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A new *Dendropsophus* Fitzinger, 1843 (Anura: Hylidae) of the *parviceps* group from the lowlands of the Guiana Shield

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Abstract

Many Amazonian frog species that are considered widely distributed may actually represent polyspecific complexes.. A minute tree frog from the Guiana Shield originally assigned to the allegedly widely distributed *Dendropsophus brevifrons* proved to be a yet undescribed species within the *D. parviceps* group. We herein describe this new species and present a phylogeny for the *D. parviceps* group. The new species is diagnosed from other *Dendropsophus* of the *parviceps* group by its small body size (19.6–21.7 mm in males, 22.1–24.5 mm in females), thighs dorsally dark grey with cream blotches without bright yellow patch, absence of dorsolateral and canthal stripe, and an advertisement call comprising trills (length 0.30–0.35 s) composed of notes emitted at a rate of 131–144 notes/s, generally followed by click series of 2–3 notes. Its tadpole is also singular by having fused lateral marginal papillae and absence of both labial teeth and submarginal papillae. Genetic distances (*p*-distance) are >5.3% on the 12S and >9.3% on the 16S from *D. brevifrons*, its closest relative. This species occurs from the Brazilian state of Amapá, across French Guiana and Suriname to central Guyana and is likely to also occur in adjacent Brazilian states and eastern Venezuela. This species is not rare but is difficult to collect because of its arboreal habits and seasonal activity peaks.

Key words: Amazonia, Anura, conservation, endemism, taxonomy, widespread taxa

Introduction

A large number of frog species remain to be described, particularly in tropical regions (Giam *et al.* 2011) such as Amazonia. In this region, many species that are considered widely distributed have proven to represent polyspecific complexes (*e.g.* Caminer & Ron 2014) or exhibit high levels of genetic diversity suggesting they could represent species complexes (*e.g.* Fouquet *et al.* 2007; Funk *et al.* 2012; Gehara *et al.* 2014). Gaining resolution of basic metrics such as the actual number of species and their respective distribution in Amazonia is radically changing inferences about biodiversity structure and the adequacy of conservation strategies (Bickford *et al.* 2007). As pristine habitats are dwindling at an alarming speed (Davidson *et al.* 2012) and multiple drivers of amphibian diversity loss are synergistically aggravating the conservation status of many species (Pounds *et al.* 2006), this process is also a race against time.

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Dendropsophus Fitzinger, 1843 is a speciose genus of small hylid frogs currently containing 96 nominal species (Frost 2015), which form a well-supported clade, but with only putative morphological and karyological (2N=30) synapomorphies (Faivovich *et al.* 2005; Suárez *et al.* 2013). Nine species groups are currently recognized within the genus, one of them is the *D. parviceps* group (Faivovich *et al*. 2005). This group is not supported by any morphological synapomorphy and was recurrently recovered as polyphyletic via molecular data analyses *e.g.* Fouquet *et al.* 2011; Pyron & Wiens 2011; Motta *et al.* 2012. The group is still recognized on a practical level (Orrico *et al.* 2014) and currently contains 14 species: *D. bokermanni* (Goin, 1960); *D. brevifrons* (Duellman & Crump, 1974); *D. frosti* Motta, Castroviejo-Fisher, Venegas, Orrico, & Padial, 2012; *D. giesleri* (Mertens, 1950); *D. grandisonae* (Goin, 1966); *D. koechlini* (Duellman & Trueb, 1989); *D. luteoocellatus* (Roux, 1927); *D. microps* (Peters, 1872); *D. parviceps* (Boulenger, 1882); *D. pauiniensis* (Heyer, 1977); *D. ruschii* (Weygoldt & Peixoto, 1987); *D. schubarti* (Bokermann, 1963); *D. subocularis* (Dunn, 1934); *D. timbeba* (Martins & Cardoso, 1987). Among them, 10 occur in Amazonia (see below), three in the Atlantic forest (*D. microps*, *D. giesleri*, and *D. ruschii*) and one in Panama, Chocó and middle Río Magdalena Valley in Colombia (*D. subocularis*). A well supported Amazonian subclade formed by *D. brevifrons*, *D. koechlini*, *D. frosti*, and *D. parviceps* was previously recovered in Motta *et al.* (2012), while *D. timbeba* and *D. schubarti*, two other Amazonian species, were recovered in different subclades. However, four Amazonian species have never been included in molecular phylogenies (*D. bokermanni*, *D. grandisonae*, *D. luteoocellatus*, *D. pauiniensis*).

Dendropsophus brevifrons was described from Santa Cecilia in Ecuador (Duellman & Crump 1974), and in their description the authors mention conspecific populations in French Guiana and near Belém, Pará State, Brazil. However, molecular distances of over 10% in the mitochondrial marker 16S between populations identified as *D. brevifrons* from French Guiana and western Amazonia suggested the existence of an additional species occurring in French Guiana (Fouquet *et al.* 2007, 2011).

New material of the *Dendropsophus parviceps* group collected throughout Amazonia and the examination of material collected near the type locality of *D. brevifrons* confirmed that specimens from the Eastern Guiana Shield do not correspond to any nominal taxon. We, thus, describe it as a new species.

Material and methods

Fieldwork and deposition of specimens. Fourteen adult specimens of the new species were collected in French Guiana at six localities (Fig. 1): Montagne de Kaw (2 specimens), Grande Montagne Tortue (5 specimens), Camp Arataie, Reserve Naturelle des Nouragues (3 specimens), Saut Aikoupai (1 specimen), Tolenga (1 specimen), and Crique Limonade, Saül (2 specimens). Seven additional specimens were collected in Guyana at Mabura Hill Forest Reserve and 11 in Suriname in Sipaliwini (3 specimens) and in Nassau Mountain (8 specimens). All these 32 specimens were euthanized using an injection of Xylocaine® (lidocaine chlorhydrate). Tissue samples (liver pieces) were removed and stored in 95% ethanol, while specimens were tagged and fixed (using formalin 10%; except the specimens from Guyana which were fixed in 70% ethanol) before being transferred to 70% ethanol for permanent storage. Type specimens were deposited at Museum National d'Histoire Naturelle (MNHN), State Museum of Natural History Stuttgart (SMNS) and National Zoological Collection of Suriname (NZCS).

These specimens were compared to material from Ecuador collected near the type locality of *Dendropsophus brevifrons* by one of us (SR). Specimens of *D. bokermanni*, *D. giesleri*, *D. koechlini*, *D. microps*, *D. pauiniensis*, *D. ruschii*, *D. schubarti*, *D. timbeba* and *D. parviceps* from various localities (Appendix 1) were also examined by two of us (SR and VGDO).

Morphology. Webbing formulae follow Savage & Heyer (1967) as subsequently modified by Myers & Duellman (1982). All other terminology is that of Duellman (1970) or Kok & Kalamandeen (2008). Abbreviations used throughout the text are: SVL, Snout-Vent Length; TiL, Tibia Length; ThL, Thigh Length (from vent to outer edge of flexed knee); TaL, Tarsus Length; FL, Foot Length (from proximal edge of inner metatarsal tubercle to tip of fourth toe); 4TD, Disc width of Toe IV; 3FD, Disc width of Finger III; 1FiL, Length of Finger I (from proximal edge of palmar tubercle to tip of Finger I); HaL, Hand Length (from proximal edge of palmar tubercle to tip of Finger III); ETS, Eye-Tip to Snout distance (straight line between anterior corner of eye and tip of snout); EN, Eye to Nostril distance (straight line between anterior corner of eye and posterior edge of nostril); HL, Head Length (straight line from posterior corner of mouth to the tip of snout); HW, Head Width (at jaw junction); ED, horizontal

Eye Diameter; IOD, Interorbital Distance (between the anterior margins of the orbits), and TYD, Tympanum Diameter. All 16 measurements (in mm) were taken (by QM for the French Guiana and Suriname material and by RE for the Guyana material) for 18 males and five females under a stereomicroscope, using electronic digital calipers (0.05 mm accuracy rounded to the nearest 0.1 mm).

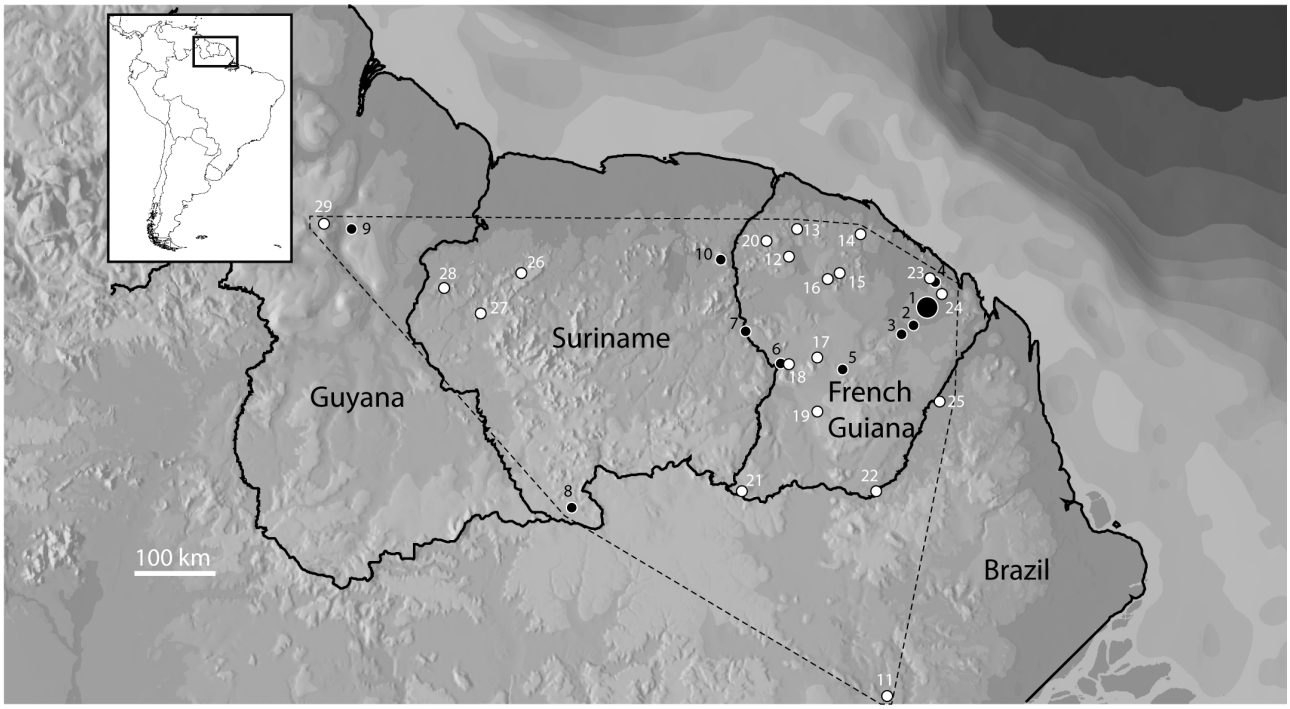


FIGURE 1. Occurrence records of *Dendropsophus counani* sp. nov. Black dots represent presence records (1–10) with material included (specimens, DNA -type locality represented with a large dot) and white dots (11–29) represent additional occurrence records: Grande Montagne Tortue (1), Arataie (2), Saut Aikoupai (3), Kaw (4), Saül (5), Inini (6), Kotika (7), Sipaliwini (8), Mabura (9), Nassau mountain (10), UHE Santo Antonio (11), Saut Tamanoir (12), Crique Saint-Pierre (13), Crique Grégoire (14), Trinité Aimara (15), Trinité Aya (16), Montagne Nivrée Dorlin (17), Haut Inini (18), Flat de la Waki (19), Cascades Voltaires (20), Mitaraka (21), Région de Trois Sauts (22), Montagne Trésor (23), Crique Wapou (24), Memora (25), Bakhuis mountains (26), Kabalebo (27), Tributary Kabalebo River (28), Konawaruk Camp (29).

Sex was determined by calling activity, the presence or absence of vocal slits, or direct examination of the gonads. Relative lengths of digits were estimated by adpressing adjacent digits to one another. Color pattern in life was taken from field notes and color photographs.

A clutch of the new species (eggs not counted) was collected at Abattis Kotika, French Guiana and tadpoles were raised. Three reached stage 31 (Gosner 1960) and were fixed in formalin and one reached stage 36 and was fixed in ethanol as tissue, providing the possibility of assigning the tadpoles to the species using molecular data. The following 17 measurements were taken by the same person (QM) according to McDiarmid & Altig (1999) using a Stemi 2000C Zeiss stereomicroscope connected to an Axiocam ERC 5S: TL, Total length (from tip of the snout to tip of the tail); BL, Body Length (from tip of snout to junction of posterior body and tail musculature); TAL, Tail Length (from junction of posterior body and tail musculature to tip of tail); BW, Body Width (highest width of body); BH, Body Height (highest height of body); HW, Head Width (at level of eyes); TMH, Tail Muscle Height (at base of tail); UTF, Upper Tail Fin Height (highest height of upper fin, from upper margin of tail musculature to upper margin of upper fin); LTF, Lower Tail Fin height (highest height of lower fin, from lower margin of lower fin to lower margin of tail musculature); TMW, Tail Muscle Width (at base of tail); MTH, Maximum Height of Tail; END, Eye-Naris Distance (from anterior corner of eye to posterior margin of nostril); NSD, Naris-Snout Distance (from anterior margin of naris to tip of snout); SSD, Snout-Spiracle Distance (from tip of snout to posterior margin of spiracle); IND, Internarial Distance (distance between the median margins of nares); IOD, Interorbital Distance; ED, Eye Diameter (greatest length of orbit from anterior margin to posterior margin of eye). Another clutch containing 50 eggs was photographed in Sipaliwini, Suriname (Fig. 6d) but the tadpoles were fixed at an early stage (field number AF2233). A third clutch containing 79 eggs was laid by a collected amplectant

pair (SMNS12014–5) in Mabura Hill, Guyana. The tadpoles of this third clutch were raised and photographed. They are similar to the ones examined from French Guiana.

Bioacoustics. Four call recordings of the new species were analyzed. An unvouchered specimen from Camp Aratai was recorded using a tape recorder Sony WM-D6C (tape: UX-Pro90) and a microphone Sennheiser MKH60 on 21 January 1996 at night (20:30; ~23°C). This record was published in Marty & Gaucher (1999) under the name *Hyla brevifrons*. The call from Tolenga (MNHN 2015.0114) was recorded using an Olympus Linear PCM Recorder (LS-11), 24bit /96 kHz, on 12 February 2012 at dusk (18:00; ~23°C). An unvouchered specimen from Camp Aratai was recorded using an Olympus Linear PCM Recorder (LS-11), 24bit /96 kHz, on 24 February 2014 at night (20:00; ~22°C). Calls from Mabura Hill Forest Reserve were recorded using a Sony WM-D6C tape recorder and Sony ECM-Z157 directional microphone on 19 April 2004 (18:00; 24–25°C) and were digitized at a sample rate of 22.050 kHz.

We compared these recordings with the available calls for other species of the *Dendropsophus parviceps* group belonging to the Amazonian clade: *D. brevifrons* and *D. bokermanni* from Ecuador. *Dendropsophus brevifrons* was recorded in Limoncocha (Provincia Sucumbíos, QCAZ43079) and Lorocachi (Provincia Pastaza, QCAZ55848). The recording from Limoncocha was made on 11 June 2009, at 22:00. The recording from Lorocachi was made on 15 June 2013, at 20:38. *Dendropsophus bokermanni* was recorded in Tambococha (Provincia de Orellana, QCAZ55324) on 9 March 2013, air temperature 25.2 °C. All recordings were made with a Sennheiser ME-67 directional microphone an Olympus Linear PCM Recorder (LS-10). Recorded individuals were also sequenced to ensure proper identification.

Additional comparisons were made using publically available acoustic recordings for *Dendropsophus parviceps* from Peru, Tambopata (Crocroft *et al.* 2001) and Bolivia (Marquez *et al.* 2002); *D. koechlini* from Peru Tambopata (Crocroft *et al.* 2001). These records perfectly match the calls described in Duellman & Crump (1974), Duellman (1978) and Duellman & Trueb (1989).

We also compared our recordings with the published descriptions of calls in Duellman (1978) of *Dendropsophus bokermanni*, in Duellman (1970) of *D. subocularis*, and in Rivero (1969) of *D. luteoocellatus*. The terminology used in these papers for acoustic parameters was unambiguous. The call of *Dendropsophus timbeba* has been published previously (see Orrico *et al*. 2013), but this species is morphologically very distinctive and was thus not included in the bioacoustics analysis.

The calls were analyzed at a sampling rate of 44.1 kHz using Audacity (http://audacity.sourceforge.net/). We measured the following variables of the two types of calls (trills and click series): call duration (beginning of first to the end of the last note of a call); inter call intervals (end of one call to the beginning of the next); call rate (number of calls per minute); number of notes per call (a call is here defined as a series of identical notes emitted in groups between longer silent intervals); note duration (beginning of the note to the end of the note); internote interval (end of one note to beginning of the next). Dominant frequency of the call and for each of the two main harmonics of the notes were measured from a spectral slice taken through one entire call (using Blackman function; frequency resolution = 43 Hz, cf. Kok & Kalamandeen 2008).

Molecular analysis. Genomic DNA was extracted using Promega DNA extraction kit from 11 tissue samples of the new species preserved in 95% ethanol (including one tadpole) and 30 tissue samples from other species of the *D. parviceps* group. We targeted two mitochondrial loci (12S and 16S) that were already available for 12 specimens belonging to species of the *D. parviceps* group, as well as 29 congeneric species representing all major *Dendropsophus* clades and three terminals used as outgroups (*Xenohyla truncata*, *Pseudis paradoxa*, *Scarthyla goinorum*, the two last ones were used to root the tree; Appendix 2). The final dataset contained 86 terminals. Fragments were amplified by standard PCR techniques using previously described primers (Fouquet *et al.* 2012) and PCR conditions. Sequencing was performed using ABI Big Dye V3.1 (ABI Foster City USA) and resolved on an automated sequencer. Sequences were preliminary aligned and edited with CodonCode Aligner v.3.5.2 (http://www.codoncode.com/aligner/download.htm) and Geneious 5.4.4 software (GeneMatters Corp.). Laboratory procedures for QCAZ samples were similar except DNA was extracted using standard phenol–chloroform extraction protocols (Sambrook *et al.* 1989) and sequencing was carried out by the Macrogen Sequencing Team (Macrogen Inc., Seoul, Korea). Novel sequences were deposited in Genbank (Appendix 2).

Sequences were aligned with MAFFT v6 (Katoh *et al.* 2002) under default parameters except for the use of the E-INS-i strategy, which is adapted to sequences with conserved domains and long gaps. We obtained a final 1455 base pairs (bp) alignment (940 bp for 12S and 515 bp of 16S). The final dataset is incomplete for the last *ca*. 500 bp

for 18 terminals of 12S and the entire 16S fragment for 31 terminals. The first portion of the 12S was used as the backbone of the alignment and all major lineages were represented by at least one complete terminal.

We used MEGA 6.06 (Tamura *et al*. 2013) to select the substitution model that best fits the data under Bayesian Information Criterion. The resulting model was employed in a Bayesian analysis (BA) with MrBayes 3.2 (Huelsenbeck & Ronquist 2001). The BA consisted of a $50x10^6$ generations run starting with random trees and 10 Markov chains (one cold) sampled every 1000 generations. Adequate burn-in was determined by examining likelihood scores of the heated chains for convergence on stationarity as well as the effective sample size of values in Tracer 1.5 (Rambaut & Drummond 2007). We considered relationships to be strongly supported when posterior probabilities were equal to or higher than 0.95.

We calculated *p*-distances with MEGA 6.06 (Tamura *et al.* 2013) among major groups recovered from the phylogenetic analysis using 395 bp of 12S, where all the sequences overlap, and a 375 bp region of 16S, absent for two lineages of the *D. parviceps* clade.

Results

Phylogenetic analysis

The Dendropsophus parviceps species group is recovered paraphyletic (Fig. 2) as it was in previous publications (*e.g.* Pyron & Wiens 2011, Fouquet et al. 2011; Motta et al. 2012). Moreover, we added *Dendropsophus microps* in the present analysis, which is nested in a poorly supported clade with species of the *D. microcephalus* group. This result adds up to the many instances of paraphyly in that group strengthening the view that this species group needs to be redefined. However, this lies outside the scope of this study.

Nevertheless, one strongly supported clade is formed by Amazonian members of the *Dendropsophus parviceps* group including *D. parviceps*. This clade will be called the *D. parviceps* clade hereafter. The new species is nested within this clade as the sister group of *Dendropsophus brevifrons* with *p*-distance >5.3% on the 12S and >9.3% on the 16S (Table 1). The new species is divided by low genetic distances in three lineages corresponding to the three different countries where the species was sampled. *Dendropsophus brevifrons* is composed of three highly distant lineages (>5% on 16S) corresponding to geographically distant populations from Ecuador (type locality), Peru and Rondônia (Brazil). The clade formed by the new species and *D. brevifrons* is sister of a clade formed by *D. bokermanni, D. frosti*, and a putative new species recovered as sister of *D. frosti*. *Dendropsophus bokermanni* is composed of three highly distant lineages (>5% on 16S) corresponding to geographically distant populations from Acre (type locality), Peru, and Ecuador (Fig. 2).

TABLE 1. Mean genetic distances (*p* distance) among major lineages of *Dendropsophus* using pairwise deletion on 12S (below diagonal) and on 16S (above diagonal).

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
1. *D. counani*_SUR		0.006	0.006	0.093	0.103	NA	0.142	0.114	0.110	0.125	0.094	0.105
2. *D. counani*_FG	0.004		0.012	0.099	0.099	NA	0.143	0.121	0.115	0.127	0.095	0.112
3. *D. counani*_GUY	0.017	0.014		0.096	0.109	NA	0.145	0.119	0.110	0.125	0.100	0.111
4. *D. brevifrons*_EC	0.053	0.055	0.061		0.103	NA	0.129	0.113	0.121	0.137	0.124	0.124
5. *D. brevifrons*_RO	0.053	0.054	0.060	0.053		NA	0.158	0.140	0.139	0.159	0.125	0.145
6. *D. brevifrons*_PE	0.058	0.059	0.060	0.059	0.052		NA	NA	NA	NA	NA	NA
7. *D. parviceps*	0.100	0.099	0.100	0.106	0.101	0.105		0.124	0.124	0.151	0.127	0.116
8. *D. bokermanni*_PE	0.091	0.091	0.087	0.099	0.095	0.103	0.087		0.065	0.072	0.063	0.058
9. *D. bokermanni*_EC	0.096	0.094	0.093	0.106	0.106	0.109	0.093	0.041		0.084	0.074	0.054
10. *D. bokermanni*_AC	0.075	0.075	0.071	0.084	0.085	0.087	0.081	0.038	0.037		0.094	0.096
11. *D.* sp.	0.105	0.101	0.098	0.106	0.109	0.117	0.091	0.051	0.040	0.046		0.052
12. *D. frosti*	0.096	0.095	0.098	0.101	0.109	0.102	0.097	0.054	0.054	0.041	0.035	

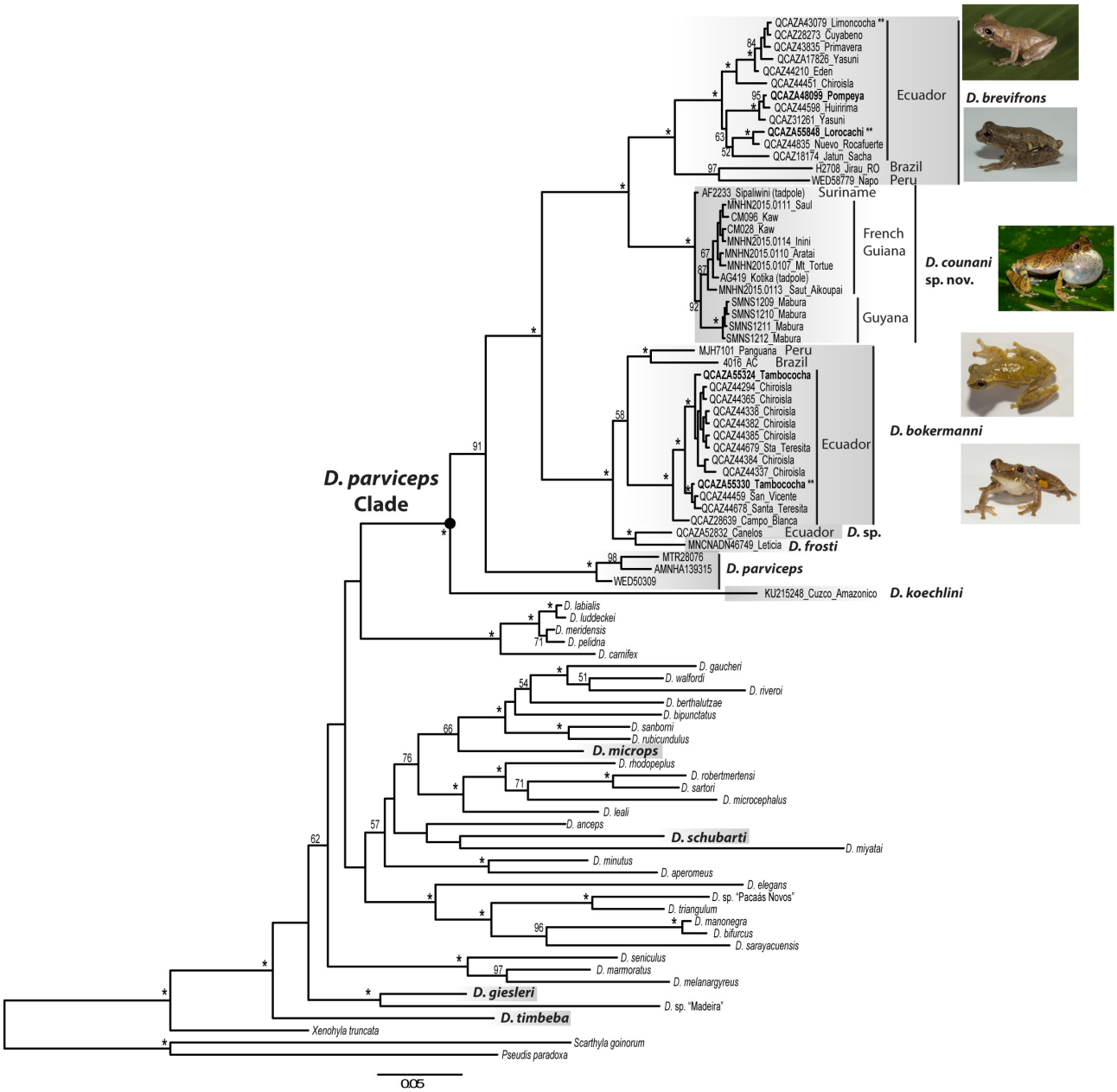


FIGURE 2. Phylogram (50% majority rule consensus with frequencies of all observed bipartitions) hypothesized from Bayesian analysis using 1455 bp of mtDNA sequences of species of the genus *Dendropsophus.* Posterior probabilities are indicated before each node (* indicates pp = 1.0 and 0.99 and pp < 0.5 are not indicated). Species of the *D. parviceps* group are in bold and the *D. parviceps* clade is indicated. Within this clade, specimens for which photos are shown are in bold and specimens for which audio record is available are indicated with **.

Dendropsophus counani **sp. nov.**
(Figs. 3–4)

Hyla brevifrons—Duellman and Crump 1974; Lescure and Marty (2000); Ernst *et al*. (2005); Salducci *et al*. (2005)
Dendropsophus brevifrons—Ernst *et al*. (2006); Fouquet *et al*. (2007); Ernst and Rödel (2008); Ouboter and Jairam (2012); Marty and Vacher (2013)
Dendropsophus cf. *brevifrons*—Dewynter *et al*. (2008); Fouquet *et al*. (2011); Orrico *et al.* (2013)

Holotype. MNHN2015.0101 (field number AF1345). An adult male from "Grande Montagne Tortue", (4.292663, -52.349539, 400 m elevation), municipality of Régina, French Guiana, collected by Antoine Fouquet, Benoit Villette, and Quentin Martinez on 26 December 2013.

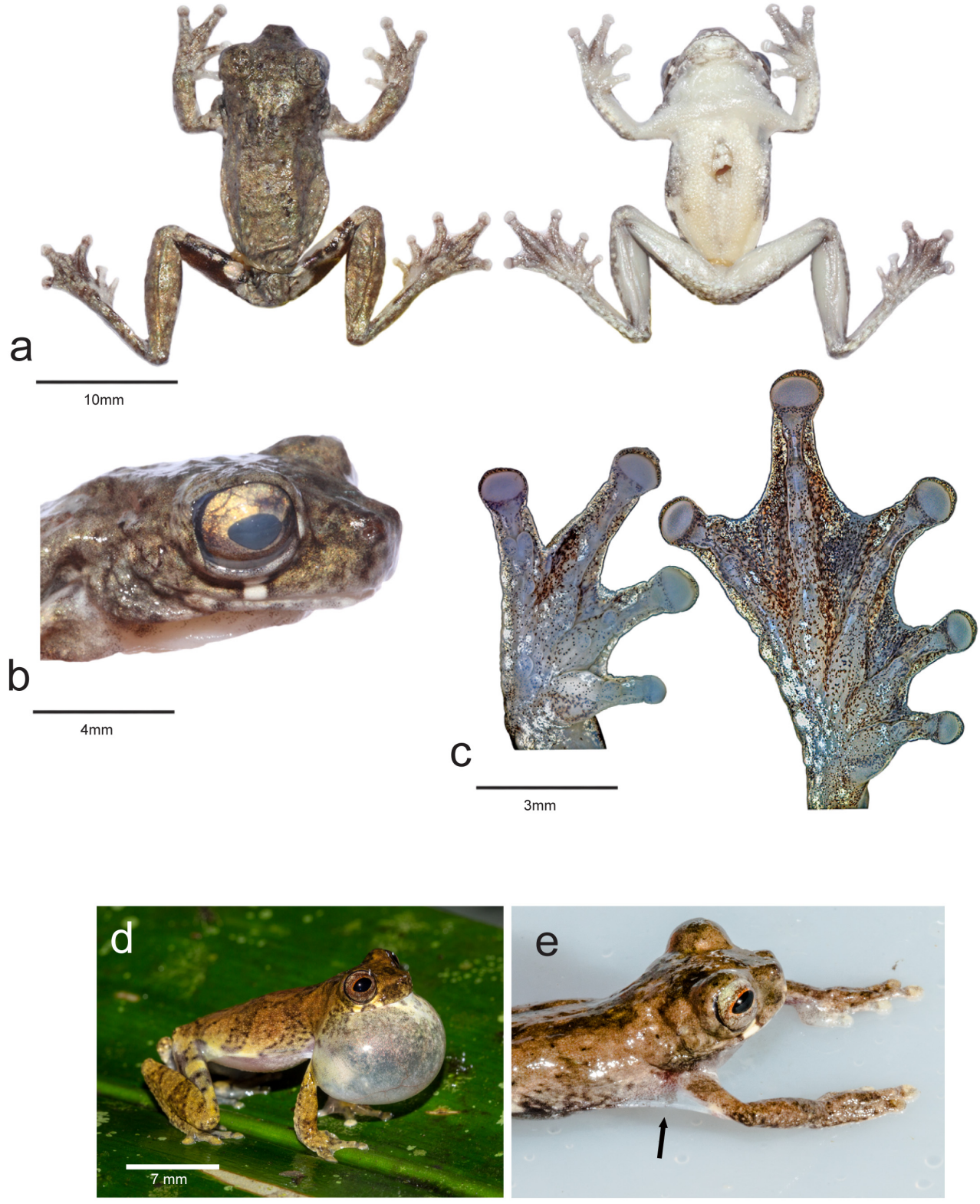


FIGURE 3. a–c) Holotype (MNHN2015.0101) of *Dendropsophus counani* sp. nov.; d) calling male (not collected); e) extended axillary membrane (MNHN2015.0112).

Paratypes. MNHN2015.0104–7 (field number AF1346–9) two adult males and two adult females collected with the holotype. MNHN2015.0102-3 (field numbers AF0017, AF0935) two adult males from Montagne de Kaw (4.548056, -52.151944, 250 m elevation), municipality of Roura, French Guiana, collected by Antoine Fouquet on 17 December 2005 and the 10 February 2013, respectively. MNHN2015.0108–10 (field numbers AF1405,

AF1406, AF1413) three adult males from Camp Arataie, Reserve Naturelle des Nouragues (3.99047, -52.57662, 100 m elevation), municipality of Régina, French Guiana, collected by Antoine Fouquet and Jennifer Devillechabrolle on 17 December 2013. MNHN2015.0113 (field number AF1417) an adult male from Saut Aikoupai (4.086343, -52.462338, 100 m elevation), municipality of Régina, French Guiana, collected by Maël Dewynter on 16 December 2013. MNHN2015.0114 (field number AM021) an adult male from Tolenga, Inini River (3.663159, -53.928308, 150 m elevation), municipality of Maripassoula, French Guiana, collected by Maël Dewynter and Kévin Pineau on 10 February 2012. MNHN2015.0111–2 (field numbers AF1676–1677) two adult males from Crique Limonade (3.573170, -53.198510, 100 m elevation), municipality of Saül, French Guiana, collected by Antoine Fouquet, Elodie Courtois, and Jean-Pierre Vacher on 24 February 2014. SMNS12009–11 (field numbers MABH1203, 1303, 1703), two adult males and one adult female from Mabura Hill Forest Reserve, Guyana (5.155278, -58.699722, 60 m elevation), collected by Raffael Ernst on 12 May 2003 and 10 June 2003, respectively. SMNS12012–15 (field numbers MABH0304, 0404, 1104, 1204), three adult males and one adult female from Mabura Hill Forest Reserve, Guyana, collected by Raffael Ernst on 19 April 2004 and 29 April 2004. MNHN2015.0115, NZCSA2332, MNHN2015.0116 (field numbers AF2121, AF2198, AF2199) two adult males and one female from Sipaliwini (2.09753, -56.1472, 100 m elevation), Sipaliwini District, Suriname, collected by Antoine Fouquet and Jean-Pierre Vacher on 24 April 2014. MNHN2015.0117–8, NZCS A2333–4, MNHN2015.0119–22 (field numbers AF2511–2, AF2516–9, AF2532–3) seven adult males and one female from Nassau mountain (4.802620, -54.615020, 400 m elevation), Sipaliwini District, Suriname, collected by Antoine Fouquet and Rawien Jairam on 20 December 2014.

Etymology. The specific epithet refers to the utopic and short-lived "independent state of Counani" which was founded by French settlers and existed from 1886 to 1891 at the border of what is now French Guiana and the Brazilian Amapá State. It was governed by the self-proclaimed "Gros 1er".

Diagnosis. We assigned the new species to the genus *Dendropsophus* on the basis of previous (Fouquet *et al.* 2007, 2011) and present molecular results (Fig. 2) and the overall similarity with other species of the genus (Figs. 3–4). *Dendropsophus counani* sp. nov. is diagnosed by the following combination of traits: (1) a small sized member of the *D. parviceps* group, (SVL 19.40–21.73 mm in 11 adult males, 22.10–24.50 mm in two females) (Table 2); (2) inconspicuous sexual dimorphism, throat with dark flecks in male vs. plain cream in female, translucid glandular nuptial pads visible under a magnifying stereoscope in adult males; (3) head short, wider than body; (4) snout truncate in dorsal and lateral views, nostrils slightly protuberant; (5) large prominent eyes (ED/HW=0.36–0.41); (6) Tibia length 51–56% SVL; (7) Femur length 37–42 % SVL; (8) palpebral membrane pigmented on its border; (9) small tympanum (TYD/ED = 0.33–0.41); (10) well developed axillary membrane; (11) distal subarticular tubercle on finger IV strongly bifid; (12) hands webbing formula I 2^{-}—2^{-} II 2½—2^{-} III 2^{+}—2^{-} IV, (13) feet webbing formula I 2½—2 II 1^{+}—2^{-} III 1^{+}—2^{+} IV 2^{+}—1^{+} V; (14) no inner tarsal fold, supernumerary tarsal tubercles absent; (15) heel and calcar tubercles absent; (16) fringe from postaxial edge of Finger IV prolonged into a series of tubercles on forearm; (17) cloacal opening covered by a sheath on its dorsal third; (18) in life, dorsal surfaces with a few scattered tubercles, light brown in life to gray in preservative with dark transversal markings in most cases; (19) two (sometimes only one) white subocular and two white rostral (sometimes inconspicuous) markings in the upper lip, (20) neither rostral nor canthal stripes; lateral surfaces of body with whitish and dark transversal markings, (21) no dorsolateral lines; (22) dorsal surface of thighs generally black to dark gray with 0–3 cream transversal blotches situated anteriorly (sometimes inconspicuous) in either live or preserved specimens, (23) yellow blotches on thighs or tibia absent in either live or preserved specimens; (24) belly and throat white (anterior part of chin with black blotches in males), (25) ventral surface of thighs and tibia light grey and smooth, anterior surface of belly cream and granular, less granular posteriorly; (26) flanks without dorsolateral stripes, unpigmented on the axilary region, with a dark oblique marking medially followed by one or two cream markings; (27) distal parts of the ventral surfaces of hands and feet dark grey to black; (28) iris copper; (29) Advertisement call either a short trill (0.33 s) or click series (0.45 s), trills consist of 41–50 notes and click series consists of 3–6 clicks, each with 1–3 notes, these notes have a dominant frequency 3.8–4.0 kHz with a slight frequency modulation in trills; (30) in life, tadpoles light brown dorsally and marbled with black and light brown laterally, dark pigmentation concentrated on the posterior part of the tail but the tip is mostly unpigmented at the exception of a central dark marking, the tail is long with pointed tip, no row of denticles, jaw sheath finely serrated and one ventral row of blunt marginal papillae.

See comparison with other species of the *parviceps* group (Table 5).

TABLE 2. Morphological measurements (abbreviations and acronyms are explained in the text) of adults of *Dendropsophus counani* sp. nov. and other species of the *D. parviceps* species group. Measurements of *D. brevifons* are from Duellman and Crump (1974), of *D. bokermanni* from Goin (1960), of *D. pauiniensis* from Heyer (1977), and of *D. frosti* from Motta *et al.* (2012). X = mean and sd = standard deviation.

	D. counani				*D. brevifrons*		*D. bokermanni*	*D. pauiniensis*	*D. frosti*		
	M (n=18)	X (sd)	F (n=5)	X (sd)	M	F	F (holotype)*	M (holotype)	M	X (sd)	F
SVL	19.40–21.73	20.53 (0.73)	22.10–24.50	23.00 (0.95)	17.0–21.4	20.1–23.2	17.8	20.2	21.1–25.2	22.1 (0.9)	25.9
TiL	9.90–11.20	10.42 (0.34)	12.00–12.65	12.10 (0.43)			8.5	9.9	11.8–12.3	12.0 (0.2)	12.9
ThL	9.20–11.10	9.90 (0.40)	11.40–12.10	11.70 (0.30)			8.2	9.5	11.5–12.0	11.8 (0.3)	12.3
TaL	5.50–6.50	5.97 (0.27)	6.50–7.10	6.79 (0.24)							
FL	7.20–8.80	8.01 (0.42)	8.70–9.70	9.21 (0.37)			11.7	7.8	9.5–9.9	9.7 (0.2)	10.3
4TD	0.70–1.00	0.86 (0.07)	0.90–1.30	1.05 (0.15)							
3FD	0.70–1.17	0.96 (0.13)	1.10–1.30	1.18 (0.08)					1.0–1.4	1.2 (0.2)	1.0
1FiL	2.50–3.20	2.74 (0.21)	2.70–3.40	3.06 (0.38)							
HaL	5.36–7.00	5.85 (0.39)	5.40–6.90	6.30 (0.58)							
ETS	2.52–3.30	2.87 (0.20)	3.00–3.40	3.26 (0.15)							
EN	1.4.3–2.50	2.01 (0.30)	1.85–2.30	2.21 (0.24)							
HL	5.03–7.20	6.47 (0.57)	6.38–7.60	7.10 (0.51)			5.1		7.1–8.1	7.5 (0.4)	8.6
HW	6.30–7.50	6.77 (0.28)	7.30–7.70	7.56 (0.15)			5.1	6.8	7.3–8.8	8.0 (0.7)	8.2
ED	2.50–3.10	2.78 (0.17)	2.80–3.00	2.88 (0.13)					3.4–3.8	3.6 (0.2)	3.2
IOD	2.60–3.00	2.74 (0.23)	2.70–3.00	3.24 (0.25)							
TYD	0.90–1.10	1.00 (0.06)	1.00–1.20	1.08 (0.11)					0.9–1.4	1.2 (0.2)	1.5

*= It is noteworthy that the specimen of *D. bokermanni* designed as holotype by Goin (1960) may in fact be immature given the smallest female measured by us from Ecuador was 23.4 mm and by Duellman (1978) 22.5 mm.

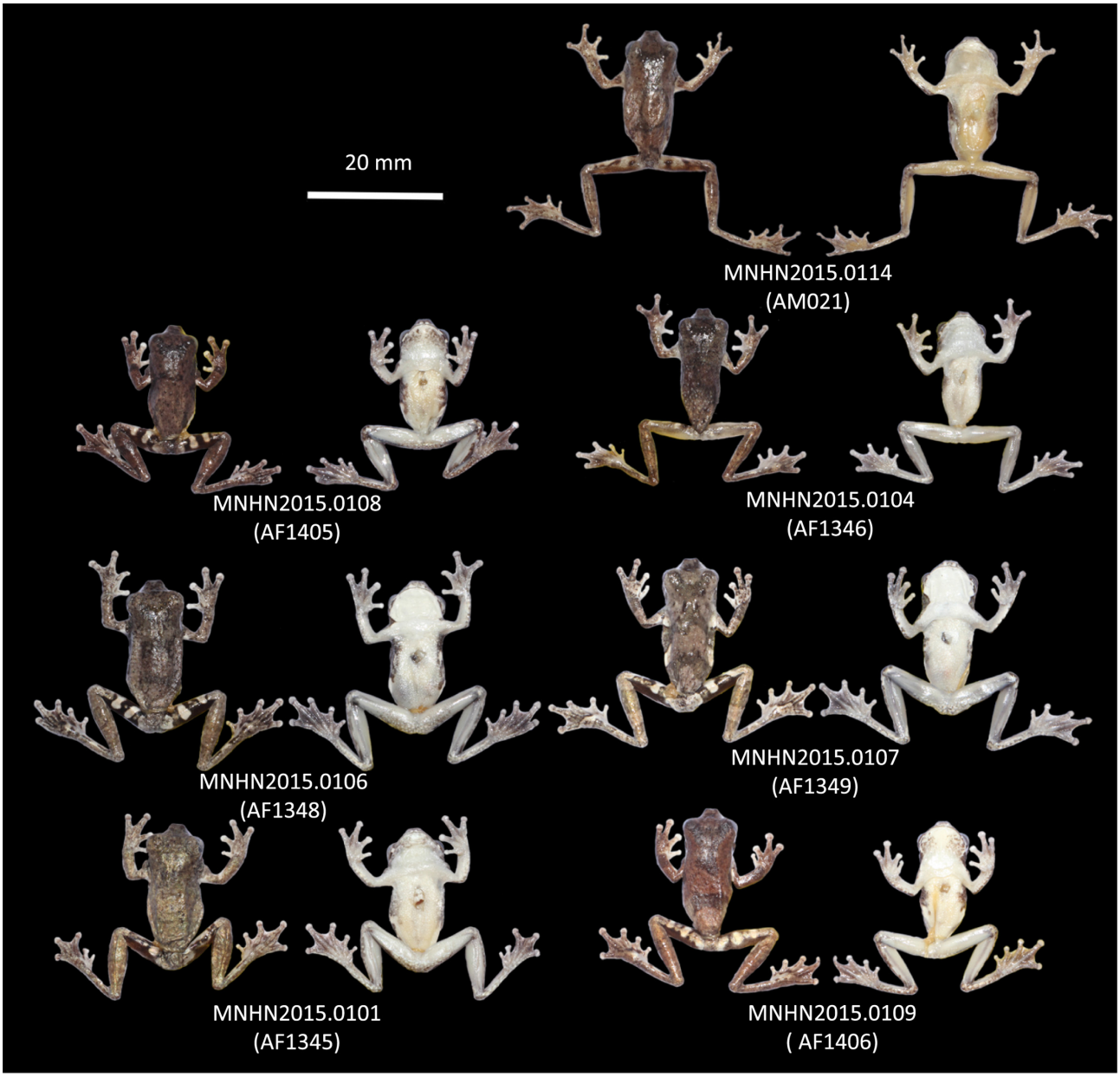


FIGURE 4. Dorsal and ventral views of seven specimens of the type series of *Dendropsophus counani* sp. nov.

Description of holotype. (Fig. 3) Adult male, SVL 20.9 mm; body slender; head wider than body, wider than long, HW/HL=1.1, widest behind eyes; snout truncate in dorsal and lateral views; canthus rostralis inconspicuous, curved; loreal region concave; nostrils slightly protuberant, directed laterally. Interorbital area flat; eyes large (ED/HW=0.3) and protuberant; palpebral membrane translucent, with brown pigmentation on its border. Tympanum small (TYD/FD=1.4), distinct but inconspicuous dorsally, directed laterally. Supratympanic fold absent. Proximal part of upper arm thickened anteriorly and slender distally, bearing an axillary membrane reaching half of upper arm ventrally; forearm angular, enlarged laterally, with tubercles on the posteroventral edges (6 on the right arm and 8 on the left) aligned with the fringe on the postaxial edge of Finger IV; fingers short, bearing round discs; relative length of fingers I < II < IV < III; subarticular tubercles large and prominently bifid on finger IV, slightly bifid on finger III, divided on finger II, round and single on finger I, most prominent on finger I; supernumerary tubercles absent; inner metacarpal tubercle flat, elongate; outer metacarpal tubercle flat large, bifid; inconspicuous white nuptial excrescences on the dorsolateral edge of finger I; webbing formula I 2^{-}—2^{-} II $2^{½}$—2^{-} III 2^{+}—2^{-} IV. Hindlimb long and slender; TL/SVL = 0.5; row of tubercles instead of a proper tarsal fold; calcar and heel tubercles absent; toes bearing round discs, as large as those on fingers; relative lengths of toes I < II < V < III < IV;

subarticular tubercles round; supernumerary tubercles absent; inner metatarsal tubercle flat, elongate; outer metatarsal tubercle flat, round; webbing formula I $2^{½}$—2 II+1^{+}—2^{-} III 1^{+}—2^{+} IV 2^{+}—1^{+} V. Skin on dorsum, head, dorsal surfaces of forearms and thighs, flanks and groin with homogeneously scattered tubercles; skin strongly granular on belly and posterior side of thighs, finely granular on chest and smooth on ventral surfaces of thighs, shanks, and throat. Cloacal opening directed posteriorly at midlevel of thighs, covered by cloacal sheath dorsally; cloacal tubercles absent. Tongue cordiform, barely free behind; dentigerous process of vomers evident, in two transverse series, separated and positioned obliquely to choanae, each having three vomerine teeth; choanae large, rounded; vocal slits moderately long, extending from midlateral base of tongue, almost reaching to angle of jaws; vocal sac single, median, subgular.

In alcohol, dorsal surfaces bronze grey with a few small black flecks; loreal region dark grey, one cream subocular mark finely delimited by black lines, two small cream spots on the tip of the upper lip, a small white spot at the anterior tip of eye, upper and forearm as the back but with a dark grey chevron, tibia and tarsus as back but with two dark grey chevrons, thighs white grey anteriorly and ventrally, black with a large and a few smaller cream spots dorsally, half black half grey posteriorly, venter creamy white, ventral sides of tibia, chest and throat white grey except the chin which is cream with black flecks; iris copper.

Measurements of holotype (in mm). SVL:20.9; TiL:10.4; ThL:9.8; TaL:5.7; FL:8.3; 4TD:0.9; 3FD:0.8; 1FiL:2.7; HaL:6.0; ETS:2.9; EN:2.3; HL:7.2; HW:7.5; ED:2.8; IOD:2.9; TYD:1.0 (Table 2).

TABLE 3. Call variables obtained from four calls of *Dendropsophus counani* sp. nov. and calls of *D. bokermanni* and *D. brevifrons*.

	D. counani sp. nov.				*D. bokermanni*	*D. brevifrons*
	Aratai	Inini	Saül	Mabura	Ecuador	Ecuador
Trill duration (s)	0.348 (0.001)	0.310 (0.008)	0.313	0.215 (0.001)	0.326 (0.0275)	0.443 (0.012)
Inter trill silence (s)	6.635 (NA)	10.62 (8.866)	23.9 (NA)	1.593 (NA)	52.553	0.975 (NA)
Trills/min	10 (NA)	8 (NA)	4 (NA)	NA	1 (NA)	3 (NA)
Notes/trill	50 (0)	41.5 (1)	44 (0)	33 (0)	34.0 (2.828)	15.5 (0.5)
Note duration (s)	0.0053 (0.001)	0.005 (0.000)	0.005 (0)	0.004 (0)	0.005 (0)	0.0113 (0)
Inter note silent (s)	0.001 (0)	0.001 (0)	0.001 (0)	0.002 (0)	0.003 (0)	0.0177 (0)
Rate (notes/s)	143.679	134.0 (2.549)	140.4	153.1 (0.502)	104.3 (2.202)	NA
Trill dom. freq. (Hz)	3855 (2)	3960 (12)	3578 (17)	3915 (4)	4204 (151)	4243 (60)
Trill 2nd freq. (Hz)	8038 (36)	7650 (102.)	NA	NA	8167 (404)	7990 (2)
Trill 3rd freq. (Hz)	11922 (4)	11163 (726)	NA	NA	12434 (33)	12919 (428)
Click series duration (s)	0.407 (0.004)	0.497 (0.140)	0.539	0.331 (0.079)	0.618 (0.072)	0.751 (0.109)
Inter click series silence	2.538 (0.585)	5.41 (0.532)	2.192 (0.36)	1.409 (0.312)	2.807 (1.848)	1.635 (0.262)
Click series/min	24 (NA)	12 (NA)	24 (NA)	30 (NA)	20 (NA)	18 (0)
Clicks/series	4 (0)	4.667 (1.528)	4.5 (0.577)	3.5 (0.577)	6 (0.816)	4.667 (0.471)
Notes/click	2.062 (0.239)	2.622 (0.038)	1.487	1.646 (0.105)	1 (0)	1 (0)
Inter click silence (s)	0.103 (0.004)	0.114 (0.004)	0.129	0.096 (0.006)	0.110 (0.016)	0.183 (0.009)
Rate (Clicks/s)	9.835 (0.089)	9.355 (1.222)	8.379	10.701	NA	NA
Click series dom. freq.	3796 (21)	3878 (83)	3428 (46)	3787 (3)	4373 (48)	4112 (18)
Click series 2nd freq.	NA	7801 (77)	NA	NA	8598 (182)	7970 (9)
Click series 3rd freq. (Hz)	11506 (117)	10826 (NA)	NA	NA	11634 (NA)	12311 (4)

Color variation of type series. *Dendropsophus counani* **sp. nov.** has a polychromatic dorsum (Fig. 4) and, as most hylids, displays a nocturnal and a diurnal coloration (Fig. 3). Given the specimens were fixed during the day the variation reported here concerns the diurnal colouration. The background colouration varies from dark brown to grey. The dorsal markings varies from a conspicuous "X" extending from the head to the flanks and a "V"

extending from the posterior part of the back to the inguinal region (MNHN2015.0107), to irregular transversal marks (MNHN2015.0109) to almost absent (MNHN2015.0101). The dorsal surface of the thighs is also very variable, typically including three conspicuous cream blotches (one inconspicuous pericloacal, one largest and conspicuous central and one before the knee) elongated transversally and located on the anterior part of the dorsal surface of the thigh (MNHN2015.0108); to inconspicuous (MNHN2015.0104). The loreal region comprises one or two subocular cream blotches. The gular region is generally spotless white in female but with black flecks on the anterior part in males.

Advertisement call. The following description is based on four recordings (Table 3). Three of them are from uncollected individuals from Camp Aratai (Réserve Naturelle des Nouragues, French Guiana, available in Marty & Gaucher 1999), Crique Limonade (Saül, French Guiana) and Mabura Hill forest Reserve (Guyana) and one collected (MNHN2015.0114) from Inini (French Guiana).

The call of *Dendropsophus counani* sp. nov. consists of trills and clicks series (Fig. 5). The trills are short (range = 0.21–0.35 s), comprise 33–50 notes (range = 134–153 notes/s) and are emitted between silent intervals of 1.6–23.9 s. These trills are generally followed by click series (range = 3–6 clicks/serie; 8.4–10.7 clicks/s) consisting of generally 2–3 notes per click. However, single click series are emitted more frequently than trills (between silent intervals of X = 3.7 s; range = 2.2–5.4 s), and last *c.a.* 0.45 s (range = 0.33–0.54 s).

The spectral structure of trills and clicks are similar and consist of three main harmonics, with the fundamental frequency dominating (dominant frequency X = 3.9 kHz, range = 3.78–3.97 kHz). Two secondary harmonics are visible, having a frequency of *ca.* 7.6–8.1 and 10.6–11.9 kHz, respectively (Fig. 5). See comparison with other species of the *parviceps* group (Table 5).

TABLE 4. Morphological measurements of three tadpoles of *Dendropsophus counani* sp. nov. at stage 31 (abbreviations are explained in the text).

	Range	Mean (sd)
TL	12.6–14.5	13.55 (1.34)
BL	4.2–4.6	4.33 (0.23)
TAL	8.2–10.1	9.15 (1.34)
BW	2.8–3.2	2.93 (0.23)
BH	2.1–2.3	2.17 (0.11)
HW	2.5–3.0	2.70 (0.26)
TMH	0.9–1.0	0.97 (0.06)
UTF	0.7–0.8	0.75 (0.07)
LTF	0.6–0.8	0.70 (0.14)
TMW	1.0–1.3	1.20 (0.17)
MTH	2.3–2.7	2.50 (0.28)
END	0.8–0.9	0.83 (0.06)
NSD	0.6–0.7	0.67 (0.06)
SSD	3.3–3.4	3.33 (0.06)
IND	1.2–1.3	1.27 (0.06)
ED	0.6–0.8	0.70 (0.10)
IOD	1.5–1.7	1.57 (0.11)

Tadpole description. The following description is based on three individuals at stage 31 (Fig. 6). Type 4 tadpole (Orton 1953); exotrophic; body skin smooth; TL 12.6–14.5 mm; BL 4.2–4.6 mm, 29–36% of TL, 1.3–1.6 times BW, 1.8–2.2 times BH; BW 1.3–1.4 times BH; body depressed, ovoid with blunt snout and posterior edges of body in dorsal view; snout round in lateral view; eyes positioned and directed laterally; ED 0.6–0.8 mm, 35–53% of IOD; IOD less than IND; nares frontally positioned and directed laterodorsally; narial opening reniform in lateral view; END 0.8–0.9 mm. Spiracular tube sinistral, conical, projecting posterodorsally, its tip located 74–78 % of BL from snout. Lateral-line system conspicuous. Caudal musculature highest at body-tail junction, tapering

posteriorly, terminating at tail tip; tail tip pointed; upper fin originating at junction of body and tail, gradually increasing in height to about 2/3 of tail; UTF 70–80 % of TMH; LTF 0.6–0.8 % of TMH; lower fin similar in proportion but slightly lower; MTH 16–21 % TL.

Mouth small, directed anteroventrally, oral disc width 0.66 mm (from edges of marginal papillae (0.38 from edges of sheaths). No labial teeth. Single posterior row of large and blunt marginal papillae with two pairs partially fused, one pair single and three lateral marginal papillae partially fused into a vertical fold on each side; anterior labium bare; submarginal papillae absent; jaw sheaths robust and finely serrated.

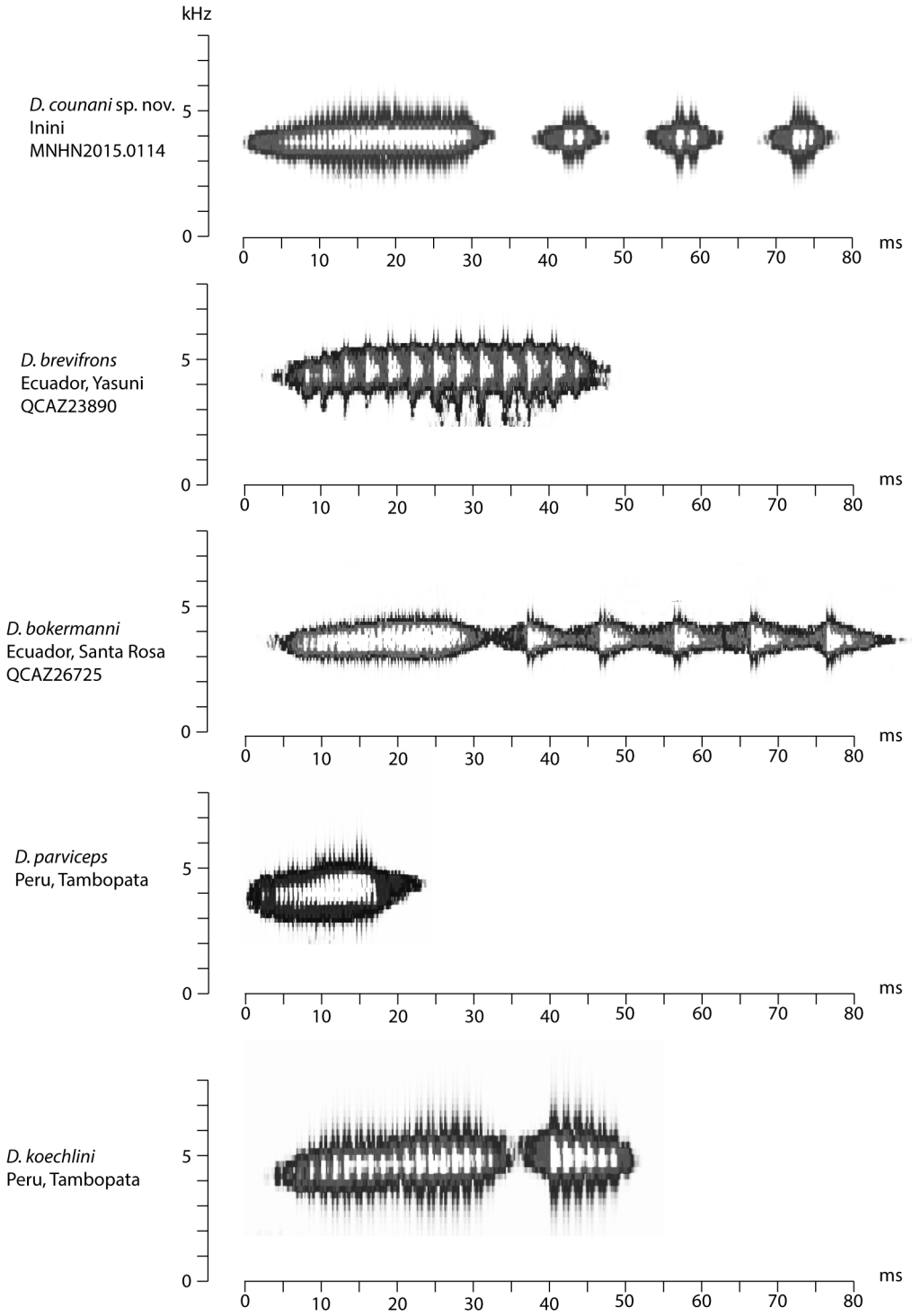


FIGURE 5. Sonograms of five Amazonian species of the *Dendropsophus parviceps* group. Recording of *D. counani* sp. nov. is from a male (SVL = 19.9 mm; MNHN2015.0114) from Inini, French Guiana. Records of *D. parviceps* and *D. koechlini* are from Cocroft *et al.* (2001).

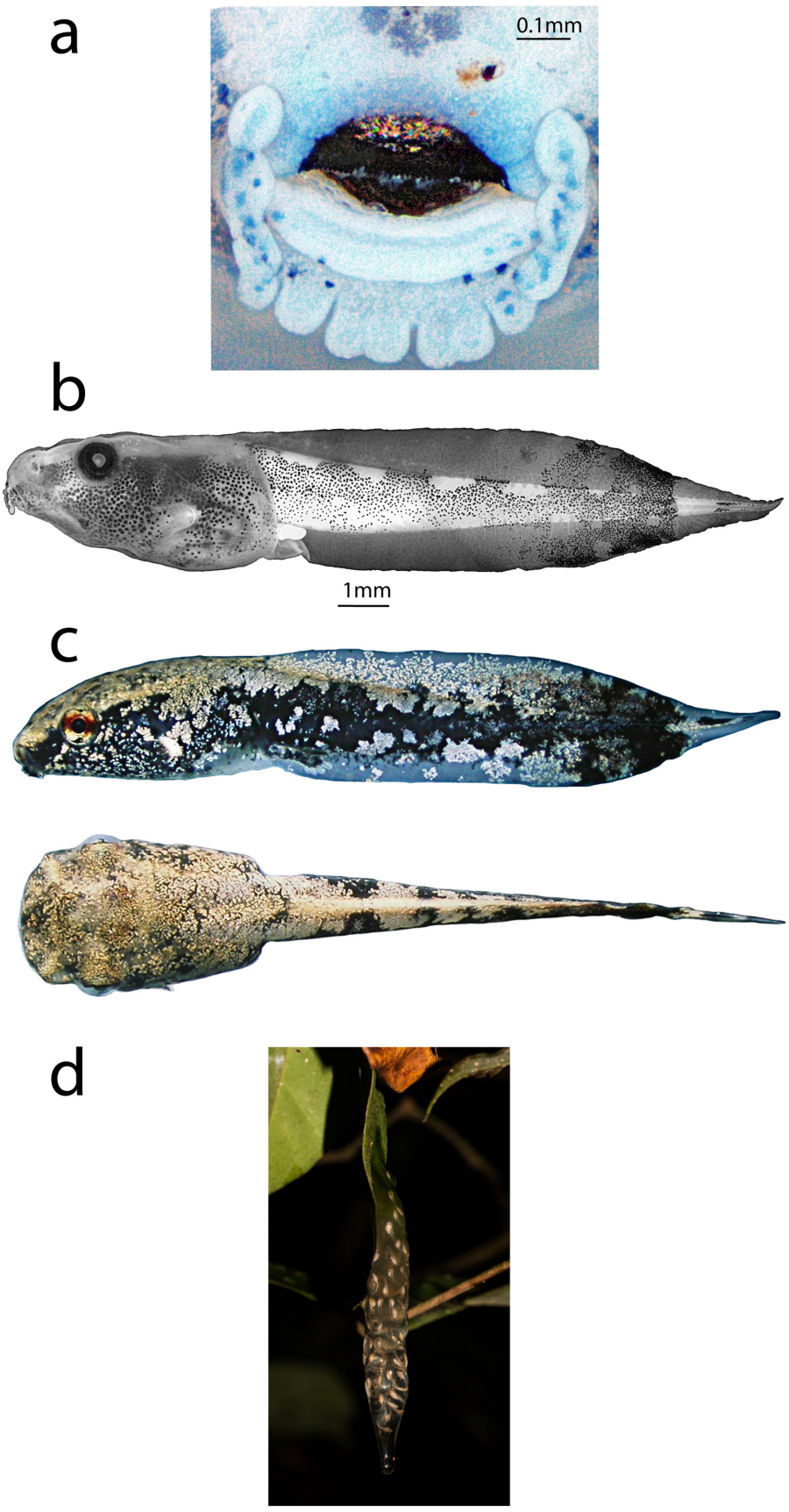


FIGURE 6. *Dendropsophus counani* sp. nov. tadpole: a) mouth and b) lateral view of specimen raised from a clutch collected at Kotika, French Guiana (MB field number AG419A) preserved at stage 31; c) lateral and dorsal views of a living specimen at stage 36 raised with AG419A; d) mature clutch hanging over water containing 50 eggs photographed at Sipaliwini, Suriname.

TABLE 5. Comparison of some diagnostic characters among species of the *Dendropsophus parviceps* group (*D. schubarti, D. microps, D. giesleri, D. timbeba* were omitted given they do not cluster with the *parviceps* clade and are unambiguously morphologically distinct).

	D. counani sp. nov.	*D. brevifrons*	*D. bokermanni*	*D. frosti*	*D. koechlini*	*D. ruschii*	*D. luteoocellatus*	*D. subocularis*	*D. pauiniensis*	*D. parviceps*
Thighs colour	dorsally dark grey with cream blotches anterodorsally and ventrally pale grey translucent	same as *D. counani* but generally less conspicuous and with an orange spot anteriorly in some specimens	large yellow/orange blotch on anterior surfaces of thighs	plain black	plain black	plain cream	large yellow/orange blotch on anterior surfaces of thighs	large yellow/orange blotch on anterior surfaces of thighs	large yellow/orange blotch on anterior surfaces of thighs	large yellow/orange blotch on ventral surface of tibia
Venter	anteriorly white and granular and posterolaterally translucent grey	same as *D. counani*	entirely cream and granular	entirely cream and granular	with black flecks	entirely cream and granular	entirely cream	entirely cream and granular	granular with melanophores	dark posteriorly
Thighs skin texture	smooth	smooth	smooth	granular	granular	granular	???	???	???	smooth
Dorsum	dark brown to grey, few scattered tubercles	tan yellowish to dark brown, smooth	light yellow to mustard, smooth	smooth	finely shagreen	smooth or with very few nat scattered tubercles	smooth	smooth	tuberculate	smooth
Flanks	pale grey on the axillary and the inguinal regions separated by a series of oblique dark and cream patches extending from the dorsum, and no dorsolateral stripes	dorsolateral stripes in females	dorsolateral stripes	black flanks	plain pale brown dorsally, marbled grey ventrally	dorsolateral stripe in most specimens	dorsolateral stripes	dorsolateral stripes	???	brown with cream marks posteriorily
Body size (mm)	19.40–21.73 M, 22.10–24.50 F	17.0–21.4 M, 20.1–23.2 F	22.7 M, 25.6 F (Duellman & Crump 1974)	21.1–25.2 M, 25.9–28.F	17.5–23.8 M, 23.9–28.1 F	24.5–27.9 M, 26.7–29.0 F	23.1 M, 28.0 F	23.1 mm M, 26.1 F	20.2–20.3 M, 23.0–24.0 F	18.3 M, 26.1 mm F
Canthal/ rostral stripe	absent	canthal and rostral	canthal	canthal	rostral	canthal and rostral	canthal	canthal and rostral	canthal and rostral	absent
Advertisement call	Trills X = 0.30 s, 33–50 notes/trill click series X = 0.45 s, 3–6 clicks, each with 1 to 3 notes	trills X = 0.47 s, 14 notes/trill (Duellman & Crump 1974); 0.44 s, 15–16 notes/trill click series X = 0.75 s, 4–5 single notes clicks in QCAZ5848	trills X = 0.32 s, 34–36 notes/trill clicks X = 0.62s, 5–7 single note clicks in QCAZ26725	???	trills >0.4s	???	trills >0.4s	Trills >0.4s	???	Trills < 0.2 s

In life, tail musculature and the flanks of the body below a line extending from snout to the upper edge of fin are black with golden patches; back and dorsal side of the flanks golden with black flecks. The fin is translucent with golden fleck anteriorly and black patches on the posterior third; the iris is golden with a reddish transversal mark.

Tadpoles of *Dendropsophus counani* sp. nov. can be distinguished from those of *D. koechlini*, *D. parviceps*, *D. ruschii*, and *D. brevifrons* by the fusion of the lateral marginal papillae; from *D. bokermanni* by the absence of secondary papillae ventrally, and from *D. subocularis* by the fusion of the few ventral marginal papillae. They can also be distinguished from *D. koechlini*, *D. parviceps*, *D. ruschii*, *D. bokermanni*, and *D. subocularis* by the shape and the coloration of the fin (reaching its max height around 2/3rd of the length and harboring black pigmentation before the tip in *D. counani*).

Distribution, ecology, and conservation. In addition to the material examined, above 13 additional occurrences in French Guiana were retrieved from the personal observations of various persons (Appendix 3), as well as three in Suriname (Ouboter & Jairam 2012; pers. obs.), two in Amapá (acoustic record from J. Dias Lima; pers. obs.) and one in Guyana (Cole *et al.* 2013) (Fig. 1). The absence of previous records in Amapá (Dias Lima 2008) and Northern Pará (Avila-Pires *et al.* 2010) is noteworthy. Lima *et al.* (2006) provide details on *Dendropsophus brevifrons* from Reserva Adolfo Ducke but the species probably belongs to the *D. microcephalus* group. . Our identification is based on the visual examination of the pictures, the video record provided, and personal examination by one of us (VGDO).

This species inhabits primary and secondary forest and is encountered only when breeding, in temporary ponds, as well as flooded parts of stream and river beds after heavy rain. Males call on vegetation (on small branches or leaves) overhanging or nearby water. They often start calling in the late afternoon and continue at night. Outside these reproduction activity events, the species likely dwells in the canopy and thus remains difficult to detect. Even when active, calling males often remain high in the trees and descend only after heavy rains. This is likely the cause for the failure to detect the species during previous surveys undertaken in Amapá (Dias Lima 2008) and Northern Pará (Ávila-Pires *et al.* 2010). Clutches (50–79 eggs) are deposited on vegetation above water and tadpoles drop from the gelatinous clutch after a few days. Six days before hatching, clutches have already a typical elongated shape and exhibit drip-tips at the distal end (Fig. 6d).

Dendropsophus counani occurs from the Brazilian state of Amapá across French Guiana and Suriname to Central Guyana and is likely to extend its range into adjacent Brazilian states and eastern Venezuela. The single specimen from Belém (KU127846) that was examined by Duellman & Crump (1974) cannot be unambiguously identified as *D. counani* sp. nov. This specimen, which was not included in the type series by Duellman and Crump (1974), was examined by us via pictures provided by the curators of the herpetological collection of KU and is very similar to specimens of *D. counani* sp. nov. *i.e.* from the other side of the Amazon River. Nevertheless, some differences exist (*e.g*. white flash mark on flanks and on dorsal side of legs are quite different). Given that there is only a single individual available from south of the Amazon River and molecular data is missing, it is difficult to draw any conclusions about the identity of the Belém population.

In French Guiana, *Dendropsophus counani* sp. nov. occurs throughout the territory and can be locally abundant when breeding, as it is probably also the case in Suriname and Amapá. In Guyana, throughout the entire study period, the species appeared only sporadically (only on very few days/nights), very localized (only two localities), and in low densities (only 24 calling males during 393.5 hrs of standardized visual and acoustic transect sampling, or 0.06 individuals/transect hour) (Ernst *et al.* 2006; Ernst & Rödel 2008).

Both (B1) the extent of occurrence (>20.000 km^2) and (B2) the area of occupancy (>2000 km^2) of *Dendropsophus counani* are largely over the threshold of the IUCN threatened categories. Moreover, its range lies in the Guiana Shield, which is relatively well preserved, the range of *D. counani* is putatively continuous and no noticeable decline has been observed nor is expected in the upcoming years. Therefore, the species should be listed as Least Concern.

Discussion

Tropical regions, such as Amazonia, still harbour a vast number of undescribed species (Giam *et al.* 2011). This is the case in the genus *Dendropsophus*, in which the accumulation curve of described species seems to be far from

stabilization (Motta *et al.* 2012). The present work exemplifies that pattern with the description of *D. counani* from the Guiana Shield. Additionally, and despite our very limited geographical sampling, genetic distances (>5% on 16S) among populations from western Amazonia suggest the existence of at least five undescribed species along with five nominal species (*D. frosti*, *D. koechlini*, *D. parviceps*, *D brevifrons* and *D. bokermanni*). These populations deserve further integrative taxonomical investigation to check whether differences in calls and morphology will corroborate the genetic distinctiveness. The *D. brevifrons* population from Belém also deserves investigation. Given that many species of anurans believed to be co-distributed across the Amazon River display pronounced molecular differentiation on opposite sides of the river, often suggesting specific subdivision (*e.g.* Fouquet *et al*. 2007; Funk *et al.* 2012; Gehara *et al.* 2014), the Belém population may also correspond to an undescribed species.

Cryptic diversity seems common in Amazonian frogs (Fouquet *et al.* 2014; Funk *et al.* 2012; Gehara *et al.* 2014). The case of *Hypsiboas fasciatus* is a striking example. Funk *et al.* (2012) revealed the existence of many lineages having restricted range across Amazonia, each displaying bioacoustic differences. Later, Caminer & Ron (2014) demonstrated that *H. fasciatus* was restricted to a narrow western range in Amazonia and describe four new species from Ecuador and Peru, all the other populations previously identified as *H. fasciatus* let for future investigation. The case of the *Dendropsophus parviceps* group may be similar. Given the existence of multiple amazonian areas of endemism (Cracraft 1985; Haffer & Prance 2001) a denser sampling of the entire *D. parviceps* groups across Amazonia is also needed.

This new species also exemplifies the underestimation of the endemism of the Guiana Shield given that *Dendropsophus counani* is likely an additional endemic for the region. Regional herpetofauna references for French Guiana (Lescure & Marty 2000), Suriname (Ouboter & Jairam 2012), and the lowlands of Guyana (Cole *et al.* 2013) reach similar estimations of 104–110 amphibians. Only about a third of these species are currently considered endemic to the Guiana Shield. However, evidence accumulates that species previously believed to be widely distributed across Amazonia in fact represent polyspecific complexes. Our perception of the diversity across the entire Amazonian region may thus be seriously flawed (Fouquet *et al.* 2007) and regional endemism within Amazonia may actually be much higher than currently assumed.

Morphologically, *Dendropsophus counani* sp. nov. is very similar to *D. brevifrons*. However, their advertisement call is highly distinct. As already highlighted by many previous works (e.g. Giaretta & Costa 2007; Caminer & Ron 2014; Feinberg *et al.* 2014), the examination of acoustic data often allows species that are morphologically indistinguishable to be efficiently discriminated. The fact that *D. counani* sp. nov. remained undescribed until now exemplifies the underuse of acoustic characters for species discrimination because calls from *D. counani* sp. nov. and *D. brevifrons* were available since 1999 (Duellman & Crump 1974; Marty & Gaucher 1999). We thus advocate for active acoustic searches in surveys aiming at documenting anuran communities.

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APPENDIX 1. Material examined.

D. bokermanni
QCAZ 28639, Ecuador, Sucumbíos, Campo Blanca, 0.211223, -76.2339, Male; QCAZ 44294, Ecuador, Orellana, Chiroisla, -0.57997, -75.9177, Male; QCAZ 44337, Ecuador, Orellana, Chiroisla, -0.57997, -75.9177, Male; QCAZ 44338, Ecuador, Orellana, Chiroisla, -0.57997, -75.9177, Male; QCAZ 44365, Ecuador, Orellana, Chiroisla, -0.57997, -75.9177, Female; QCAZ 44459, Ecuador, Orellana, San Vicente, -0.67901, -75.6511, Male; QCAZ 44678, Ecuador, Orellana, Santa Teresita, -0.90087, -75.4136, Male; QCAZ 44679, Ecuador, Orellana, Santa Teresita, -0,90087, -75,4136, Male; QCAZ 55324, Ecuador, Orellana, Tambococha, -0.97366, -75.4353, Male; QCAZ 55330, Ecuador, Orellana, Tambococha, -0.97366, -75.4353, Female.

D. brevifrons
QCAZ 18174, Ecuador, Napo, JatunSacha, -0.10645, -77.6128, Male; QCAZ 28273, Ecuador, Sucumbíos, Playas del Cuyabeno, -0.26543, -75.8917, Female; QCAZ 31261, Ecuador, Orellana, Pompeya-Iro road, 109 km from Pompeya along the road, -0.69157, -75.9196, Male; QCAZ 43079, Ecuador, Sucumbíos, Limoncocha, -0.40624, -76.6195, Male; QCAZ 43835, Ecuador, Sucumbíos, Primavera, -0.44427, -76.7869, Male; QCAZ 44210, Ecuador, Orellana, Eden, -0.49833, -76.0711, Female; QCAZ 44451, Ecuador, Orellana, Chiroisla, -0.57997, -75.9177, Male; QCAZ 44598, Ecuador, Orellana, Huiririma, -0.71163, -75.6240, Male; QCAZ 44835, Ecuador, Orellana, Nuevo Rocafuerte, -0.91651, -75.4231, Male; QCAZ 48099, Ecuador, Orellana, Pompeya, -0.69136, -76.4500, Male; QCAZ 55848, Ecuador, Pastaza, Lorocachi, -0.16131, -75.9867, Male.
D. giesleri
MCNAM6018, Brazil, Minas Gerais, Lagoa próxima ao trevo de Santa Rita do Ouro Preto, Ouro Preto, Male; MCNAM6019, Brazil, Minas Gerais, Lagoa próxima ao trevo de Santa Rita do Ouro Preto, Ouro Preto, Male; MCNAM7338, Brazil, Minas Gerais, Lagoa do Physalaemus maximus, Ouro Preto, Male; MCNAM7854, Brazil, Minas Gerais, Nova Lima, Male; MCNAM7855, Brazil, Minas Gerais, Nova Lima, Male; MNRJ41730, Brazil, Minas Gerais, Ouro Preto, Male; MNRJ41731, Brazil, Minas Gerais, Ouro Preto, Male; MNRJ41732, Brazil, Minas Gerais, Ouro Preto, Male; MNRJ37343, Brazil, Rio de Janeiro, REBIO União, Rio das Ostras, Male; MNRJ2532, Brazil, Rio de Janeiro, Angra dos Reis, Female; MNRJ28387, Brazil, Espírito Santo, Sítio do Bozza, Santa Teresa, Female.

D. koechlini
MZUSP49893, Brazil, Amazonas, Boca do Pauiní, Female

D. microps
CFBH14864, Brazil, São Paulo, São Luis do Paraitinga, Male; CFBH24548, Brazil, São Paulo, Fazenda Intervales, Ribeirão Grande, Male; CFBH24549, Brazil, São Paulo, Fazenda Intervales, Ribeirão Grande, Male; CFBH7498, Brazil, Minas Gerais, Camanducaia, Male.

D. parviceps
TG2887, Brazil, Acre, Mata da Infraero, Cruzeiro do Sul, Male.

D. pauiniensis
MZUSP49892, Brazil, Amazonas, Boca do Pauíni, Male.

D. ruschii
MNRJ47851, Brazil, Minas Gerais, Pedra Dourada, Male; MNRJ47852, Brazil, Minas Gerais, Pedra Dourada, Male; MNRJ47853, Brazil, Minas Gerais, Pedra Dourada, Male; MNRJ47854, Brazil, Minas Gerais, Pedra Dourada, Male; MNRJ47855, Brazil, Minas Gerais, Pedra Dourada, Male; MNRJ47856, Brazil, Minas Gerais, Pedra Dourada, Male; MNRJ47857, Brazil, Minas Gerais, Pedra Dourada, Male; MNRJ31548, Brazil, Espírito Santo, Parque e Nascente do Rio Juai, Pedra Azul, Female; MNRJ31549, Brazil, Espírito Santo, Parque e Nascente do Rio Juai, Pedra Azul, Female.

D. schubarti
MZUSP73651, Brazil, Rondônia, Ji-Paraná, Male; MZUSP73652, Brazil, Rondônia, Ji-Paraná, Male; MZUSP58175, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58176, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58177, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58178, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58179, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58180, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58181, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58182, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58183, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58184, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58185, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male; MZUSP58186, Brazil, Pará,

PARNA da Amazonia (Rio Tapajós), Male; MZUSP92582, Brazil, Acre, Tarauacá, Male; MZUSP60412, Brazil, Rondônia, Santa Cruz da Serra, Male; MZUSP53939, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Uruá, Male; MZUSP56056, Brazil, Pará, Parque Rio Tapajós, Male; MZUSP56057, Brazil, Pará, Parque Rio Tapajós, Male; MZUSP56058, Brazil, Pará, Parque Rio Tapajós, Male; MZUSP60488, Brazil, Rondônia, Nova Brasília, Male; MZUSP60489, Brazil, Rondônia, Nova Brasília, Male; MZUSP60491, Brazil, Rondônia, Nova Brasília, Male; MZUSP92583, Brazil, Rondônia, Ji-Paraná, Male; MZUSP58174, Brazil, Pará, PARNA da Amazonia (Rio Tapajós), Male

D. timbeba
MZUSP60560, Brazil, Acre, caminho para Vila Boa Vista, Xapuri, Male.

APPENDIX 2. Molecular data included in the phylogenetic analysis. Bracketed numbers in the locality column refers to locality numbers on the map. Newly added sequences have their accession numbers in bold.

Species	Voucher (Field number)	Locality	Country	Latitude	Longitude	12S	16S
D. bokermanni	MJH7101	Huanuco, Panguana	Peru	-9.60393	-74.93580	AY843611	AY843611
D. bokermanni	(TG2632, 4016)	FLONA Riozinho Liberdade, AC	Brazil	-7.95556	-72.07694	**KT721835**	**KT721792**
D. bokermanni	QCAZ55324	Tambococha	Ecuador	-0.97366	-75.43526	**KT721828**	**KT721785**
D. bokermanni	QCAZ55330	Tambococha	Ecuador	-0.97366	-75.43526	**KT721829**	**KT721786**
D. bokermanni	QCAZ28639	CampoBlanca	Ecuador	0.211223	-76.23394	**KT721807**	NA
D. bokermanni	QCAZ44294	Chiroisla	Ecuador	-0.57997	-75.91769	**KT721811**	NA
D. bokermanni	QCAZ44337	Chiroisla	Ecuador	-0.57997	-75.91769	**KT721812**	NA
D. bokermanni	QCAZ44338	Chiroisla	Ecuador	-0.57997	-75.91769	**KT721813**	NA
D. bokermanni	QCAZ44365	Chiroisla	Ecuador	-0.57997	-75.91769	**KT721814**	NA
D. bokermanni	QCAZ44384	Chiroisla	Ecuador	-0.57997	-75.91769	**KT721816**	NA
D. bokermanni	QCAZ44678	Santa Teresita	Ecuador	-0.90087	-75.41357	**KT721821**	NA
D. bokermanni	QCAZ44382	Chiroisla	Ecuador	-0.57997	-75.91769	**KT721815**	NA
D. bokermanni	QCAZ44385	Chiroisla	Ecuador	-0.57997	-75.91769	**KT721817**	NA
D. bokermanni	QCAZ44459	San Vicente	Ecuador	-0.67901	-75.65112	**KT721819**	NA
D. bokermanni	QCAZ44679	Santa Teresita	Ecuador	-0.90087	-75.41357	**KT721822**	NA
D. brevifrons	QCAZ43079	Limoncocha	Ecuador	-0.40624	-76.61948	**KT721825**	**KT721782**
D. brevifrons	QCAZ48099	Pompeya	Ecuador	-0.69136	-76.45002	**KT721826**	**KT721783**
D. brevifrons	QCAZ55848	Lorocachi	Ecuador	-0.16131	-75.98673	**KT721830**	**KT721787**
D. brevifrons	QCAZ17826	Yasuni	Ecuador	-0.67819	-76.39656	**KT721824**	NA
D. brevifrons	QCAZ18174	JatunSacha	Ecuador	-0.10645	-77.61285	**KT721805**	NA
D. brevifrons	QCAZ43835	Primavera	Ecuador	-0.44427	-76.78685	**KT721809**	NA
D. brevifrons	QCAZ44835	Nuevo Rocafuerte	Ecuador	-0.91651	-75.42306	**KT721823**	NA
D. brevifrons	QCAZ28273	Cuyabeno	Ecuador	-0.26543	-75.89173	**KT721806**	NA
D. brevifrons	QCAZ31261	Yasuni	Ecuador	-0.69157	-75.91959	**KT721808**	NA
D. brevifrons	QCAZ44451	Chiroisla	Ecuador	-0.57997	-75.91769	**KT721818**	NA
D. brevifrons	QCAZ44598	Huiririma	Ecuador	-0.71163	-75.62395	**KT721820**	NA
D. brevifrons	QCAZ44210	Eden	Ecuador	-0.49833	-76.07112	**KT721810**	NA
D. brevifrons	(WED58779)	Napo	Ecuador			DQ380351	NA

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APPENDIX 2. (Continued)

Species	Voucher (Field number)	Locality	Country	Latitude	Longitude	12S	16S
D. brevifrons	(H2708)	Jirau, RO	Brazil	-9.59132	-65.04918	**KT721802**	**KT721779**
D. counani	MNHN2015.0107	Grande Montagne Tortue (1)	French Guiana	4.29266	-52.34954	**KT721794**	**KT721771**
D. counani	MNHN2015.0110	Arataie (2)	French Guiana	3.99047	-52.57662	**KT721795**	**KT721772**
D. counani	MNHN2015.0113	Saut Aikoupai (3)	French Guiana	4.08634	-52.46234	**KT721796**	**KT721773**
D. counani	(CM096)	Kaw (4)	French Guiana	4.71667	-52.13333	**KT721801**	**KT721778**
D. counani	(CM028)	Kaw (4)	French Guiana	4.71667	-52.13333	EF376022	EF376058
D. counani	MNHN2015.0111	Saül (5)	French Guiana	3.57317	-53.19851	**KT721797**	**KT721774**
D. counani	MNHN2015.0114	Inini (6)	French Guiana	3.66316	-53.92831	**KT721800**	**KT721777**
D. counani	(AG419 tadpole)	Kotika (7)	French Guiana	3.95331	-54.26702	**KT721799**	**KT721776**
D. counani	(AF2233 tadpole)	Sipaliwini (8)	Suriname	2.03253	-56.11449	**KT721798**	**KT721775**
D. counani	SMNS1209	Mabura (9)	Guyana	5.155278	-58.69972	**KT721831**	**KT721788**
D. counani	SMNS1210	Mabura (9)	Guyana	5.155278	-58.69972	**KT721832**	**KT721789**
D. counani	SMNS1211	Mabura (9)	Guyana	5.155278	-58.69972	**KT721833**	**KT721790**
D. counani	SMNS1212	Mabura (9)	Guyana	5.155278	-58.69972	**KT721834**	**KT721791**
D. frosti	MNCN:ADN46749	Leticia to Tarapacá road	Colombia	-4.10788	-69.94996	JQ088283	JQ088283
D. koechlini	KU15248	Cuzco Amazonico	Peru			AY819369	NA
D. parviceps	(95248)	Plácido de Castro, AC	Brazil	-10.30120	-67.14859	AF308080	AF308111
D. parviceps	AMNH A-139315	Centro Experim. Univ., AC	Brazil	-9.95364	-67.87334	AY843652	AY843652
D. parviceps	(WED50309)	?	?			DQ380367	NA
D. sp.	QCAZ52832	Canelos	Ecuador	-0.16016	-77.75764	**KT721827**	**KT721784**
D. gaucheri	ZUEC17681	Oriximiná, PA	Brazil			JF973308	JF973300
D. berthalutzae	CFBH5418	Duque de Caxias, RJ	Brazil			AY843607	AY843607
D. walfordi	MJH129	?	Brazil			AY843683	AY843683
D. riveroi	KU217613	Sucumbios	Ecuador			DQ380372	NA
D. anceps	CFBH5797	Linhares, ES	Brazil			AY843597	AY843597
D. schubarti	(WED57619)	?	?			DQ380374	NA
D. sanborni	MACN38638	Entre Rios	Argentina			AY843663	AY843663
D. rubicundulus	(IT-H 0653)	Buri, SP	Brazil			AY843661	AY843661
D. bipunctatus	(MRT5946)	Serra do Teimoso, Jussari, BA	Brazil			AY843608	AY843608
D. labialis	(Guadalupe08)	Bogota	Colombia			JF422603	JF422603

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APPENDIX 2. (Continued)

Species	Voucher (Field number)	Locality	Country	Latitude	Longitude	12S	16S
D. elegans	(LM3135)	?	?			DQ380355	NA
D. luddeckei	(Chiquinquira03)	Andalucia	Colombia			JF422599	JF422599
D. meridensis	?	La Carbonera	Colombia			JF422585	JF422585
D. pelidna	KU181108	Betania	Venezuela			AY819434	AY819434
D. carnifex	DFCH-USFQ 899	Tandayapa	Ecuador			AY843616	AY843616
D. minutus	(CM114)	Kaw	French Guiana			EF376027	KJ833303
D. giesleri	CFBHS/N	Ubatuba, SP	Brazil			AY843629	AY843629
D. timbeba	KU215190	Cuzco Amazonico	Peru			DQ380348	NA
D. rhodopeplus	MHZ462	Jenaro Herrera	Peru			AY843658	AY843658
D. robertmertensi	MZFC15824	Zanatepec	Mexico			AY819452	NA
D. sartori	MZFC16014	Guerrero	Mexico			AY819453	NA
D. microcephalus	UTA A-50632	Aldea Rio Viejo	Honduras			AY843643	AY843643
D. aperomeus	KU212083	Venceremos	Peru			AY819450	NA
D. seniculus	CFBH5761	Angra dos Reis, RJ	Brazil			AY843666	AY843666
D. marmoratus	MJH7116	Panguana	Peru			AY843640	AY843640
D. melanargyreus	(PG047)	Kaw	French Guiana			JF973313	JF973305
D. sp.	MTR25656	Pacaás Novos, RO	Brazil			**KT721804**	**KT721781**
D. triangulum	KU202745	Misahualli	Ecuador			AY326053	AY326053
D. microps	(MTR15283)	Pinheirinho, SP	Brazil			**KT721803**	**KT721780**
D. leali	MNHN2005.0013	Pidima	French Guiana			JN206640	JN206639
D. manonegra	MHUA:A7336	?	?			KF009943	KF009943
D. bifurcus	?	?	?			AY362975	AY362975
D. sarayacuensis	MJH7143	Panguana	Peru			AY843664	AY843664
D. miyatai	LSUMZH-12939	Sucumbios	Ecuador			AY843647	AY843647
D. sp.	(VOGT2211)	Cachoeirinha, Rio Madeira, AM	Brazil			**KT721836**	**KT721793**
Xenohyla truncata	CFBH7600	Restinga de Marica, RJ	Brazil			AY843775	AY843775
Pseudis paradoxa	(DCC3284)	Fazenda Santa Helena, SP	Brazil			AY326032	AY326032
Scarthyla goinorum	QULC2340	Igarape Nova Empresa, AM	Brazil			AY843752	AY843752

APPENDIX 3. Additional occurence records.

Locality	Country	Latitude	Longitude	Reference
UHE Santo Antonio (11)	Amapá	-0.05194	-52.52167	Dias Lima J. record
Saut Tamanoir (12)	French Guiana	5.15427	-53.75466	Rufray V. - Pelletier V. pers. obs.
Crique Saint-Pierre (13)	French Guianafv	4.84827	-53.84047	Blanc M. pers. obs.
Crique Grégoire (14)	French Guiana	5.09666	-53.04971	Rufray V. - Fouquet A. - Courtois E. pers. obs.
Trinité Aimara (15)	French Guiana	4.67093	-53.28426	Blanc M. - Dewynter M. pers. obs.
Trinité Aya (16)	French Guiana	4.60252	-53.41425	Blanc M. - Dewynter M. pers. obs.
Montagne Nivree Dorlin (17)	French Guiana	3.73422	-53.52856	Rufray V. pers. obs.
Haut Inini (18)	French Guiana	3.65525	-53.84404	Blanc M. - Cochard A. pers. obs.
Flat de la Waki (19)	French Guiana	3.08361	-53,41210	Vacher J.-P. pers. obs.
Cascades Voltaires (20)	French Guiana	5.02913	-54.08932	Blanc M. - Cochard A. pers. obs.
Mitaraka (21)	French Guiana	2.23577	-54.44928	Fouquet A. pers. obs.
Region de Trois Sauts (22)	French Guiana	2.24801	-52.87465	Lescure J. pers. obs.
Montagne Trésor (23)	French Guiana	4.60892	-52.27929	Villette B. pers. obs.
Crique Wapou (24)	French Guiana	4.43487	-52.14725	Blanc M. - Dewynter M. pers. obs.
Memora (25)	Amapá	3.31294	-52.18036	Fouquet A. pers. obs.
Bakhuis mountains (26)	Suriname	4.72462	-56.76380	Fouquet A. pers. obs.
Kabalebo (27)	Suriname	4.22179	-57.26629	Ouboter & Jairam 2012
Tributary Kabalebo River (28)	Suriname	4.49976	-57.67078	Ouboter & Jairam 2012
Konawaruk Camp (29)	Guyana	5.21682	-59.00002	Cole *et al.* 2013

All in-text references underlined in blue are linked to publications on ResearchGate, letting you access and read them immediately.