebmann *et al.* (2008) and Escalona *et al.* (2019a), respectively.

Species	NT	ST	NN	CL	FF	DF
<i>B. albomarginata</i> (n = 3)	Simple	Pulsed	1	175 (166–185)	1188.6 (1136.9–1231.7)	2331.3 (2196.4–2446.2)
<i>B. faber</i> (n = 6)	Simple	Pulsed	1	86 (75–121)	402.4 (344.5–447.9)	1114.0 (990.5–1274.8)
<i>B. lundii</i> (n = 2)	Simple	Pulsed	4 (1–8)	1031 (834–1228)	512.1 (506.2–517.9)	512.1 (506.2–517.9)
<i>B. pardalis</i> (n = 5)	Simple	Pulsed	1	133 (117–143)	647.7 (602.5–826.9)	647.7 (602.5–826.9)
<i>B. exastis</i> (n = 12)	Simple	Pulsatile	3 (2–4)	1040 (807–1229)	320.0 (270.0–360.0)	1420.0 (1300.0–1510.0)
<i>B. pugnax</i> (n = 8)	Simple	Pulsed	1	209 (156–258)	623.4 (562.5–750.0)	1486 (562.5–1687.5)
<i>B. rosenbergi</i> (n = 2)	Simple	Pulsed	6 (4–8)	655 (551–759)	607.3 (568.5–646)	607.3 (568.5–646)
<i>B. crepitans</i> (n = 7)	Simple	Pulsed	2	427 (368–473)	842.6 (689.1–937.5)	842.6 (689.1–937.5)
<i>B. platanera</i> sp. nov. (n = 31)	Complex	Pulsed	5 (4–6)	284 (200–451)	713.7 (542.7–1125.0)	1280.4 (562.5–2287.5)
<i>B. xerophylla</i> ¹ (n = 8)	Simple	Pulsed	1	97 (79–125)	827.0 (617.3–964.7)	1443.6 (656.2–1966.7)
<i>B. xerophylla</i> ² (n = 6)	Complex	Pulsed	4 (3–6)	261 (210–297)	859.2 (618.7–974.3)	1533.7 (909.8–1938.4)

¹Call type I (see Results for details).

²Call type II (see Results for details).

Vocalization of *Boana xerophylla* north of the Orinoco River. Frogs from these populations produced a complex and biphasic (sensu Littlejohn 2001) advertisement call formed by five pulsed notes (minimum and maximum: 4–6 notes) (Fig. 2A and C, Table 3). The notes are composed by two to four pulses. The first phase corresponds to the first note, while the second phase corresponds to the segment of the call between the second and the last note. The amplitude and duration of pulses increase from the second note (Fig. 2C). The first phase lasts, on average, 44 ms (minimum and maximum: 28–71 ms) and it is followed by a silent interval, highly variable, that lasts on average 35 ms (11–89 ms). The second phase lasts 205 ms (137–312 ms). Total call length is 284 ms (200–451 ms). The call amplitude is modulated. The relative amplitude in the first note was around 50 % the relative amplitude at the end of the call; it increases progressively in the beginning of the second note, reaching the highest value at the first pulse of the last note and then decreasing abruptly (Fig. 2C).

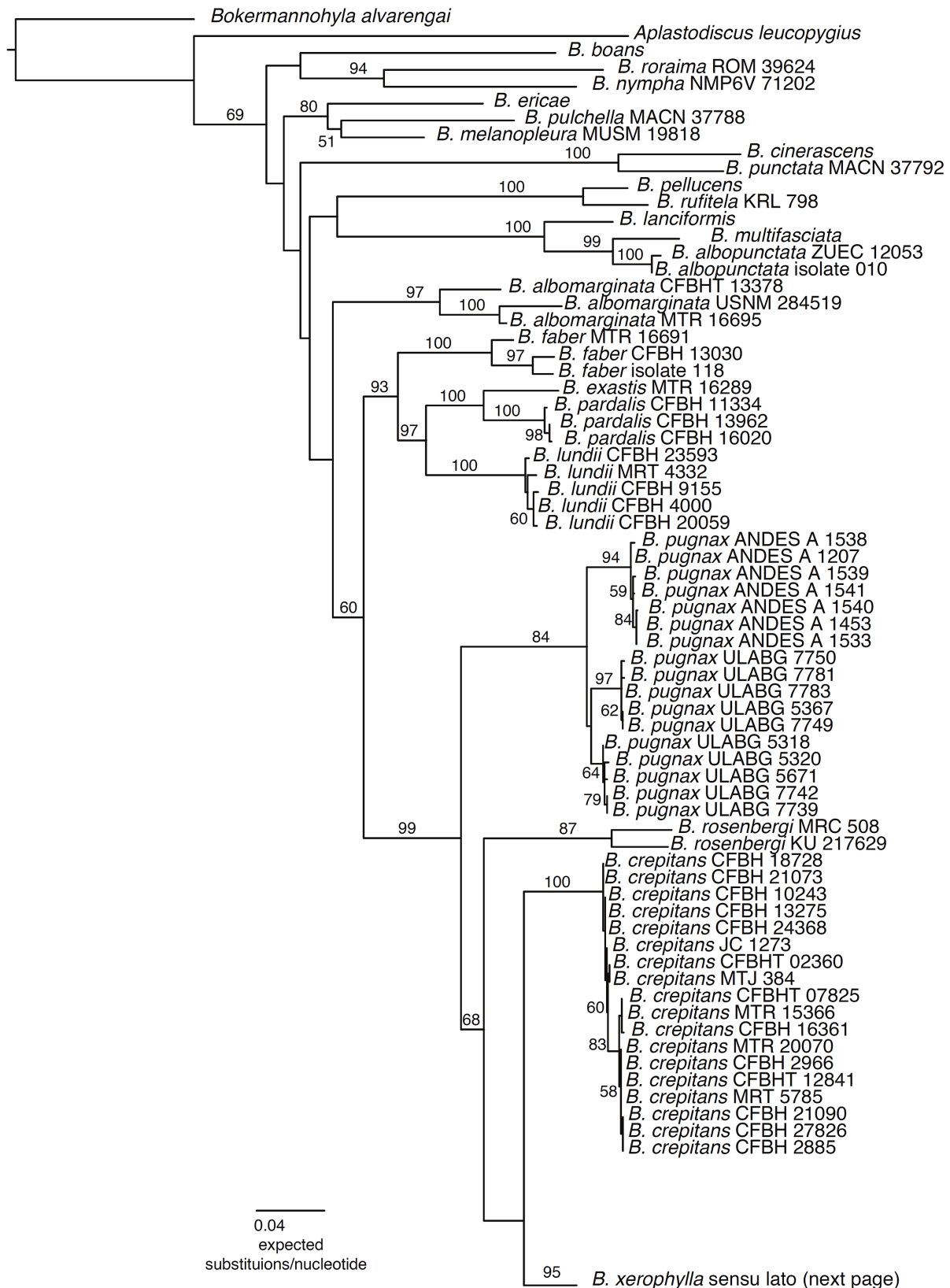


FIGURE 1. Maximum likelihood phylogenetic tree of the *Boana faber* species group and outgroups inferred from concatenated DNA sequences of fragments of the mitochondrial genes 12S, 16S, and COI, totaling 2820 aligned base pairs. The best models of molecular evolution were used per fragment and codon position. Numbers on internal branches are the percentage ($\geq 50\%$) of 1,000 nonparametric bootstrap pseudoreplicates. The updated taxonomy of *B. xerophylla* following the results of this work is on the right of the black bars.

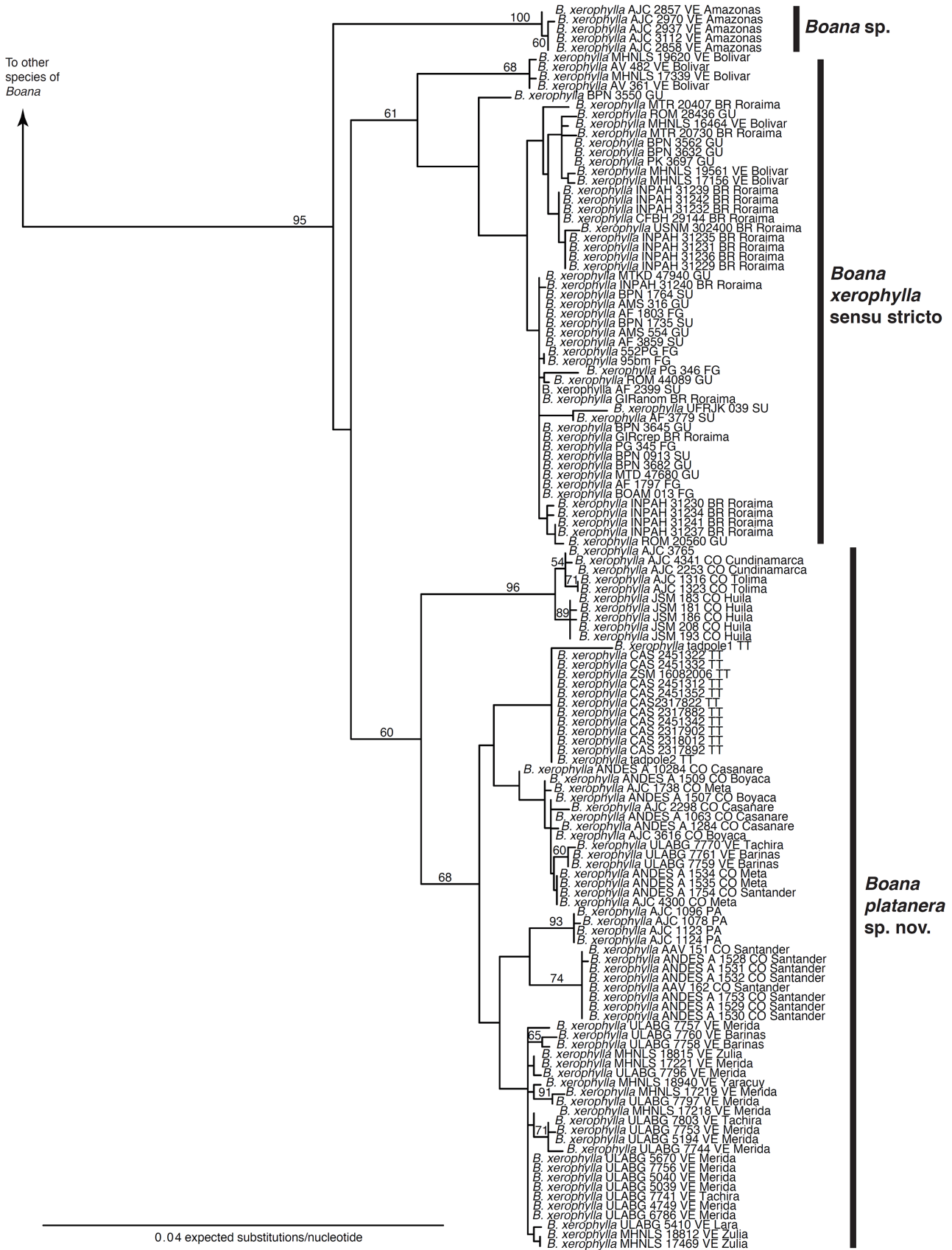


FIGURE 1. (Continued)

TABLE 3. Eigenvalue, variance explained (in %), and loadings for the six principal components obtained from the principal component analysis of the advertisement call of *Boana platanera* **sp. nov.** (n = 31) and the call types I (n = 8) and II (n = 6) of *B. xerophylla*. Highest loading are shown in bold. NN = number of notes; 1st NL = first note length; 2nd PL = second phase length; CL = call length; PI = pulse interval; FF = fundamental frequency; SFB = second frequency band.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Eigenvalue	3.62685	1.44539	0.671059	0.619474	0.485245	0.111824
Variance (%)	51.8	20.6	9.6	8.8	6.9	1.6
Loadings						
NN	0.42115	0.40979	-0.35279	0.087963	0.10258	0.018553
1 st NL	-0.35444	-0.38066	-0.13209	0.382	0.68007	0.24324
2 nd PL	0.34672	-0.069226	0.67326	0.63023	-0.11482	0.0014711
CL	0.43806	0.28769	-0.29811	0.28225	0.34315	0.092649
PI	0.37391	-0.075023	0.44534	-0.6069	0.49494	0.20317
FF	-0.34582	0.52799	0.27574	0.024572	0.3775	-0.61844
SFB	-0.35425	0.56143	0.20391	0.023667	-0.092643	0.71285

TABLE 4. Acoustic measurements (average, minimum, and maximum values) of the advertisement call of *Boana platanera* **sp. nov.** and call types I and II of *B. xerophylla*. The measurements for the holotype, two paratypes, and one non-collected topotype (recording “MES_SO2”) of *B. platanera* are shown separately. N = number of individuals. Abbreviations as follow: 1st NL = first note length (ms); 2nd PL = second phase length (ms); CL = call length (ms); DF = dominant frequency (Hz); FF = fundamental frequency (Hz); SFB = second frequency band (Hz); NN = number of notes; PI = pulse interval (ms).

	ULABG 7758 (holotype)	ULABG 7759 (paratype)	ULABG7760 (paratype)	Topotype 1 (unvouchered)
NN	5 (4–5)	5 (4–6)	5 (5–6)	5 (5–5)
CL	400	320	340	378
1st NL	59	50	45	37
2nd PL	255	245	259	270
PI	19	18	21	16
FF	562.5	600.0	562.5	750.0
SFB	1312.5	1350.0	1218.8	1500.0
DF	562.5	600.0	937.5	1500.0

Continued.

	<i>B. platanera</i> (n = 31)	<i>B. xerophylla</i> - call type I (n = 8)	<i>B. xerophylla</i> - call type II (n = 6)
NN	5 (4–6)	1	4 (3–6)
CL	284 (200–451)	97 (79–125)	261 (210–297)
1st NL	44 (28–71)	97 (79–125)	94 (85–110)
2nd PL	205 (137–312)	NA	108 (73–150)
PI	16 (11–23)	13 (12–14)	12 (11–14)
FF	713.7 (542.7–1125.0)	827.0 (617.3–964.7)	859.2 (618.7–974.3)
SFB	1656.7 (1033.6–2306.26)	1840.5 (1500.0–2101.7)	1870.7 (1593.8–2058.2)
DF	1280.4 (562.5–2287.5)	1443.6 (656.2–1966.7)	1533.7 (909.8–1938.4)

The advertisement call has two frequency bands in most recordings, which have about the same relative amplitude (Fig. 2E). The fundamental frequency is on average 713.7 Hz (542.7–1125.0 Hz) and the second frequency band is 1656.7 Hz (1033.6–2306.26 Hz). Usually, the second frequency band is the dominant (Table 4). The dominant frequency is 1280.4 Hz (562.5–2287.5 Hz), which is usually modulated, increasing gradually towards the end of the call; the dominant frequency is 680.0 Hz (516.8–1106.3 Hz) in the first note and 1449.6 Hz (551.2–2343.8

Hz) at the end of the call (average change in dominant frequency = 790.2 Hz, -51.7–1541.8 Hz). The second frequency band is emphasized only in the second-half of the second phase (Fig. 2G).

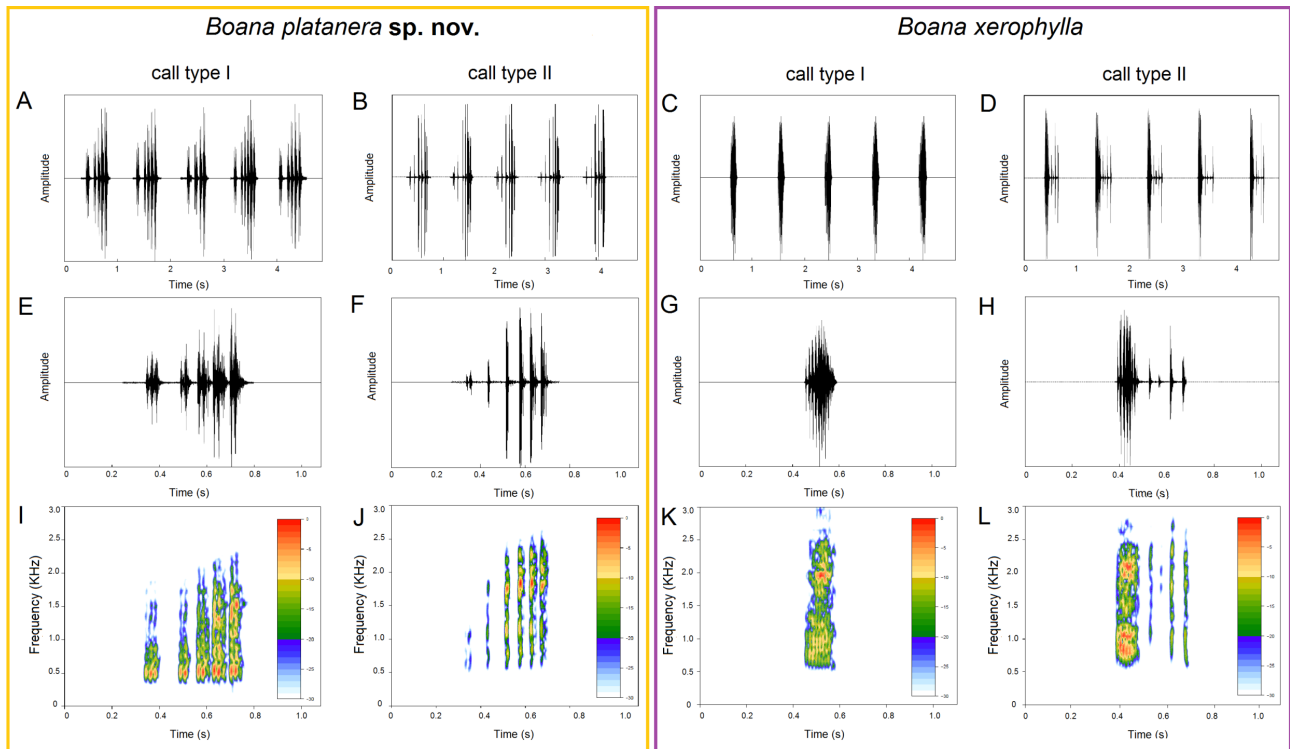


FIGURE 2. Calls of *Boana platanera* sp. nov. (A, B, E, F, I and J) and *B. xerophylla* (C, D, G, H, K and L). (A and E) Oscillograms and (I) spectrogram of the advertisement call (call type I) of *B. platanera*. Illustrated calls from the holotype, ULABG 7758, temperature and humidity at time of recording unknown (recording “MES_SO1”). (B and F) Oscillograms and (J) spectrogram of the presumably territorial call (call type II) of *B. platanera*. Illustrated calls from a non-collected specimen from Caparú lagoon, Mérida state, Venezuela, temperature and humidity at time of recording unknown (recording “MES_CA6”). (C and G) Oscillograms and (K) spectrogram of the advertisement call (call type I) of *B. xerophylla*. (D and H) Oscillograms and (L) spectrogram of the presumably territorial call (call type I) of *B. xerophylla*. Both illustrated calls from specimen AAG-UFU 5550, from Rancho do Papito, road BR-432, on the road from Boa Vista to Cantá, Roraima state, Brazil, air and water temperature at time of recording 26 °C and 32 °C, respectively (recording “Hypsib_crepitansCantaRR2bAAG”).

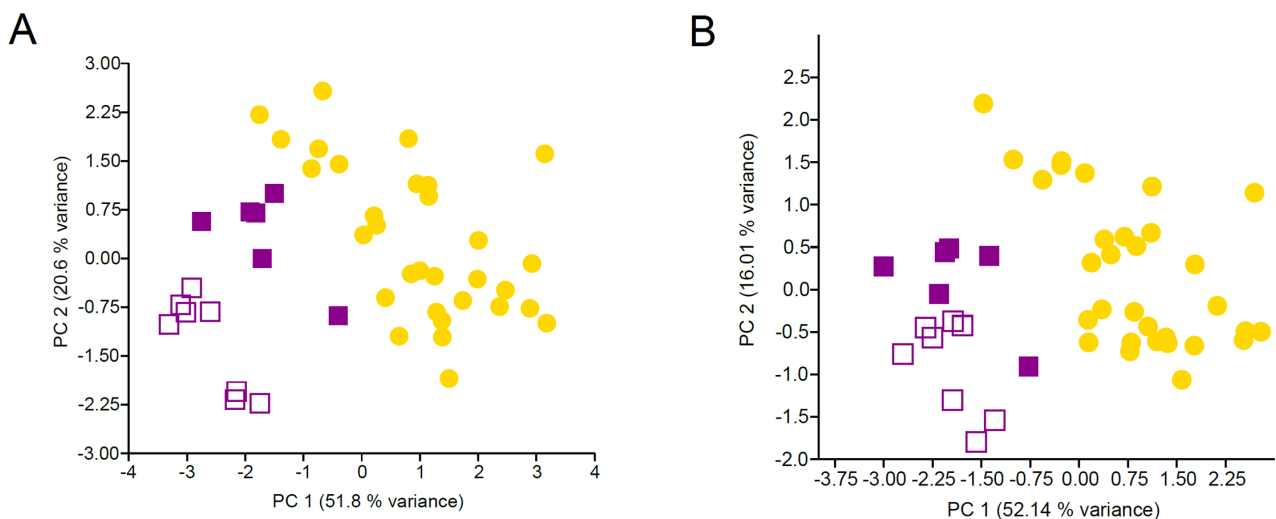


FIGURE 3. Scatter plot of the first two principal components obtained of the principal component analysis (PCA) of the call variables measured for *Boana xerophylla* sensu stricto and *B. platanera* sp. nov. Values between brackets are the variance explained by each component. Yellow dots are *B. platanera* specimens (n = 31); purple empty and filled squares are *B. xerophylla* specimens with call type I (n = 8) and II (n = 6), respectively.

TABLE 5. Measurements of external morphology and webbing formulas of some type specimens of *Boana platanera* sp. nov. (holotype in bold) and average, minimum, and maximum values per sex. Sample included all type and referred specimens measured (Appendix 3). All measurements are in mm. Abbreviations: SVL, snout-vent length; FL, femur length; TL, tibia length; TaL, tarsus length; FoL, foot length; AL, arm length; FaL, forearm length; HL, hand length; DIIIW, disc width of finger III; HW, head width; IED, inter-eye distance; IND, inter-nostril distance; HeL, head length; TW, tympanic membrane width; ETD, eye-tympanum distance; EL, eye length; END, eye-nostril distance; Hwb, hand webbing; and Fwb, foot webbing.

	ULABG 7758	ULABG 7759	ULABG 7760	ULABG 7761	Females (N = 76)	Males (N = 195)
SVL	52.87	54.01	53.93	55.50	63.10 (54.33–74.74)	54.32 (46.57–63.34)
FL	28.70	30.50	28.87	30.21	34.12 (27.52–40.89)	29.65 (23.49–35.98)
TL	28.50	31.31	28.22	31.07	34.89 (30.22–39.53)	30.69 (25.17–36.28)
TaL	16.10	17.18	15.81	17.20	19.04 (16.06–22.37)	16.84 (14.30–20.09)
FoL	21.45	23.37	22.44	21.99	25.49 (21.22–29.74)	22.28 (18.26–26.01)
AL	8.30	9.53	8.87	10.06	10.46 (7.11–13.38)	9.18 (6.66–12.63)
FaL	9.01	10.23	10.05	11.03	11.34 (9.29–13.97)	9.49 (7.42–11.37)
HL	16.47	16.47	16.08	15.86	18.25 (15.14–21.29)	16.24 (13.72–19.80)
DIIIW	2.19	3.17	2.93	2.87	3.07 (2.11–3.85)	2.60 (1.48–3.44)
HW	18.35	18.99	18.21	19.17	21.10 (18.14–24.94)	18.62 (14.58–20.85)
IED	5.40	6.17	6.16	5.95	6.62 (5.23–8.71)	5.92 (4.62–7.56)
IND	3.70	4.05	3.58	3.94	4.08 (3.34–5.00)	3.60 (2.87–4.23)
HeL	17.27	17.84	17.18	17.56	20.27 (17.50–23.54)	17.83 (15.39–21.05)
TW	4.25	4.27	4.43	4.52	4.87 (3.48–5.87)	4.37 (3.02–5.16)
ETD	2.05	2.12	1.74	1.76	2.28 (1.42–3.16)	1.97 (0.96–2.78)
ED	4.86	5.21	4.97	6.00	6.16 (4.90–7.75)	5.44 (4.31–6.68)
END	5.19	5.70	5.44	5.44	6.09 (4.68–7.74)	5.32 (4.37–6.93)
Hwb	III ⁺ –IIII ^{1/2} –2 ⁺ IV	III ^{1/2} –2 ⁺ IV	III ^{1/2} –2 ⁺ IV	III–IIII ^{1/2} –2 ⁺ IV	-	-
Fwb	I ^{1/2} –1 ⁺ II ⁺ –2 ⁺ III ⁺ –3 ⁺ IV ⁺ –3 ⁺ V	II ⁺ –3 ⁺ III ⁺ ; IV ⁺ –3 ⁺ V	III ⁺ –2 ⁺ IV ⁺ ; IV ⁺ –3 ⁺ V	II ⁺ –2 ⁺ III ⁺ ; IV ⁺ –3 ⁺ V	-	-

Vocalizations of *Boana xerophylla* from the eastern Guiana Shield. Descriptive statistics of the acoustic variables are shown in Table 2 and 4. We found two call types in six of the eight analyzed recordings. The most common call type (53 %), hereafter call type I, is the one analyzed by Escalona *et al.* (2019a). This is a simple pulsed call formed by one note (Fig. 2B and D) with average duration of 97 ms (minimum and maximum: 79–125 ms). Call amplitude is modulated, progressively increasing, and reaching its highest value at the middle of the call, after which it decreases progressively (Fig. 2D). This call has two frequency bands (Fig. 2F). The fundamental frequency is 827.0 Hz (617.3–964.7 Hz) and the dominant frequency at 1443.6 Hz (656.2–1966.7 Hz). Only one individual (AAG-UFU 5549) emitted calls with the fundamental frequency being the dominant frequency. Dominant frequency was modulated in most of cases, increasing towards the end of the call (average change in the dominant frequency = 854.4 Hz, 722.6–1042.2 Hz).

The second type of vocalization, hereafter call type II, is a complex call formed by four notes (minimum and maximum: 3–6 notes; Fig. 2C, F and I), which is basically formed by a call type I, with the addition of two to five spaced short notes. This call, following Littlejohn (2001), is biphasic. Average call length is 262 ms (210–296 ms), with the first note lasting 94 ms (85–110 ms) and the second phase (group of short notes) lasting 105 ms (73–150 ms). This type of call has two frequency bands (Fig. 2I); the fundamental frequency is 907.3 Hz (843.8–974.3 Hz) and the dominant frequency is 1637.9 Hz (909.8–1938.0 Hz). Call type II has a dominant frequency modulation, but not as steep as that observed in call type I (average change in the dominant frequency = 489.4 Hz, 93.8–956.2 Hz). In both call types, the second frequency band is emphasized in the first note (Fig. 2H, I).

Morphological data. In addition to the morphometric data of Escalona *et al.* (2019a), we measured 76 adult females from populations north of the Orinoco River and around 30 individuals from the other species of the *B. faber* species group. Table 5 summarize character variation. Detailed morphological comparisons are presented in the systematics section. Morphological characters are illustrated in Figs. 4–6, 8–10.

Data integration. The observed phylogenetic, morphological, and acoustic variation reported in this study and Escalona *et al.* (2019a) consistently and congruently indicate that *Boana xerophylla*, as currently understood, includes more than one independently evolving lineage. While the specimens from the eastern Guiana Shield can be clearly associated with the binomen *Boana xerophylla* sensu stricto, those north of the Orinoco River are considered as part of a new species that we name and describe below. Based on the molecular phylogenetic analyses and genetic differentiation, we flag the specimens from the western Guiana Shield clade as members of an unconfirmed candidate species.

***Boana platanera* sp. nov. La Marca, Escalona, Castellanos, Rojas-Runjaic, Crawford, Señaris, Fouquet, Giaretta, and Castroviejo-Fisher**
(Figs. 2, 4–6, 8J, 10)

Suggested common name: Banana tree dwelling frog (rana platanera, in Spanish).

Boana xerophylla—populations north of the Orinoco River, Dubois (2017); Rojas-Runjaic & Infante-Rivero (2018); populations north of the Orinoco River, Barrio-Amorós *et al.* (2019); populations north of the Orinoco River, Escalona *et al.* (2019a); Cañizales (2020).

Hypsiboas xerophyllus—populations from north Orinoco River, Orrico *et al.* (2017).

Hypsiboas crepitans—populations from north Orinoco River, Faivovich *et al.* (2005); populations from north Orinoco River, Köhler (2010); Lehtinen (2014); Guarnizo *et al.* (2015).

Hyla crepitans—Lutz (1927); Shreve (1947); Alemán (1953); Ginés (1959); Röhl (1959); Rivero (1961); Fouquette (1966); Solano de Chacín (1968); Kenny (1969); populations from north Orinoco River, Duellman (1970, 1997, 2001); populations from north Orinoco River, Cochran & Goin (1970); Donoso-Barros & Leon (1972); Yústiz (1976); Kluge (1979); La Marca (1992); Kime *et al.* (2000); Lynch & Vargas Ramírez (2000); Lynch & Suárez-Mayorga (2001); Bernal *et al.* (2004); Nava (2005); populations from Colombia and Panama, Vanzolini & Myers (2015).

Holotype. Adult male, ULABG 7758 (field number MES 018; Figs. 2, 4), from 2 km of La Soledad, on the road from Barinitas to Santo Domingo, Barinas state, Venezuela (08°48'26" N, 70°30'46" W [datum: WGS 84]; 947 m asl; Fig. 7A), collected by Enrique La Marca, Moisés Escalona, and Iván Mendoza, on June 13, 2012.

Paratypes. Three adult male specimens, ULABG 7759–7761, topotypes, same data as holotype (Fig. 5). Three adult male specimens, ULABG 7762–7764, from La Soledad, Barinas state, Venezuela (08°48'35" N, 70°31'31"

W [datum: WGS 84] 980 m asl), collected by Enrique La Marca, Moisés Escalona, and Iván Mendoza, on June 13, 2012.

Referred specimens. Up to 497 specimens were used to describe the genetic and phenotypic variation, although they are not included in the type series. In addition, we analyzed the calls of eleven non-vouchered specimens. See Appendices 1–3 for details.

Generic placement. The new species is assigned to *Boana*, within the *B. faber* group (sensu Faivovich *et al.* 2005), based on the results of the phylogenetic analyses (Fig. 1).



FIGURE 4. Dorsal and ventral view of *Boana platanera* sp. nov. preserved holotype, ULABG 7758 (field number MES 018) from 2 km of La Soledad, on the road Barinitas to Santo Domingo, Barinas state, Venezuela. White scale bar represents 20 mm. Photos: Michelle Castellanos and Enrique La Marca.

Definition. The new species is defined by the combination of the following characters: (1) moderately large size, snout-vent length (SVL) 54.33–74.74 mm in females ($n = 76$) and 46.57–63.34 mm in males ($n = 195$); (2) head narrower than body, flat in dorsal view; (3) snout truncated (slightly rounded in some individuals) in dorsal and lateral view; nostrils protuberant; (4) horizontal pupil; first half of palpebral membrane densely pigmented with black dots; (5) supratympanic fold extends posteriorly from posterior eye corner and slopes downward to a point above arm insertion; (6) distance between tympanum and eye equal to or shorter than half tympanum diameter; (7) forearm relatively more robust than arm; fingers moderately long and slender with large rounded discs; (8) adult males with prepollical spine, protruding through distal end in some cases; (9) hand-web formula $\text{I0-0II}(1-1^+)-(1-1^+)\text{III } 1.5-(2^-2^+)\text{IV}$; (10) foot-web formula $\text{II } 1.5-1^+\text{II}(2^-2^+)-(2-3^-)\text{III}3-(2^-3^-)\text{IV}(3-3^-)-(3^-3^+)\text{V}$; (11) cloacal opening at thighs upper level, with supraclacal fold directed posteriorly; pericloacal region dark-brown with a white-colored crenulated supraclacal fold; (12) skin granular on throat, chest, belly, and ventral surfaces of thighs; (13) dorsal skin smooth, slightly granulated on flanks; (14) poorly developed ulnar fold extending along finger IV external side; (15) tarsal fold poorly evident; (16) calcars absent; (17) adult males with vocal sac simple, median, subgular, and moderately distensible (Fig. 6H); (18) dorsal coloration is variable at night, from almost uniform pale

yellowish ocher, reddish brown, to conspicuously marbled with more or less well defined dark-brown marks, and an irregular or broad X-shaped on the mid dorsum; (19) in preservative, palms and soles pale cream-colored, hand and foot webs cream with dark brown flecks, especially on foot.

Diagnosis. Character states of compared species are given in parentheses. *Boana platanera* is sister of *B. xerophylla* (Fig. 1) and it can be diagnosed from the latter by the following combination of adult male characters: a pale orange-yellow or light brown coloration on dorsum (dark brown to green tones; Fig. 8I, J); presence of black or dark brown speckles in the anterior half of the palpebral membrane (absent; Fig. 9); pericloacal region dark brown (cream); advertisement call with shorter, 28–71 ms, first note length (79–124 ms in call type I and 85–110 ms in call type II), composed of five notes (one note in call type I). Although not diagnostic, the following characters may help to differentiate both species: the new species has a statistically significant larger body (46.57–63.34 mm) than *B. xerophylla* (45.13–56.71 mm) (Table 2 in Escalona *et al.* 2019a); in preservative, the gular region is cream with dark brown or black flecks near to the jaw border (cream and sometimes with few dark brown speckles on the border of the jaw; Fig. 9); advertisement call with statistically significant longer pulse interval (11–23 ms) than *B. xerophylla* (12–14 ms in call type I and 11–14 ms in call type II); statistically significant longer second phase length (137–312 ms) than *B. xerophylla* (73–150 ms in call type II).



FIGURE 5. Dorsal and ventral views of preserved paratypes, ULABG 7759–7764. Details in the text. Photos: Michelle Castellanos and Enrique La Marca.

Boana platanera is sympatric with *B. pugnax* in lowland western and central Venezuela. The new species is distinguished from *B. pugnax* by having a pale orange-yellow or light brown coloration on dorsum (dark-brown to dark-grey tones; Fig. 8G, J); the anterior half of the palpebral membrane densely pigmented (poorly pigmented); dorsal surfaces of finger and toe discs usually cream, when pigmented, pale gray (dark); calcar absent (poorly developed); a complex advertisement call composed of five notes (simple call of one note). Although not diagnostic, *B. platanera* is distinguished from *B. pugnax* by having a statistically significant smaller body (males: *B. platanera*: 46.57–63.34 mm; *B. pugnax*: 55.85–74.80 mm [sample from western Venezuela]; Table 4); and a statistically significant longer advertisement call (*B. platanera*: 200–451 ms; *B. pugnax*: 156–258 ms).

The new species differs from *Boana crepitans* by having a pale orange-yellow or light brown coloration on dorsum (gray-cream tones to dark brown; Fig. 8H, J); advertisement call composed of five notes (two notes). Although not diagnostic, the new species has a statistically significant shorter ETD (eye to tympanum distance; *B.*

platanera: 0.96–2.78 mm) than *B. crepitans* (1.99–3.29 mm) (Tables 1–2 in Escalona *et al.* 2019a); statistically significant shorter advertisement call (*B. platanera*: 200–451 ms; *B. crepitans*: 368–473 ms), with a statistically significant shorter second phase (*B. platanera*: 137–312 ms; *B. crepitans*: 278–367 ms) (Tables 2, 3 in Escalona *et al.* 2019a).

Boana platanera differs from *B. rosenbergi* by having a smooth dorsum, thighs, and flanks (rough or with tubercles in at least one of these regions; Fig. 8); smaller body size (males: *B. platanera*: 46.57–63.34 mm; *B. rosenbergi*: 75.55–83.98 mm); presence of black dots on anterior half of the palpebral membrane (absent); ulnar fold smooth (slightly crenulated); and a complex advertisement call (simple in *B. rosenbergi*) with shorter duration (*B. platanera*: 200–451 ms; *B. rosenbergi*: 551–759 ms) (Table 2).

The new species differs from *Boana exastis* by having a smooth dorsum, thighs, and flanks (rough or with tubercles in at least one of these regions; Fig. 8); smaller body size (males: *B. platanera*: 46.57–63.34 mm; *B. exastis*: 81.1–99.0 mm); presence of black dots on anterior half of the palpebral membrane (absent); poorly-defined dermal fringes on limbs (crenulated dermal fringes), less webbing in hands and feet (more extensive webbing in hands and feet), absence of cloacal plate (presence); absence of calcars (presence); complex advertisement call (simple in *B. exastis*), with shorter duration (*B. platanera*: 200–451 ms; *B. exastis*: 807–1229 ms) (Table 2).

Boana platanera differs from *B. lundii* by having a smooth dorsum, thighs, and flanks (rough or with tubercles in at least one of these regions; Fig. 8); presence of black dots on anterior half of the palpebral membrane (absence); poorly-defined dermal fringes on limbs (well defined); less webbing in hands and feet (more webbing in hands and feet); absence of calcars (presence); complex advertisement call (simple), with shorter duration (*B. platanera*: 200–451 ms; *B. lundii*: 834–1228 ms) (Table 2).

The new species differs from *Boana pardalis* by having a smooth dorsum, thighs, and flanks (rough or with tubercles in at least one these regions; Fig. 8); presence of black dots on first half of the palpebral membrane (absence); poorly-defined dermal fringes on limbs (crenulated); less webbing in hands and feet (more webbing in hands and feet); absence of cloacal plate (presence); absence of calcars (presence); complex advertisement call (simple), with longer duration (*B. platanera*: 200–451 ms; *B. pardalis*: 117–143 ms), composed of 4–6 notes (one) (Table 2).

Boana platanera differs from *B. faber* by having a smaller body size (males: *B. platanera*: 46.57–63.34 mm; *B. faber*: 77.90–97.08 mm); presence of black dots on anterior half of the palpebral membrane (absence); ulnar fold present (absent); cream gular coloration with dark-brown flecks near to the jaw border (dark); complex advertisement call (simple), longer advertisement call (*B. platanera*: 200–451 ms; *B. faber*: 75–121 ms), composed of 4–6 notes (one note), with higher fundamental frequency (*B. platanera*: 542.7–1125.0 Hz; *B. faber*: 344.5–447.9 Hz) (Table 2).

Boana platanera is readily distinguishable from *B. albomarginata* by having a smooth dorsal skin (slightly granular in *B. albomarginata*), a pale orange-yellow coloration with dark-brown marks, irregular or broad X-shaped on the dorsum and dark-brown bars on flanks and thighs (green with some white spots on the dorsum; Figs. 8A, J); supratympanic fold slopes downward to a point above arm insertion (supratympanic extends posteriorly until half of the laterodorsal region); absence of calcar (presence); complex advertisement call (simple), with longer duration (*B. platanera*: 200–451 ms; *B. albomarginata*: 166–185 ms), with 4–6 notes (one note), and lower fundamental frequency (*B. platanera*: 542.7–1125.0 Hz; *B. albomarginata*: 1136.9–1231.7 Hz) (Table 2). Although not diagnostic, the new species is larger bodied (males: *B. platanera*: 51.97–59.08 mm; *B. albomarginata*: 44.68–53.6 mm).

Holotype description. Adult male in a good state of preservation (Fig. 4), with a piece of tissue sampled from the right thigh. Morphometric measurements of the holotype are presented in Table 5. Body slender; head longer than wide (HW/HeL = 1.06); snout truncated in lateral and dorsal views; nostrils protuberant, oblique and directed dorsolaterally; internarial distance smaller (66 %) than eye-to-nostril distance; eye diameter, upper eyelid width and interorbital distance approximately equal to tympanum diameter; canthus rostralis rounded, almost indistinct; loreal region concave; lips not flared; eyes large (ED/HeL = 0.28), protruding; interorbital region and dorsal surface of snout slightly concave. Tympanum conspicuous, nearly circular; tympanic membrane differentiated; tympanic annulus well-defined, with upper border concealed by the tympanic membrane. Vocal sac single, subgular; vocal slits large, located at the posterolateral edge of the mouth floor. Tongue wider than long, cordiform, slightly notched behind; almost completely attached to mouth floor. Choanae elliptical, widely separate. Vomerine teeth massive; vomerine processes arched, slightly separate and between choanae.



FIGURE 6. Specimens of *Boana platanera* **sp. nov.** in life. Note the variation in coloration at night (A–D, G, H), the difference of the coloration during the day (E), and the coloration of a juvenile at night (F). All the specimens from Venezuela: (A, B) adult male not collected from Sabaneta sector, El Hatillo, Miranda state; (C) adult male from Río Cata, Aragua state; (D) adult male from Parque Minas de Aroa, Yaracuy state; (E) adult male from Ipika, Sierra de Perijá, Zulia state; (F) juvenile not collected, sex unknown, from Posada Ecológica Casa María, altos de Canoabo, Carabobo state; (G) adult male calling from Laguna de Caparú, Mérida state; (H) adult male calling from Posada Ecológica Casa María, altos de Canoabo, Carabobo state (not collected). The photos are not to the same scale. Photos: (A–B, D) Fernando J. M. Rojas-Runjaic; (E) Edwin Infante; (F, H) Celsa Señaris (C) Iván Mendoza; (G) Moisés Escalona.

Arms slender; forearms more robust than upper arms; an inconspicuous crenulated fringe along forearm ventro-external surface and prolatral side finger IV (more conspicuous on right forearm). Hand with an elliptical and flat palmar tubercle and a inconspicuous thenar tubercle; prepollex well-developed, with a single curved spine (Fig. 5); numerous small supernumerary tubercles scattered on the palm; relative fingers length: III>IV>II>I; subarticular tubercles single, rounded to conical and prominent; fingers discs large, expanded and nearly circular; disc on first finger slightly smaller than those of other fingers; third finger disc diameter about 50 % of eye diameter and approximately 60 % of tympanum diameter; hand-webbing formula: I0–0III⁺–1III1.5–2⁺IV.

Legs long and slender; thigh length slightly longer than shank length (FL/TL = 1.01); without calcars—the protrusion of the skin fold on the right heel, which resembles a calcar, is caused by the fixation position of the hind limbs, with the feet oriented posteriorly; tarsal fringe not evident; foot with an elliptical inner metatarsal tubercle; outer metatarsal tubercle not evident; subarticular tubercles single, rounded and prominent; supernumerary tubercles scarce, small, and flat; toes extensively webbed, with rounded and expanded disks; foot-web formula: II.5–1⁺III2⁺–2III3–3IV3–3⁺V. Skin on dorsal surfaces smooth; throat, chest, belly and inferior edge of ventral surface of thighs granulate; supraocloacal fold crenulated; pericloacal region tuberculate.

Color of euthanized holotype. The holotype was photographed two minutes after anesthesia and the following description was based in those photographs. Dorsum with a large dark brown irregular blotch over an olive background; flanks olive with vertical narrow brown bands; groin and postero-ventral part of flank orange; throat and chest dark gray; chin olive with dark brown markings; upper part of venter gray; middle and lower part of venter reddish orange, with gray tubercles; upper parts of extremities gray to olive, with brown bands or markings; foot web reddish; iris light greenish gray with fine dark venation.

Color of holotype in preservative. Dorsum pale brown with dark-brown irregular blotches without a defined pattern, darker on dorsum than on head (Fig. 4); upper surface of arms pale brown, with one dark-brown incomplete band on forearm, wider on the external edge; dorsal surface of hands with one dark-brown incomplete band (more evident on the right hand); third and fourth fingers with the same coloration of arms; first and second fingers pale cream colored; dorsal surface of thighs pale brown with dark brown bars that form an irregular reticular pattern; dorsal surface of shanks, metatarsus and toes pale brown with dark brown blotches without a defined pattern; webbing on hands cream colored with dark brown flecks. Flanks cream with dark-brown vertical lines. Pericloacal region dark brown surrounded by white.

Ventral surfaces of arms, forearms and hand palms pale cream; pattern on dorsal surface of thigh partially extended to ventral surface; lower edge of thighs pale cream; shanks pale brown with dark brown blotches; metatarsus, feet and foot-web cream with numerous dark brown flecks; throat cream with dark brown flecks, mostly in borders of the mouth; chest and belly pale cream.

Variation in morphology. The variation of external measurements, as well as hand and foot webbing formula of some type specimens and from all the specimens examined is shown in Table 5. There is sexual dimorphism in body size, with males generally smaller than females (males: 46.57–63.34 mm; females: 54.33–74.74 mm), and by the presence of a prominent prepollical spine in males (Figs. 5, 6).

Color variation in life. When active at night, adult specimens have a yellow, tan, to light brown coloration, with brown patterns (irregular in shape or with a broad X-shaped blotch near the head; some specimens have a brown vertebral line) on dorsum (Figs. 6A, 7C). Brown dots are spread on the flanks, above the upper lip, on the limbs, and on the webbings. Some specimens have a brown line delimiting the supratympanic fold. Some specimens have apparent scars on the dorsum. There is a brown blotch with a white line on the upper margin on heels and cloacal region. There are several vertical brown bars on flanks and transversal brown bars on the thighs. White coloration predominates along all the ventral surfaces, with strong orange or pinkish tones on the belly, arms, and thighs. In some specimens, the dorsal brown bars of the thighs are projected on the internal portion. The tarsus has two colorations delimited by the tarsal fold. The outer portion of the tarsus has a brown coloration with orange tones, while the internal portion has orange coloration. Some specimens have some brown spots around the mandible, on the upper portion of the thigh, and/or the webbing at the hands and feet. During the day, when normally are inactive, they have a pale cream coloration (Fig. 6E). The brown patterns and spots, when visible, are pale gray, and the bars on the flanks and thighs are dark brown almost black. Juvenile specimens have a pale green coloration with black diffuse dots on the dorsum (Fig. 6F). During the night, the iris around the pupil is metallic gray color and the outer area is pale emerald (Fig. 6A, C, D).

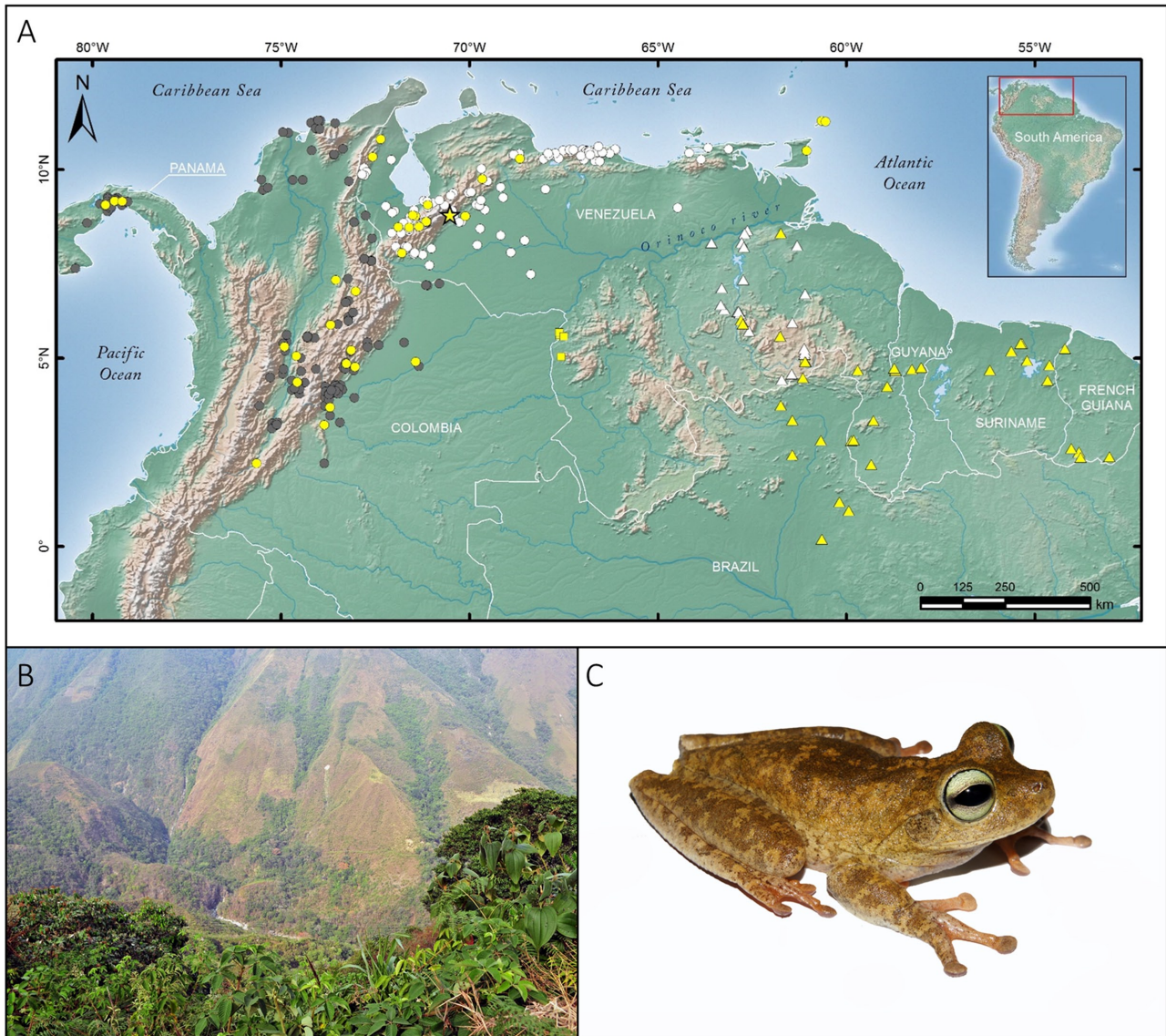


FIGURE 7. (A) Map of northern South America with confirmed localities of *Boana platanera* sp. nov. (circles and star), *B. xerophylla* (triangles), and *B. sp.* (squares). The type locality of *B. platanera* is indicated with a star; yellow symbols indicate localities of specimens with DNA sequence data analyzed in this study; white symbols indicate localities of specimens analyzed morphologically; gray symbols indicate localities of individuals according to the literature (Kluge 1979; Lynch & Suárez-Mayorga 2001). (B) Photograph illustrating the landscape around the type locality of *B. platanera*. (C) Paratype of *B. platanera* in life at night (ULABG 7763). Photos: (B) Jesús Molinari; (C) Enrique La Marca.

Color variation in preservative. Coloration pattern of paratopotypes in preservative is depicted in Fig. 5. Specimens from localities other than the type locality show some color variation, as follows: dorsum occasionally may be uniformly pale-brown (e.g., ULABG 2950, 2951, 7755, 7803), sometimes bearing two scapular dark brown spots (e.g., ULABG 5338), or few scattered small dots on sacral region (e.g., ULABG 5337, 5338) or dorsum (e.g., ULABG 7745). Some specimens tend to have an ashy background with irregular markings (e.g., ULABG 5060, 6902, 7753) and, very rarely, have a lichen aspect (e.g., ULABG 7756, 7757). More often, dorsum bears large blotches that may be irregular in shape (e.g., ULABG 1416, 3725), or sometimes with a broad X-shaped brown blotch (e.g., ULABG 2544, 4749, 4754) that could tend to be diffuse (e.g., ULAB 2949). Specimen ULABG 7744 has a white supratympanic line from posterior border of eye to posterior part of tympanum, and a white line along border of upper lip. Specimen ULABG 1417 has a dark brown line on middle of dorsum, from almost tip-of-snout to sacral region. Forearms and wrists may have brown bands (e.g., ULABG 2544). Shanks and thighs may have bands with ill-defined borders (e.g., ULABG 2544).



FIGURE 8. Species of the *Boana faber* species group in life. Note the difference in coloration, skin texture, supratympanic fold, calcar, tarsal fringe, and hand webbing. (A) *Boana albomarginata*; (B) *B. faber*; (C) *B. pardalis*; (D) *B. exastis*; (E) *B. lundii*; (F) *B. rosenbergi*; (G) *B. pugnax*; (H) *B. crepitans*; (I) *B. xerophylla*; and (J) *B. platanera* **sp. nov.** Photographs are not at the same scale. Photos: (A, B, J) Fernando J. M. Rojas-Runjaic; (C, E) Mario Sacramento; (D) Mauro Texeira Jr.; (F) Santiago Ron (Anfibios del Ecuador); (G) Iván Mendoza; (H) Omar Padilla; (I) Santiago Castroviejo-Fisher.

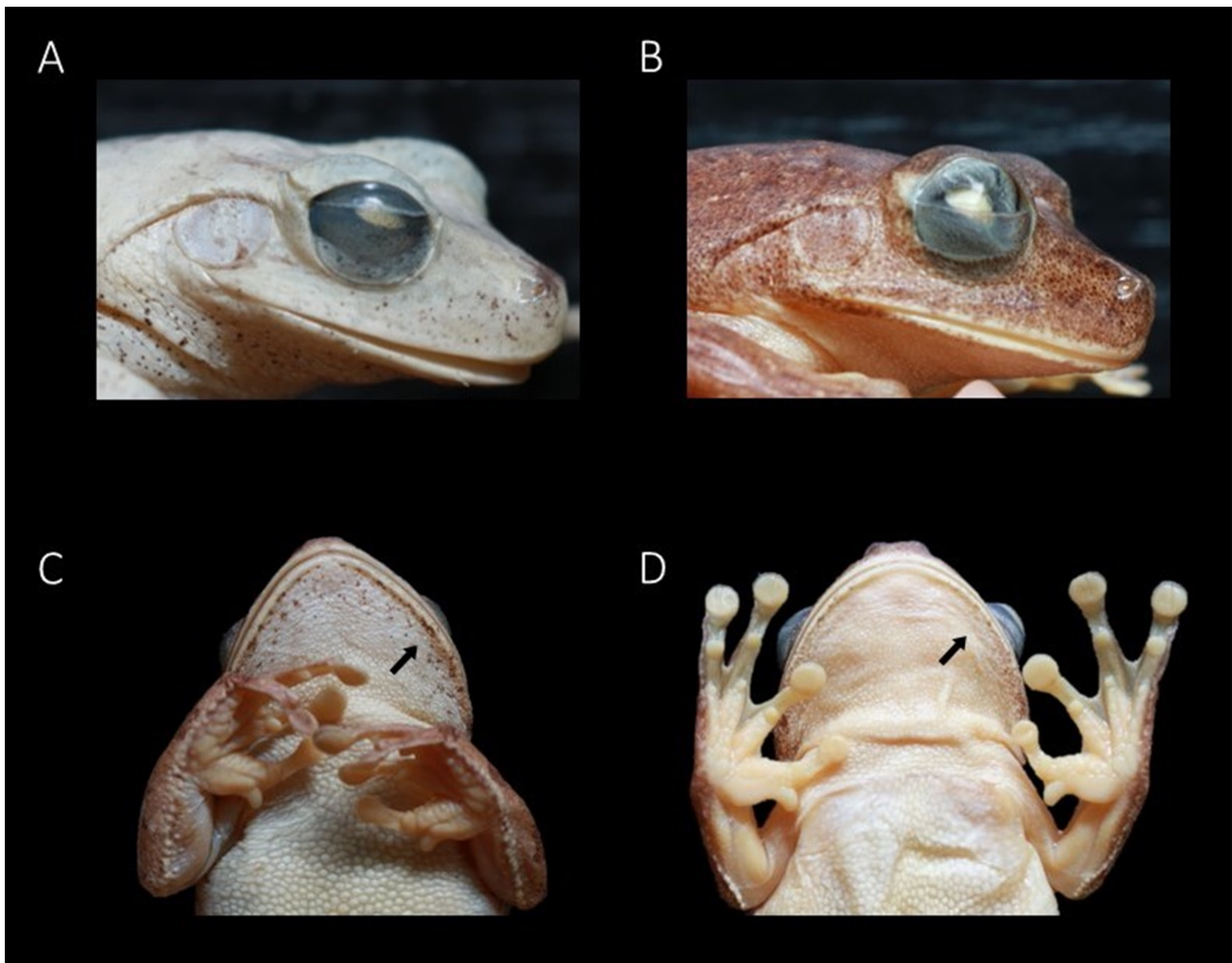


FIGURE 9. Lateral view of head of (A) *Boana platanera* sp. nov. (MHNLS 20970) and (B) *B. xerophylla* (MHNLS 15062). Ventral view of the anterior half of (A) *B. platanera* (MHNLS 5567) and (B) *B. xerophylla* (MHNLS 15062). The black arrows in the gular region indicate the difference in pigmentation between the two species. Photos are not at the same scale. Photos: Michelle Castellanos.

Natural history. All specimens from the type series were collected after dusk (around 20:00 h) in a sewage system alongside a paved road, in steep terrain, 947 m asl. These were found active on the floor, many of them vocalizing. Surrounding vegetation was disturbed second-growth forest, with primary humid forest surrounding it (Fig. 7B). No other anuran species was heard or seen at this site.

The additional museum specimens reviewed came from the Tropical and Premontane altitudinal belts of the Holdridge's system as applied to Venezuela (Ewel *et al.* 1976), within the life zones of Tropical dry forest and Tropical humid forest, as well as Premontane dry forest and PreMontane humid forest. The associated vegetation is usually that of open disturbed areas, with abundance of grasses and few trees. Field records of ELM for some of the referred specimens indicate that the species live in places with annual mean temperatures higher than 17 °C and mean annual precipitation roughly between 600 and 1500 mm. Two precipitation regimes are associated with the distribution of this species. One is the bi-seasonal pluviometry regime, with a single wet season around the middle of the year (June and July). The other is the tetra-seasonal regime with two wet seasons separated by a short mid-year period of less precipitation (Monasterio & Reyes 1980).

Males vocalize on vegetation up to 5 m (Fig. 6G), but also from the ground, on rocks, or partially submerged or floating in the water, although the latter behavior is usually observed in artificial and temporary pools (Fig. 6H). Field observations indicate that the amplexus in *Boana platanera* is axillary (*sensu* Carvajal-Castro *et al.* 2020), with the toes projected above the female shoulders (Fig. 10). Scars on the dorsum of several individuals suggest the existence of male to male combat in this species. This species can form choruses and males are separated from each



FIGURE 10. Axillary amplexus in (A) *Boana platanera* **sp. nov.** from Sabaneta sector, El Hatillo, state of Miranda, Venezuela, and (B) *B. xerophylla* from Reserva Biológica Ilha de Maracá, Roraima, Brazil. Photos: (A) Fernando J. M. Rojas-Runjaic and (B) Antoine Fouquet.

other by at least one meter. In addition, this treefrog usually lays eggs in rafts in lentic aquatic systems. The following species were detected sharing the same breeding sites as *B. platanera*: *B. lanciformis*, *B. pugnax*, *Dendropsophus microcephalus*, *Engystomops pustulosus*, *Leptodactylus fuscus*, *Pleurodema brachyops*, *Pseudis paradoxa*, *Rhinella horribilis*, *R. marina*, *Scarthyla vigilans*, and *Scinax rostratus*.

Distribution. *Boana platanera* is widely distributed north of the Orinoco River in Venezuela (states of Anzoátegui, Apure, Aragua, Barinas, Carabobo, Cojedes, Distrito Capital, Lara, Mérida, Miranda, Portuguesa, Sucre, Táchira, Trujillo, Vargas, Yaracuy, and Zulia; Fig. 7A; Appendix 3), although it is unclear if it is present in Nueva Esparta state and other islands near to mainland Venezuela. Based on our phylogenetic tree, it is also present in Panama, Colombia, and Trinidad and Tobago. Therefore, we assign all the populations of *B. xerophylla* s.l. north of the Orinoco River to *B. platanera*. The localities from Colombia and Panama published by Kluge (1979) and Lynch & Suárez-Mayorga (2001) are plotted in Fig. 7A.

Conservation status. Venezuelan populations of *Boana platanera* (as *Hyla crepitans*) were referred as abundant by Donoso-Barros & Leon (1972). This abundance is indirectly evidenced by the hundreds of samples housed at Venezuelan museums. Two recent studies provided quantitative data about how its abundance varies geographically (referred as *B. xerophylla*). Rojas-Runjaic & Infante-Rivero (2018) reported that *B. platanera* is rare between 1500 and 2000 m asl in the Sierra de Perijá. Cañizales (2020) reported this species as abundant in one locality (around 100 m asl) in western Venezuela. Our field observations agree with these observations, and point out that *B. platanera* is especially common and very abundant throughout the year in anthropic environments with aquatic habitats. Infection by the chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*) was reported, with low prevalence (1/20), in samples from the Cordillera de Mérida (referred as *Hypsiboas crepitans*) by Sánchez *et al.* (2008), absent in 16 tested individuals from Montalbán, Carabobo state, Venezuela (Señaris & Lampo, unpublished data), and present in 6 of 50 samples from across Colombia (Flechas *et al.* 2017). Experiments by Márquez *et al.* (2010) found that *B. platanera* specimens (referred as *Hypsiboas crepitans*) from the Cordillera de Mérida are susceptible to *Bd* infection, but they have the ability to overcome it within 38 days at a temperature (23 °C) purportedly ideal for *Bd* growth. Following the criteria of the IUCN Red List categories (IUCN 2012), we propose that *B. platanera* should be listed as Least Concern (LC) based on its wide geographical and elevational distribution in a broad range of habitats, its tolerance for habitat modification, and presumed large and stable populations.

Etymology. The specific epithet *platanera* is an adjective used in apposition. It is the common name given in Colombia and Venezuela to this kind of relatively large treefrogs (*i.e.*, *Boana platanera* and *B. pugnax*). The epithet “platanera” refers to the plantain or banana plant (“*plátano*”; hence, “from the plantain”), where these frogs are commonly found in the daytime. This name is widely used since the species is abundant, easy to spot, present in anthropic environments, and widely distributed. Although *B. platanera* and *B. pugnax* have been misidentified in the past (La Marca 1996; Escalona *et al.* 2017), our intention is to use the folk nomenclature as the species epithet so that it can be easily remembered by non-taxonomic experts.

Discussion

Cryptic diversity and integrative taxonomy. Speciation, the process of lineage splitting and formation of new species, could take place with little or no morphological differentiation (Coyne & Orr 2004; Bickford *et al.* 2007; Padial *et al.* 2010; Fišer *et al.* 2018). Empirical data indicate that cryptic species “classified as a single nominal species because they are at least superficially morphologically indistinguishable” (Bickford *et al.* 2007) are common and present in many animal taxa (Pfenninger & Schwenk 2007; Adams *et al.* 2014; Pérez-Ponce de León & Poulin 2016), notably amphibians (Pfenninger & Schwenk 2007; Pérez-Ponce de León & Poulin 2016; Jaramillo *et al.* 2020). The analysis of DNA sequences has greatly increased reports of cryptic species (Bickford *et al.* 2007), with anurans notably exemplifying this trend (Fouquet *et al.* 2007; Jungfer *et al.* 2013; Gehara *et al.* 2014; Castroviejo-Fisher *et al.* 2017; Vacher *et al.* 2020).

While most empirical studies have focused on how speciation may be decoupled from morphological differentiation as inferred from genetic data, evolutionary theory allows for critical phenotypic differentiation (*e.g.*, evolution of intrinsic reproductive barriers) with minimal or absence of detectable genetic differentiation (*e.g.*, de Queiroz 1998; Padial *et al.* 2010). In other words, species can be genetically cryptic. Although rarely reported in the literature, a clear example is *Osteocephalus taurinus* and *O. oophagus*. These two Amazonian treefrog species show

clear morphological, behavioral, and acoustical differences but with little genetic differentiation and even lacking reciprocal monophyly as inferred from mitochondrial and/or nuclear markers (Jungfer *et al.* 2013). Other examples are shown in Pons *et al.* (2004), Fouquet *et al.* (2019) and Chasiluisa *et al.* (2020), for coleopterans and anurans, respectively.

Herein, we found low genetic differentiation between specimens of *Boana platanera* and *B. xerophylla* compared to most other sister species of Anura. For example, the genetic distances (min. and max. at 16S: 0.7–2.2 %) are well below suggested thresholds for amphibian species (3–5 %; Vences *et al.* 2005a; Vences *et al.* 2005b; Fouquet *et al.* 2007; Vieites *et al.* 2009) and despite reciprocal monophyly in our ML analysis, we note the low BS values and the necessity of recognizing the samples from the western Guiana Shield as a different candidate species.

While most systematists would rightfully interpret these genetic results as more compatible with variation within a species than with the existence of more than one species (Hillis 2019, 2020), we found several morphological and acoustical differences between *B. platanera* and *B. xerophylla* that indicate species-level differentiation despite moderate genetic distance. These fixed phenotypic differences are indicative of divergence as expected when samples from more than one independent evolutionary lineage are studied (Padial *et al.* 2010; Padial & De la Riva 2010, 2021). Particularly relevant are the observed diagnostic differences in advertisement calls because they are likely linked to mate choice (Ryan 1980; Gerhardt 1991; Ryan & Keddy-Hector 1992) and reproductive isolation (Boul *et al.* 2007). In summary, we consider *B. platanera* and *B. xerophylla* as genetically cryptic species and a clear empirical example that suggest that false negatives using genetic thresholds may be more common than reported in the literature. Thus, we appraise to use integrative taxonomic approaches for species recognition.

Explanations behind false negatives when looking for new species with genetic data include recent speciation events (Moritz & Cicero 2004; Vences *et al.* 2005b; Vieites *et al.* 2009) coupled with evolutionary mechanisms leading to phenotypic character fixation, such as strong positive selection (Padial *et al.* 2010), introgression across species, inadequate sampling or a combination of them (Hillis 2019). We argue that for *B. platanera* and *B. xerophylla* the first scenario is more likely because the congruence among the mt and nuDNA phylogenies, and with the morphological and acoustical patterns of variation (Escalona *et al.* 2019a; this work) are incompatible with introgression. Also, our sampling comprises several individuals per locality and from across the known distribution of these treefrogs, although samples are missing from the area between the western and eastern Guiana Shield (Fig. 7A). We suggest future studies to further evaluate these species hypotheses, as well as the Orinoco River barrier hypothesis, using a wider collection of samples, genetic markers, and phenotypic data.

Acoustic differentiation. We found marked differences between the two call types of *Boana xerophylla* and the advertisement call of *B. platanera*. Differences in advertisement calls have been suggested as indicative of mating isolation among anuran species (Blair 1958; Ryan 1980; Gerhardt 1994; Vences & Wake 2007; Boul *et al.* 2007; Wollenberg *et al.* 2019). Consequently, their assessment has proven to be very effective in anuran systematics, revealing morphologically cryptic species (*e.g.*, Angulo & Reichle 2008; Funk *et al.* 2012; Köhler *et al.* 2017; Rojas-Runjaic *et al.* 2018). Our study constitutes an example in which differences in advertisement calls support the recognition of two species (*i.e.*, *B. platanera* and *B. xerophylla*).

Our results regarding acoustic differentiation between *Boana platanera* and *B. xerophylla* agree with the pattern found within the *B. faber* group. We compared the advertisement calls from species of the *B. faber* group and, even among sister species, we found that there are remarkable differences in variables such as number of notes, call length, and fundamental and dominant frequencies (Table 2). This agrees with the observations of de Andrade *et al.* (2017). Moreover, it supports the idea that the advertisement call is a multi-trait character that shows variation among species (Escalona *et al.* 2019b), which is consistent with its utility in systematics (Köhler *et al.* 2017). Marked differentiation of advertisement calls among closely related species is expected if the calls evolved under relatively strong evolutionary forces (*e.g.*, reinforcement; see Pfennig & Pfennig 2009). However, other factors can be at play. For example, variation in dominant frequency could be the byproduct of size variation (Gingras *et al.* 2013; Escalona *et al.* 2019b; Tonini *et al.* 2020), with larger species emitting sounds at lower frequencies. Concomitantly, the species composition of the communities where species occur could exert an additional selective force due to partition of the acoustic space (Wells 2007; but see Garey *et al.* 2018).

Our study also revealed two call types within *Boana platanera* and *B. xerophylla*, both emitted by males from several locations. In *B. platanera*, this is consistent with the calls reported by Fouquette (1966); however, we interpreted the call with notes fused as the advertisement call since it was the call predominantly found in all recordings analyzed. In *B. xerophylla*, the call with the simplest structure has one note and is emitted in six of the seven

recordings, while the other type of call is basically a lengthening of the simple call by the addition of two to five spaced one pulse notes (Fig. 2; Table 2). This latter call could correspond to a territorial call (*sensu* Köhler *et al.* 2017) of *B. xerophylla*, since it is relatively less common in our recordings (Toledo *et al.* 2015; Köhler *et al.* 2017). Alternatively, this two notes call represents a “mix” of territorial and advertisement call (see Gerhardt 1994). Nali & Prado (2014) showed evidence that indicate that the short note of the complex call of *Bokermannohyla ibitiguara* (composed by long and short notes) might be a territorial component, while the long note may be directed to females. Other interpretation is that the two to five spaced pulses of the call type II would be an “attractive” component, functionally similar to the chucks in *Engystomops pustulosus* (Ryan 1980) or the squawk in *E. petersi* (Boul *et al.* 2007). However, our interpretations regarding the function of the call type II are speculative and needs further observations of the behavioral context of call emission. In any case, regardless of which of the two call types of *B. xerophylla* is the advertisement call, our taxonomic conclusion is not affected since we found diagnostic differences when comparing both call types with the advertisement call of *B. platanera*.

We found a striking variation of the band of frequency corresponding to the dominant frequency in *Boana platanera* and *B. xerophylla*. In most cases, around 65 % of the specimens in both species, the dominant frequency corresponded to the second band frequency. This pattern has been reported in other hylids (Magrini *et al.* 2011 and references therein). Such variation could be explained by differences in call amplitude, because the air pressure that passes through the vocal tract could affect the dominant frequency (Martin 1972). It agrees with the modulation of the dominant frequency and the modulation of amplitude along the call in both species (Fig. 2). Finally, this variability in dominant frequency raises questions for future studies regarding female preferences based on the dominant frequency in these species.

Available names. Following the conclusions of Orrico *et al.* (2017), *Hyla doumercii* Duméril & Bibron, 1841, *Hyla fuentei* Goin & Goin, 1968, *Hyla levaillantii* Duméril & Bibron, 1841, and *Hypsiboas indris* Cope, 1867 are synonyms of *B. xerophylla*. Although *Hypsiboas indris* is considered a *nomen nudum* (Frost 2020), all these names were assigned to types from “Suriname” (“Suriname, Suriname District, Powakka” in the case of *Hyla fuentei*). Our results indicate that the observed variation in molecular, morphological, and acoustic traits of specimens from the eastern Guiana Shield is minimal, and more compatible with the existence of a single species, reinforcing the conclusions of Orrico *et al.* (2017) and Escalona *et al.* (2019a). We conclude that all the aforementioned names are synonyms of *B. xerophylla* and not applicable to *B. platanera*. We provided a list of cnesonyms for *B. platanera*, although no exhaustive.

Natural history of *Boana platanera*. Natural history knowledge of *Boana platanera* is retrieved from previous works referring to individuals as *Hyla crepitans* from populations north of the Orinoco River. Donoso-Barros & Leon (1972) commented that Venezuelan populations seem to have a cyclic reproductive season, with sexual activity in April-May, which corresponds to the start of the rainy season in the bi-seasonal precipitation regime. Moreover, they described the clutch and eggs of *B. platanera* and described the embryological and larval development from one clutch reared in the laboratory. They emphasized the similitude of the coloration of the juvenile of *B. platanera* (Fig. 6F) with the adult of *Hyalinobatrachium fleischmanni*. The tadpole of *B. platanera* was described by Kenny (1969) from populations from Trinidad. Duellman (1970) described tadpoles from Villavicencio (Colombia) and posteriorly mentioned that it differs structurally from the tadpoles described by Kenny (Duellman 2001). Mijares-Urrutia (1998) included the tadpole of *B. platanera* in a key to the tadpoles of frogs of the high Venezuelan Andes.

Available data indicate that the new species has a natural history with some similarities regarding the species of the *Boana faber* group. The amplexus observed in individuals of *B. platanera* from Venezuela is similar with the observed in other populations from Panama (Kluge, cited by Martins *et al.* 1998), as well as to other species in the *B. faber* group (*i.e.*, *B. rosenbergi* [Kluge 1981], *B. faber* [Martins & Haddad 1988], *B. pardalis* [de Andrade *et al.* 2017], *B. xerophylla* [Fig. 10B]). However, in the case of *B. rosenbergi* and *B. faber*, the hands have been observed at the angle of the female’s jaw and the fingers were projected toward the head of the female. As hypothesized by Martins & Haddad (1988), this kind of clasping would avoid hurting females with the prepollical spine in comparison to a “typical” axillary amplexus, with the hands below the female’s forelimbs. De Andrade *et al.* (2017) called this kind of amplexus as “tympanic”; however, this is debatable because neither the hands nor the fingers reach the tympanum in *B. pardalis* (the same occurs in *B. platanera* and *B. xerophylla*).

The construction of nests by males has been suggested as a potential behavioral synapomorphy of *Boana faber* group (Faivovich *et al.* 2005). *Boana platanera* shows a plastic reproductive behavior. Caldwell (1992) studied a population from Guatopo National Park, Miranda State, during reproductive activity and reported the first case of

nest building (see Duellman 1970). She found only one nest, which was at the edge of a sand spit, while most embryos or tadpoles were in small pools along the edge of the stream. Interestingly, the tadpoles found in the nest showed a faster growth. She concluded that the construction of nests by males in this species is facultative, suggesting that it depends on the substrate. Lynch & Vargas Ramírez (2000) reported 50 observations of males building nest with gravel in a population from Tayrona National Park (northern Colombia). Lehtinen (2014) found a nest with tadpoles in Trinidad and Tobago, and confirmed that this belonged to *B. crepitans* based on 16S sequences (herein referred as *B. platanera*). Based on the previous observations, we infer that there is not parental care in the nest as known for other species of the *B. faber* group (e.g., *B. rosenbergi* [Kluge 1981] and *B. faber* [Martins *et al.* 1998]).

Acknowledgments

We are thankful to the following people and institutions for helping us with this study: S. Potsch (Universidade Federal do Rio de Janeiro), the late P. E. Vanzolini, H. Zaher, and T. Grant (Museu de Zoologia, Universidade de São Paulo), J. Pombal Jr., P. Passos, D. Fernandes, C. Canedo, and L.N. Weber (Museu Nacional, Universidade Federal do Rio de Janeiro), M.T. Rodrigues, P. Pinheiro, and J. Tanaka (Universidade de São Paulo), J.E. García-Pérez (Museo de Ciencias Naturales de Guanare), S. Ron (Museo de Zoología de la Pontificia Universidad Católica del Ecuador), A. González-Chaves, S. Doreste, I. Mendoza, N. Sánchez, B.P. Noonan, L. Echevarría, A. Kwet, E. Infante-Rivero, J-P. Vacher, M. Read, R. Furtado, M. Texeira Jr., M. Sacramento, J. Molinari, I. Mendoza, Jardín Botánico de Mérida, Fonoteca Zoológica at Museo Nacional de Ciencias Naturales, and the Macaulay Library and Bioacoustics Research Program at Cornell Lab of Ornithology. The constructive criticisms of P. I. Simões, the associate editor, and two anonymous reviewers improved previous versions of our manuscript. We received financial support from: Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq (ref. 140815/2018-0 to ME and 312744/2017-0 to SC-F), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (program PrInt ref. 88887.508359/2020-00 to SC-F), Agence Nationale de la Recherche, CEBA (ref. ANR-10-LABX-25-01 to AF), and FAPEMIG (AAG). The Ministerio del Poder Popular para el Ambiente issued collecting and genetic analyses permits (refs. 0269, 2013–2014 and 0082, 2014, respectively) for Venezuela and the Instituto Chico Mendes (IC-MBio/SISBIO 30059–5) for Brazil.

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APPENDIX 1. GenBank accession number, voucher number, locality data, and reference for the gene sequences used in our DNA analyses of *Boana*. New sequences generated in this study are in bold face. Outgroups included *Aplastodiscus* and *Bokermannohyla* species. Generally, voucher codes correspond to museum acronyms or personal field numbers. AAV = Álvaro Andrés Velásquez-Álvarez; AF = Antonie Fouquet; AJC = Andrew J. Crawford; AMNH = American Museum of Natural History, New York; ANDES = Universidad de Los Andes, Bogotá, Colombia; AMS = Andrew M. Snyder; BPN = Brice P. Noonan; CAS = California Academy of Science; CFBH = Celio F.B. Haddad Collection, to be deposited in the Departamento de Zoología, Universidade Estadual Paulista, Campus de Rio Claro, São Paulo; CH = Circulo Herpetológico de Panamá; INPAH = Instituto Nacional de Pesquisas da Amazônia, Herpetology collection; JSM = Juan Salvador Mendoza; KU = University of Kansas, Museum of Natural History, Lawrence; MACN = Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; MTD = Senckenberg Naturhistorische Sammlungen Dresden (formerly MTKD: Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde), Dresden, Germany; MTKD = currently called MTD (defined above); MUSM = Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima; MVUP = Museo de Vertebrados de la Universidad de Panamá, Panamá; PG = Philippe Gaucher; PK = Philippe J. R. Kok; ROM = Royal Ontario Museum, Toronto; ULABG = Colección de Anfibios y Reptiles del Laboratorio de Biogeografía de la Universidad de Los Andes, Mérida; USNM = National Museum of Natural History, Washington, D.C.; ZSM = Zoologische Staatssammlung München, Germany; ZUEC = Museo de Historia Natural, Universidade Estadual de Campinas, Campinas. AL = Alagoas; AP = Apure; BA = Barinas; BO = Bolívar; BR = Brazil; BY = Boyacá; CA = Casanare; CO = Colombia; CU = Cundinamarca; FG = French Guiana; GU = Guyana; HU = Huila; LA = Lara; ME = Mérida; MT = Meta; PA = Panamá; PE = Pernambuco; PO = Portuguesa; SA = Santander; SG = Sangre Grande; SP = São Paulo; SU = Surinam; TA = Táchira; TL = Tolima; TO = Tobago island; TT = Trinidad and Tobago; YA = Yaracuy; VE = Venezuela; ZU = Zulia.

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>A. leucopygius</i>	USNM 303038	AY843638	AY843638	-	NA	Faivovich <i>et al.</i> (2005)
<i>B. albomarginata</i>	USNM 284519	AY549316	KF794116	-	NA	Faivovich <i>et al.</i> (2004); Faivovich <i>et al.</i> (2013)
<i>B. albomarginata</i>	MTR 16695	KX697975	-	KX698021	NA	Orrico <i>et al.</i> (2017)
<i>B. albomarginata</i>	CFBHT13378	-	-	KX698009	NA	Orrico <i>et al.</i> (2017)
<i>B. albopunctata</i>	Isolate 10	-	JQ627203	JQ627301	NA	Rodriguez & Galetti (DS)
<i>B. albopunctata</i>	ZUEC 12053	AY549317	AY549317	-	NA	Faivovich <i>et al.</i> (2004)
<i>B. cinerascens</i>	AMNH A-164105; JF isolate 2371	AY549336	AY549336	KX698010	NA	Faivovich <i>et al.</i> (2004); Orrico <i>et al.</i> (2017)
<i>B. boans</i>	RWM_17746; AV 499	AY843610	KT717077	KT717080	NA	Faivovich <i>et al.</i> (2005); Escalona <i>et al.</i> (2019a)
<i>B. crepitans</i>	CFBH 2966	AY843621	AY843621	-	BR: AL: Xingo's dam	Faivovich <i>et al.</i> (2005)
<i>B. crepitans</i>	CFBH 10243	KX697938	KX697985	-	BR: MG: Grão Mogol	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBH 2885	KX697939	KX697986	-	BR: BH: Itabuna	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBH 13275	KX697941	KX697988	-	BR: "Bahia"	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBH 16361	KX697945	KX697992	-	BR: AL: Campo Alegre	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBH 21073	KX697948	KX697995	-	BR: BH: Caetité	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBH 21090	KX697949	KX697996	-	BR: BH: Dom Basílio	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBH 18728	KX697950	KX697997	-	BR: BH: Aurelino Leal	Orrico <i>et al.</i> (2017)

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APPENDIX 1. (Continued)

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>B. crepitans</i>	CFBH 24368	KX697953	KX698000	-	BR: MG: Jaboticatubas	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBH 27826	KX697959	KX698006	-	BR: BH: Camamu	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	JC 1273	KX697967	KX698013	-	BR: BH: Mucugê	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	MRT 5785	KX697969	KX698015	-	BR: BH: Jussari	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	MTJ 384	KX697971	KX698017	-	BR: MG: Januária	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	MTR 15366	KX697972	KX698018	-	BR: PE: Buique	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	MTR 20070	KX697976	KX698022	-	BR: BH: Miguel Calmon	Orrico <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBHT 07825	-	KU495263	-	BR: AL: Campo Alegre	Lyra <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBHT 02360	-	KU495261	-	BR: MG: Grão Mogol	Lyra <i>et al.</i> (2017)
<i>B. crepitans</i>	CFBHT 12841	-	KU495262	-	BR: BH: Camamu	Lyra <i>et al.</i> (2017)
<i>B. ericae</i>	CFBH 3599	AY 549332	AY 549332	-	NA	Faivovich <i>et al.</i> (2004)
<i>B. ericae</i>	CFBH 6764	-	-	KX698012	NA	Orrico <i>et al.</i> (2017)
<i>B. exastis</i>	MTR 16289	KX697973	-	KX698019	NA	Orrico <i>et al.</i> (2017)
<i>B. faber</i>	CFBH 13030	-	-	KX697980	NA	Orrico <i>et al.</i> (2017)
<i>B. faber</i>	Isolate 118	-	JQ627206	JQ627303	NA	Rodriguez & Galetti (DS)
<i>B. faber</i>	MTR 16691	KX697974	-	KX698020	NA	Orrico <i>et al.</i> (2017)
<i>B. lanciformis</i>	MJH 564; isolate 18237	AY 843636	AY 843636	JN970768	NA	Faivovich <i>et al.</i> (2005); Funk <i>et al.</i> (2012)
<i>B. lundii</i>	CFBH 4000	-	AY 843639	-	NA	Faivovich <i>et al.</i> (2005)
<i>B. lundii</i>	CFBH 9155	KX697936	-	KX697983	NA	Orrico <i>et al.</i> (2017)
<i>B. lundii</i>	CFBH 20059	KX697944	-	KX697991	NA	Orrico <i>et al.</i> (2017)
<i>B. lundii</i>	CFBH 23593	KX697951	-	KX697998	NA	Orrico <i>et al.</i> (2017)
<i>B. lundii</i>	MRT 4332	KX697968	-	KX698014	NA	Orrico <i>et al.</i> (2017)
<i>B. melanopleura</i>	MUSM 19818	-	HM444781	-	NA	Lehr <i>et al.</i> (2010)
<i>B. multifasciata</i>	AMNH A-141040	AY 843648	AY 843648	-	NA	Faivovich <i>et al.</i> (2005)
<i>B. multifasciata</i>	ROM 28435	-	-	JN970762	NA	Funk <i>et al.</i> (2012)
<i>B. nympha</i>	NMP6V 71202/2	AY 843670	AY 843670	-	NA	Faivovich <i>et al.</i> (2005)
<i>B. pardalis</i>	CFBH 11334	KX697940	-	KX697987	NA	Orrico <i>et al.</i> (2017)
<i>B. pardalis</i>	CFBH 13962	KX697942	-	KX697989	NA	Orrico <i>et al.</i> (2017)

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APPENDIX 1. (Continued)

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>B. pardalis</i>	CFBH 16020	KX697935	-	KX697982	NA	Orrico <i>et al.</i> (2017)
<i>B. pellucens</i>	WED 53621; KU 202734	AY326058	AY326058	-	NA	Darst & Cannatella (2004)
<i>B. pellucens</i>	Isolate 23680	-	-	JN970771	NA	Funk <i>et al.</i> (2012)
<i>B. platanera sp. nov.</i>	ANDES-A 1524	-	MN967685	MT552075	CO: SA: Piedecuesta-Umpala	This study
<i>B. platanera sp. nov.</i>	ANDES-A 1525	-	MN967640	MT552033	CO: SA: Piedecuesta-Umpala	This study
<i>B. platanera sp. nov.</i>	CH 10032	-	MN967704	MN967704	PA: Lake edge, Cerro Azul	This study
<i>B. platanera sp. nov.</i>	AJC 1096 (MVUP number pending)	-	MN967653	MT552044	PA: Naranjal between Tocumen & Chepo	This study
<i>B. platanera sp. nov.</i>	AJC 1123 (MVUP number pending)	-	MN967638	MT552031	PA: road opposite Summit Gardens, off of Guillard Hwy	This study
<i>B. platanera sp. nov.</i>	CH 10017	-	MN967569	MT551971	PA: road opposite Summit Gardens, off of Guillard Hwy	This study
<i>B. platanera sp. nov.</i>	ANDES-A 1526	-	MN967651	MT552042	CO: TL: Mariquita	This study
<i>B. platanera sp. nov.</i>	ANDES-A 1527	-	MN967711	MT552102	CO: TL: Mariquita	This study
<i>B. platanera sp. nov.</i>	AJC 1738 (ANDES-A, pending)	-	MN967606	MT552004	CO: MT: San Juan de Arama	This study
<i>B. platanera sp. nov.</i>	AJC 2253 (ANDES-A, pending)	-	MN967587	MT551987	CO: CU: Vereda Ballon, Laguna Mangu	This study
<i>B. platanera sp. nov.</i>	AJC 2298 (ANDES-A, pending)	-	MN967695	MT552085	CO: CA: Orocue	This study
<i>B. platanera sp. nov.</i>	AJC 3616 (ANDES-A, pending)	-	MN967636	MT552029	CO: BY: Santa María	This study
<i>B. platanera sp. nov.</i>	ANDES-A 3057	In process.	In process.	In process.	CO: CU: Nilo	This study
<i>B. platanera sp. nov.</i>	AJC 4300 (ANDES-A, pending)	-	MN967624	MT552020	CO: MT: San Martín	This study
<i>B. platanera sp. nov.</i>	ANDES-A 3626	-	MN967593	MT551993	CO: CU: Nilo	This study

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APPENDIX 1. (Continued)

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>B. platanera</i> sp. nov.	ANDES-A 1753	-	KP149283	KP149088	CO: SA: Puente Nacional	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1529	-	KP149481	KP149269	CO: SA: Puente Nacional	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1754	-	KP149448	KP149241	CO: SA: Puente Nacional	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1530	-	KP149420	KP149215	CO: SA: Puente Nacional	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1531	-	KP149402	KP149197	CO: SA: Puente Nacional	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1532	-	KP149316	KP149120	CO: SA: Puente Nacional	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1528	-	KP149290	KP149095	CO: SA: San Vicente	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1534	-	KP149475	KP149263	CO: MT: San Juan de Arama	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1535	-	KP149477	KP149265	CO: MT: San Juan de Arama	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1507	-	KP149317	KP149121	CO: BY: Miraflores	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1509	-	KP149378	KP149176	CO: BY: Miraflores	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1063	-	KP149370	KP149168	CO: CA: Sabanalarga	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	ANDES-A 1284	-	KP149478	KP149266	CO: CA: Sabanalarga	Guarnizo et al. (2015)
<i>B. platanera</i> sp. nov.	CAS 2317822	-	KDQF01002151	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	CAS 2317882	-	KDQF01002152	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	CAS 2317892	-	KDQF01002153	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	CAS 2317902	-	KDQF01002154	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	CAS 2318012	-	KDQF01002155	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	CAS 2451312	-	KDQF01002156	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	CAS 2451322	-	KDQF01002157	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	CAS 2451332	-	KDQF01002158	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	CAS 2451342	-	KDQF01002159	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	CAS 2451352	-	KDQF01002160	-	TT: SG: Lower Manzanilla	Vacher et al. (2020)
<i>B. platanera</i> sp. nov.	JSM 181 (ANDES-A, pending)	-	MN967664	MT552055	CO: HU: Garzón	This study
<i>B. platanera</i> sp. nov.	JSM 183 (ANDES-A, pending)	-	MN967665	MT552056	CO: HU: Garzón	This study

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APPENDIX 1. (Continued)

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>B. platanera</i> sp. nov.	JSM 186 (ANDES-A, pending)	-	MN967650	MT552041	CO: HU: Garzón	This study
<i>B. platanera</i> sp. nov.	JSM 193 (ANDES-A, pending)	-	MN967642	MT552035	CO: HU: Garzón	This study
<i>B. platanera</i> sp. nov.	JSM 208 (ANDES-A, pending)	-	MN967687	MT552077	CO: HU: Garzón	This study
<i>B. platanera</i> sp. nov.	MHNLS 17218	-	In process.	In process.	VE: ME: La Azulita-Lagunillas, Quebrada Azul	This study
<i>B. platanera</i> sp. nov.	MHNLS 17219	-	In process.	In process.	VE: ME: La Azulita-Lagunillas, Quebrada Azul	This study
<i>B. platanera</i> sp. nov.	MHNLS 17221	-	In process.	In process.	VE: ME: La Azulita-Lagunillas, Quebrada Azul	This study
<i>B. platanera</i> sp. nov.	MHNLS 17469	-	In process.	In process.	VE: ZU: Fundo La Orehila, Sierra de Perijá	This study
<i>B. platanera</i> sp. nov.	MHNLS 18812	-	In process.	In process.	VE: ZU: Cerro Las Antenas, Sierra de Perijá	This study
<i>B. platanera</i> sp. nov.	MHNLS 18815	-	In process.	In process.	VE: ZU: Cerro Las Antenas, Sierra de Perijá	This study
<i>B. platanera</i> sp. nov.	MHNLS 18940	-	In process.	In process.	VE: YA: Hacienda La Guáquira	This study
<i>B. platanera</i> sp. nov.	ZSM 16082006	-	In process.	In process.	TT: TO: near 'Kings Bay', Speyside	This study
<i>B. platanera</i> sp. nov.	Tadpole 1	-	KJ642639	-	TT: TO: Parlatuvier river	Lehtinen (2014)
<i>B. platanera</i> sp. nov.	Tadpole 2	-	KJ642640	-	TT: TO: Parlatuvier river	Lehtinen (2014)
<i>B. platanera</i> sp. nov.	ULABG 4749	-	KF157564	-	VE: ME: 10 km Sta. Apolonia	Escalona <i>et al.</i> (2019a)
<i>B. platanera</i> sp. nov.	ULABG 5039	-	KF157565	-	VE: ME: Sta. Elena de Arenales	Escalona <i>et al.</i> (2019a)
<i>B. platanera</i> sp. nov.	ULABG 5040	-	KF157566	-	VE: ME: Sta. Elena de Arenales	Escalona <i>et al.</i> (2019a)

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APPENDIX 1. (Continued)

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>B. platanera</i> sp. nov.	ULABG 5194	-	KF157567	KF157616	VE: ME: Sta. Elena de Arenales	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 5410	-	KF157571	KF157598	VE: LA: Laguna El Manantial, Sanare	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 5670	-	KF157572	-	VE: BA: Reserva El Irel, Barrancas	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 6786	-	KF157574	-	VE: ME: Ciudad de Mérida	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7741	-	KF157577	-	VE: TA: Caño San Mateo	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7744	-	KF157578	KF157601	VE: ME: Sta. Elena de Arenales	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7753	-	KF157581	KF157604	VE: ME: Jardín Botánico de Mérida	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7756	-	KF157582	-	VE: ME: Laguna Caparú	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7757	-	KF157583	KF157605	VE: ME: Laguna Caparú	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7758	-	KF157584	KF157606	VE: BA: La Soledad	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7759	-	KF157585	KF157607	VE: BA: La Soledad	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7760	-	KF157586	KF157608	VE: BA: La Soledad	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7761	-	KF157587	KF157609	VE: BA: La Soledad	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7770	-	KF157588	KF157610	VE: TA: Las Cuevas, Río Doradas	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7796	-	KF157591	KF157613	VE: ME: San José de La Providencia	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7797	-	KF157592	KF157614	VE: ME: San José de La Providencia	Escalona et al. (2019a)
<i>B. platanera</i> sp. nov.	ULABG 7803	-	KF157593	KF157615	VE: ME: Caño Rico	Escalona et al. (2019a)
<i>B. pugnax</i>	ULABG 5318	-	KF157568	KF157595	NA	Escalona et al. (2019a)
<i>B. pugnax</i>	ULABG 5320	-	KF157569	KF157596	NA	Escalona et al. (2019a)
<i>B. pugnax</i>	ULABG 5367	-	KF157570	KF157597	NA	Escalona et al. (2019a)

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APPENDIX I. (Continued)

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>B. pugnax</i>	ULABG 5671	-	KF157573	KF157617	NA	Escalona <i>et al.</i> (2019a)
<i>B. pugnax</i>	ULABG 7739	-	KF157575	KF157599	NA	Escalona <i>et al.</i> (2019a)
<i>B. pugnax</i>	ULABG 7742	-	KF157576	KF157600	NA	Escalona <i>et al.</i> (2019a)
<i>B. pugnax</i>	ULABG 7749	-	KF157579	KF157602	NA	Escalona <i>et al.</i> (2019a)
<i>B. pugnax</i>	ULABG 7750	-	KF157580	KF157603	NA	Escalona <i>et al.</i> (2019a)
<i>B. pugnax</i>	ULABG 7781	-	KF157589	KF157611	NA	Escalona <i>et al.</i> (2019a)
<i>B. pugnax</i>	ULABG 7783	-	KF157590	KF157612	NA	Escalona <i>et al.</i> (2019a)
<i>B. pugnax</i>	ANDES-A 1541	-	KP149407	KP149202	NA	Guarnizo <i>et al.</i> (2015)
<i>B. pugnax</i>	ANDES-A 1207	-	KP149471	-	NA	Guarnizo <i>et al.</i> (2015)
<i>B. pugnax</i>	ANDES-A 1453	-	KP149296	KP149101	NA	Guarnizo <i>et al.</i> (2015)
<i>B. pugnax</i>	ANDES-A 1533	-	KP149417	KP149212	NA	Guarnizo <i>et al.</i> (2015)
<i>B. pugnax</i>	ANDES-A 1538	-	KP149418	KP149213	NA	Guarnizo <i>et al.</i> (2015)
<i>B. pugnax</i>	ANDES-A 1539	-	KP149327	KP149130	NA	Guarnizo <i>et al.</i> (2015)
<i>B. pugnax</i>	ANDES-A 1540	-	KP149409	KP149204	NA	Guarnizo <i>et al.</i> (2015)
<i>B. pulchella</i>	MACN 37788	AY549352	AY549352	-	NA	Faivovich <i>et al.</i> (2004)
<i>B. punctata</i>	MACN 37792	AY549353	AY549353	KU184077	NA	Faivovich <i>et al.</i> (2004); Berneck <i>et al.</i> (2016)
<i>B. roraima</i>	ROM 39624	AY843660	AY843660	-	NA	Faivovich <i>et al.</i> (2005)
<i>B. rosenbergi</i>	KU 217629	AY819438	-	-	NA	Wiens <i>et al.</i> (2005)
<i>B. rosenbergi</i>	MRC 508	KX697966	-	-	NA	Orrico <i>et al.</i> (2017)
<i>B. rufitela</i>	KRL 798; USNM 572699	AY843662	AY843662	FJ766740	NA	Faivovich <i>et al.</i> (2005); Crawford <i>et al.</i> (2010)
<i>B. sp.</i>	MHNSL 19810	-	In process.	In process.	VE: AM: Fundo Copaba, near Pto. Ayacucho	This study
<i>B. sp.</i>	MHNSL 19811	-	In process.	In process.	VE: AM: Fundo Copaba, near Pto. Ayacucho	This study

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APPENDIX 1. (Continued)

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>B. sp.</i>	MHNLS 19885	-	In process.	In process.	VE: AM: Around cerro Las Pavas, road Pto. Ayacucho-Gavilán	This study
<i>B. sp.</i>	MHNLS 19918	-	In process.	In process.	VE: AM: Raudal de Danto, Río Cuao	This study
<i>B. sp.</i>	AJC 3112	-	In process.	In process.	VE: AM: Mision Coromoto, Atures	This study
<i>B. xerophylla</i>	AF 1797	-	KDQF01000681	-	FG: AP: Piste forestière	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	AF 1803	-	KDQF01000683	-	FG: AP: Piste forestière	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	AF 2399	-	KDQF01000938	-	SU: NA: Trail 7	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	AF 3779	-	In process.	-	SU: VO: CI camp	This study
<i>B. xerophylla</i>	AF 3859	-	In process.	-	SU: Brownsberg	This study
<i>B. xerophylla</i>	AMS 316	-	KDQF01001716	-	GU: Dadanawa Ranch	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	AMS 554	-	KDQF01001756	-	GU: White Sand Camp	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	BOAM 13	-	KDQF01001861	-	FG: Borne 4	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	BPN 913	-	In process.	-	SU: Road to Apura	This study
<i>B. xerophylla</i>	BPN 1735	-	In process.	-	SU: Road to Apura near Pikin Saron	This study
<i>B. xerophylla</i>	BPN 1764	-	In process.	-	SU: Pikin Saron	This study
<i>B. xerophylla</i>	BPN 3550	-	KDQF01002058	-	GU: Potaro-Siparuni, River Lodge	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	BPN 3562	-	KDQF01002062	-	GU: Turtle Mountain, Potaro-Siparuni	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	BPN 3632	-	KDQF01002076	-	GU: Kusad Mountain	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	BPN 3645	-	KDQF01002078	-	GU: Kusad Mountain, pond	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	BPN 3682	-	KDQF01002085	-	GU: Parabara BC	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	GIRanom	-	KDQF01002567	-	BR: RR: Apiaú	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	GIRcrep	-	KDQF01002568	-	BR: RR: Apiaú	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	INPAH 31229	-	In process.	In process.	BR: RR: Rorianópolis	This study
<i>B. xerophylla</i>	INPAH 31230	-	In process.	In process.	BR: RR: Rorianópolis	This study

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APPENDIX 1. (Continued)

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>B. xerophylla</i>	INPAH 31231	-	In process.	In process.	BR: RR: Rorianópolis	This study
<i>B. xerophylla</i>	INPAH 31232	-	In process.	In process.	BR: RR: Rorianópolis	This study
<i>B. xerophylla</i>	INPAH 31234	-	In process.	In process.	BR: RR: Rorianópolis	This study
<i>B. xerophylla</i>	INPAH 31235	-	In process.	In process.	BR: RR: Rorianópolis	This study
<i>B. xerophylla</i>	INPAH 31236	-	In process.	In process.	BR: RR: Rorianópolis	This study
<i>B. xerophylla</i>	INPAH 31237	-	In process.	In process.	BR: RR: Vecinal BR-210	This study
<i>B. xerophylla</i>	INPAH 31239	-	In process.	In process.	BR: RR: Vecinal BR-210	This study
<i>B. xerophylla</i>	INPAH 31240	-	In process.	In process.	BR: RR: São João de Baliza, BR 210	This study
<i>B. xerophylla</i>	INPAH 31241	-	In process.	In process.	BR: RR: São João de Baliza, BR 210	This study
<i>B. xerophylla</i>	INPAH 31242	-	In process.	In process.	BR: RR: São João de Baliza, BR 210	This study
<i>B. xerophylla</i>	Isolate BM095	KX697962	EU201107	KX698011	FG: Mont Saint Marcel	Orrico <i>et al.</i> (2017); Fouquet <i>et al.</i> (2007)
<i>B. xerophylla</i>	MHNLS 15062	KT717075	KT717075	KT717075	VE: BO: Raudales Wareipa	Escalona <i>et al.</i> (2019a)
<i>B. xerophylla</i>	MHNLS 15662	KT717076	KT717076	-	VE: BO: Rio Purumay	Escalona <i>et al.</i> (2019a)
<i>B. xerophylla</i>	MHNLS 16464	-	In process.	In process.	VE: BO: Quebrada de Jaspe	This study
<i>B. xerophylla</i>	MHNLS 17156	-	In process.	In process.	VE: BO: Salto Karuay	This study
<i>B. xerophylla</i>	MHNLS 19561	-	In process.	In process.	VE: BO: Kavanayén, Ca-naima National Park	This study
<i>B. xerophylla</i>	MHNLS 19620	-	In process.	In process.	VE: BO: Sierra de Imataca	This study
<i>B. xerophylla</i>	MTD 47680	-	KDQF01003023	-	GU: Iwokrama	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	MTKD 47940	-	In process.	-	GU: Iwokrama	This study
<i>B. xerophylla</i>	MTR 20407	KX697977	KDQF01003451	KX698023	BR: RR: E.E. Maracá	Orrico <i>et al.</i> (2017); Vacher <i>et al.</i> (2020)

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APPENDIX 1. (Continued)

Species	Voucher/isolate ID	12S	16S	COI	Locality	Reference
<i>B. xerophylla</i>	MTR 20730	KX697978	KDQF01003500	KX698024	BR: RR: Pacaraima	Orrico <i>et al.</i> (2017); Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	PG 345	-	KDQF01003859	-	FG: Haut Marwini	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	PG 346	-	KDQF01003860	-	FG: Haut Marwini	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	PG 552	KX697932	KDQF01003897	KX697979	FG: Haute Wanapi	Orrico <i>et al.</i> (2017); Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	PG 555	-	KDQF01003898	-	FG: Haute Wanapi	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	PK 3697	-	KDQF01004021	-	GU: Close to Iwokrama field station	Vacher <i>et al.</i> (2020)
<i>B. xerophylla</i>	ROM 44089	JN970519	JN970655	JN970774	GU: Parish Hill	Funk <i>et al.</i> (2012)
<i>B. xerophylla</i>	ROM 28436	JN970518	JN970654	JN970773	GU: Paramakatoi	Funk <i>et al.</i> (2012)
<i>B. xerophylla</i>	ROM 20560	JN970517	JN970653	JN970772	GU: Kurupukari	Funk <i>et al.</i> (2012)
<i>B. xerophylla</i>	UFRJK 39	-	In process.	-	SU: Lelygeberge, Sili-pawini	This study
<i>Bok. ahvarengai</i>	UFMG BDT ANI700000	KY829114	KY829114	KY829114	NA	Lima <i>et al.</i> (2017)

APPENDIX 2. Species, record code, voucher, locality, and air temperature for the acoustic records analysed in the present study. AAG-UFU = Coleção de Anuros da Universidade Federal de Uberlândia; AF = Antoine Fouquet; AE = Anfíbios del Ecuador, Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (<https://bioweb.bio/faunaweb/amphibiaweb/>); AMNH = American Museum of Natural History, New York; ELM = Enrique La Marca (tape recordings stored at ULABG); FNZ = Fonozoo, Museo Nacional de Ciencias Naturales de Madrid (<http://www.fonozoo.com/>); MES = Moisés Escalona (tape recordings stored at ULABG); ML = Macaulay Library at the Cornell Lab of Ornithology, Ithaca, New York (<https://www.macaulaylibrary.org/>); SCF = Santiago Castroviejo-Fisher; ULABG = Colección de Anfíbios y Reptiles del Laboratorio de Biogeografía de la Universidad de Los Andes, Mérida. BR = Brazil; CO = Colombia; FG = French Guiana; VE = Venezuela.

Species	Sound record code:	voucher code	Author	Locality	Date	Average air temperature (°C)
<i>Boana albomarginata</i>	FNZ 17475/6330: ?		Axel Kwet	BR: Santa Catarina: near Brusque	11/15/2003	23.0
<i>B. albomarginata</i>	FNZ 17470/6329: ?		Axel Kwet	BR: Santa Catarina: near Brusque	11/15/2003	23.0
<i>B. albomarginata</i>	FNZ 17226/6203: ?		Axel Kwet	BR: Santa Catarina: Praia dos Naufragados	10/19/2002	21.5
<i>B. faber</i>	FNZ 16648/5890: ?		Axel Kwet	BR: Rio Grande do Sul: Pró-Mata, pond T10	?	20.5
<i>B. faber</i>	FNZ 16825/5980: ?		Axel Kwet	BR: Rio Grande do Sul: Pró-Mata, pond T10	12/03/1997	13.0
<i>B. faber</i>	FNZ 16705/5919: ?		Axel Kwet	BR: Rio Grande do Sul: Parque Turvo	12/12/1996	21.0
<i>B. lundii</i>	FNZ 22371/10294: unvouchered		Raissa Souza	BR: Goiás: Floresta Nacional de Silvânia	4/17/2010	17.9
<i>B. lundii</i>	FNZ 22374/10295: unvouchered		Raissa Souza	BR: Goiás: Floresta Nacional de Silvânia	10/27/2012	17.7
<i>B. pardalis</i>	ML 201301: USNM 243593		Stanley Rand	BR: São Paulo: Boraceia biological station	03/11/1983	NA
<i>B. pardalis</i>	ML 201369: USNM 247834		Stanley Rand	BR: São Paulo: Boraceia biological station	04/12/1984	19.4
<i>B. pardalis</i>	ML 201391: USNM 247836		Stanley Rand	BR: São Paulo: Boraceia biological station	06/12/1984	21.5
<i>B. pardalis</i>	ML 201393: unvouchered		Stanley Rand	BR: São Paulo: Boraceia biological station	06/12/1984	NA
<i>B. platanera sp. nov.</i>	ML 218303: unvouchered		William Pyburn	CO: Meta: Finca Santa Terrasita [= Teresita?]	06/18/1969	22.0
<i>B. platanera sp. nov.</i>	ML 194817: KUH 169499		William Duellman	CO: Norte de Santander: 11 km N Ocaña	07/03/1974	20.0
<i>B. platanera sp. nov.</i>	FNZ 7110: KU 77018		William Duellman	PA: Canal Zone: Camp Chagras	06/18/1963	25.0
<i>B. platanera sp. nov.</i>	FNZ 7111: KU 77019		William Duellman	PA: Canal Zone: Camp Chagras	06/18/1963	25.0
<i>B. platanera sp. nov.</i>	FNZ 7643: KU 101550		William Duellman	PA: Panama: 3 km WSW Chepo	06/05/1966	25.6
<i>B. platanera sp. nov.</i>	24 H. crepitans.wav: unvouchered?		Ibáñez R., Rand A.S., Ryan M.J., Jaramillo C.A.	PA: Monumento Natural Barro Colorado, Parque Nacional Soberanía or surrounding áreas	?	NA
<i>B. platanera sp. nov.</i>	ML 208456: unvouchered		Martin Fouquette Jr.	PA: Canal Zone: 5 mile marker on Chiva Chiva Trail (C-21)	05/24/1956	24.8
<i>B. platanera sp. nov.</i>	ML 208467: unvouchered		Martin Fouquette Jr.	PA: Canal Zone: K-2, 5.2 miles from K-55	08/15/1956	25.9
<i>B. platanera sp. nov.</i>	ML 204279: unvouchered		Addison Wynn	TT: St. George: Arima, near Simla Research Station	07/13/1989	23.6

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APPENDIX 2. (Continued)

Species	Sound record code: voucher code	Author	Locality	Date	Average air temperature (°C)
<i>B. platanera</i> sp. nov.	ML_204280: USNM 306154	Addison Wynn	TT: St. George: Arima, near Simla Research Station	07/13/1989	23.6
<i>B. platanera</i> sp. nov.	JCS Carabobo_Casa Maria: unvouchered	J. Celsa Señaris	VE: Carabobo: Posada Ecológica Casa María, altos de Canoabo	05/23/2018	NA
<i>B. platanera</i> sp. nov.	EI VE_Casigua-El_Cubo: unvouchered	Edwin Infante	VE: Zulia: Casigua-El Cubo	?	NA
<i>B. platanera</i> sp. nov.	MES_SO1: ULABG 7758 (Holo-type)	Moisés Escalona	VE: Barinas: 2 km of La Soledad	06/13/2012	NA
<i>B. platanera</i> sp. nov.	MES_SO2: unvouchered	Moisés Escalona	VE: Barinas: 2 km of La Soledad	06/13/2012	NA
<i>B. platanera</i> sp. nov.	MES_SO3: ULABG 7759 (Para-type)	Moisés Escalona	VE: Barinas: 2 km of La Soledad	06/13/2012	NA
<i>B. platanera</i> sp. nov.	MES_SO4: unvouchered	Moisés Escalona	VE: Barinas: 2 km of La Soledad	06/13/2012	NA
<i>B. platanera</i> sp. nov.	MES_SO5: ULABG 7760 (Para-type)	Moisés Escalona	VE: Barinas: 2 km of La Soledad	06/13/2012	NA
<i>B. platanera</i> sp. nov.	MES_LC1: ULABG 7770	Moisés Escalona	VE: Táchira: Las Cuevas	08/01/2012	19.1
<i>B. platanera</i> sp. nov.	MES_EP1: ULABG 7744	Moisés Escalona	VE: Mérida: Santa Elena de Arenales	05/12/2012	NA
<i>B. platanera</i> sp. nov.	MES_EP2: ULABG 7745	Moisés Escalona	VE: Mérida: Santa Elena de Arenales	05/12/2012	NA
<i>B. platanera</i> sp. nov.	MES_EP3: unvouchered	Moisés Escalona	VE: Mérida: Santa Elena de Arenales	05/12/2012	NA
<i>B. platanera</i> sp. nov.	MES_EP4: unvouchered	Moisés Escalona	VE: Mérida: Santa Elena de Arenales	05/12/2012	NA
<i>B. platanera</i> sp. nov.	MES_EP5: unvouchered	Moisés Escalona	VE: Mérida: Santa Elena de Arenales	05/12/2012	NA
<i>B. platanera</i> sp. nov.	MES_JB1: ULABG 7753	Moisés Escalona	VE: Mérida: Jardín Botánico de Mérida	05/30/2012	22.6
<i>B. platanera</i> sp. nov.	MES_JB2: ULABG 7754	Moisés Escalona	VE: Mérida: Jardín Botánico de Mérida	05/30/2012	22.6
<i>B. platanera</i> sp. nov.	MES_JB4: ULABG 7755	Moisés Escalona	VE: Mérida: Jardín Botánico de Mérida	05/30/2012	19.9
<i>B. platanera</i> sp. nov.	MES_JB5: unvouchered	Moisés Escalona	VE: Mérida: Jardín Botánico de Mérida	05/30/2012	NA
<i>B. platanera</i> sp. nov.	MES_CA1: unvouchered	Moisés Escalona	VE: Mérida: Caparú lagoon	06/09/2012	NA
<i>B. platanera</i> sp. nov.	MES_CA2: ULABG 7756	Moisés Escalona	VE: Mérida: Caparú lagoon	06/09/2012	NA
<i>B. platanera</i> sp. nov.	MES_CA3: ULABG 7757	Moisés Escalona	VE: Mérida: Caparú lagoon	06/09/2012	NA
<i>B. platanera</i> sp. nov.	MES_CA4: unvouchered	Moisés Escalona	VE: Mérida: Caparú lagoon	06/09/2012	NA
<i>B. platanera</i> sp. nov.	MES_CA5: unvouchered	Moisés Escalona	VE: Mérida: Caparú lagoon	06/09/2012	NA

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APPENDIX 2. (Continued)

Species	Sound record code: voucher code	Author	Locality	Date	Average air temperature (°C)
<i>B. platanera</i> sp. nov.	MES_CA6: unvouchered	Moisés Escalona	VE: Mérida: Capatú lagoon	06/09/2012	NA
<i>B. platanera</i> sp. nov.	MES_CA7: unvouchered	Moisés Escalona	VE: Mérida: Capatú lagoon	06/09/2012	NA
<i>B. rosenbergi</i>	AE MR-FWE-H-rosenbergi-bilsa: unvouchered	Morley Read	EC: Esmeraldas: 200 m W to Bilsa scientific station	?	NA
<i>B. rosenbergi</i>	AE MR-H-rosenbergi-rio-Toachi: unvouchered	Morley Read	EC: Pichincha: valley of Toachi river	?	NA
<i>B. xerophylla</i>	ML_204254: MZUSP 65684	Celso Morato de Carvalho	BR: Roraima: Reserva Biologica Ilha de Maracá	05/26/1986	NA
<i>B. xerophylla</i>	AF_LS100411 Hypsiboas crepitans maraca: unvouchered	Antoine Fouquet	BR: Roraima: Reserva Biologica Ilha de Maracá	05/20/2011	NA
<i>B. xerophylla</i>	AF_LS100543 Hypsiboas sp. aff. crepitans_serra do Apiiau: unvouchered	Antoine Fouquet	BR: Roraima: Serra do Apiáu	11/16/2011	NA
<i>B. xerophylla</i>	AF_LS100544 Hypsiboas sp. aff. crepitans_serra do Apiiau: unvouchered	Antoine Fouquet	BR: Roraima: Serra do Apiáu	11/16/2011	NA
<i>B. xerophylla</i>	AF_LS100555 Hypsiboas sp aff. crepitans_Serra do apiiau: unvouchered	Antoine Fouquet	BR: Roraima: Serra do Apiáu	11/20/2011	NA
<i>B. xerophylla</i>	AF_STE-071_H_crepitans_13_3_2014_layonB_Apatou: AF1797	Jean-Pierre Vacher	FG: Apatou	03/13/2014	NA
<i>B. xerophylla</i>	SCF008: AMNH 20089	Santiago Castroviejo-Fisher	BR: Roraima: Rorainópolis	06/30/2011	24.8
<i>B. xerophylla</i>	Hypsib_crepitansCantaRR1aAAG: AAG-UFU 5549	Ariovaldo Giarretta	BR: Roraima: Cantá	07/22/2016	27.0
<i>B. xerophylla</i>	Hypsib_crepitansCantaRR2bAAG: AAG-UFU 5550	Ariovaldo Giarretta	BR: Roraima: Cantá	07/22/2016	26.0
<i>B. xerophylla</i>	Hypsib_crepitansCantaRR3aAAG: AAG-UFU 5551	Ariovaldo Giarretta	BR: Roraima: Cantá	07/22/2016	26.0
<i>B. xerophylla</i>	Hypsib_crepitansCantaRR4aAAG: AAG-UFU 5559	Ariovaldo Giarretta	BR: Roraima: Cantá	07/25/2016	27.0

APPENDIX 3. Countries, states, localities, and voucher numbers for examined specimens (^aspecimens with advertisement calls; ^bspecimens with DNA sequences; ^cspecimens with morphometric data) following the taxonomy resulting from this work. Museum acronyms are stated in Materials and Methods. All specimens are adult males unless otherwise stated.

***Boana* sp.** VENEZUELA:—AMAZONAS: Fundo Copaiba, alrededores de Puerto Ayacucho, Municipio Atures (MHNLS 19810^b); Charca alrededores Cerro Las Pavas, Carretera Puerto Ayacucho-Gavilán, Municipio Atures (MHNLS 19885^b); Campamento junto a las turbinas, Raudal de Danto, Río Cuao, Municipio Autana (MHNLS 19918^b).

Boana albomarginata. BRAZIL:—PARANÁ: Morretes (MCP 6443^c).—SANTA CATARINA: Blumenau, Parque Nacional da Serra do Itajaí (MCP 11564^c, 11567^c, 11571^c); Florianópolis, Praia de Naufragados (MCP 6380^c, 6381^c); São Francisco do Sul (MCP 12815^c).—RIO DE JANEIRO: Itaguaí, Ilha de Itacuruça (MCP 12237^c).

Boana crepitans. BRAZIL:—ALAGOAS: Faz. do Prata, São Miguel dos Campos (MNRJ 9673, 9674).—BAHÍA: Faz. Pedra Formosa, Ibirapitanga (MNRJ 29185); Faz. Caititu, Urucuca (MNRJ 26476); Conquista (MNRJ 2626, 12304–12305, 12307, 16945); Caetitê (MNRJ 25078, 25068–25085); Serra do Teimoso, Yussari (MNRJ 21607–21610); Fazenda Tiririca, Conde (MNRJ 16978–16980); Fazenda Orion, Arataca (MNRJ 28930–28931); Ilhéus, CEPLAC (MZUSP 71881).—GOIÁS: Mambá (MNRJ 27833–27838); Jatobazinho (MNRJ 3140, 13475).—MINAS GERAIS: Berilo (MNRJ 21597–21599, 21607–21610); Distrito de Peixe Cru, Turmalina (MNRJ 21592–21596); Faz. Cabrali, Cristália (MNRJ 21600–21602); Itacarambi (MCP 9505^c); Lagoa Santa, Lapinha (MCP 9504, 9506, 9507^c); Mocambinho, Manga (MNRJ 16943–16947); Teófilo Otoni (MZUSP 112750–112754).—PERNAMBUCO: Poçoão, Mun. De Pesqueira (MNRJ 239, 5230–5232); Serra dos Cavalos (MZUSP 63141).—SERGIPE: Faz. Cruzeiro, Cristinópolis (MNRJ 16938).

Boana exastis. BRAZIL:—BAHÍA: Estação Ecológica Estadual Wenceslau Guimarães (MTR 22280^c).

Boana faber. BRAZIL:—PARANÁ: Morretes (MCP 2093^c).—RIO GRANDE DO SUL: Dom Pedro de Alcântara, Canto do Hilário (MCP 412^c); Dom Pedro de Alcântara, Canto dos Leffa (MCP 1528^c); Barracão, Parque Estadual do Espigão Alto (MCP 681^c, 682^c, 684^c); Planalto, Quarta Seção (MCP 1362^c); Barão, Arroio Canoas (MCP 1536^c); Mariana Pimentel (MCP 1592^c); Nova Prata, Bairro São Cristóvão (MCP 1754^c); São Francisco De Paula, Potreiro Novo (MCP 1797^c).—SANTA CATARINA: Peritiba (MCP 580^c); Ita (MCP 644^c); Porto Belo, Bombinhas (MCP 1013^c); Balneario Picarras, Praia de Picarras (MCP 1544^c).

Boana lundii. BRAZIL:—GOIÁS: Minaçu, UHE Serra da Mesa (MCP 2998^c, 3000^c).—MINAS GERAIS: Capitólio (MCP 11360^c–11372^c).

Boana pardalis. BRAZIL:—ESPÍRITU SANTO: Reserva Biológica Augusto Ruschi, Santa Tereza (MTR 34653^c, 34728^c, 34863^c, 34873^c, 34880^c, 34890^c).—RIO DE JANEIRO: Teresópolis, Agriões (MCP 3578^c).

Boana platanera. Females. VENEZUELA:—ANZOÁTEGUI: Valle de Guanape (MHNLS 5571^c).—APURE: Modulo Fernando Corrales (MCNG 292^c, 652^c).—ARAGUA: Río Cata, aguas arriba de la represa, Municipio Costa de Oro (MHNLS 21376^c).—BARINAS: Calderas (MCNG 608^c); Barinas (MCNG 613^c, 633^c); Estación El Irel, Barrancas (CVULA IV-2541^c, 2545^c, 2546^c, 2552^c, 2553^c, 5661^c–5664^c, 5669^c, 6917^c, 6918^c, 6969^c; ULABG 5661^c–5664^c, 5669^c); Estación experimental [de la] ULA, Reserva Forestal Caparo (ULABG 5595^c); Finca “La Recanera”, Parroquia Sta. Rosa, Municipio Rojas (CVULA IV-6947^c, 6949^c); Santa María de Caparo (CVULA IV-6379^c); Vía Suripá, Dto. Pedraza (CVULA IV-4846^c).—GUÁRICO: Río Memo, carretera Altagracia de Orituco Lezama (MHNLS 5684^c).—LARA: Caserío Guadalupe, cerca de Quibor (MCNG 2029^c).—MIRANDA: Fundo Ecológico Santa María, sector Sabaneta de Cañaverl, municipio El Hatillo (MHNLS 20968^c).—MÉRIDA: 5 km cerca de Santa Apolonia, Municipio Tulio Febres Cordero (ULABG 4732^c); 10 km cerca de Santa Apolonia, Municipio Tulio Febres Cordero (ULABG 4749^c, 4751^c, 4755^c); Cerca de Guayabones, 22 km NE de El Vigía (CVULA IV-133^c, 135^c–138^c, 140^c); Finca El Palmar, 9.5 km Santa Elena de Arenales (ULABG 5039^c, 5041^c, 5042^c, 5044^c, 5049^c, 5087^c, 5250^c, 5287^c, 5288^c, 7747^c); Gavilanes, vía Caño Zancudo (CVULA IV-1381^c, 4570^c); Invernadero [de] botánica, Fac. Ingeniería [forestal] (CVULA IV-1597^c); La Azulita, 915 m. asl (ULABG 2951^c); Las Virtudes, 700 m. asl (MCNG 1588^c); Palmarito (CVULA IV-1524^c); Pedregosa Alta (CVULA IV-3354^c); Río Albarregas (La Parroquia) [Río Albarregas a la altura de La Parroquia, Ciudad de Mérida] (CVULA IV-2159^c); San Jacinto (CVULA IV-925^c); Vía La Azulita-Caño Zancudo (CVULA IV-1799^c, 1940^c).—PORTUGUESA: Barrio Coromoto, Guanare (MCNG 1523^c); Carretera Guanare-Papelón (MCNG 963^c); Colonia agrícola Turén (CVULA IV-406^c); Dique oeste, Módulo de UNELLEZ [Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamora] (MCNG 2122^c); Guanare (MCNG 612^c, 639^c).—TÁCHIRA: Doradas, Uribante (CVULA IV-3571^c); Vía San Cristobal-Macanilla, c.a. 21 km San Cristobal; 10.4 km de Chorro del Indio, 1150 m. asl (ULABG 3248^c).—TRUJILLO: Vía Monte Carmelo (ULABG 5526^c).—ZULIA: Hacienda Las Delicias, Santa Cruz del Zulia (CVULA IV-4571^c); Santa Cruz del Zulia (CVULA IV-973^c, 4303^c, 4304^c); Trayecto hacia la primera antena, abajo de la intersección con el camino a Río Lajas; cerro Las Antenas; Municipio Rosario de Perijá (MHNLS 18815^c); Vía Santa Barbara-Encontrados (ULABG 6941^c). Males. VENEZUELA:—ANZOÁTEGUI: Valle de Guanape (MHNLS 5567^c).—APURE: Hato El Frío (ULABG 6971^c); Modulo Fernando Corrales (MCNG 291, 292, 652); Dique oeste, Módulo de UNELLEZ (MCNG 2122); Vía Elorza (CVULA IV-3044^c).—ARAGUA: Aguas arriba del Río Cepe, Municipio Santiago Mariño (MHNLS 21274, 21275); Estación Biológica de Rancho Grande (MHNLS 7460–7462); Estación de Fauna Silvestre “El Limón”, Maracay (ULABG 1416–1418); Quebrada El Cumbre, Hacienda El Cumbre, Choroni (MHNLS 14241); Río Cata, aguas arriba de la represa, Municipio Costa de Oro (MHNLS 21377^c).—BARINAS: 1 km O Calderas (CVULA IV-1743^c); 2 km La Soledad (ULABG 7758^{abc}, 7759^{abc}, 7760^{abc}, 7761^{bc}); Barinitas (CVULA IV-1322^c, IV-2249^c); Estación El Irel, Barrancas (CVULA IV-2547^c, IV-2548^c–2550^c, IV-2919^c, IV-

6916^c, IV-6919; ULABG 5670^{bc}); Hato La Candelaria (CVULA IV-769^c); Hato San Martín, 30 km ENE de Puerto Nutrias (ULABG 1688, 1689^c–1691^c); La Soledad (CVULA IV-2139^c, IV-2140^c, IV-2239^c–2244^c, IV-2690^c, IV-2691^c, IV-2721^c, IV-2722^c; ULABG 7762–7764); Puente de La Soledad (ULABG 6795^c, 6796^c); Pedraza La Vieja (ULABG 1928^c); Reserva Forestal de Caparo (ULABG 7318^c); Río Canaguá, Barinas (CVULA IV-6548^c, IV-6549^c); Santa Rosa, Barinas (CVULA IV-6948^c); vía La Caramuca-Barinas (CVULA IV-2222).—CARABOBO: Bahía de Patanemo (MHNLS 6086, 6254–6262, 6285); Bahía de Patanemo, Yapascua (MHNLS 6275); Ibarre, Bahía de Patanemo (MHNLS 6327–6330).—DISTRITO CAPITAL: Caracas (MHNLS 2682, 2683, 2967); El Valle, Caracas (MHNLS 3670); Instituto Botánico, Caracas (MHNLS 4680); La Quebradita, Caracas (MHNLS 152); Ojo De Agua, Tacagua (MHNLS 1149); Parque Los Caobos, Municipio Libertador (MHNLS 18996); Parque Zoológico Caricuao, área de reserva, quebrada La Tomita, 80 m aguas arriba de la primera bifurcación (MHNLS 14120); San Bernardino, Caracas (MHNLS 489); Tacagua (MHNLS 1363).—LARA: Caserío Guadalupe, cerca de Quibor (MCNG 2030).—MÉRIDA: 1.5 km Vía Zea-El Vigía (ULABG 3190^c–3192^c); 1.5 km del puente sobre el río Chama, entrada a El Vigía (ULABG 5706^c–5710^c); 5 km cerca de Santa Apolonia (ULABG 4733^c–4735^c); 10 km cerca de Santa Apolonia (ULABG 4749, 4750^c, 4752^c–4754^c); Barrio Chamita, Mérida, Municipio Libertador (MHNLS 21144); Finca El Palmar, 9.5 km desde Santa Elena de Arenales, cuenca Río Limones (ULABG 5039^c–5045^c, 5047^c–5050^c, 5057^c, 5059^c–5062^c, 5073^c, 5078^c, 5079^c, 5086^c, 5127^c–5130^c, 5194^{bc}, 5195^c, 5196^c, 5221^c–5223^c, 5229^c, 5248^c, 5249^c, 5260^c, 5261^c, 5275^c–5286^c, 5289^c–5292^c, 5302^c, 5447^c, 7744^{abc}, 7745^{ac}, 7746^c); Finca Santa Lucía, vía entre El Vigía y El Quince (ULABG 4101^c); Jardín Botánico de Mérida (ULABG 7671^c, 7753^{bc}, 7754^{ac}, 7755^{ac}); La Azulita (CVULA IV-1470^c, IV-2161^c, IV-2162^c, IV-2223, IV-7035^c, IV-7036^c); La Azulita, 915 m (ULABG 2948, 2949, 2950^c, 2951); Laguna Caparú, 900 m (ULABG 2002^c, 3076, 7396^c, 7756^{abc}, 7757^{abc}); La Macana (MHNLS 17912); La Pedregosa Alta (CVULA IV-3349^c–3351^c, IV-3355^c–3362^c); Laguna La Sucia, sector La Sucia, Páramo De Mariño, carretera Tovar-Zea, Municipio Tovar (MHNLS 20418); Los Llanitos de Tabay (ULABG 2947^c); Monte Zerpa, ciudad de Mérida (MCNG 1583^c); Manzano Alto (ULABG 2858^c); San José de la Providencia, Mesa Bolívar (ULABG 7796^{bc}, 7797^{bc}); San Juan de Lagunillas (CVULA IV-3043^c, IV-6658^c–6661^c); Sector Caño Rico, entre Caño Zancudo y Guayabones, carretera hacia la Sierra de La Culata (ULABG 7803^{bc}); Truchicultura, El Salado, cerca de La Azulita (ULABG 5337^c, 5338^c); Urbanización Humboldt, ciudad de Mérida (CVULA IV-1129^c, IV-1130^c); Urbanización Santa María Sur, ciudad de Mérida (ULABG 6786^{bc}); Vía Jají, 22 km NO de Mérida (CVULA IV-1505^c); Municipio Pinto Salinas, sector La Macana, 9.2 Km desde puente en Santa Cruz de Mora, 1360 m (ULABG 6902).—MIRANDA: Baruta (MHNLS 217); Carenero (MHNLS 1586); Carretera Chuspa-Higuerote (MHNLS 3546–3568, 3703, 3886); Casa de Juvenal Cárdenas, 1km aguas arriba de Capayita, Río Araira, Municipio Zamora (MHNLS 20637, 21292); El Marques (MHNLS 6227); Fundo Ecológico Santa María, sector Sabaneta de Cañaverál, Municipio El Hatillo (MHNLS 20967–20969, 20970^c, 20971); Hacienda El Latón (MHNLS 2968, 2969, 3669, 4310, 4311); La Providencia, Turgua (MHNLS 144); La Toma, Capaya (MHNLS 4973); Los Dos Caminos (MHNLS 145, 3691); Los Teques (MHNLS 2402); Paracotos (MHNLS 1770, 2256–2259, 3009, 4433); Quebrada camino arriba de Casa de Juvenal Cárdenas, 1km aguas arriba de Capayita, Río Araira, Municipio Zamora (MHNLS 21302); Quebrada de Salmeron (MHNLS 2965); Quebrada Guacarapa, Guarenas (MHNLS 12683); Quebrada Las Palmas, hoyo del Río Tuy (MHNLS 222); Río Araira, 2km aguas arriba de Capayita, Municipio Zamora (MHNLS 21786, 21787); Santa Teresa del Tuy (MHNLS 154); Urbanización Macaracuay, Av. Manaure, Quinta Mis Hermanos, Caracas (MHNLS 17115).—MONAGAS: Sector Cachipo, Reserva Forestal de Guarapiche (MHNLS 13717^c, 13718^c).—PORTUGUESA: 6 km cerca del río Saguaz, cerca de Biscucuy (ULABG 3725^c); Carretera Biscucuy-Chabasquén (ULABG 3862^c); Carretera Guanare-Guanarito (MCNG 1584^c); Colonia Agrícola Turén (CVULA IV-0405^c); El Potrero, vía Suruguapo, a 12.6 km en la carretera Acarigua-Guanare (ULABG 5369^c, 5424^c, 5425^c, 5427^c, 5428^c, 5430^c); Fundaguanare, Calle Florida, Guanare (MCNG 2119^c); Mesa Alta, Mesa de Cavaca (MCNG 1938^c); Guanare (MCNG 610^c); Pozo Blanco, Acarigua (CVULA IV-5949^c).—SUCRE: Entre Cariaco y Chacopata (MHNLS 9152–9155); Finca Vuelta Larga, 9.7 Km SE Guaraunos (MHNLS 11789); Playa Colorada, 3 km al este de San Juan de las Galdonas, Península de Paria (MHNLS 9544^c).—TÁCHIRA: Doradas, Uribante (CVULA IV-3572^c, IV-5816^c); El Potosí, Uribante (CVULA IV-3559^c, IV-3560^c); La Honda (CVULA IV-5359^c); Laguna cercana al caño San Mateo (ULABG 7740^{ac}, 7741^{bc}); Las Cuevas, vía hacia el río Doradas (ULABG 7770^{abc}); Los Caños, cerca de Coloncito (ULABG 7738^c); Uribante-Caparo (CVULA IV-5139–5141).—TRUJILLO: Escuela Técnica Industrial, Trujillo (ULABG 1142^c–1144^c); La Loma, 4 km del puente de San Jacinto (ULABG 1146^c, 1163^c); Vía Monte Carmelo (ULABG 5527^c); Vía Trujillo-San Lazaro, cerca de Sabanetas (ULABG 2666^c).—VARGAS: Cagüita, Hacienda El Limón (MHNLS 2970, 2971, 3004, 3093, 422283, 4284, 4345, 4528, 4703, 4758, 4788); Chichiriviche de La Costa, sector Vega Arriba, Parroquia Carayaca, Municipio Vargas (MHNLS 20317); Los Caracas (MHNLS 1710, 1711).—YARACUY: Hacienda La Guaquirá, Macizo de Nirgua (MHNLS 18940, 18941, 19300, 19301); Laguna de La Capilla, sector El Silencio, Sierra de Aroa, Municipio Bolívar (MHNLS 21154^c); Laguna en “La Sabana”, Hacienda La Guáquirá, Macizo De Nirgua (MHNLS 19749^c–19752); Quebrada antes de la estación biológica, Hacienda La Guáquirá, Sector La Marroquina, Municipio San Felipe (MHNLS 21186); Sector Mayorica, Granja “Vista Al Yurubi”, Municipio San Felipe (MHNLS 21011–21012).—ZULIA: Aguas arriba de la cascada Kusare frente a Ipika, Cuenca del Río Tokuko, Sierra de Perijá (MHNLS 18544); Carretera hacia el río Lajas, cerca de la intersección con el trayecto hacia la primera antena, Cerro Las Antenas, Sierra De Perijá, Municipio El Rosario (MHNLS 18812^c); Comunidad Indígena Yukpa de Ipika, Sierra de Perijá (MHNLS 18084); Hacienda El Guamal, area de desborde del Río El Palmar (MHNLS 16980); Ipika, Sierra de Perijá (MHNLS 18120–18122); Kunana, Hoya del Río Negro, Perijá (MHNLS 401–406); Misión El Tukuko, Sierra de Perijá (MHNLS 11861); Río Yasa (MHNLS 1580; 2966); Santa Bárbara del Zulia (CVULA IV-4552); Santa Cruz del Zulia (CVULA IV-4572^c, IV-4573^c); Trayecto hacia la primera antena, abajo de la intersección con el

camino a Río Lajas, Cerro Las Antenas, Municipio Rosario De Perijá (MHNLS 18815^c).

Boana pugnax. VENEZUELA:—APURE: Hato El Cedral, cerca al campamento Matiyure (ULABG 7781^{abc}, 7782^c, 7783^{abc}, 7790^c, 7791^c); Hato Fernando Corrales (CVULA IV-3417^c; MCNG 0168^c, 0169^c, 0651^c); Paso El Burro (CVULA IV-7078^c).—BARINAS: 40 km S de Barinas (CVULA IV-0502^c); Estación El Irel, Barrancas (CVULA IV-2544^c, IV-0255^c; ULABG 5666^c, 5668^c); Reserva Forestal de Caparo (ULABG 5594^c).—MÉRIDA: 1.5 km del puente sobre el río Chama, entrada a El Vigía (ULABG 5671^{abc}, 5672^c–5675^c); Brisas del Chama, 3 km desde El Vigía-Caja Seca, justo luego del puente (ULABG 5712^c, 5713^c); Finca Santa Lucía, vía entre El Vigía y El Quince (ULABG 4100^c); Las Virtudes (MCNG 1587^c).—PORTUGUESA: Fundaguanare, Guanare (MCNG 0627^c); Fundo El Drago (MCNG 0801^c–0803^c); Mesa de Cavacas (MCNG 0638^c); Río Tucupido (MCNG 0809^c).—TÁCHIRA: Puente de Piedra (CVULA IV-2907^c).—ZULIA: Santa Bárbara del Zulia (CVULA IV-0968^c, IV-0971^c–0974^c, IV-3745^c, IV-4531^c, IV-4824^c); Vera de Agua, 10 km El Vigía road to Santa Bárbara (ULABG 5320^{bc}).

Boana rosenbergi. ECUADOR:—ESMERALDAS: Cachavi (MZUSP 109521^c, 109523^c, 109524^c–109526^c, 109529^c, 109531^c–109533^c, 109535^c); San Javier (MZUSP 10554^c).

Boana xerophylla. BRAZIL:—RORAIMA: Floresta, Rorainópolis (AMNH 20089^a); Mucajaí (MZUSP 65984–65986). VENEZUELA:—BOLÍVAR: Base del cerro Taute; aproximadamente a 3.6 km al suroeste de la laguna de Canaima; Parque Nacional Canaima (MHNLS 15859^c, 15874^c); Campamento Purumay, 300 m upstream río Cucurital, Gran Sabana (MHNLS 15662^{bc}); Canaima; Parque Nacional Canaima (MHNLS 15880^c); Kavanayén, Parque Nacional Canaima (MHNLS 19561^b); Laguna-morichal en la sabana; margen izquierda del Río Purumay (MHNLS 14936^c); Quebrada Atapere, cuenca alta del río Cucurital, Gran Sabana (MHNLS 16046^c, 17339^c); Quebrada de Jaspe; Km 273 via El Dorado-Santa Elena de Guairen; La Gran Sabana (MHNLS 16464^{bc}, 16465^c, 16466^c); Raudales Wareipa-Aurauri, Río Cucurital, Gran Sabana (MHNLS 15062^{bc}, 15064^c, 15066^c); Sabana con morichal; aproximadamente a 3.7 km al sur de laguna de canaima; parque nacional canaima (MHNLS 15886^c, 15895^c, 15896^c); Salto Karuay (MHNLS 17156^b); Sierra de Imataca (MHNLS 19620^b).