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Resolving the taxonomic puzzle of *Boana cinerascens* (Spix, 1824), with resurrection of *Hyla granosa gracilis* Melin, 1941 (Anura: Hylidae)

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Abstract

Expeditions to unexplored or little explored places are important for discovering new species and also for collecting new samples (including specimens and tissues for DNA sequencing) that may help resolve a plethora of taxonomic problems. In the 19th century, several naturalists explored a number of localities in Amazonia, describing species for which type material was deposited, mostly, in European museums of natural history. Some of these types were lost or destroyed in World War II and recent expeditions have focused on sampling new material from the type localities. material from *Boana cinerascens*, which allowed us to infer phylogenetic relationships of the *Boana punctata* group (i.e., green *Boana*), based on DNA sequence data, and to revaluate the status of *B. cinerascens* and its synonyms. We designate, redescribe and illustrate a neotype for *B. cinerascens, w*hich was described by Spix in 1824, from the Municipality of Tefé, State of Amazonas, Brazil. We revalidate, redescribe, and illustrate *Hyla granosa gracilis* Melin, 1941(= *Boana gracilis*). Corroborating previous studies, the green *Boana* were not recovered as a monophyletic group. *Boana cinerascens* is sister of *B. gracilis* plus a clade containing *B. atlantica* + *B. punctata* (both species not recovered as monophyletic).

Keywords: Amphibia, Cophomantinae, Molecular, Neotype, Phylogeny, Systematics, Taxonomy, Amazonia

Introduction

Recent expeditions to Amazonia have revealed that our knowledge about the species diversity of anurans is still incomplete. New species continue to be found even in well-known and well-studied places, and several species have been shown to consist of several cryptic lineages (e.g., Ferreira *et al.* 2017; Fouquet *et al.* 2016; Orrico *et al.* 2014; Peloso *et al.* 2014, 2016; Simões *et al.* 2013; Sturaro & Peloso 2014). For example, several species of *Boana* Gray, 1825 were recently named or revalidated for Amazonian populations, whereas authors also highlighted that many additional taxa still await formal description or revalidation (Caminer & Ron 2014; Fouquet *et al.* 2016; Peloso *et al.* 2018). This corroborates that we are far from understanding the full spectrum of amphibian diversity in Tropical South America.

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As currently defined *Boana* comprises 92 species distributed in Central and South America, from Nicaragua to Argentina (Duellman *et al.* 2016; Faivovich *et al.* 2005; Frost 2019). In their systematic review of the family Hylidae, Faivovich *et al.* (2005) recognized seven species groups in the genus (then referred to as *Hypsiboas*): *Boana albopunctata*, *B. benitezi*, *B. faber*, *B. pellucens*, *B. pulchella*, *B. punctata* and *B. semilineata*. The systematics of the *Boana punctata* group and the taxonomy of some species within it have long and convoluted taxonomic histories.

The Green Gladiator Frogs Clade (Boana punctata *species group*)

Faivovich *et al.* (2005) recognized the group (referred to as the *Hypsiboas punctatus* group) based exclusively on DNA sequence data—no morphological synapomorphies were provided. They included in the group most former members of the *Hyla granosa* and *Hyla punctata* species groups. However, because they included only the nominal species *Hyla granosa* in their analysis, the inclusion of *Hyla alemani*, *H. atlantica*, *H. hobbsi*, and *H. ornatissima* in the group was done tentatively, based on their previous assignments. In a phylogeny based on DNA sequences, Faivovich *et al.* (2013) recovered *Boana ornatissima* nested in the *B. benitezi* group, transferring to that group.

After the review of Faivovich *et al.* (2005), two other green frogs were named and included in the *B. punctata* group based on their overall similarity to *Boana cinerascens*: *Boana liliae* (Kok 2006), and *Boana jimenezi* (Señaris & Ayarzagüena 2006)—but Pinheiro *et al*. (2019) transferred *Boana liliae* (Kok, 2006) to *Myersiohyla* based on a phylogenetic analysis of DNA sequence data. Therefore, as currently defined the *Boana punctata* group is composed of eight valid nominal taxa: *Boana alemani* (Rivero, 1964), *Boana atlantica* (Caramaschi & Velosa, 1996), *Boana cinerascens* (Spix, 1824), *Boana hobbsi* (Cochran & Goin, 1970), *Boana jimenezi* (Señaris & Ayarzagüena, 2006), *Boana picturata* (Boulenger, 1899), *Boana punctata* (Schneider, 1799), and *Boana sibleszi* (Rivero, 1971). Several studies have, however, suggested that the group is not monophyletic (Duellman *et al.* 2016; Faivovich et al. 2013; Pinheiro *et al.* 2019; Pyron & Wiens 2011; Wiens *et al.* 2010)—e.g., the phylogenetic position of *B. sibleszi* is poorly supported, and the taxon has been recovered within the *B. benitezi* or *B. semilineata* species groups.

A brief taxonomic history of Boana cinerascens *(Spix, 1824)*

Despite some attempts to clarify the taxonomic status of several populations of species in the *Boana punctata* group, the species boundaries, and geographical ranges of most taxa remain controversial. The identification of species in this group has been largely based on external morphology, which can be misleading due to the similar morphology and variable color pattern in many species of the group (Hoogmoed 1979; Kok 2006; Kok & Kalamandeen 2008). Below, we summarize the complex taxonomic history involving *Boana cinerascens*, a species described almost two centuries ago, but for which the species limits and geographical range remain largely uncertain. *Boana cinerascens* was originally named as *Hyla cinerascens* by Spix (1824), with its description based on specimen(s) deposited at Zoologische Staatssammlung München (ZSM 2498/0 according to Duellman 1977), from "pagum Ecga prope flumen Teffe" (= Tefé, State of Amazonas, Brazil, according to Vanzolini [1981, 1996]). The specimens were collected probably around November and December 1819, during the visit of the Bavarian explorers Johann Baptist Spix and Karl Friedrich Philipp Martius to the region.

In the original description, Spix (1824) does not mention how many specimens he examined, and only one was illustrated (Spix 1824, plate VIII, figure 4; reproduced in Fig. 1A). Peters (1872) mentions only one specimen ("badly preserved and discolored") in his study about the amphibians collected by Spix deposited in the Zoologische Staatssammlung München. However, two syntypes were reported by subsequent authors (Cochran 1955; Duellman 1977; Glaw & Franzen 2006) —both syntypes are now apparently lost (Duellman 1977; Glaw & Franzen 2006). It is important to note that Hoogmoed and Gruber (1983) suggested that it is likely that Spix used only one specimen and the second one was included after the ZSM catalogue was produced (between 1872 and early twenty century). Peters (1872) considered *Hyla cinerascens* as a synonym of *Hyla albomarginata*, justifying that the examined syntype was "a very poorly preserved copy of *H. albomarginata* Spix". Lutz (1951a; b [1949]), however, considered unlikely that Spix's species was conspecific with the Atlantic Forest species *H. albomarginata*, and therefore treated *H. cinerascens* as a distinct species. Furthermore, this synonymy was considered doubtful by several authors such as Duméril and Bibron (1841), Lutz (1951; 1973), Bokermann (1966).

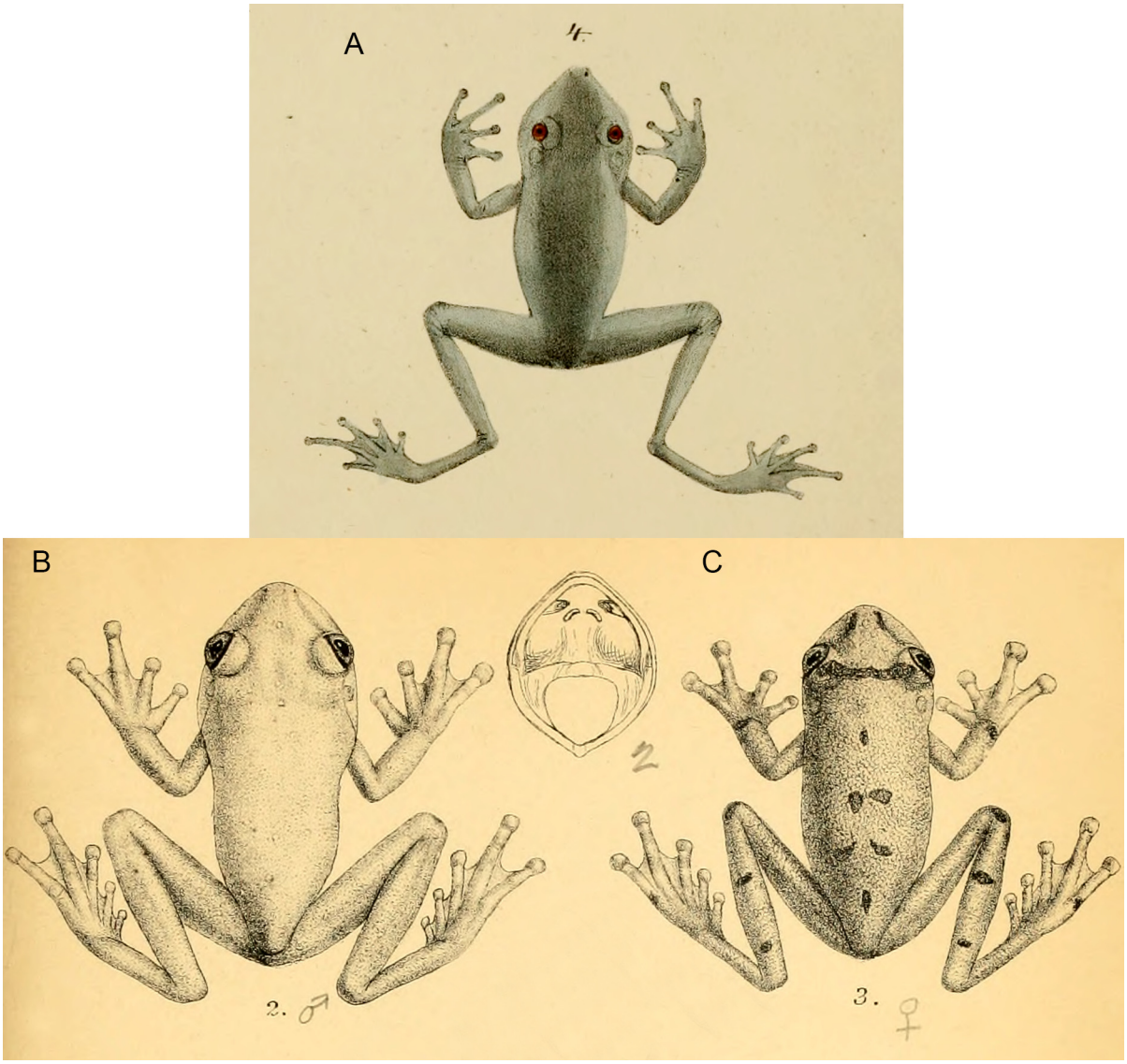

FIGURE 1. Illustrations of type specimens currently referred to *Boana cinerascens* in this study. (A) Holotype of *Hyla cinerascens* as figured in Spix (1824), plate VIII, figure 4—scanned copy from the Ernst Mayr Library Museum of Comparative Zoology, from Harvard University, Massachusetts (available at www.biodiversitylibrary.org/bibliography/3665#/summary). (B) BMNH 1947.2.12.99, lectotype, and (C) BMNH 1947.2.12.97, paralectotype, of *Hyla granosa*, as figured in Boulenger (1882), plate XXIV, figures 2 and 3—scanned copy from Natural History Museum Library, London (available at www.biodiversitylibrary.org/bibliography/8307#/summary).

Hyla granosa was described by Boulenger (1882) based on a series of specimens from scattered localities around Amazonia: Guyana, Demerara Falls (The Natural History Museum – BMNH 1947.2.12.93[1]), Santarém, Brazil (BMNH 1947.2.12.94–96); Interior of Brazil (BMNH 1947.2.12.97–98); and Ecuador, Canelos (BMNH 1947.2.12.99). Two of these specimens (BMNH 1947.2.12.99 and BMNH 1947.2.12.97) were illustrated by Boulenger (1882, plate XXIV, figures 2 and 3, following Hoogmoed [1979], reproduced here in Fig. 1B and 1C, respectively). In the original description, Boulenger (1882) suggested that males and females might show remarkable differences in color pattern ("males with a few scattered white dots on the head and back; females with a cross-streak between the eyes, a streak from the nostril, and a few spots on the back, forearms, and tibiae, purple; upper eyelid rose, as in *H. punctata*"). However, no sympatric specimens of the opposite sex were available in his sample. Lutz (1951a;b [1949]) noted that Boulenger's type series may have more than one form under the same name—she suggested, that the plain form could be called *Hyla inornata* and, by implication, that the patterned form should retain

1 Numbers represent the current collection numbers at the BMNH.

the name *Hyla granosa.* However, this proposal was an informal suggestion without nomenclatural value and no type specimen was designated for *Hyla inornata*. Although it could be inferred that she was referring to the animal illustrated in Boulenger (1882: BMNH 1947.2.12.99), we agree with Duellman (1974) that the name *Hyla inornata* Lutz, 1951 [1949] must be considered a *nomen nudum*, because there is no designed type for this name.

Hyla ornatissima was named and described by Noble (1923), based on a single female specimen from Meamu, Mazaruni R., British Guiana, currently Guyana (AMNH 13491). Lutz (1951a; b [1949]) suggested *H. ornatissima* might be identical to *H. granosa*, but did not formally synonymize them.

Hyla granosa gracilis was named and described by Melin (1941) based on two male syntypes from Rio Uaupés (north of Ipanoré), Brazil (both specimens catalogued with same number in Naturhistoriska Museet, Göteborg, Sweden, NHMG 467) (Fig. 2), according to Duellman (1974).

FIGURE 2. Syntypes of *Hyla granosa gracilis* Melin, 1941 (NHMG 467). Photos available at the NHMG website.

Rivero (1961) briefly reviewed the taxonomy of the aforementioned taxa, and considered *Hyla ornatissima* a synonym of *H. granosa.* He also suggested that the name *Hyla granosa gracilis* is unnecessary and rejected the diagnostic characters provided by Melin (1941), synonymizing *H. g. gracilis* with *H. granosa*. The status of *H. granosa gracilis* was further discussed by a series of papers that dealt with the species, but do not mention each other (likely because each author was unaware of the work of others). Cochran & Goin (1970) explicitly considered

H. granosa gracilis as synonym of *Hyla punctata*. Rivero (1972) formally proposed that *H. granosa gracilis* should be considered a synonym of *H. granosa.*

Duellman (1974), in his taxonomic reassessment of several Neotropical hylids, once again reviewed the status of the taxa mentioned above. He designated one of the syntypes of *H. granosa* as lectotype (BMNH 1947.2.12.99, from Canelos, Pastaza, Ecuador). It is worth mentioning that Cochran & Goin (1970) restricted the type-locality of *Hyla granosa* to Demerara Falls, Guyana, without indicating a lectotype. Only one of Boulenger's specimens was collected at that locality (BMNH 1947.2.12.93). However, Duellman (1974: 8) explicitly designated a lectotype (BMNH 1947.2.12.99), and consequently, the type-locality of *H. granosa* became Canelos, Ecuador. When reassessing the status of *H. granosa gracilis*, Duellman (1974) concurred with Rivero (1972) that the taxon was to be considered a synonym of *H. granosa*, and consequently neither a synonym of *H. punctata* (as suggested by Cochran & Goin 1970), nor a subspecies of *H. granosa* (as suggested by Lutz 1951a; b [1949], 1973).

The status of most species was reviewed again by Hoogmoed (1979). Based on morphological, ecological, and acoustical evidence, he removed *Hyla ornatissima* from the synonymy of *Hyla granosa.* Hoogmoed (1979) did not comment on the status of *H. cinerascens.* A few years later, Hoogmoed and Gruber (1983), in a systematic review of Spix's material, considered that *Hyla granosa* Boulenger, 1882 was a junior synonym of *Hyla cinerascens* Spix, 1824 but made the following remark: "As *H. granosa* is a well-established name (Hoogmoed, 1979) it seems undesirable to replace it by a name which for a long time has been considered a synonym of a superficially similar species and of which the type has been destroyed. We therefore will propose the International Commission on Zoological Nomenclature to suppress *H. cinerascens* Spix, 1824 in order to stabilize the nomenclature of this taxon". The formal petition to ICZN was never submitted and the name *Hyla granosa* continued to be widely used for another 20 years, until Barrio-Amorós (2004) and Frost *et al.* (2006) used the name *Hyla cinerascens* for the taxon until then known as *H. granosa*. The use of *H. cinerascens* was widely followed and the name has become the standard for what was once known as *H. granosa*.

The status of the species treated above has remained unchanged, except for generic reallocations. Faivovich *et al.* (2005) placed them in *Hypsiboas*, and Dubois (2017) corrected the generic name to *Boana* (by implication). As per our interpretation of historical literature, *Boana cinerascens* (Spix, 1824) is a valid name, and *Boana granosa* (Boulenger, 1882) and *Boana granosa gracilis* (Melin, 1941) are junior synonyms of it.

Three recent expeditions to the Rio Negro and Rio Solimões regions (State of Amazonas, Brazil) of Amazonia yielded important material that allowed us to revisit the taxonomic issues mentioned above.

Recent Fieldwork

M.S. Hoogmoed, T.C.S. Avila-Pires and M.T. Rodrigues collected 11 green hylids of the *B. punctata* group on the east bank of the Rio Negro, opposite the Anavilhanas Archipelago, State of Amazonas, Brazil, between 8 and 15 April 2006. From 15–21 January 2017, some of the authors (AOM, MJS, PLVP) visited Tefé, Amazonas, Brazil (the type-locality of several Amazonian frogs) to search for some of the species named by Spix (1824) from that locality. We obtained five specimens of *Boana cinerascens* (Fig. 3A–B), together with tissue samples and advertisement call recordings (see below).

Later that same year (February to March 2017), some of us (MJS, JCLC and PLVP) made collections at Parque Nacional do Jaú (PNJ), Novo Airão, Amazonas, Brazil. At PNJ we collected two distinct syntopic species of green treefrogs that could be assigned to *B. cinerascens* (as currently understood: *sensu* Hoogmoed 1979). Upon closer examination and comparison of this material with material deposited at MPEG, AMNH, and MHNLS ((collection acronyms are listed below) we concluded that part of the material is identical with *B. cinerascens* (Fig. 3C–D), whereas the rest resemble either of the types of *Hyla granosa gracilis* (Fig. 4).

In addition to the Brazilian material, DPM visited the type locality of *H. granosa* (Canelos, Ecuador) in December 2013. The fieldtrip resulted in the collection of a topotypic specimen of *H. granosa*. The Brazilian and Ecuadorian material provided us with the opportunity to try to solve the century-old taxonomic problems involving the names *Hyla cinerascens* and *H. granosa.*

Here, we designate, diagnose, describe, and illustrate a neotype for *Boana cinerascens*—based on the material collected at the type-locality. Moreover, we provide a phylogenetic analysis of recently collected material, complemented with GenBank (Benson *et al.* 2013) sequences, and conclude that the name *Boana gracilis* is available for

the second species collected at PNJ. Additional specimens unambiguously assignable to *Boana gracilis* exists at the AMNH, MPEG and MHNLS—this material is used to provide a redescription and analysis of variation of the species.

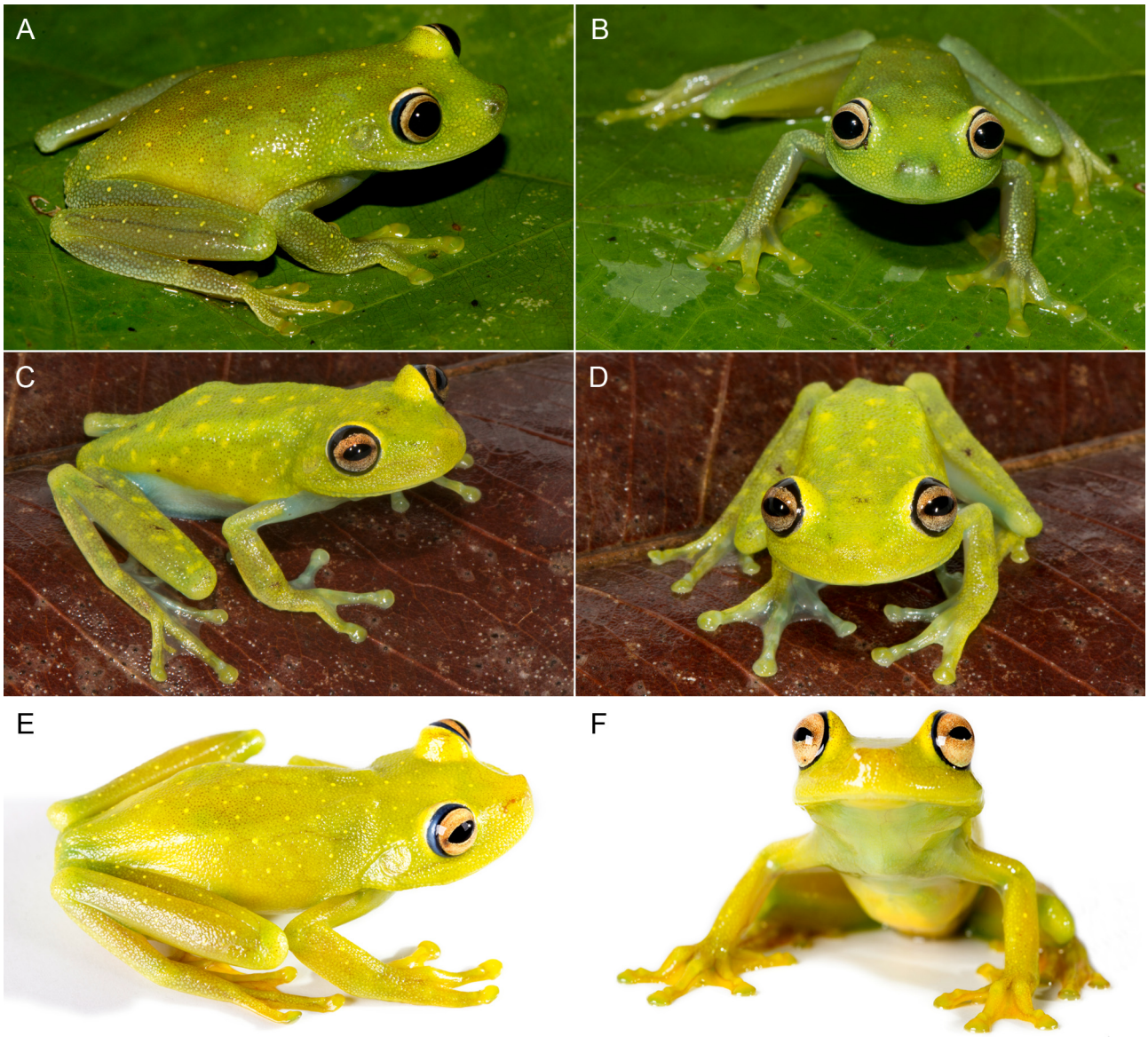

FIGURE 3. Recently collected specimens of green tree frogs included in this study—*Boana cinerascens*. (A) Dorsolateral and (B) frontal profiles of MPEG 40282 (neotype), from Tefé, Amazonas, Brazil. (C) Dorsolateral and (D) frontal profiles of MPEG 40287 from Parque Nacional do Jaú, Amazonas, Brazil. (E) Dorsolateral and (F) frontal profiles of QCAZ-A 56580 from quebrada Pupalyacu, Canelos, Pastaza, Ecuador.

Material and methods

Morphological analysis

For the descriptions and comparisons, we examined specimens deposited in the herpetological collections of the following institutions: American Museum of Natural History, New York, USA (AMNH); Coleção de Anfíbios Célio F. B. Haddad, Universidade Estadual Paulista, Rio Claro, Brazil (CFBH); Coleção Herpetológica Osvaldo Rodrigues da Cunha, Museu Paraense Emilio Goeldi, Belém, Brazil (MPEG); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museo de Historia Natural La Salle, Caracas, Venezuela (MHNLS) (complete list of material examined is given in Appendix 1). We also examined, from photographs, the syntypes of *Hyla granosa*

gracilis (NHMG 467) deposited in the Herpetological Collection of Naturhistoriska Museet, the two specimens illustrated by Boulenger (1882) as *Hyla granosa*, deposited in the Natural History Museum, London, UK (BMNH), and the BMNH specimens illustrated by Lutz (1951a; b [1949]) and Hoogmoed (1979).

We took 12 measurements (under a stereomicroscope, using a digital caliper, to the nearest 0.1 mm) following Peloso *et al.* (2014, 2016, 2018): SVL (snout-vent length); HL (head length; from snout to angle of the jaw); HW (head width; between the angles of jaws); ED (eye diameter; between anterior and posterior corner of the eye); ELW (eyelid width); IOD (interorbital distance; distance between anterior corner of the eyes); IND (internarial distance); END (eye-nostril distance; from the anterior corner of the eye to the posterior margin of nostril); TD (tympanum diameter; measured horizontality at the widest portion); THL (thigh length; from the middle of the cloacal opening to the outer edge of the flexed knee); TBL (tibia length; from the outer edge of the flexed knee to the heel); FL (foot length; from tibiotarsal articulation to tip of fourth toe). Fingers and toes were indicated as FI–IV and TI–V.

The color in life was described based on field notes and photographs taken in the field by the authors, and on literature (only papers with photographs, in addition to written descriptions of color, and with listed reference material).

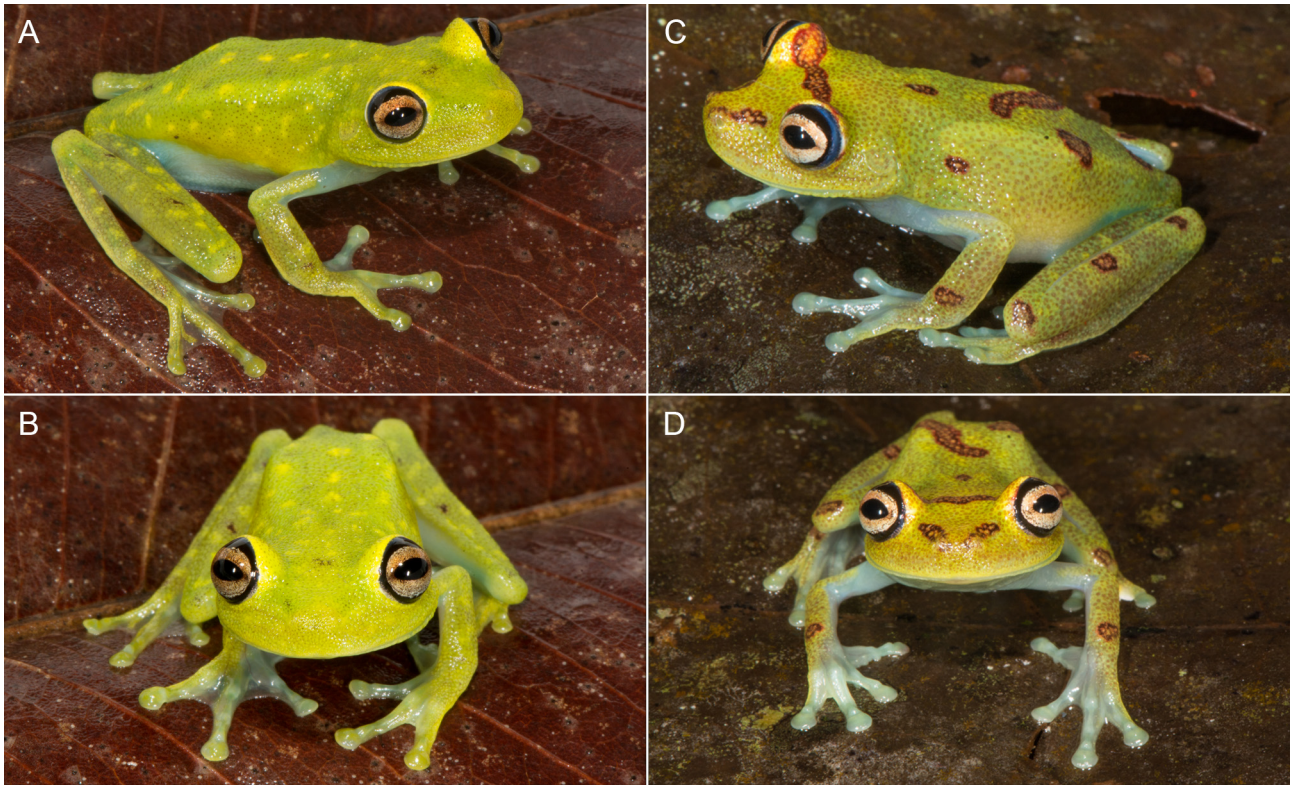

FIGURE 4. Recently collected specimens of Green Tree Frogs included in this study—*Boana gracilis* (see text for nomenclatural clarification). (A) Dorsolateral and (B) frontal profiles of MPEG 40292. (C) Dorsolateral and (D) frontal profiles of MPEG 40288 Both specimens from Parque Nacional do Jaú, Amazonas, Brazil.

Acoustic analysis

During fieldwork in Tefé, Amazonas, Brazil one of us (PLVP) recorded the advertisement call of a male *Boana cinerascens* (MPEG 40282), on 15 January 2017, at Igarapé Tapiranema, Rio Tefé (03°16'47"S, 64°45'09"W). Another call of a male *Boana cinerascens* (MPEG 40290) was recorded by PLVP on 26 February 2017 at the PNJ (02°18'04"S, 62°28'07"W). Both recordings were made with a Marantz PMD620 digital recorder using the internal, built-in, microphone, with 16 bits resolution, 44 kHz sampling frequency. Calls were recorded about 1 m from the specimen. We generated the spectrograms in Raven, version 1.5.0 (Bioacoustics Research Program 2014) at a sampling frequency of 55.2 kHz and a frequency resolution of 10.8 Hz. We measured twelve acoustic parameters to describe the structure of each call, following Köhler *et al.* (2017): (1) call duration, (2) call interval, (3) call rise time, (4) notes per call, (5) note duration, (6) note rate, (7) inter-note interval, (8) pulses per note, (9) pulses per call,

(10) inter-pulse interval, (11) bandwidth per call, and (12) bandwidth per note. The recordings were labeled "Pedro Luiz Peloso Digital Recordings" (PLPDR) and deposited in the Coleção Sonora UNESP-Rio Claro, Universidade Estadual Paulista, Campus Rio Claro, São Paulo, Brazil.

Phylogenetic Analysis

We sequenced two mitochondrial loci (16S: 16S large subunit ribosomal RNA; and COI: Cytochrome Oxidase I) from two *Boana cinerascens* from Tefé (topotypical material) and from the two morphotypes (four specimens in total) from PNJ, to test if these specimens represented an unknown color morph of *B. cinerascens* or a distinct species. Primers used for PCR amplification and sequencing were the same used in Peloso *et al.* (2014, 2016).

We checked and edited all sequences in Geneious R9 (Kearse *et al.* 2012). Following the phylogenetic hypothesis and taxonomy proposed by Faivovich *et al.* (2005), we combined our new data with sequences of *Boana punctata* species group and outgroups representing the other six currently recognized species groups of *Boana*, and three *Aplastodiscus* (the sister clade of *Boana*), mostly download from GenBank (Benson *et al.* 2013) (Appendix II).

We aligned the sequences independently for each gene with MAFFT online, version 7 (Kuraku *et al.* 2013), using the E-INS-i strategy for both genes under default parameters. We concatenated the data of two genes, using Sequencing Matrix, version 1.7.8 (Vaidya *et al.* 2011), including question marks on both sides for missing data due to different fragment lengths. We tested the best partition scheme and substitution models with PartitionFinder, version 2.1.1 (Lanfear *et al.* 2017), under the corrected Akaike Information Criterion (AICc), as suggested by the authors, considering all possible combinations of subsets (default).

We performed a maximum likelihood (ML) analysis to infer the phylogeny, using RAxML, version 8.2.9 (Stamatakis 2014), under default parameters using the best partition scheme and substitution models from PartitionFinder. We ran 100 independent searches, for the best likelihood tree. To estimate nodal support values, we performed 1000 bootstrap pseudoreplicates, drawing bipartition information on the best likelihood tree. We performed the phylogenetic analysis in CIPRES Science Gateway, version 3.3 (Miller *et al*. 2010).

Results

Phylogenetic relationships

The combined molecular dataset included 95 terminals and 2208 aligned characters (16S: 1486 bp, COI: 722 bp). Maximum likelihood analysis recovered a tree with ln likelihood = -26131.372239 (Fig. 5). The best partition scheme and substitution models were: 16S (GTR+I+G), first codon position of COI (GTR+G), second codon position of COI (GTR+I+G) and third codon position of COI (GTR).

We did not recover the monophyly of the *Boana punctata* species group. *Boana sibleszi* was recovered as the sister taxon of the *Boana benitezi* group, although with no significant support (bootstrap value < 50%). The *B. benitezi* group was recovered as paraphyletic due to the nesting of *B. jimenezi* within it, as the sister taxon of *B. lemai*). *Boana picturata* is the sister of *Boana pellucens* group (bootstrap value < 50%). The *Boana semilineata* group was recovered as the sister group of a clade containing all remaining sampled members of the *Boana punctata* group (*Boana cinerascens*, *Boana punctata*, *B. atlantica* and the clade formed by the specimens morphologically similar to *Hyla granosa gracilis*). Because of weak node supports for some clades, number of molecular markers, and limited taxon sampling in- and outside of *Boana*, we refrain from any discussion of relationships outside the *B. punctata* group, and do not propose any rearrangements regarding the contents of species groups within *Boana.* However, as previously shown by Pinheiro *et al.* (2019), Duellman *et al.* (2016), Pyron & Wiens (2011) and Wiens *et al.* (2010), it seems clear that some rearrangements in the contents of the groups will be necessary in the near future.

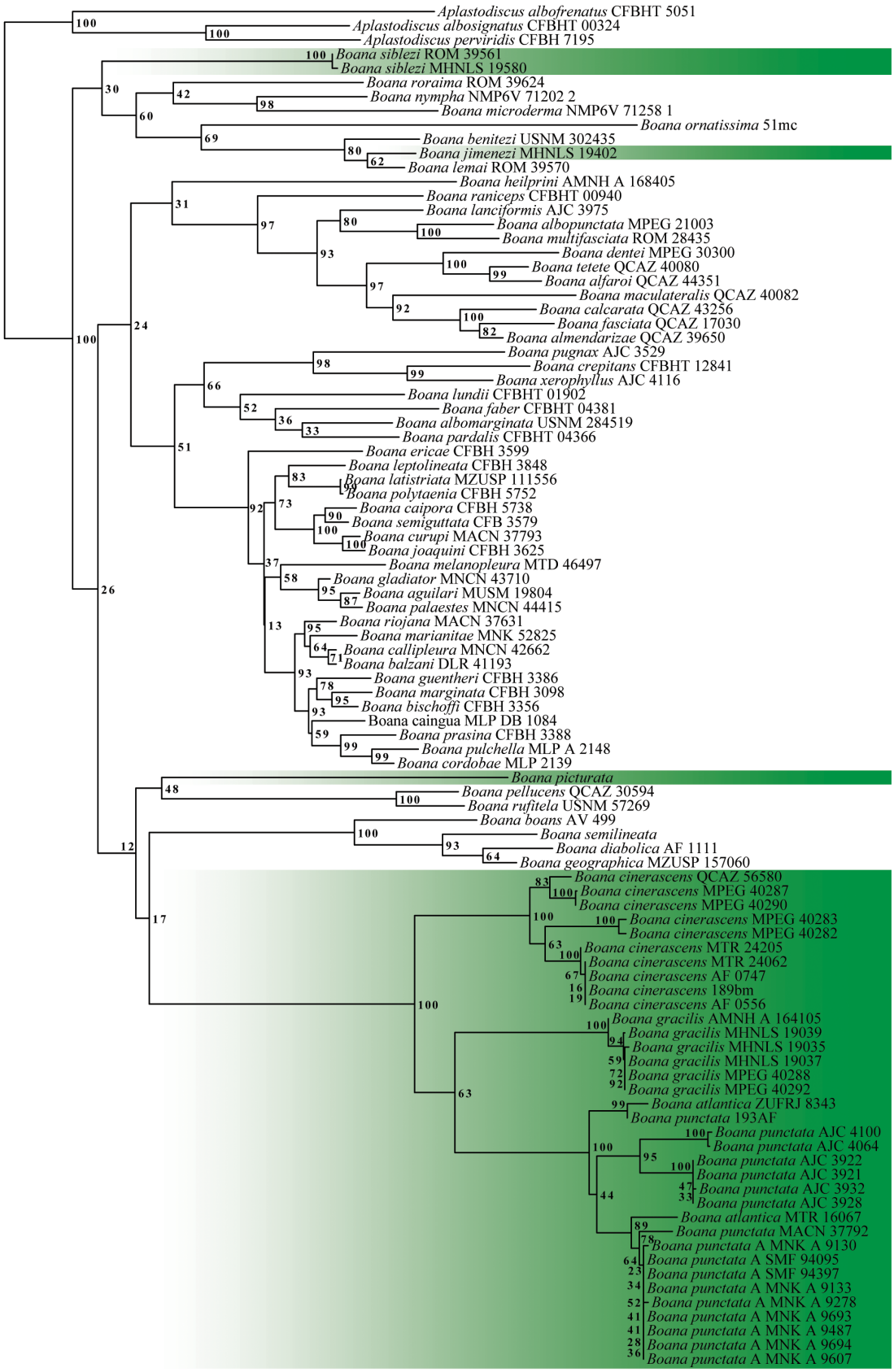

FIGURE 5. Maximum likelihood tree of *Boana*, evidencing paraphyly of the "*Boana punctata* group" (green *Boana*), based on 16S and COI under best partition and substitution models (see text for more details) (ln = -26131.372239). Numbers at nodes = bootstrap proportions. Members of the *Boana punctata* group, as defined by Faivovich *et al.* (2005), are represented by green color.

Boana cinerascens (*sensu stricto*, based on the position of the topotypical material from Tefé, MPEG 40282–40283) is the sister species of a clade containing specimens from Guiana (AMNH), Venezuela (MHNLS) and Brazil (MPEG 40288 and 40293), which resemble *Hyla granosa gracilis*, and another clade formed by *B. atlantica* and *B. punctata*—the latter two species were not recovered as monophyletic (Fig. 5).

Taxonomy

Boana cinerascens Spix, 1824 was described based on specimens from Tefé, and we have collected topotypes to include in our analyses—a neotype is designated below. The integration of the phylogenetic and morphological data (see comparisons section for more details) corroborate our assessment that at least two taxa were collected at PNJ, and that at least some of the specimens represent a taxon distinct from *Boana cinerascens* Spix, 1824. Two names could be applicable to that taxon*:* the older *Hyla granosa* Boulenger, 1882, and the younger *H. granosa gracilis* Melin, 1941.

The examination of the type series of *Hyla granosa* Boulenger, 1882 revealed that at least two taxa are present among the specimens. Boulenger (1882) considered differences in color pattern to be a product of sexual dimorphism (see Fig. 1B and 1C). However, given the results of our phylogenetic analysis, and the examination of a larger series of animals than the one which was available to Boulenger (including both males and females) we conclude that two distinct species were illustrated by Boulenger—BMNH 1947.2.12.99 (Fig. 1B) is most similar to topotypic specimens of *B. cinerascens* whereas BMNH 1947.2.12.97 (Fig. 1C) is similar to *B. gracilis.* This potential taxonomic problem was solved, perhaps unintentionally, by Duellman's (1974) designation of BMNH 1947.2.12.99 as the lectotype of *Hyla granosa* (specimen Canelos, Pastaza, Ecuador). The examination and inclusion in our phylogenetic analysis of a specimen of Canelos (QCAZ 56580) leaves little doubt that the specimen is more closely related to *B. cinerascens* then they are to *B. gracilis* (Fig. 5). Therefore, we concur with previous authors who suggested that *H. granosa* Boulenger, 1882 is a junior synonym of *B. cinerascens* Spix, 1824. On the other hand, the syntypes of *Hyla granosa gracilis* Melin, 1941 are distinct from *B. cinerascens* Spix, 1824 (topotypical material). Given the morphological similarity, and geographical proximity of the PNJ specimens to the type-locality of *H. granosa gracilis*, we hypothesize that these specimens are conspecific. Therefore, the combination *Boana gracilis* (Melin, 1941) is used.

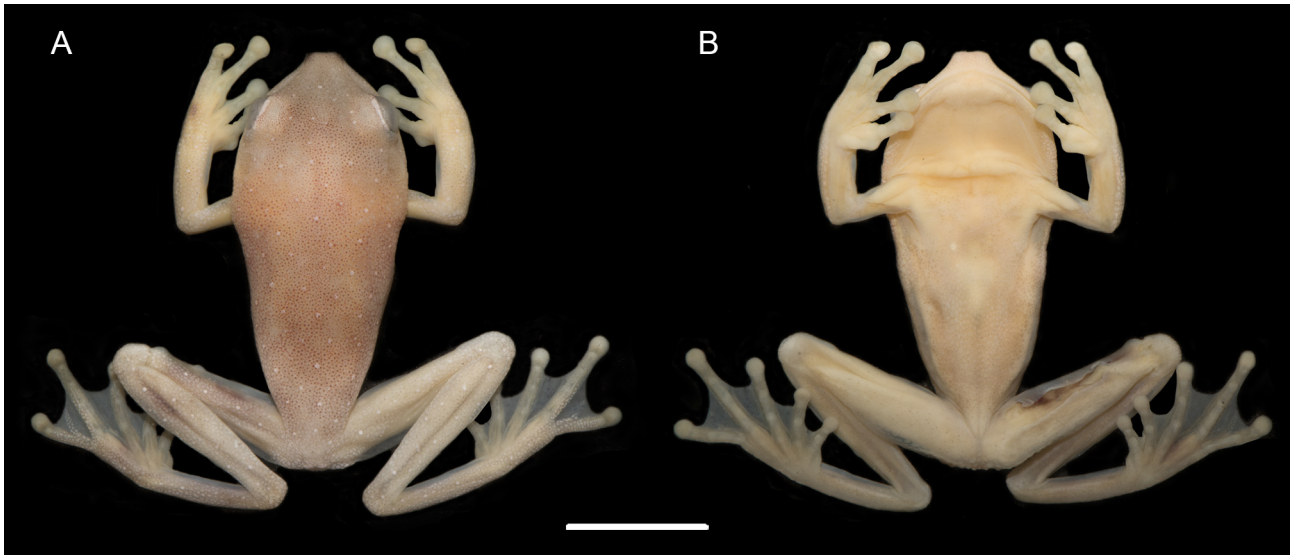

FIGURE 6. Neotype of *Hyla cinerascens* Spix, 1824 (= *Boana cinerascens*) (MPEG 40282). (A) Dorsal and (B) ventral views of male specimen from Tefé, Amazonas, Brazil. Scale bar = 10 mm.

Species accounts

Boana cinerascens **(Spix, 1824)**
(Figs. 3, 6–7)

Hyla cinerascens Spix, 1824: 35 (Syntypes: ZSM 2498/0 [two specimens], type-locality: "Ecgá prope flumen Teffe" (= Tefé, state of Amazonas, Brazil, according to Vanzolini [1981, 1996], both lost, according to Duellman [1977], Hoogmoed & Gruber [1983], and Glaw & Franzen [2006]); Lutz 1951a "1949": 315; Lutz 1951b "1949": 331; Duellman 1977: 26; Barrio-Amorós 2004: 13; Glaw & Franzen 2006: 166.

Hyla granosa Boulenger, 1882: 358 (BMNH 1947.2.12.99 [formerly 80.12.5.181] (type-locality: Ecuador: Canelos), according to Condit [1964], designated lectotype by Duellman [1974: 8], restricting the type-locality to Canelos by lectotype designation); Lutz 1951a "1949": 310; Lutz 1951b "1949": 326; Hoogmoed, 1979: 5 (partly); Hoogmoed & Gruber (1983): 366; Galatti *et al*, 2007: 83.

"Hyla inornata" (*nomen nudum*) Lutz 1951a "1949": 311; Lutz 1951b "1949": 328.

Hypsiboas cinerascens Duellman *et al.,* 2016 (partly).

Boana cinerascens Dubois, 2017: 28.

Neotype (MPEG 40282, field number PLVP 402). An adult male, from Tefé (03°16'47"S and 64°45'09"W), Amazonas, Brazil (Fig. 10), collected by Adriano Oliveira Maciel, Marcelo J. Sturaro and Pedro L.V. Peloso, on January 15, 2017 (Fig. 6–7).

Diagnosis. Based on the molecular phylogenetic analysis, *Boana cinerascens* should be considered a member of the *B. punctata* group. *Boana cinerascens* is defined, morphologically by the following combination of characters: (1) medium sized *Boana* (SVL males 32.3–37.5, mean 34.9 mm, N = 8); (2) snout truncate in both dorsal and lateral views; (3) skin on dorsum granular; (4) forearm moderately hypertrophied; (5) prepollex small and non-protruding as a prepollical spine; (6) mental gland present; (7) in life, dorsum green with small yellow spots and numerous reddish-brown dots (melanophores); (8) in preservative, dorsum cream with numerous white spots, and numerous brown and reddish-brown small dots (melanophores); (9) dorsolateral stripe absent; (10) subgular, single vocal sac.

Description of the neotype. An adult male, SVL 32.3 mm. Head wider than long (HW/HL = 1.18), widest at corner of the mouth; snout truncate in both dorsal and lateral views; interorbital distance more than two and a half times the distance between the nostrils (IOD/IND = 2.57) (Fig. 6A); eye diameter slightly greater than eye-nostril distance (ED/END = 1.05); *canthus rostralis* indistinct, rounded in cross-section; nostrils protuberant, nearly elliptical, directed dorsolaterally; internarial area slightly concave, interorbital area flat, loreal area concave. Eyes large and protuberant, directed laterally, larger than tympanum diameter (ED/TD = 1.77); pupil horizontally elliptical; nictitating membrane transparent without any trace of reticulation, its border with brown spots (Fig. 7A).

Supratympanic fold present; tympanum small (TD/ED = 0.56), round, completely covered by skin but tympanic annulus evident. Vocal sac subgular, single, extending slightly over the forearms. Choanae small, elliptical, not concealed by palatal shelf, larger than vomerine odontophores; a pair of vomerine odontophores present (four vomerine teeth on right side, six on left side); tongue cordiform, nearly one fourth of posterior end free; vocal slits present, extending diagonally from lateral base of tongue (anterior third) almost to angle of jaw.

Arms robust, moderately hypertrophied; axillary membrane absent (Fig. 6B). Lateral margins of arm and forearm with small tubercles, but not forming a fringe; finger tips round; finger disks present on all fingers, disk on FI smallest; relative lengths of fingers I < II < IV < III; subarticular tubercles round, narrower than finger width; subarticular tubercles on FI and FIV of nearly the same size, larger than those of FII and FIII; supernumerary tubercles present; inner metacarpal tubercle flat, elliptical; prepollex small with prepollical spine not protruding out of skin; outer metacarpal tubercle small, heart shaped. Hand webbing between FI and FII absent, present but not extensive between FII–FIII and FIII–FIV. Webbing formula I–II2^{-}–3^{-}III 2½–2^{+}IV on both sides. Details of hand shown in Figure 7B.

Legs long and slender, lacking appendages (e.g. fringes, folds, or tubercles). Ankle without appendices or tubercles. All toes well developed, disks present on all toes, disks on TI and TII smallest; relative lengths of toes I < II < V < III < IV. Subarticular tubercles round; inner metatarsal tubercle flat, slightly elliptical; outer metatarsal tubercle hardly visible, elliptical. Webbing formula: I 2^{-}–2^{+}II1^{+}–2½III1^{+}–3^{-}IV2^{+}–1V on left foot and I2^{-}–2^{+}II1^{-}–2½III1^{+}–3^{-}IV2^{+}–1^{+}V on right foot. Details of foot shown in Figure 7C. Skin on dorsum, head, dorsal surfaces of limbs, flanks, and groin granular; skin on chest, belly and undersurfaces of thigh areolate; oval mental gland; skin on

vocal sac granular; skin on ventral parts of fore limb and tibia smooth. Cloacal opening directed posteriorly; cloacal region with tubercles.

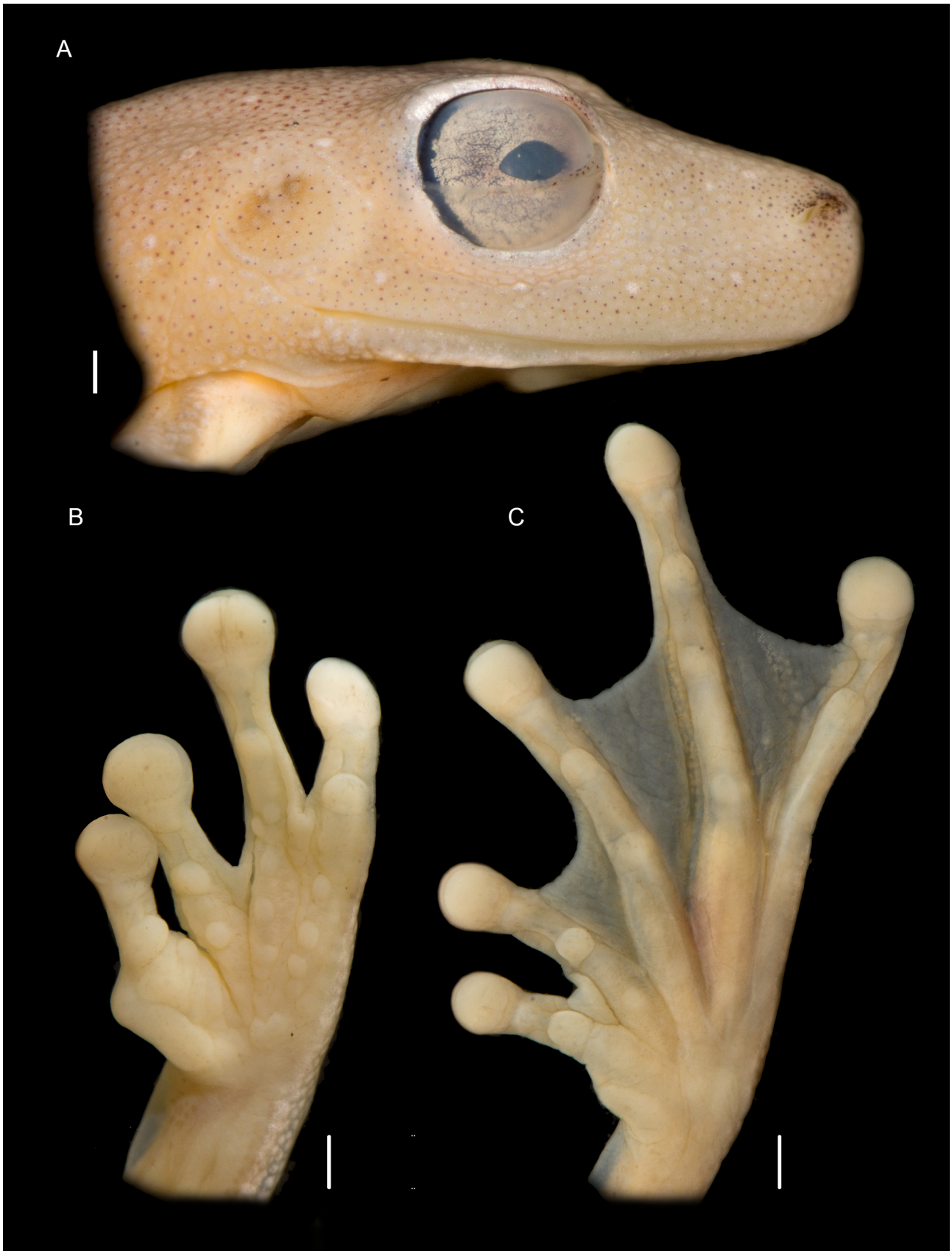

FIGURE 7. Neotype of *Hyla cinerascens* Spix, 1824 (= *Boana cinerascens*) (MPEG 40282). (A) Lateral view of head, (B) palm of hand, and (C) palm of foot of male specimen, from Tefé, Amazonas, Brazil. Scale bar = 1 mm.

Measurements of the neotype (in mm): SVL = 32.3; HL = 11.3; HW = 13.3; ED = 3.9; ELW = 2.4; IOD = 7.2; IND = 2.8; END = 3.7; THL = 18.6; TBL = 16.8; FL = 23.0; TD = 2.2.

Color in preservative. Dorsum cream with white spots, and brown and reddish-brown small melanophores (Fig. 6A). Flanks predominantly cream with brown and reddish-brown melanophores on upper region. Inguinal region, anterior, and posterior region of thighs cream. Thigh dorsally cream with white spots and brown and reddish-brown small melanophores; anteriorly and posteriorly cream. Upper arms, forearms, and tibiae dorsally cream with white spots and brown and reddish-brown small melanophores. Gular region cream with light-brown melanophores. Chest and belly translucent cream, with light-brown melanophores and white visceral peritonea covering the organs visible. Ventral surface of forearms and hindlimbs cream with light brown spots. Ventral surface of hands and feet cream (Fig. 6B).

Color in life. Dorsum yellowish green with light yellow spots and brown and reddish-brown small melanophores. Flanks predominantly yellow with brown and light yellow blotches and reddish-brown melanophores on upper region. Inguinal region, anterior and posterior region of the thighs light lemon green. Dorsal surface of thighs, forearms, and tibiae same as dorsum (Fig. 3). Gular region, chest and belly translucent light lemon green.

Advertisement call. Calls from one adult male (MPEG 40290) from PNJ, Novo Airão, Amazonas, Brazil (02°18'04"S, 62°28'07"W) and one adult male (MPEG 40282, neotype) from Tefé, Amazonas, Brazil (Fig. 8). Specimens were calling perched 3 m above the ground near the edge of the river. The call of the PNJ specimens consists of one to two notes (mean duration of 0.034 s, SD=0.0016) separated by short intervals (mean inter-note interval = 0.11 s). The advertisement call has a mean duration of 0.19 s (SD = 0.05) with an average dominant frequency of 1814 Hz (SD = 96.99), mean rise time of 0.095 s (SD = 0.026), and mean frequency bandwidth of 1616.96 Hz (SD = 17.25) (Fig. 8). The call from Tefé consists of two to three notes (mean duration of 0.037 s, SD = 0.0019) separated by short intervals (mean inter-note interval = 0.12 s). The advertisement call has a mean duration of 0.26 s (SD = 0.080) with an average dominant frequency of 1874 Hz (SD = 127.31), mean rise time of 0.13 s (SD = 0.041), and mean frequency bandwidth of 1762 Hz (SD = 17.09).

TABLE 1. Summary of acoustic parameters for vocalizations of adult males of the *Boana punctata* group.

Species	Dominant frequency (Hz)	Call duration (s)	Number of notes	Note duration (s)	Additional information	References
Boana atlantica	840–1280	0.19–0.44	4−8	0.012–0.022	Advertisement and courtship calls[a]	Napoli & Cruz (2005)
Boana cinerascens (Tefé)	1874	0.26	2–3	0.037	-	This study
Boana cinerascens (Jaú)	1814	0.19	1–2	0.034	-	This study
Boana hobbsi	2240–2260	–	One	0.24-0.31	Consists of a tonal note followed by trills	Simões *et al.* (2019)
Boana jimenezi	3010–3488	0.158–-0.197	Three	0.0098–0.026	Call can also have four notes[b]	Señaris & Ayarzaguëna (2006)
Boana punctata	Variable	0.17–0.52	3–8	0.018–0.025	Short and long advertisement calls; Territorial call; Courtship call; Aggressive call; Fighting call; Release call[c]	Brunetti *et al.* (2015)
Boana sibleszi	1680–2231	0.42–0.6	1	0.42–0.6	Occasionally two notes	Señaris & Ayarzaguëna (2006)

[a]Data only for advertisement call presented
[b]Data only for the three-note call presented
[c]Data only for short advertisement call presented

According to Hoogmoed (1979), Crawford & Jones (1933), firstly described the call of *Hyla granosa* as a medium-pitched "pink", however for him this call was more similar to that of *H. punctata* and for him, specimens of both species were confused. He provided sonograms of calls of both species from Suriname, without comments on temporal or spectral parameters. Later, the advertisement call of *Hyla granosa* was described by Duellman (1978) as a two- to four-note call, usually: "boop-boop-boop". The duration of the notes was 0.078 seconds and the average dominant frequency was 1390 Hz. Subsequently, De la Riva et al. (1997) described the call as a series of two to seven short notes that decrease in intensity, with one average dominant frequency of 1327 Hz. Calls from studies in Ecuador (Pareja *et al*., unpublished) show values close to those found by Duellman and De la Riva *et al*.; the dominant frequency varies between 1560.41 Hz up to 1839.50 Hz. *Boana cinerascens* from the Guyanes has a call of 1–2 notes with a dominant frequency between 1260–2500 Hz (Lescure and Marty, 2000). The call of *Boana cinerascens* differs from the other advertisement calls of the group: *Boana jimenezi*´s advertisement call is composed of 3–4 notes with a dominant frequency at 3010–3488 Hz., and *Boana punctata* calls with 5–15 notes and a dominant frequency between 689–1540 Hz (Hödl, 1977; Lescure and Marty, 2000; Marquez et al., 1993; Señaris and Ayarzaguëna, unpublished data). Finally, the mating call of *Boana sibleszi* usually consists of one note, occasionally two, with the dominant frequency at 1680–2231 Hz. Information regarding the advertisement calls of the *Boana punctata* group are summarized in Table 1.

Distribution. *Boana cineracens* is known with certainty from the type locality Tefé, Amazonas, Brazil; Parque Nacional do Jaú, Novo Airão, Amazonas, Brazil; and Canelos, Ecuador (Fig. 10). This species occurs syntopically with *B. gracils* and may occur more widely.

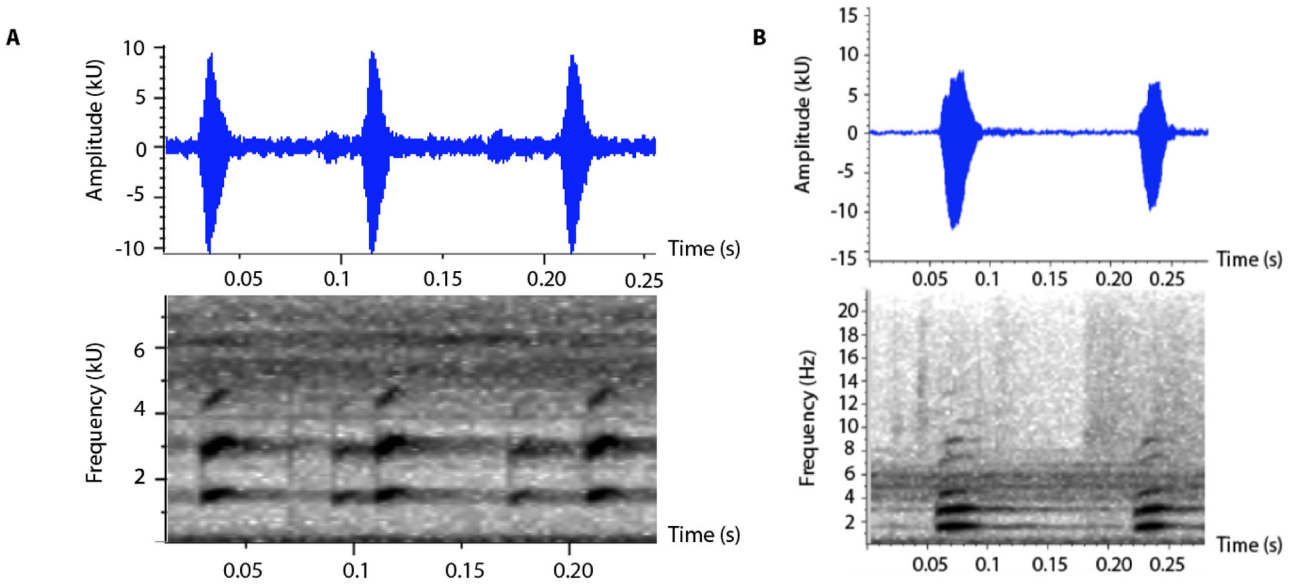

FIGURE 8. Advertisement calls of *Boana cinerascens*— oscillogram (above) and spectrograms (below). (A) Tefé, Amazonas, Brazil (MPEG 40282, neotype). (B) Parque Nacional do Jaú, Novo Airão, Amazonas, Brazil (MPEG 40290).

Boana gracilis **(Melin, 1941), revalidated, new combination**
(Figs. 2, 4, 9)

Hyla granosa gracilis Melin 1941: 21; Lutz 1951 a [1949]: [map].
Hyla granosa Rivero 1961: 100; Rivero 1972: 182; Duellman 1974: 8; Hoogmoed 1979: 5 (partly, material from Canaripó); Galatti *et al.,* 2007 (only Fig. 5 which shows a specimen from PNJ).
Hyla punctata Cochran & Goin 1970: 224.
Hypsiboas granosa Faivovich *et al*., 2005: 85.
Hypsiboas cinerascens Frost *et al*., 2006: 65; Pyron & Wiens 2011: 570; Faivovich *et al.,* 2013: 50; Duellman *et al.,* 2016 (partly); Pinheiro *et al.,* 2019
Boana cinerascens Frost, 2019: [website].

Diagnosis. Based on the molecular phylogenetic analysis, *Boana gracilis* should be considered a member of the

B. punctata group. *Boana gracilis* is diagnosed morphologically by the following combination of characters: (1) medium sized *Boana* (SVL males 33.7–37.2, mean 35.9 mm, N = 26); (2) snout truncate in both dorsal and lateral views; (3) skin on dorsum granular; (4) forearm slightly hypertrophied; (5) prepollex small prepollical spine not protruding out of skin; (6) mental gland present; (7) number of vomerine teeth up to 10; (8) lacking small tubercles on postaxial side forearm and supernumerary tubercles on hand; (9) round subarticular tubercles on fingers I and IV , by not having supernumerary tubercles on hands; (10) in life, dorsum predominantly yellowish-green with large yellow blotches, scattered reddish-brown dots (melanophores) and reddish-brown irregular blotches within the white blotches (most of the examined specimens), a reddish-brown transversal interorbital bar (expanded on eyelid); (11) in preservative, dorsum cream with large white blotches and scattered brown small melanophores, and brown irregular blotches within the white blotches (most of the examined specimens); a brown transversal interorbital bar (expanded on eyelid); (12) dorsolateral stripe absent; (13) subgular, single vocal sac.

Comparisons with congeners in the *Boana punctata* group. Because of the phylogenetic position of this taxon, we limit the comparisons to species in the *B. punctata* group. We made the comparisons by direct examination of preserved specimens, photographs (especially for color in life) and/or the literature. Character states for the species under comparison are given in parentheses. *Boana gracilis* differs from *B. alemani* in dorsal color pattern (in preservative: cream with dark spots; color in life unknown) and its larger size (SVL 30.5 mm). *Boana gracilis* differs from *B. atlantica* in dorsal color pattern (in preservative: white with yellow dorsolateral stripes and sparse spots; in life: green with reddish brown dorsolateral stripes and sparse spots) and its smaller size (male SVL > 37 mm) (examined specimens and Caramaschi & Velosa 1996; Haddad *et al.* 2013). *Boana gracilis* differs from *B. cinerascens* by its higher number of vomerine teeth (up to 10 *vs*. up to six in *B. cinerascens*), by lacking small tubercles on postaxial side forearm (present), and supernumerary tubercles on hand (present), dorsal color pattern (in preservative: cream with scattered, very small, white spots; in life: green, with sparse small white spots). *Boana gracilis* differs from *B. hobbsi* in dorsal color pattern (cream with few and sparse dark brown spots and two dorsolateral dark brown stripes) and its small size (holotype *B. hobbsi* SVL = 42.5 mm) (examined specimen, and Cochran & Goin 1970). It differs from *B. picturata* (Boulenger, 1899) in dorsal color pattern (in preservative: cream with reticulate violet blotches margined by purplish red) and much smaller size (SVL > 47mm in all examined specimens). *Boana gracilis* differs from *B. punctata* in dorsal color pattern (in preservative: cream with sparse white spots and, in most individuals, dorsal lateral white and red stripes) (examined specimens and photo of the holotype provided in Milto & Barabanov 2011). It differs from *B. sibleszi* in dorsal color pattern (sexual dimorphism [Hoogmoed, 1979], in life: green speckled by white or brown, with or without yellow dorsolateral stripes; in preservative: cream speckled by brown and a transversal brown bar between eyes), mental gland (absent) (Cole *et al.* 2013; Hoogmoed, 1979; Kok & Kalamandeen 2008; Rivero 1972). *Boana gracilis* and *B. sibleszi* are not sister species in our phylogeny (Fig. 5). *Boana gracilis* differs from *B. jimenezi* by the shape of the subarticular tubercles on fingers I and IV (bifid), by not having supernumerary tubercles on hands (present), by the presence of a mental gland (absent) and dorsal color pattern (in life: pale green with numerous small tan or reddish-brown chromatophores, with or without dorsolateral white stripes; in preservative: cream with numerous small chromatophores, with or without immaculate white dorsolateral stripes) (Señaris & Ayarzagüena 2006).

Description. SVL adult males 32.7–37.2 mm (35.4 ± 1.4; N = 22) and SVL adult females 28.1–33.2 mm (30.4 ± 2.1; N = 4). Head as wide as long (HW/HL = 0.88–1.13, 1.04 ± 0.05; N = 26), widest at corner of the mouth; snout truncate in both dorsal and lateral views; interorbital distance more than two and a half times the distance between the nostrils (IOD/IND = 2.44–3.72, 2.84 ± 0.33; N = 26); eye diameter slightly smaller than eye–nostril distance (ED/END 0.80–1.17, 0.99 ± 0.09; N = 26); *canthus rostralis* indistinct; nostrils protuberant, nearly elliptical, directed dorsolaterally; internarial area slightly concave, interorbital area flat, loreal area concave. Eyes large and protuberant, directed laterally, larger than tympanum diameter (ED/TD 1.52–2.31, 1.76 ± 0.18; N = 26); pupil horizontally elliptical; nictitating membrane transparent without any trace of reticulation, its border with brown spots.

Supratympanic fold barely evident; tympanum small (TD/ED 0.43–0.66, 0.58 ± 0.05; N = 26), round, completely covered by skin with tympanic annulus barely evident. Vocal sac subgular, single, extending slightly over the forearms. Choanae small, elliptical, not concealed by palatal shelf, larger than vomerine odontophores; a pair of vomerine odontophores present with 4–10 (7.5 ± 1.5; N = 17) vomerine teeth on right side; tongue cordiform, nearly one fourth of posterior end free; vocal slits present, extending diagonally from lateral base of tongue (anterior third) almost to angle of jaw.

Arms slender, only slightly hypertrophied; axillary membrane absent. Lateral margins of upper arm and fore-

arm without tubercles or fringes; finger tips round; finger disks present on all fingers, disk on FI smallest; relative lengths of fingers: I < II < IV < III; subarticular tubercles round, narrower than finger width; subarticular tubercles on FIV larger than those of FI–III; supernumerary tubercles absent; inner metacarpal tubercle flat, elliptical, outer metacarpal tubercle absent; prepollex small prepollical spine not protruding out of skin; outer metacarpal tubercle small, almost round, barely distinguishable. Webbing between FI and FII absent, present but not extensive between FII–FIII and FIII–FIV. Variation in finger webbing: **II**(2^{-}–2)–(2½–3^{+})**III**(2^{+}–2½)–(2–2^{+})**IV**.

Legs long and slender, lacking appendages (e.g., fringes, folds, or tubercles). Ankle without appendices or tubercles. All toes well developed, disks present on all toes, disk on TI and TII smallest; relative lengths of toes: I < II < V < III < IV. Subarticular tubercles round, single; inner metatarsal tubercle flat, slightly elliptical; outer metatarsal tubercle hardly visible. Variation in foot webbing formula : **I**2^{-}–(2–2^{+})**II**(1–1^{+})–(2–2^{+})III(1–1^{+})–(2–2^{+})**IV**(2–2^{+})–(1–1^{+})**V**. Skin on dorsum, head, dorsal surfaces of limbs, flanks and groin granular; skin on chest, belly and undersurfaces of thigh areolate; oval mental gland; skin on vocal sac granular; skin on ventral parts of fore limbs and tibiae smooth. Cloacal opening directed posteriorly; cloacal region with tubercles.

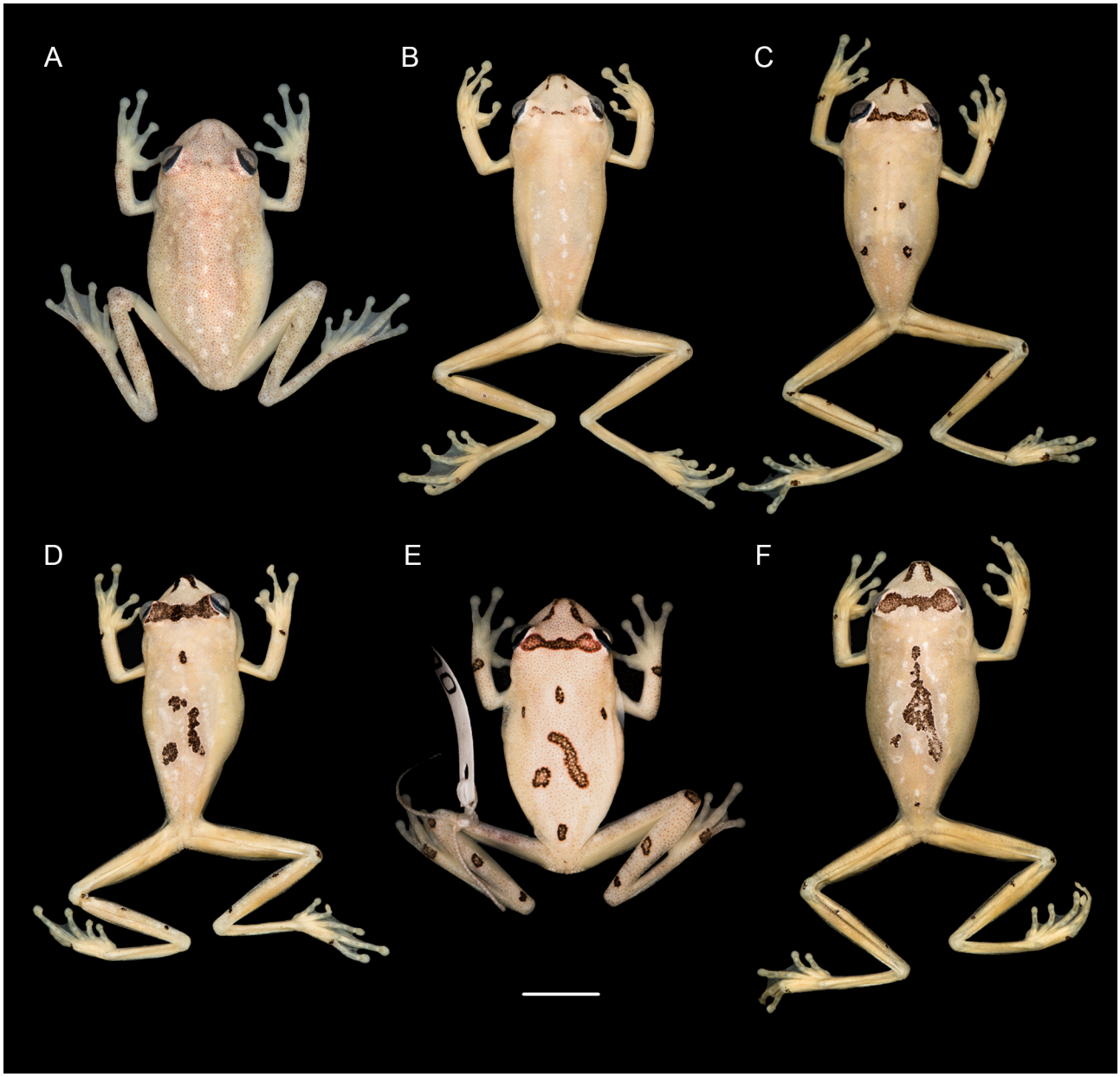

FIGURE 9. Dorsal color pattern variation in *Boana gracilis.* (A) MPEG 40292, from Parque Nacional do Jaú, Novo Airão, Amazonas, Brazil; (B) MPEG 41573, (C) MPEG 41571, (D) MPEG 41568, from Parque Nacional de Anavilhanas, Novo Airão, Amazonas, Brazil; (E) MPEG 40288, from Parque Nacional do Jaú, Novo Airão, Amazonas, Brazil; (F) MPEG 41567, from Parque Nacional de Anavilhanas, Novo Airão, Amazonas, Brazil.

Color in preservative **(Fig. 9).** Dorsum cream with large white blotches, with brown and reddish-brown small melanophores. Many individuals with a brown transverse interorbital bar (expanded on eyelid). Dorsum may have large brown spots. Flanks predominantly cream with brown and reddish-brown melanophores on upper region. Inguinal region, anterior and posterior region of the thighs cream. Thigh dorsally cream with white blotches and brown and reddish-brown small melanophores; anteriorly and posteriorly cream. Upper arms, forearms, and tibiae dorsally cream with white blotches and brown and reddish-brown small melanophores—commonly showing a higher concentration of melanophores forming spots and stains. Gular region cream with light-brown melanophores. Chest and belly translucent cream, with light-brown melanophores, and white visceral peritonea covering the organs visible. Ventral surface of forearms and hindlimbs cream with light brown spots. Ventral surface of hands and feet cream.

Color in life **(Fig. 4).** Dorsum yellowish green with light yellow blotches, with or without concentrations of brown and reddish-brown small melanophores (Fig. 4); region between eyes with brown blotches. Flanks predominantly yellow; light yellow blotches and reddish-brown melanophores on upper region. Inguinal region, anterior and posterior region of the thighs light lemon green. Dorsal surface of thighs, forearms and tibiae as same as dorsum (Fig. 4). Gular region, chest and belly translucent light lemon green.

Distribution. *Boana gracilis* is known with certainty from the type locality "Rio Uaupes (north of Ipanoré), Brazil; the Municipality of Novo Airão (Parque Nacional do Jaú, and Parque Nacional de Anavilhanas), State of Amazonas, Brazil; Canaripó, Venezuela (Hoogmoed 1979), San José de Chipiro, boca del río Ventuari, Venezuela, Macuruco, confluencia Orinoco-Ventuari, Venezuela; and from Iwokrama, Guyana (Fig. 10). This species occurs syntopically with *B. cinerascens* and may occur more widely.

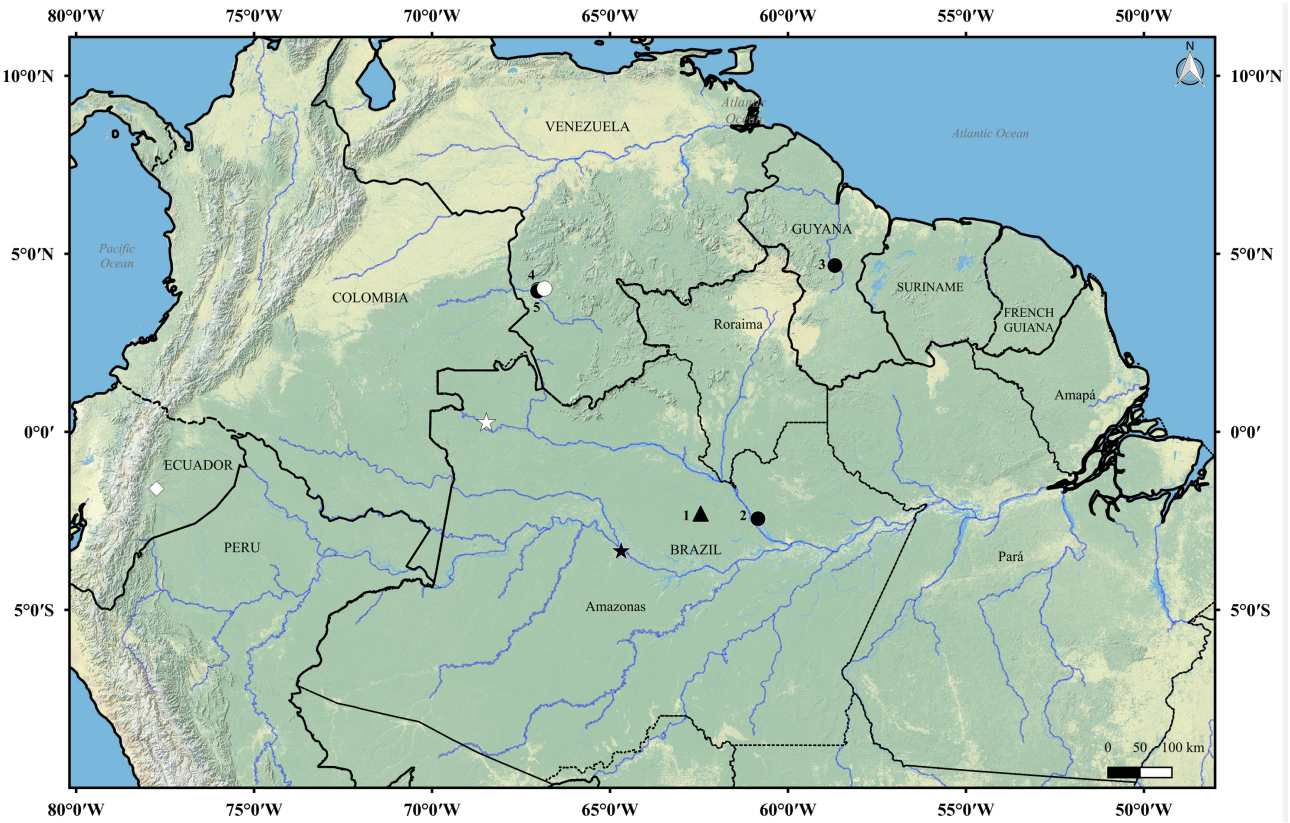

FIGURE 10. Geographic distribution of *Boana cinerascens* and *Boana gracilis* based on the localities of type specimens and samples included in our analyses. Black-star = Tefé, Amazonas, Brazil (type-locality of *Boana cinerascens*). White-star = Rio Uaupés (north of Ipanoré), Amazonas, Brazil (type-locality of *Boana gracilis*). White-rhombus = Canelos, Ecuador (type-locality of *Hyla granosa*). Circles = *Boana gracilis*. Triangle = both species. 1 = Parque Nacional do Jaú, Novo Airão, Amazonas, Brazil. 2 = Parque Nacional de Anavilhanas, Novo Airão, Amazonas, Brazil. 3 = Muri, Scrub Camp, Iwokrama, Guyana. 4 = San José de Chipiro, Boca del río Ventuari, Alto Orinoco, Amazonas, Venezuela. 5 = Macuruco, confluencia Orinoco-Ventuari, Alto Orinoco, Amazonas, Venezuela. White-ball = Canaripó, río Ventuari, Amazonas, Venezuela.

Discussion

Our results corroborate that the *Boana punctata* species group, as currently defined, is not monophyletic (see also Duellman *et al.* 2016; Pyron & Wiens 2011; Wiens *et al.* 2010; Faivovich *et al.* 2013; Pinheiro *et al.* 2019). However, new studies with more complete sampling of species and characters (e.g., molecular, morphological, and acoustical data) will be necessary to clarify the relationships within *Boana* and the composition of most species groups.

Boana cinerascens and *B. gracilis* are sympatric at Parque Nacional do Jaú, Brazil, and at Iwokrama, Guyana—both species are apparently widely distributed in Amazonia. This suggests the necessity of a broader and more inclusive study in order to establish more precisely the geographical range of both species.

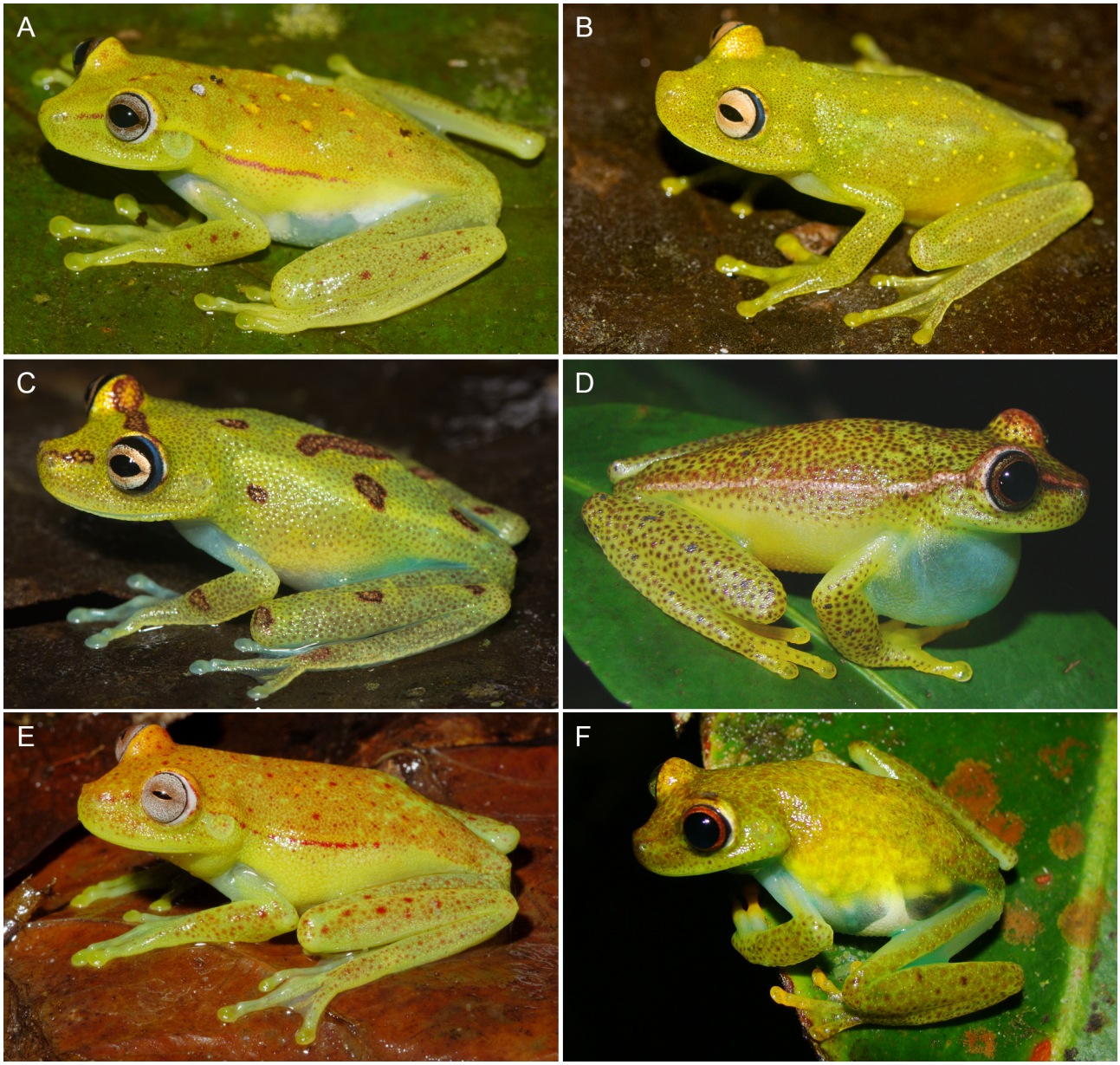

FIGURE 11. Some representatives of the paraphyletic *Boana punctata* species group. (A) *B. atlantica*, CFBH 27814, from Camamu, Bahia, Brazil, photo by PLVP; (B) *B. cinerascens*, MPEG 40287, from Parque Nacional do Jaú, Amazonas, Brazil, photo PLVP; (C) *B.* gracilis, MPEG 40288 from Parque Nacional do Jaú, Amazonas, Brazil, photo PLVP; (D) *B. jimenezi*, MHNLS 19400, from Parque Nacional Canaima, Gran Sabana, Bolívar, Venezuela, photo FJMR-R; (E); *B. punctata* from Aruaguatins, Tocantins, Brazil, photo PLVP; (F) *B. sibleszi*, MHNLS 19536, from Parque Nacional Canaima, Gran Sabana, Bolívar, Venezuela, photo FJMR-R.

Integrative approaches (e.g., combining morphological, bioacustical and molecular evidences) have been useful to understand and delimit the species boundaries in Amazonian amphibians. Such an integrative approach is especially valuable for groups for which many species may have superficially similar external morphologies (Padial *et al.* 2010; Peloso *et al.* 2014). This is the case for most species in the *Boana punctata* group, which are green with a variable degree of dorsal ornamentation (Fig. 11). The present work is a first step towards a better understanding of the species diversity and limits of green treefrogs in Amazonia. By designating a neotype for *B. cinerascens* and clarifying the status of its known synonyms, we open a venue for a more inclusive taxon and geographical sampling, which should help detect additional taxa currently hidden under the name *B. cinerascens*. *Boana atlantica* and *B. punctata*, two morphologically very similar species were recovered in our phylogenetic analysis as non-reciprocally monophyletic but forming a clade with genetic structure, suggesting the occurrence of a species complex composed by several cryptic species. A careful review of voucher specimens and comparisons of advertisement calls of these two species is required in order to clarify their taxonomic status (see also Napoli & Cruz 2005). In any case, the situation is no less complicated than that involving *B. cinerascens* because there are plenty of synonyms of *B. punctata*, some of which do not have extant type specimens (Frost 2018; Hoogmoed & Gruber 1983).

Recently, the taxonomy of other *Boana* groups was revised using integrative approaches, resulting in a large number of new or candidate species and/or revalidations (Caminer & Ron 2014; Fouquet *et al.* 2016; Orrico *et al.* 2017; Peloso et al., 2018). In most cases, including the one we presented involving *B. cinerascens* and *B. gracilis*, the collection of new material, which enabled the incorporation of DNA sequence evidence, was crucial to resolve long-standing taxonomic problems. This demonstrates the importance to keep exploring new sites and older ones, especially in Amazonia, where the species diversity is still underestimated (Angulo & Icochea 2010; Ferreira *et al.* 2017; Peloso *et al.* 2010). The necessity to conduct expeditions to the type localities of lost/unknown types is needed to facilitate future taxonomic work. In many cases, topotypic samples are small (or inexistent in case of lost types), and very often there is no genetic and acoustic data associated to these populations. The importance of fresh topotypic material is shown by the present study, and by the recent collection of topotypes of *Hyla geographica* Spix, 1824, which allowed the recognition of several unnamed candidate species previously hidden under that name (Fouquet *et al.* 2016; Peloso *et al.* 2018).

Although the taxonomic studies have been losing space and prestige to more "impressive, attention grabbing" studies, it should be obvious that taxonomy is still one of the most important, basic areas in biology (Padial & De la Riva 2007). The true species diversity in the Neotropics is still unknown, but large natural areas are destroyed every year—vanishing before they can be properly inventoried. Without the proper incentives for continuous studies in taxonomy (biological inventories and systematic reviews) we will never be able to understand the true diversity existing in Amazonia, and we can only effectively preserve what we know.

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APPENDIX 1. Specimens examined

Boana alemani (N = 1) **VENEZUELA:** Cagua, Edo. Aragua (MHNLS 238, holotype).

Boana atlantica (N = 2). **BRAZIL: Bahia:** Camamu: Brejo, Zumbi dos Palmares (CFBH 27814, CFBH 27820).

Boana cinerascens (N = 9). **BRAZIL: Amazonas:** Tefé (MPEG 40282–40286); Novo Airão, Parque Nacional do Jaú (MPEG 40287, MPEG 40290–40291). **ECUADOR: Pastaza:** Canelos, Quebrada Pupalyacu (QCAZ-A 56580).

Boana gracilis (N = 26). **BRAZIL: Amazonas:** Novo Airão, Parque Nacional do Jaú (MPEG 40288, MPEG 40292), Parque Nacional de Anavilhanas (MPEG 41564–41574); Rio Uaupés (north of Ipanoré) (NHMG 467, syntypes, examined from photographs). **GUYANA: Iwokrama:** Muri, Scrub Camp (AMNH 164104–164108). **VENEZUELA: Amazonas:** Atabato, San José de Chipiro, boca del rio Ventiaru, Alto Rio (MHNLS 19035–19039); Caño detrás de Macuruco, confluencia Orinoco-Ventuari (MHNLS 20789–20791).

Boana hobbsi (N = 1). **COLOMBIA: Amazonas:** Cano Guacaya, a tributary of the Rio Apaporis (MCZ 28052, holotype, examined from photographs).

Boana jimenezi (N = 1). **VENEZUELA: Bolívar:** Gran Sabana, P.N. Canaima, Campamento Guayacara, sabana de Guayaraca (MNHLS 19400).

Boana picturata (N = 10): **COLOMBIA: Cauca:** Quebrada Guanguí, 0.5km above Rio Patia (AMNH 88936–88943); **Nariño:** Guayacana (AMNH 87921).

Boana punctata (N = 13). **BRAZIL: Acre:** Feijó (MPEG 36525), Xapuri (36510–36511). **Amazonas:** Lago Amanã (MPEG 17648–17651). **Pará:** Afuá, Ilha de Marajó, Rio Preto (MPEG 37618–37619), Monte Alegre (MPEG 20129–20130), São Geraldo do Araguaia, Parque Serra das Andorinhas (MPEG 36342–36343).

Boana ornatissima (N = 3). **BRAZIL: Amapá:** Mazagão: Cachoeira Itaboca, Rio Camaipi, tributary of Rio Maracá (MPEG 809). GUYANA (originally given as British Guiana): Meamu, Mazaruni River (AMNH-A 164105, holotype). **SURINAM: Marowijne:** Loe Creek, Camp Hofwijks VII (AMNH 90790)

Boana sibleszi (N = 2). **VENEZUELA: Bolívar:** Sierra de Lema, Troncal 10, a 6 km de la alcabala (MHNLS 19580). Gran Sabana, P.N. Canaima, Chivatón (MHNLS 19536).

APPENDIX II

Specimens included in the phylogenetic analysis of green *Boana*. The list includes collection numbers or field series numbers (when available) associated with the specimens, locality data and reference from previous studies (for sequences retrieved from Genbank).

Species	Voucher/Field Number	16S	COI	Locality	References
Aplastodiscus albofrenatus	CFBHT 5051	KU184021	KU184058	Brazil: Rio de Janeiro, Rio de Janeiro, Tijuca	Berneck ***et al.*** (2016)
Aplastodiscus albosignatus	CFBHT 00324	KU495134	KU494341	Brazil: São Paulo, São Luis do Paraitinga	Lyra ***et al.*** (2017)
Aplastodiscus perviridis	CFBH 7195	KU184016	KU184049	Brazil: Sao Paulo, Santo Antonio do Pinhal	Berneck ***et al.*** (2016)
Boana aguilari	MUSM 19804	HM444783	–	Peru: Junin, Pampa Hermosa	Lehr ***et al.*** (2010)
Boana albomarginata	USNM 284519	AY549316	–	Brazil: Pernambuco, Near Caraurucu, on way to Serra dos Cavalos	Faivovich ***et al.*** (2004)
Boana albopunctata	MPEG 21003	MN781650	MN781637	Brazil: Mato Grosso: Querência, Fazenda Tanguro	This study
Boana alfaroi	QCAZ 44351	JN970549	JN970682	Ecuador: Provincia Orellana: Río Napo, Chiroisla	Funk ***et al.*** (2011)
Boana almendarizae	QCAZ 39650	JN970530	JN970665	Ecuador: Provincia Morona Santiago: General Leonidas Plaza, "Limón", on the road to Gualaceo	Caminer & Ron (2014)
Boana atlantica	MTR 16067	MN781651	MN781638	Brazil: Bahia: Camacan, Serra Bonita	This study
Boana atlantica	ZUFRJ 8343/ ACC 0216	MN781652	MN781639	Brazil: Alagoas: São Jose da Laje, Usina Serra Grande	This study
Boana balzani	DLR 41193	AY549323	–	Bolivia: Departamento. La Paz, Prov. Noryungas, Serrania Bellavista	Faivovich ***et al.*** (2004)
Boana benitezi	USNM 302435	AY843606	–	Venezuela: Brazil, Roraima, Villa Pacaraima, border marker BV (Brazil) 8	Faivovich ***et al.*** (2005)
Boana bischoffi	CFBH 3356	AY549324	–	Brazil: Santa Catarina, Rancho Queimado	Faivovich ***et al.*** (2004)
Boana boans	AV 499	KT717077	KT717080	Venezuela: Cachiri stream, road Purumay-Vena fall	Unpublished data from GenBank
Boana caingua	MLP-DB 1084	AY549326	–	Argentina: Misiones, Posadas	Faivovich ***et al.*** (2004)
Boana caipora	CFBH 5738	EU077268	–	Brazil: Sao Paulo, Serra do Mar, Serra de Paranapiacaba, Municipio de Pilar do Sul	Antunes ***et al.*** (2008)
Boana calcarata	QCAZ 43256	JN970580	JN970713	Ecuador: Provincia Orellana: Estación Científica Yasuní, Universidad Católica del Ecuador	Funk ***et al.*** (2011)

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APPENDIX II (Continued)

Species	Voucher/Field Number	16S	COI	Locality	References
Boana callipleura	MNCN 42662	HM480426	–	Bolivia: Cochabamba: between Los Guácharos and El Palmar	Köhler ***et al.*** (2010)
Boana cinerascens	189bm	EU201113	–	French Guiana: Trinité	Fouquet ***et al.*** (2007)
Boana cinerascens	AF 0556	KR811175	–	French Guiana: Savane Virginie	Fouquet ***et al.*** (2015)
Boana cinerascens	AF 0747	KR811174	–	French Guiana: Saint Georges	Fouquet ***et al.*** (2015)
Boana cinerascens	MPEG 40282	MN781653	MN781640	Brazil: Amazonas: Tefé (neotype)	This study
Boana cinerascens	MPEG 40283	MN781654	MN781641	Brazil: Amazonas: Tefé	This study
Boana cinerascens	MPEG 40287	MN781655	MN781642	Brazil: Amazonas: Nova Airão: Parque Nacional do Jaú	This study
Boana cinerascens	MPEG 40290	MN781656	MN781643	Brazil: Amazonas: Nova Airão: Parque Nacional do Jaú	This study
Boana cinerascens	MTR 24062	KR811173	–	Brazil: Amapá: Oiapoque	Fouquet ***et al.*** (2015)
Boana cinerascens	MTR 24205	KR811176	–	Brazil: Amapá: Lourenço	Fouquet ***et al.*** (2015)
Boana cinerascens	QCAZ-A 56580	-		Ecuador: Pastaza: Canelos, quebrada Pupalyacu	This study
Boana cordobae	MLP 2139	AY549329	–	Argentina: Cordoba, Tanti	Faivovich ***et al.*** (2004)
Boana creptans	CFBHT 12841	KU495262	KU494469	Brazil: Bahia: Camamu	Lyra ***et al.*** (2017)
Boana curupi	MACN 37793	AY549359	–	Argentina: Misiones, Depto. Guarany, San Vicente	Faivovich ***et al.*** (2004)
Boana dentei	MPEG 30300	MN781657	MN781644	Brazil: Pará: Almeirim, Reserva Biológica Maicurú	This study
Boana diabolica	AF 1111	KU168872	–	French Guiana: Mana	Fouquet ***et al.*** (2016)
Boana ericae	CFBH 3599	AY549332	–	Brazil: Goiás, Alto Paraíso de Goiás	Faivovich ***et al.*** (2004)
Boana faber	CFBHT 04381	KU495265	KU494472	Brazil: Rio de Janeiro: Petrópolis	Lyra ***et al.*** (2017)
Boana fasciata	QCAZ 17030	JN970535	JN970669	Ecuador: Provincia Morona Santiago, Tiink, Río Zamora	Funk ***et al.*** (2011)
Boana geographica	MZUSP 157060	KU168903	–	Brazil: Amazonas: Tefe	Fouquet ***et al.*** (2016)
Boana gladiator	MNCN 43710	HM480413	–	Peru: Cusco: Valle de Marcapata, between San Miguel and Marcapata	Köhler ***et al.*** (2010)
Boana gracilis	AMNH-A 164105	AY549336	–	Guyana: Iwokrama: Muri Scrub camp, 80 m	Faivovich ***et al.*** (2005)

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APPENDIX II (Continued)

Species	Voucher/Field Number	16S	COI	Locality	References
Boana gracilis	MHNLS 19035	MN781658	MN781645	Venezuela: Amazonas: San José de Chipiro, boca del rio Ventuari, municipio Atabapo, alto Orinoco	This study
Boana gracilis	MHNLS 19037	MN781659	MN781646	Venezuela: Amazonas: San José de Chipiro, boca del rio Ventuari, municipio Atabapo, alto Orinoco	This study
Boana gracilis	MHNLS 19039	MN781660	MN781647	Venezuela: Amazonas: San José de Chipiro, boca del rio Ventuari, municipio Atabapo, alto Orinoco	This study
Boana gracilis	MPEG 40288	MN781661	MN781648	Brazil: Amazonas: Nova Airão: Parque Nacional do Jaú	This Study
Boana gracilis	MPEG 40292	MN781662	MN781649	Brazil: Amazonas: Nova Airão: Parque Nacional do Jaú	This study
Boana guentheri	CFBH 3386	AY843631	–	Brazil: Rio Grande do Sul, Terra de Areia	Faivovich ***et al.*** (2005)
Boana heilprini	AMNH A-168405	AY843632	–	Pet trade	Faivovich ***et al.*** (2005)
Boana jimenezi	MHNLS 19402	MN688742	MN683994	Venezuela: Bolívar: Gran Sabana, Campamento Guayaraca, Sabana de Guayaraca, P.N. Canaima	This study
Boana joaquini	CFBH 3625	AY549339	–	Brazil: Santa Catarina: Urubici	Faivovich ***et al.*** (2004)
Boana lanciformis	AJC 3975	KP149371	KP149169	Colombia: Casanare: Sabanalarga, Sabanalarga	Guarnizo ***et al.*** (2015)
Boana latistriata	MZUSP111556	AY549360	–	Brazil: Minas Gerais: Município Itamontes	Faivovich ***et al.*** (2004)
Boana lemai	ROM 39570	AY843637	–	Guyana: Mount Ayanganna	Faivovich ***et al.*** (2005)
Boana leptolineata	CFBH 3848	AY549341	–	Brazil: Santa Catarina: Município de São Domingos	Faivovich ***et al.*** (2004)
Boana lundii	CFBHT 01902	KU495270	KU494477	Brazil: Minas Gerais: São Roque de Minas	Lyra ***et al.*** (2017)
Boana maculateralis	QCAZ 40082	JN970541	JN970675	Ecuador: Provincia Napo: Comunidad Santa Rosa	Funk ***et al.*** (2011)
Boana marginata	CFBH 3098	AY549342	–	Brazil: Rio Grande do Sul: São Francisco de Paula	Faivovich ***et al***. (2004)
Boana marianitae	MNK 52825	AY549343	–	Bolivia: Santa Cruz: Caballero, Canton San Juan, Amboro National Park	Faivovich ***et al.*** (2004)
Boana melanopleura	MTD 46497	HM444777	–	Peru: Junin,:San Ramon	Lehr ***et al.*** (2010)
Boana microderma	NMP6V 71258/1	AY843644	–	Peru: Anguilla: 50 km W of Iquitos	Faivovich ***et al***. (2005)

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APPENDIX II (Continued)

Species	Voucher/Field Number	16S	COI	Locality	References
Boana multifasciatus	ROM 28435	JN970643	JN970762	Guyana: Potaro-Siparuni: Paramakatoi, pond near camp Paramakatoi	Funk ***et al.*** (2011)
Boana nympha	NMP6V 71202/2	AY843670	–	Peru: 50 km W of Iquitos	Faivovich ***et al.*** (2005)
Boana ornatissima	51mc	EF376056	–	French Guiana: Chutes Voltaires	Salducci ***et al.*** (2005)
Boana palaestes	MNCN 44415	HM480414	–	Peru: Cusco: Río Kimbiri, La Convención	Köhler ***et al.*** (2010)
Boana pardalis	CFBHT 04366	KU495275	KU494482	Brazil: Rio de Janeiro: Petrópolis	Lyra ***et al.*** (2017)
Boana pellucens	QCAZ 30594	JN970651	JN970770	Ecuador: El Oro Avanzada-Playón road, km 8	Funk ***et al.*** (2011)
Boana picturata	KU 202737	AY326055	–	Ecuador: Pichincha: Tinalandia: 15.5 km SE Santo, Domingo de Colorados; 700 m	Darst & Cannatella (2004)
Boana polytaenia	CFBH 5752	AY843655	–	Brazil: Rio de Janeiro, Itatiaia, Maringá	Faivovich ***et al.*** (2005)
Boana prasina	CFBH 3388	AY549347	–	Brazil: Santa Catarina: Rio Vermelho	Faivovich ***et al.*** (2004)
Boana pugnax	AJC 3529	KP149296	KP149101	Colombia: Santander: San Vicente de Chucuri, Vereda las Margaritas, Reserva el arboretum, Quebrada los Cauchos	Guarnizo ***et al.*** (2015)
Boana pulchella	MLP A 2148	AY549349	–	Argentina: Buenos Aires: Sierra de la Ventana	Faivovich ***et al.*** (2004)
Boana punctata	193AF	EU201112	–	French Guiana: Mana	Fouquet ***et al.*** (2007)
Boana punctata	AJC 3921	KP149469	KP149258	Colombia: Meta, San Juan de Arama, Caserio Miraflores, Vereda La Balastrera, Finca Los Almendros (duenos, Ernesto y Gloria Alvarez), Caserillo Miraflores, Vereda La Balastrera, Municipio San Juan de Arama	Guarnizo ***et al.*** (2015)
Boana punctata	AJC 3922	KP149390	KP149186	Colombia: Meta, San Juan de Arama, Caserio Miraflores, Vereda La Balastrera, Finca Los Almendros (duenos, Ernesto y Gloria Alvarez), Caserillo Miraflores, Vereda La Balastrera, Municipio San Juan de Arama	Guarnizo ***et al.*** (2015)

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APPENDIX II (Continued)

Species	Voucher/Field Number	16S	COI	Locality	References
Boana punctata	AJC 3928	KP149392	KP149188	Colombia: Meta, San Juan de Arama, Caserio Miraflores, Vereda La Balastrera, Finca Los Almendros (duenos, Ernesto y Gloria Alvarez), Caserillo Miraflores, Vereda La Balastrera, Municipio San Juan de Arama	Guarnizo ***et al.*** (2015)
Boana punctata	AJC 3932	KP149476	KP149264	Colombia: Meta, San Juan de Arama, Caserio Miraflores, Vereda La Balastrera, Finca Los Almendros (duenos, Ernesto y Gloria Alvarez), Caserillo Miraflores, Vereda La Balastrera, Municipio San Juan de Arama	Guarnizo ***et al.*** (2015)
Boana punctata	AJC 4064	KP149397	KP149193	Colombia: Casanare, Sabanalarga, Sabanalarga	Guarnizo ***et al.*** (2015)
Boana punctata	AJC 4100	KP149307	KP149111	Colombia: Casanare, Sabanalarga, Sabanalarga	Guarnizo ***et al.*** (2015)
Boana punctata	MACN 37792	AY549353	KU184077	Argentina: Chaco: Resistencia: Camino a Isla del Cerrito	Faivovich ***et al.*** (2004)
Boana punctata	MNK A 9130/ AS 0039	JF790120	–	Bolivia: Santa Cruz: Ñuflo de Chavez, San Sebastián	Jansen ***et al.*** (2011)
Boana punctata	MNK A 9133/ AS 0150	JF790121	–	Bolivia: Santa Cruz: Ñuflo de Chavez, San Sebastián	Jansen ***et al.*** (2011)
Boana punctata	MNK A 9278/ AS 0469	JF790126	–	Bolivia: Beni: Yucuma, Los Lagos	Jansen ***et al.*** (2011)
Boana punctata	MNK A 9487/ AS 0164	JF790122	–	Bolivia: Santa Cruz: Ñuflo de Chavez, San Sebastián	Jansen ***et al.*** (2011)
Boana punctata	MNK A 9607/ AS 0299	JF790123	–	Bolivia: Santa Cruz: Velasco, Caparu	Jansen ***et al.*** (2011)
Boana punctata	MNK A 9693/ AS 0396	JF790124	–	Bolivia: Santa Cruz: Ñuflo de Chavez, San Sebastián	Jansen ***et al.*** (2011)
Boana punctata	MNK A 9694/ AS 0397	JF790125	–	Bolivia: Santa Cruz: Ñuflo de Chavez, San Sebastián	Jansen ***et al.*** (2011)
Boana punctata	SMF 94095/AS 183	KF723062	–	Bolivia: San Sebastián	Schulze ***et al.*** (2015)
Boana punctata	SMF 94097/AS 510	KF723063	–	Bolivia: Los Lagos	Schulze ***et al.*** (2015)
Boana raniceps	CFBHT 00940	KU495281	KU494488	Brazil: São Paulo: Santa Fé do Sul	Lyra ***et al.*** (2017)
Boana riojana	MACN 37631	AY549354	–	Argentina: Catamarca, Depto. Belen, Rio El Bolson, prox. Villa Vil	Antunes ***et al.*** (2008)
Boana roraima	ROM 39624	AY843660	–	Guyana: Mount Ayanganna	Faivovich ***et al.*** (2005)

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APPENDIX II (Continued)

Species	Voucher/Field Number	16S	COI	Locality	References
Boana rufitela	USNM 57269	AY843662[a]	FJ766740[b]	Panama: Cocle, El Cope, Parque Nacional 'Omar Torrijos'	Faivovich ***et al.*** (2005)[a]; Crawford ***et al.*** (2010)[b]
Boana semiguttata	CFB 3579	AY549357	–	Brazil: Paraná: Piraquara	Faivovich ***et al.*** (2004)
Boana semilineata	–	KM390786	KU234701	Brazil: Rio de Janeiro	unpublished data from Genbank
Boana sibleszi	MHNLS 19580	MN688743	MN683995	Venezuela: Bolívar: Gran Sabana, Sierra de Lema, Troncal 10.6 km al S de la alcabala	This study
Boana sibleszi	ROM 39561	AY843667	–	Guyana: Mount Ayanganna	Faivovich ***et al.*** (2005)
Boana tetete	QCAZ 40080	JN970539	JN970673	Ecuador: Provincia Napo: Comunidad Santa Rosa	Funk ***et al.*** (2011)
Boana xerophylla	AJC 4116	KP149478	KP149266	Colombia: Casanare: Sabanalarga, Sabanalarga	Guarnizo ***et al.*** (2015)