VERTEBRATE ZOOLOGY
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69 (3): 227–246
2019

SENCKENBERG

A new striped species of *Dendropsophus* (Anura: Hylidae) with a composite advertisement call and comments on the *D. rubicundulus* group

Martin Jansen[1,2], Diego José Santana[3], Bernardo Franco da Veiga Teixeira[4] & Gunther Köhler[1]

[1] Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt a.M., Germany — [2] Correspondence: martin.jansen@senckenberg.de —[3] Universidade Federal de Mato Grosso do Sul, Instituto de Biociências, Laboratório de Zoologia, Av. Costa e Silva, 79070-900, Campo Grande, Mato Grosso do Sul, Brazil — [4] Laboratório de Taxonomia, Ecologia Comportamental e Sistemática de Anuros Neotropicais, Universidade Federal de Uberlândia, Faculdade de Ciências Integradas do Pontal, Rua 20, 1600, Bairro Tupã, 38304-402. Ituiutaba, MG, Brazil

Submitted December 19, 2018.
Accepted June 20, 2019.
Published online at www.senckenberg.de/vertebrate-zoology on August 15, 2019.
Published in print Q4/2019.

Editor in charge: Raffael Ernst

Abstract

Herein we describe *Dendropsophus rozenmani* sp. nov. based on morphological, bioacoustic, and molecular data. This new species is distinguished from other species of *Dendropsophus* by its small size (SVL 18.7–21.1 mm in adult males and 19.6–23.2 mm in females); in life, dorsal ground coloration brown, with two anterior parallel and straight, dark brown stripes and a middorsal sacral stripe; and lateral limits of dorsal coloration above tympanum. In addition, the new species differs from all other species of the *D. rubicundulus* group (along with *D. anataliasiasi*) by having a composite advertisement call, i.e., a series of calls consisting of two call types. In a phylogenetic tree based on 494 bp of the 16S mitochondrial gene, four species of *Dendropsophus*, *D. cruzi*, *D. juliani,* and *D. sanborni* and one candidate species, *D. juliani* A, are positioned within the *rubicundulus* species group which poses questions on the monophyly of this group as well as its morphological definition. The occurrence of both single and composite calls in the *D. rubicundulus* group suggests future studies on the call evolution in that group as well as the whole genus.

Key words

Advertisement call; Amphibia; bioacoustics; Cerrado; Chiquitanía; *Dendropsophus tritaeniatus*; species delimitation; taxonomy.

Introduction

The Neotropical realm sensu Wallace (1876) has a greater amphibian diversity than any other region of the world (Duellman, 1999; Amphibiaweb, 2018). A recent update of Wallace's zoogeographic regions acknowledged that South America, and especially the southern part of this continent, harbors a significant number of phylogenetically distinct lineages (Holt *et al*., 2013). Several recent studies in South America suggested that cryptic diversity is high in frogs, and that many species possibly have smaller distributions and smaller population sizes than previously thought (e.g., Fouquet *et al*., 2007; Jansen *et al*., 2011; Gehara *et al*., 2013, 2014; Ortega-Andrade *et al*., 2015; Ferrão *et al*., 2016; Caminer *et al*., 2017; Vacher *et al*., 2017). Despite this repeated discovery of candidate species in the Neotropics, a taxonomic assessment of most of these species or lineages is still lacking. Because of the frequent failure of DNA extraction of museum specimens and/or often lacking additional (bioacoustic or larval) data from old species descriptions, new topotypic material and data are important for the clarification of many taxonomic problems (e.g., Jansen *et al*., 2011; Teixeira *et al*., 2013; Teixeira & Giaretta,

2015). Bioacoustic data from type localities have a large potential of for species delimitation, and thus, a standardized bioacoustical methodology for the use in integrative taxonomy of anurans was recently proposed (KÖHLER *et al*., 2017).

A DNA barcoding study by JANSEN *et al*. (2011) identified several lineages of frogs in the eastern lowlands of Bolivia (Chiquitano and Beni / Moxos Plains regions) with some of these possibly corresponding to unnamed distinct species. The Chiquitano region has a moderate to high amphibian diversity with up to 45 species at one locality (e.g., SCHULZE *et al*., 2009, 2015; JANSEN *et al*., 2011; BÁLINT *et al*., 2018). This might be due to its biogeographical position as a transition zone (sensu FERRO & MORRONE, 2014) between the wet forests of Amazonia, the dry and often impenetrable forests of the Chaco, and the open savannas of the Cerrado, leading to a mosaic of overlapping natural habitats. Indeed, some of the open areas in the lowlands correspond to the western outliers of the Brazilian Cerrado (i.e., the Cerrado of the Chiquitano region, and the Cerrado of Beni; IBISCH & MÉRIDA, 2004; KILLEEN *et al*., 2006). The patchy horizontal structure of habitats of the Chiquitano region may have led to local endemism as proposed for similar and neighboring regions (COLLI *et al*., 2002; RODRIGUES & JUNCÁ, 2002; RODRIGUES *et al*., 2008), and in fact, some evidence for the distinctiveness of the Chiquitano herpetofauna has been provided by JANSEN *et al*. (2007, 2009), JANSEN & KÖHLER (2008), and CAMINER *et al*. (2017).

The *Dendropsophus rubicundulus* group (fide NAPOLI & CARAMASCHI, 1998) is currently composed of nine species. Briefly, these species can be morphologically grouped into those with an immaculate (predominant green) dorsum [*D. cachimbo* (Napoli & Caramaschi, 1999a), known only from type locality, and *D. elianeae* (Napoli & Caramaschi, 2000), distributed from east-central Paraguay to east central and southern Brazil)], and those with stripes [*D. tritaeniatus* (Bokermann, 1965), *D. araguaya* (Napoli & Caramaschi, 1998), *D. cerradensis* (Napoli & Caramaschi, 1998), *D. jimi* (Napoli & Caramaschi, 1999b), *D. rhea* (Napoli & Caramaschi, 1999b), *D. anataliasiasi* (Bokermann, 1965), *D. rubicundulus* (Reinhardt & Lütken, 1862)]. The first five of those species compose the *tritaeniatus* species complex sensu NAPOLI and CARAMASCHI (1999b) who stated that these species are always associated with permanent springs and streams (as opposed to the remaining species of the group that occur at permanent or temporary ponds), and are further characterized by two anterior parallel brown stripes from the posterior corner of the eyes to nearly the middle of the body, followed by a single sacral stripe.

In this study, we taxonomically re-evaluate populations from the eastern lowlands of Bolivia formerly assigned to *Dendropsophus tritaeniatus* (e.g., DE LA RIVA *et al*., 2000; MÁRQUEZ *et al*., 2002; JANSEN *et al*., 2011; in the following: *D.* cf. *tritaeniatus* "Bolivia") based on new available (topotypic) molecular, bioacoustic, and morphological data of the *D. rubicundulus* group (TEIXEIRA *et al*., 2013; TEIXEIRA & GIARETTA, 2015; this study). The aim of this work is to describe these populations as a new species.

Materials & Methods

Field methods and morphology

Voucher specimens were collected during several field trips from November 2004 to February 2012. Collected specimens were euthanized by injection of T61®, fixed with a preservative solution of 5 ml formalin (36%) in 1 L ethanol (94%), and stored in 70% ethanol. Tissue samples (muscle) for DNA analyses were preserved in 96% non-denaturated ethanol. Measurements are given in millimetres (mm) and were taken to the nearest 0.1 mm under a dissecting microscope using digital callipers. Webbing formulae follow MYERS & DUELLMAN (1982), and all other terminology and definitions of morphometric measurements follow WATTERS *et al*. (2016). Abbreviations for measurements used are: EN = eye to nostril distance, ED = horizontal eye diameter, UEW = upper eyelid width, FL = foot length, HL = head length, HW = head width, IOD = interorbital distance, SVL = snout–vent length, TD = tympanum diameter, and TL = tibia length. Specimens examined are listed in Appendix 1. The capitalized colors and color codes (the latter in parentheses) are those of KÖHLER (2012). Terminology of markings used in color descriptions follows KÖHLER (2012). Institutional acronyms used are those listed in SABAJ (2016) except for MNKA (= NKA) Museo Noel Kempff Mercado, Santa Cruz de la Sierra (amphibians).

Bioacoustics

Calls of frogs were recorded in the field using a digital recorder (Olympus DM-550) and external directional microphones (Sennheiser ME80/M66), using a sampling rate of 44.1 kHz (32-bit resolution) and were saved as uncompressed .wav files. Recordings were deposited in the Animal Sound Archive (www.tierstimmenarchiv.de; for accession numbers see Appendix 2). Advertisement calls were computer-analysed using the software RAVEN PRO 1.5 (BIOACOUSTICS RESEARCH PROGRAM 2011). Frequency information was obtained through Fast Fourier Transformation (FFT, width 1024 points). Spectrograms were obtained at Hanning window function with 256 bands resolution. Temporal measurements of calls such as repetition rates, duration of notes, and number of pulses, were measured on the waveforms. Graphs of the audiospectograms and waveforms were built with the SEEWAVE R package (SUEUR *et al*., 2008). Terminology in call descriptions follows KÖHLER *et al*. (2017). In contrast to TEIXEIRA & GIARETTA (2015) who used a note-centered approach sensu KÖHLER *et al*. (2017) by terming the two distinct emissions of *Dendropsophus anataliasiasi* "note

type A and B", we here follow the call-centered approach sensu Köhler *et al*. (2017) by using the terms "call type A and B" for the two types of emissions existent in *D. anataliasiasi* and the new species described herein. A series starting with emission of one call type A and subsequent calls of type B (e.g., ABBBBB) is herein referred to a "composite call". All statistics were conducted in R (R Core Team, 2017).

Molecular methods

Additionally to the 16S rRNA sequence data already used in an earlier study (Jansen *et al*., 2011; Schulze *et al*., 2015), we included new sequence data and complemented our data set with selected sequences from GenBank (see list of sequences in Appendix 3). The nomenclature used herein follows Frost (2018). Additionally, we used the terminology of candidate species suggested by Jansen *et al*. (2011) for unnamed distinct lineages in Bolivia (e.g., *Dendropsophus cachimbo* A). We selected sequences from GenBank based on the following criteria: for phylogenetic analyses we chose available sequences attributed to species of *Dendropsophus* including all 16S rRNA sequences of the *D. microcephalus* species group available, but excluding those sequences that could not be aligned to the other sequences (*D. berthalutzae* KU495201 and KU495202, *D. leali* AY819550 and MG030717, *D. microcephalus* AF308109, AF308110, AY819503, *D nanus* AY819505, EF376062, EU201104, JF973304, GQ366298, *D. robertmertensi* AY819551, *D. sartori* AY819552), and additionally one member of each of the other species groups of *Dendropsophus*, i.e., *D. columbianus* (Boettger), *D. labialis* (Peters), *D. leucophyllatus* (Beireis), *D. marmoratus* (Laurenti), *D. minimus* (Ahl), and *D. parviceps* (Boulenger) species groups. As outgroup and to root the trees we chose *Xenohyla truncata* (Izecksohn), the sister taxon of *Dendropsophus* according to Faivovich *et al*. (2005). An alignment of 494 bp containing 122 sequences in total was performed in Mega6 (Tamura *et al*., 2013) with the implemented ClustalW algorithm (Higgins *et al*., 1994). The best nucleotide substitution model for our dataset was identified using PartitionFinder2 (Lanfear *et al*., 2016), with linked branch lengths.

Phylogenetic analyses were performed with the aligned sequences and with the implemented GTR+G+I best-fit model following the Akaike Information Criterion with a correction for finite sample sizes (AICc). Bayesian Inference analysis (BI) was performed with MrBayes 3.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Runs were performed in duplicate with 1,000,000 generations each, trees sampled every 100 generations, and convergence assessed graphically. Of each run, the first 1250 trees were discarded as "burn-in".

Maximum-likelihood (ML) analysis was performed using the iqtree webserver (Trifinopoulos *et al*., 2016). To estimate clade support we run an analysis using 10,000 ultrafast bootstrap approximation (UFBoot) replicates with 10,000 maximum iterations and Minimum correlation coefficient of 0.99 plus 10,000 replicates of Shimodaira-Hasegawa approximate likelihood ratio (SH-aLRT), which proved to be accurate with a high statistical power (Guindon *et al*., 2010). We used FigTree 1.3.1 for tree viewing (http://tree.bio.ed.ac.uk/software/figtree/). We followed De Queiroz *et al*. (2002) in the definition of weak (50 – 69 bootstrap percentages), moderate (70 – 89), and strong (90 – 100) support. However, we emphasize that the goal of this study is to call attention to the degree of genetic differentiation among populations, and not to provide an in-depth or comprehensive analysis of phylogenetic relationships within *Dendropsophus* at any level. This would require more comprehensive data sets, e.g., including additional molecular markers.

For members of the *Dendropsophus rubicundulus* group including additional species that are positioned in the same clade according our analyses (*D. cruzi*, *D. juliani*, *D. juliani* A, and *D. sanborni*, see below) we estimated evolutionary genetic divergence for the 16S gene among sequences, computing uncorrected pairwise p-distances with Mega 6 (Tamura *et al*., 2013) to assess the degree of intra- and interspecific differences, using a Bootstrap estimation method of 10,000 replications.

Results

The analysis of our molecular data revealed several distinct genetic clusters among *Dendropsophus* species (Fig. 1 and 2). The recovered phylogeny shows the candidate species within a major clade containing species of the *D. rubicundulus* species group plus *D. cruzi*, *D. juliani*, *D. juliani* A, and *D. sanborni*. This clade received weak support by ML (69%) and by Bayesian analyses (62 posterior probabilities). Within this clade, in the ML analysis our candidate species is sister to a clade formed by *D. sanborni* along with *D. cachimbo* A and *D. elianeae* (Fig. 1). In the Bayesian analysis our candidate species is sister to *D. cachimbo* (Fig. 2). In both cases, our candidate species forms a group with strong support (ML: 100%; Bayesian: 1.0), and is separated by genetic distances to the other members of the clade as follows (p-distances, followed by K2-distance in parentheses of closest relatives; see also Tab. 1 for more details): *D.* cf. *tritaeniatus* "Bolivia" differs from *D. anataliasiasi* (mean) by 7.2 (7.7)%, *D. cachimbo* (UFU 1632) by 6.1 (6.4)%, from *D. cachimbo* A (mean) by 5.7 (6.0)%, from *D. elianae* (mean) by 5.7 (6.0)%, and *D. sanborni* (AY843663) by 5.1 (5.3)%. The voucher specimen of the sequence AY843661 of *D. rubicundulus* from GenBank most probably was misidentified and actually belongs to *D. elianeae* instead of *D. rubicundulus* according to (1) the position in the tree and (2) 7.5% genetic p-distance from AY843661 to the sequence of *D. rubicundulus* from Serra do Cipó (ca. 60 km distant from type locality) used herein.

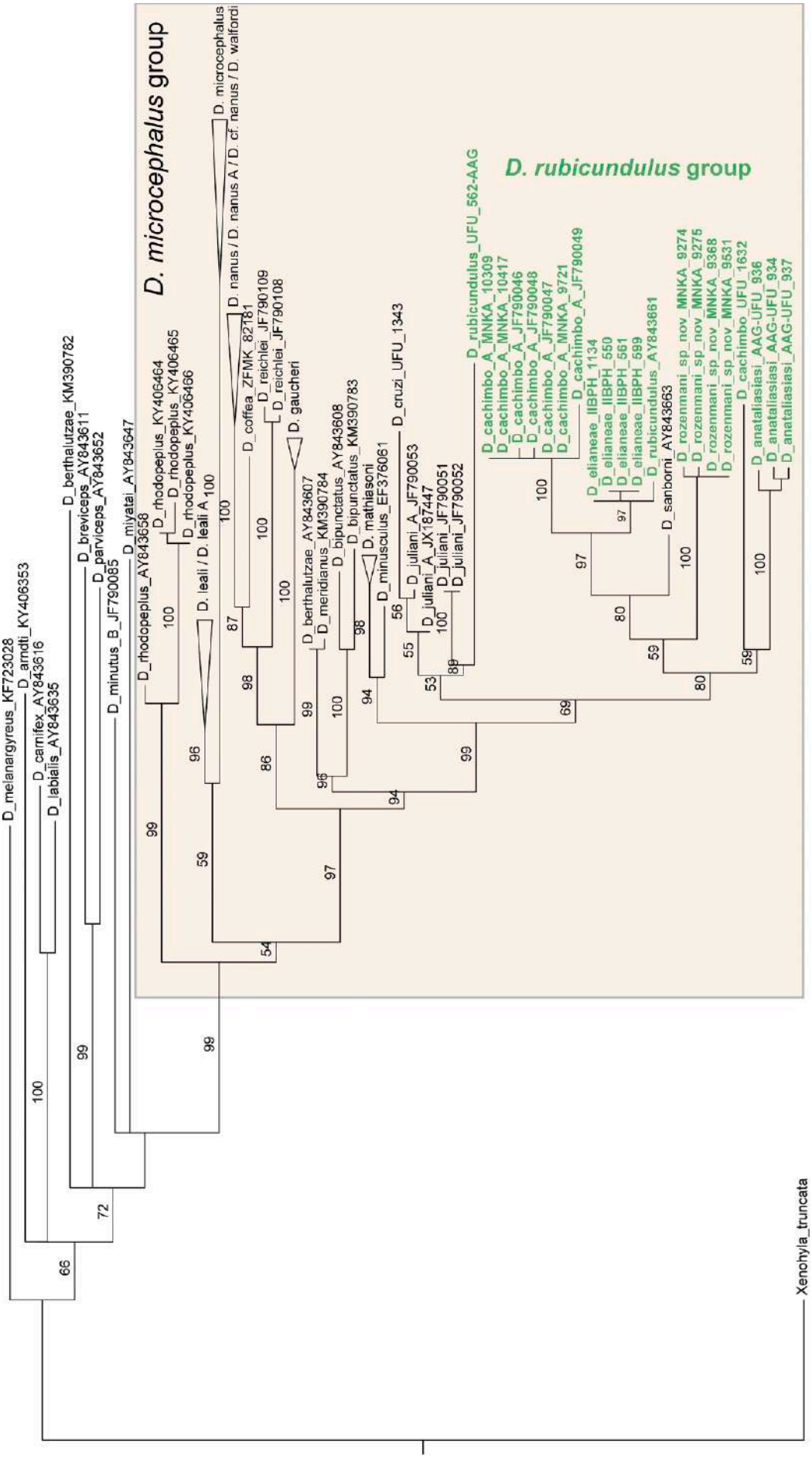

Fig. 1. Phylogenetic tree of *Dendropsophus* species based on Maximum Likelihood analysis of partial sequences of the 16S rRNA gene (494 bp). *Xenohyla truncata* was used as outgroup. Numbers at nodes show support from bootstrap analysis (not shown if bootstrap values < 50). Clade containing species of the *Dendropsophus microcephalus* species group marked. Numbers after species names refer to GenBank accession numbers (see Appendix 3).

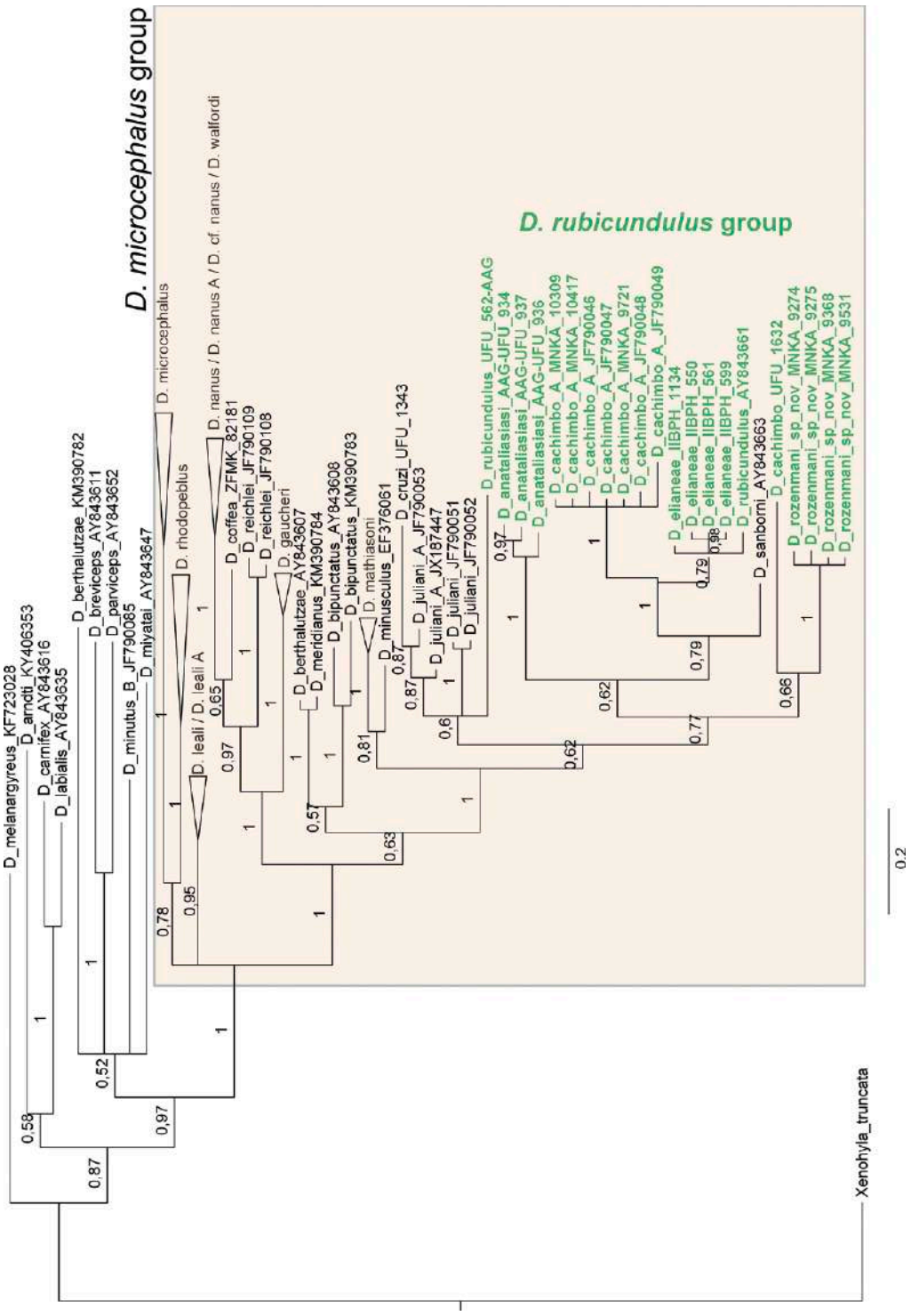

Fig. 2. Phylogenetic tree of *Dendropsophus* species based on Bayesian analysis of partial sequences of the 16S rRNA gene (494 bp). *Xenohyla truncata* was used as outgroup. Numbers at nodes show support from Bayesian posterior probabilities (not shown if posterior probability < 0.50). Clade containing species of the *Dendropsophus microcephalus* species group marked. Numbers after species names refer to GenBank accession numbers (see Appendix 3).

Regardless of the affiliation to any species group (see discussion below) we describe the populations *Dendropsophus* cf. *tritaeniatus* "Bolivia" as a new species due to divergences from other species in the genus in morphology, bioacoustics and molecular data.

Dendropsophus rozenmani sp. nov.

ZOOBANK urn:lsid:zoobank.org:act:8D7B2428-4473-46AD-AE1F-6E8CEE4441F7 (Figures 3, 4, 6, Appendix 4)

Dendropsophus tritaeniatus – Jansen *et al*. (2011)
Hyla tritaeniata – Reichle & Köhler (1996), Reichle (1997), Reichle & Köhler (1998), De la Riva *et al*. (2000), Márquez *et al*. (2002)

Holotype. MNKA 11504, adult male, Caparú Ranch, outpost Las Lagunitas (-14.836217, -61.177783, 185 m asl), Provincia Velasco, Department of Santa Cruz, Bolivia, collected on 17 January 2006 by M. Jansen; original field tag MJ 805.

Paratypes. All (4 specimens) from Caparú Ranch, outpost Las Lagunitas, Provincia Velasco, Department of Santa Cruz, Bolivia: MNKA 9922, SMF 88450, -14.812300, -61.171967, 184 m asl,

Table 1. Estimates of evolutionary divergence of *D. rozenmani* sp. nov. to other species of the clade (Fig. 1 and 2). The pairwise genetic distances between sequences or mean genetic divergence between groups (when more than one sequence referred to the same species were available) are shown.

	p-Distance	K2-distance
D. anataliasiasi	0.072	0.077
D. cachimbo (UFU 1632)	0.061	0.064
D. cachimbo A (mean)	0.057	0.060
D. cruzi (UFU 1343)	0.061	0.064
D. elianae (mean)	0.057	0.060
D. juliani (NMP 6V72799)	0.051	0.053
D. juliani A	0.056	0.059
D. rubicundulus (UFU 562)	0.091	0.097
D. sanborni (Entre Rios, Brazil, AY843663)	0.051	0.053

collected on 18 February 2012 by M. JANSEN and O. BARROSO; SMF 88490, -14.812500, -61.169050, 160 m asl, collected on 19 February 2012 by M. JANSEN and O. BARROSO; MNKA 9531, male, collected on 3 December 2009 by A. SCHULZE.

Referred specimens. Seven specimens. BOLIVIA: Beni: Los Lagos, -12.768367, -65.815250, 136 m asl: SMF 88449, SMF 88491, SMF 88453, MNKA 9368, MNKA 9276–78.

Diagnosis. A species of the genus *Dendropsophus* that is assigned to the *D. microcephalus* species group based on the results of a molecular analysis of a fragment of the 16S rRNA gene, general morphological appearance, and overall call structure. Further, it is tentatively assigned to the *D. rubicundulus* group (fide NAPOLI & CARAMASCHI, 1998) based on morphological and molecular data awaiting further studies on the monophlyly of this group. *Dendropsophus rozenmani* is distinguished from other species of *Dendropsophus* by the following combination of characters: (1) small size, SVL 18.7–21.1 mm in adult males and 19.6–23.2 mm in females; (2) head longer than wide; (3) snout short, rounded in dorsal view, acute to protruding in lateral view; (4) canthus rostralis rounded, loreal region slightly concave; (5) tympanum indistinct or not visible; (6) skin on dorsal surfaces smooth; (7) in life, dorsal ground coloration brown, with two anterior parallel and straight, dark brown stripes and a middorsal sacral stripe; (8) lateral limits of dorsal coloration above tympanum; (9) composite advertisement call consisting of two types of pulsed calls (type "A" and type "B") that are emitted usually in series starting with one call type A and followed by 1 to 12 calls type B; call type A is 42 seconds in average long and has 3–9 pulses; type B is in average 12 ms long and has 1–3 pulses; dominant frequency of both call types is around 4100 Hz.

Comparisons. External morphology and comparisons of a sequence of the 16S rRNA gene indicate that *Dendropsophus rozenmani* sp. nov. is related to species currently placed in the *D. rubicundulus* group (fide NAPOLI & CARAMASCHI, 1998).

In external appearance, *Dendropsophus rozenmani* sp. nov. is most similar to *D. tritaeniatus*, mainly because of similar dorsal markings composed of two, well defined straight and parallel anterior dorsal brown stripes, and a middorsal sacral stripe (NAPOLI & CARAMASCHI, 1999b) [character states of *D. rozenmani* sp. nov. in brackets in the following]. However, *D. tritaeniatus* as well as all the other species of the *D. rubicundulus* group, has a green dorsal ground coloration [brown in *D. rozenmani* sp. nov.]. In addition, *D. tritaeniatus* is readily distinguished from *D. rozenmani* sp. nov. by having only one single call type [versus two different call types forming a composite call (TEIXEIRA *et al*., 2013; JANSEN, own data)]. Such qualitative characters in anuran advertisement calls have been suggested to be very valuable for delimitation of different species (see KÖHLER *et al*., 2017). Besides this qualitative difference, *D. tritaeniatus* has 3.4 pulses in average (2–4) per call [5.5 pulses in average (3–9) per call type A; 1.8 pulses (1–3) per call type B], and an average of 32 ms (17–49) call duration [42 ms (18–66) in call type A; 12 ms (4–23) in call type B]. Furthermore, *D. tritaeniatus* differs from *D. rozenmani* sp. nov. its habitat preferences: *D. tritaeniatus* is associated with permanent springs and streams (NAPOLI & CARAMASCHI, 1998) whereas *D. rozenmani* sp. nov. inhabits permanent and temporary ponds as well as inundated areas of savannas (Fig. 4B).

The other species of the *rubicundulus* group having a striped dorsal pattern (*D. anataliasiasi*, *D. araguaya*, *D. cerradensis*, *D. jimi*, *D. rhea*, *D. rubicundulus*) differ from *D. rozenmani* sp. nov. by exhibiting the following characters (NAPOLI & CARAMASCHI, 1998, 1999a,b, 2000): *D. anataliasiasi*, *D. araguaya* *D. cerradensis*, *D. jimi*, *D. rhea*, and *D. rubicundulus* have a green dorsal ground coloration in life [brown], and a violet dorsal ground coloration in preservative [brown]. In addition, *D. jimi*, and *D. rubicundulus* have a single advertisement call type [composite call]; *D. anataliasiasi* and *D. rubicundulus* do not have a single sacral stripe [present], and sometimes these two species have a middorsal pin stripe [absent]; *D. anataliasiasi* has two anterior divergent dorsal brown stripes, fused with two brown sacral stripes, or, if parallel, stripes are irregular or marked with blotches [two straight, well defined and parallel anterior dorsal brown stripes, and a middorsal sacral stripe]; *D. rubicundulus* has a head as long as wide [longer than wide]; *D. araguaya* has interrupted dorsal stripes that might diverge [well defined and parallel stripes]; *D. cerradensis* has dorsal stripes that always diverge [parallel stripes]; *D. jimi* has irregular dorsal stripes [well defined]; *D. rhea* has divergent dorsal stripes [parallel].

Two species of the *rubicundulus* group, namely *Dendropsophus cachimbo* and *D. elianeae*, as well as *D. cachimbo* A, another candidate species fide JANSEN *et al*. (2011), are readily distinguished from *D. rozenmani* sp. nov. by having an immaculate green dorsum [striped dorsal pattern on brown dorsal ground color]; the lateral limits of the dorsal coloration below the tympanum [above]; advertisement call composed of only a single call type

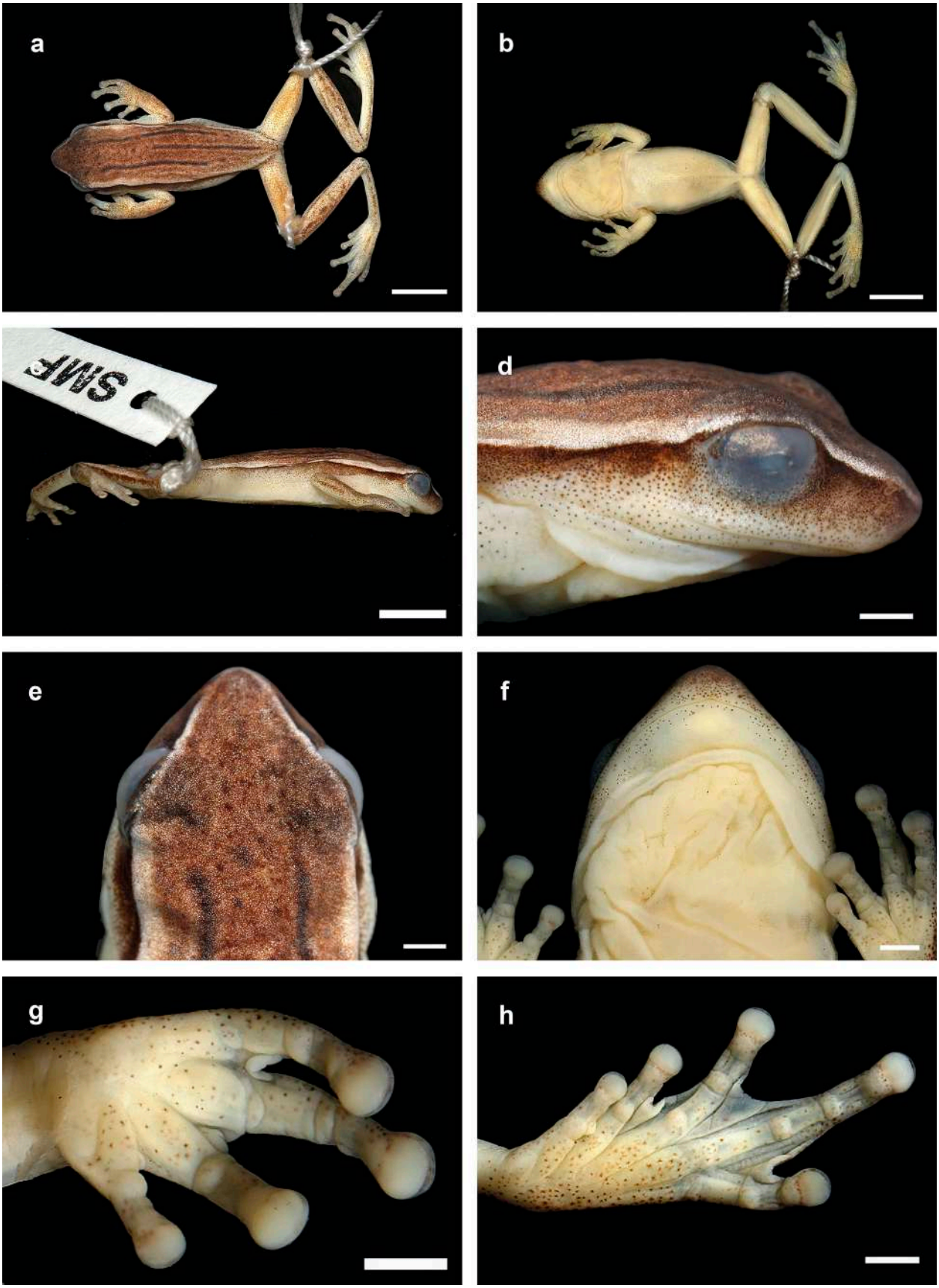

Fig. 3. Holotype of *Dendropsophus rozenmani* sp. nov. (MNKA-11504): (a) dorsal view (b) ventral view (c) lateral view (d) lateral view of head (e) dorsal view of head (f) ventral view of head (g) ventral surface of right hand (h) ventral surface of left foot. Scale bars = 5.0 mm in a – c and 1.0 mm in d – h. Photos: G. Köhler.

Table 2. Selected measurements and proportions of type material of *Dendropsophus rozenmanni*. Range is followed by mean value and standard deviation in parentheses. For abbreviations see text.

		D. rozenmanni (5 males, 2 females)
SVL	males	18.7–21.1 (19.7±0.9)
	females	19.6–23.2 (21.4±1.8)
TL/SVL	males	0.474–0.506 (0.489±0.012)
	females	0.456–0.578 (0.517±0.086)
FL/SVL	males	0.295–0.353 (0.332±0.024)
	females	0.289–0.381 (0.335±0.065)
HW/ SVL	males	0.265–0.296 (0.280±0.012)
	females	0.263–0.296 (0.280±0.025)
HL/SVL	males	0.246–0.299 (0.283±0.019)
	females	0.251–0.287 (0.269±0.025)
EN/HL	males	0.147–0.202 (0.175±0.019)
	females	0.191–0.236 (0.213±0.032)
IOD/HW	males	0.285–0.384 (0.327±0.034)
	females	0.318–0.457 (0.388±0.099)

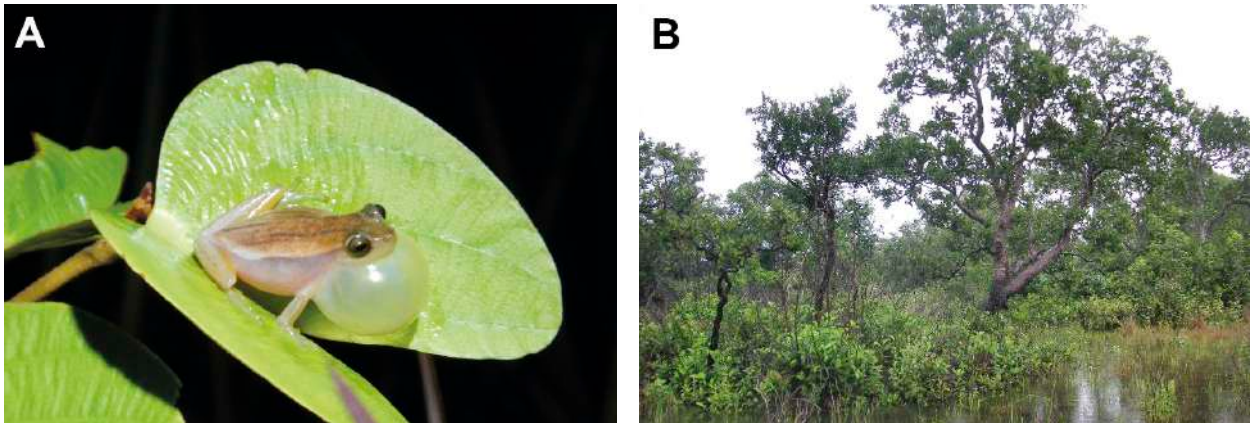

Fig. 4. (A) Calling paratype *Dendropsophus rozenmani* sp. nov. (MNKA 9922); (B) temporary inundated Cerrado at the type locality Caparú Ranch, Bolivia, the typical habitat of *Dendropsophus rozenmani* sp. nov. Photos: M. Jansen

[two call types forming a composite call]. In addition, *D. elianeae* has a larger SVL of around 20 to 26 mm in males and 25 to 26 mm in females [around 19 to 21 mm in males and 23 mm in females] (NAPOLI & CARAMASCHI, 1999a,b, 2000; MARTINS & JIM, 2004; JANSEN *et al*., 2011; TEIXEIRA & GIARETTA, 2015; JANSEN own data).

Because *Dendropsophus cruzi* (Pombal & Bastos, 1998), *D. juliani* Moravec, Aparicio & Köhler, 2006, *D. juliani* A, and *D. sanborni* (Schmidt, 1944) are nested in the same clade (Fig. 1 and 2; see discussion), we herein include these species in the comparisons with the new species. *Dendropsophus cruzi* mainly differs from *D. rozenmani* sp. nov. by having a brown dorsum with variable, but often X-shaped dorsal pattern [brown dorsum with well-defined stripes], a small SVL of 16 to 20 mm in males [around 19 to 21 mm in males], as well as in advertisement call composed of a single note or type with two pulses [two call types with up to 10 pulses]. *Dendropsophus juliani* mainly differs from *D. rozenmani* sp. nov. by having a pale yellowish-tan to reddish-tan dorsum with inconspicuous dark brown markings [brown dorsum with well-defined stripes]. *Dendropsophus juliani* A mainly differs from *D. rozenmani* sp. nov. by having a reddish-tan dorsum without markings [brown dorsum with well-defined stripes]. *Dendropsophus sanborni* mainly differs from *D. rozenmani* sp. nov. by having a brown dorsum with fine punctuations [brown dorsum with well-defined stripes], an average SVL of 16 mm in males [20 mm] (SCHMIDT, 1944; POMBAL & BASTOS, 1998; MARTINS & JIM, 2003; MORAVEC *et al*., 2006; JANSEN *et al*., 2011).

Similar to *D. anataliasiasi* and *D. rozenmani* sp. nov., two different call types were reported for *D. sanborni* ("introductory note" and "typical advertisement call" in chorus situations, MARTINS & JIM, 2003) and *D. juliani* ("initial note" and "subsequent notes", MORAVEC *et al*., 2006). Indeed, following the call centered approach of KÖHLER *et al*. (2017), we argue that the different "note types" in *D. sanborni* and *D. juliani* actually are different call types. However, because such "initial" or "introductory" calls are often skipped and therefore not strictly linked, we doubt that the call types in *D. sanborni* and *D. juliani* form a composite call (in *D. rozenmani* sp. nov., call types "A" and "B" are usually emitted together, and thus, might, have a straight functional linkage).

Table 3. Some characteristics of advertisement calls of *D. rozenmani* sp. nov. (365 calls; n=10 individuals) and related species of the *D. rubicundulus* group where call data are available. Range followed by mean ± standard deviation in parentheses. See text for more details.

Bioacoustic traits	***D. rozenmani* sp. nov.** (n=10)		***D. anataliasiasi*** (n=10)		***D. cachimbo*** (n=14)	***D. elianeae*** (n.d.)*	***D. jimi*** (n.d.)*	***D. rubicundulus*** (n=13)	***D. tritaeniatus*** (n=5)
	type A	type B	type A	type B					
call duration [ms]	42±9 (18–66)	12±3 (4–23)	52.1±4.6 (21–69)	22.7±3.1 (13–34)	15.0±1.9 (5–34)	18.0±2.9 (14–26)	52.4±9.6 (37–72)	19.3±3.2 (10–32)	32±4.8 (17–49)
pulses per call	5.5±**1.1** (3–9)	1.8±**0.5** (1-3)	7.0±0.6 (5–9)	3.2±0.4 (2–4)	2.1±0.2 (1–3)	3±1 (2–5)	4±2 (3–9)	3.6±0.4 (2–5)	3.4±**0.2** (2–4)
pulse duration[ms]	5±**1** (2–10)	5±**2** (2–17)	7.6±**0.2** (5–10)	6.9±**0.3** (5–13)	7.5±**0.7** (4–17)	4.9±**0.8** (2–6)	6.0±**1.0** (3–6)	5.3±**0.4** (2–11)	9.9±**1.0** (3–14)
pulse rate [pulses per second]	131±17 (82–167)	154±41 (43–250)	135.2±8.7 (95.2–381.0)	142.9±6.5 (90.9–200.0)	148.2±18.7 (66.7–333.3)	n.d.	n.d.	190.4±17.7 (125–300)	107.3±8.6 (82–133)
Dominant frequency [Hz]	4136±211 (3531–4593)	4135±209 (3531–4565)	4024±113.6 (3843–4312)	4023±118 (3843–4312)	4166±153.2 (3890–4406)	3200–3300	3900	3730±235.8 (3093–4171)	3191±104.3 (2924–3533)
Source	this study		Teixeira & Giaretta (2015)		Teixeira & Giaretta (2015)	Martins & Jim (2004)	Martins & Jim (2004)	Teixeira & Giaretta (2015)	Teixeira *et al.*, (2013)

n.d. = no data; * = in chorus situation

Therefore, the existence of a composite call in *D. rozenmani* sp. nov. distinguishes this species readily from *D. juliani* and *D. sanborni*. Nevertheless, the "typical advertisement call" of *D. sanborni* differs quantitatively from the one of *D. rozenmani* sp. nov. by having a dominant frequency of 4000 to 5500 Hz (Martins & Jim, 2003) [3575–4593]; in average 5.0 (3–8) pulses [call type A: 5.5 (3–9) pulses per call; call type B: 1.8 (1–3)], and a mean call duration of 38 ms (26–65) [call type A: 42 ms (18–66), call type B: 12 ms (4–23)]. Explicit values for the "initial note" (=call, see above) of *D. juliani* were not given, but both note (call) types have 3.8 pulses in average (3–6) [call type A: 5.5 (3–9) pulses per call; call type B: 1.8 (1–3)], and mean note (call) duration is 17.6 ms (11–26) [call type A: 42 ms (18–66), call type B: 12 ms (4–23)]. See Tab. 3 for an overview of comparative bioacoustic data.

Description of holotype. Adult male as indicated by presence of vocal slits and large vocal sac; SVL 21.1; head about same width as body, longer than wide (HW/HL = 0.86); snout short, in dorsal view rounded, rounded in lateral view; distance from nostril to eye less than diameter of eye (EN/ED = 0.59); canthus rostralis distinct, rounded; loreal region slightly concave, sloping to upper lip; nostrils barely protuberant, openings directed laterally; eye quite large (ED 2.3); tympanic membrane round, indistinct, hardly visible, its diameter more than one third of eye length; tympanic annulus not visible; supratympanic fold absent; UEW = 1.65; IOD = 1.7; forelimbs not hypertrophied; abbreviated axillary membrane present, extends along proximal upper arm; minute ulnar tubercles absent; finger discs round, wider than digit (Finger III: digit width/disc width = 0.72); relative length of fingers I<II<IV<III; webbing vestigial between Finger I and II, basal between Fingers II to IV; remaining webbing formula I 2.5–3 II 2+–3 III 2⅔–2.5 IV; distal subarticular tubercle in fourth finger not bifid; supernumerary tubercles not visible; palmar tubercle flat, elliptical; subarticular tubercle large, rounded; nuptial excrescences absent; hind limbs long, slender, lacking calcar tubercles, tarsal fold absent; TL = 10.7; FL = 8.0; toes moderately long, toe discs round (Toe IV: toe width/disc width = 0.82); relative

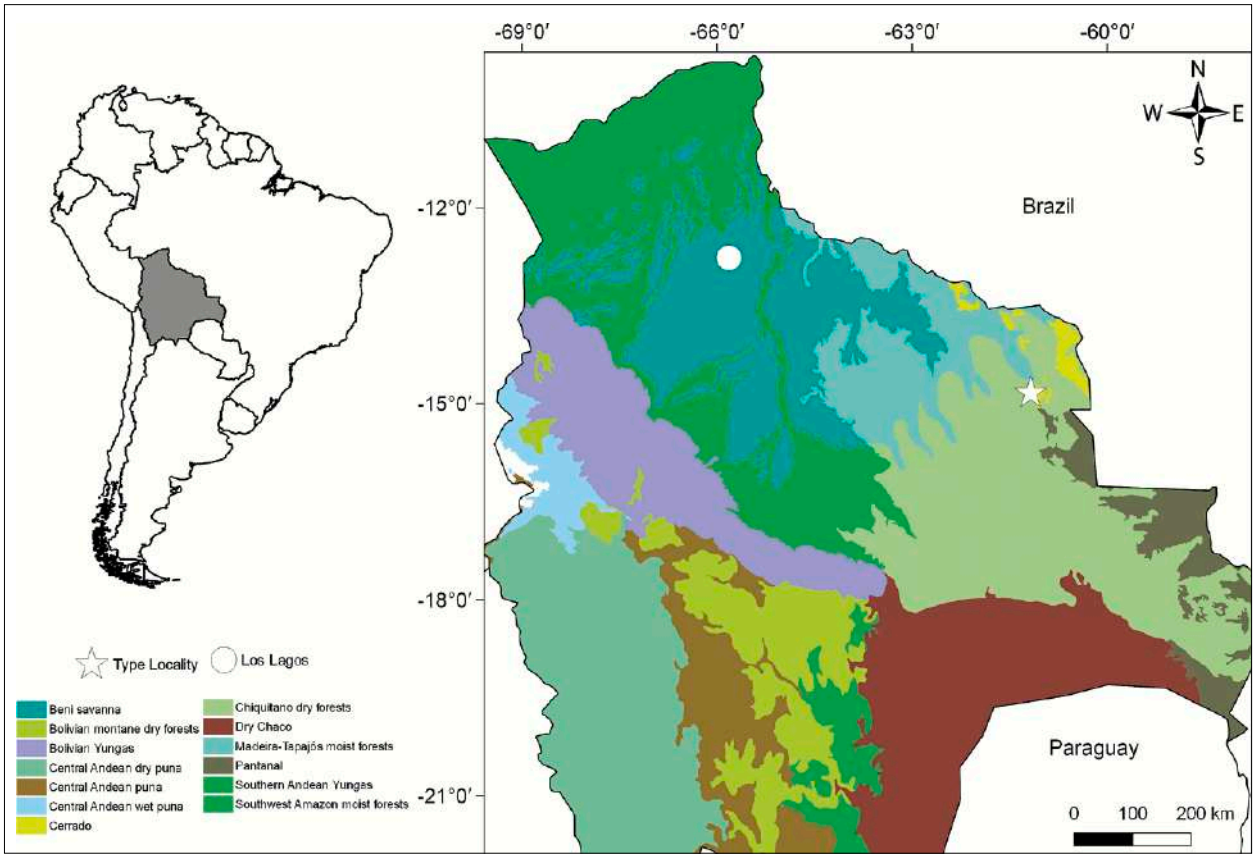

Fig. 5. Map showing type locality (star) and locality of referred specimens (circle) of *Dendropsophus rozenmani* sp. nov.

length of toes I<II<III<IV<V; outer metatarsal tubercle not visible; inner metatarsal tubercle large, flat, elliptical; subarticular tubercles large, rounded; supernumerary tubercles minute, subconical; toe webbing formula I 2–2.5 II 1.5–3 III 1.75–3 IV 2+–1.5 V; dorsal surfaces of head and ventral surfaces of limbs smooth; dorsum with scattered minute tubercles; skin on belly coarsely granular; cloacal opening directed posteriorly at upper level of thighs; cloacal sheath wrinkled and long, covering almost the entire cloacal opening; cloacal folds present; vomerine odontophores present; choanae clearly visible; tongue approximately round, clearly notched and free posteriorly; pectoral fold absent; vocal slit extends from midlateral base of tongue nearly to angle of lower jaw; vocal sac single, median, folds visible in gular region.

Coloration after almost nine years preservation in 70% ethanol was as follows: Dorsal surface of head Verona Brown (37); dorsal surface of body Raw Umber (23), grading into Pale Pinkish Buff (3) laterally and with Sepia (279) longitudinal stripes; hidden portions of limbs Pale Pinkish Buff (3) with a suffusion of Yellow Ocher (15); a Burnt Sienna (38) longitudinal lateral line along body, heavily suffused with Verona Brown (37) below; ventral surfaces Pale Pinkish Buff (3).

Variation. The paratypes agree well with the holotype in terms of general morphology and coloration. For variation of selected morphometric characters see Tab. 2. Coloration in life of an adult male (MNKA 9922) was recorded as follows: Dorsal surfaces of head, body, and non-hidden portions of limbs Dark Yellow Buff (54) with a suggestion of Dark Salmon Color (59); lateral surface of head Straw Yellow (53); lateral surface of body Pinkish White (216), suffused with Drab-Gray (256); fingers and distal portions of toes as well as dorsal surface of digital discs Dark Yellow Buff (54); iris Kingfisher Rufous (296).

Vocalization. The composite advertisement call consists of two distinct types of pulsed calls. Call type A (Fig. 5A) is usually the initial call followed by a series of calls of type B (Fig. 5B), e.g. ABBBBB (see example call in Fig. 6). A composite call (A+nB) consists of one call type A followed by 1–12 calls type B (2.48±2.27, n=114 composite calls from 9 individuals). However, call type A can be emitted solely as well.

We recorded and analysed advertisement calls of 10 individuals, including the holotype and three paratypes (MNKA 9922, SMF 88450, SMF 88490; Tab. 3). All but one emitted composite calls, resulting in 114 composite calls composed of 114 calls type A and 284 calls type B from 9 individuals. Additionally, 45 solely emitted calls type A from all 10 individuals were included in the analyses. In total, 5 to 30 (16.77±8.53) calls type A and 0 to 64 (29.22±19.48) calls type B were analysed per individual. Call duration of a composite call was 143 to 1563 ms (337 ms±276). In a composite call, intervals between calls of type A and B or B and B were 77–119 ms (99 ms

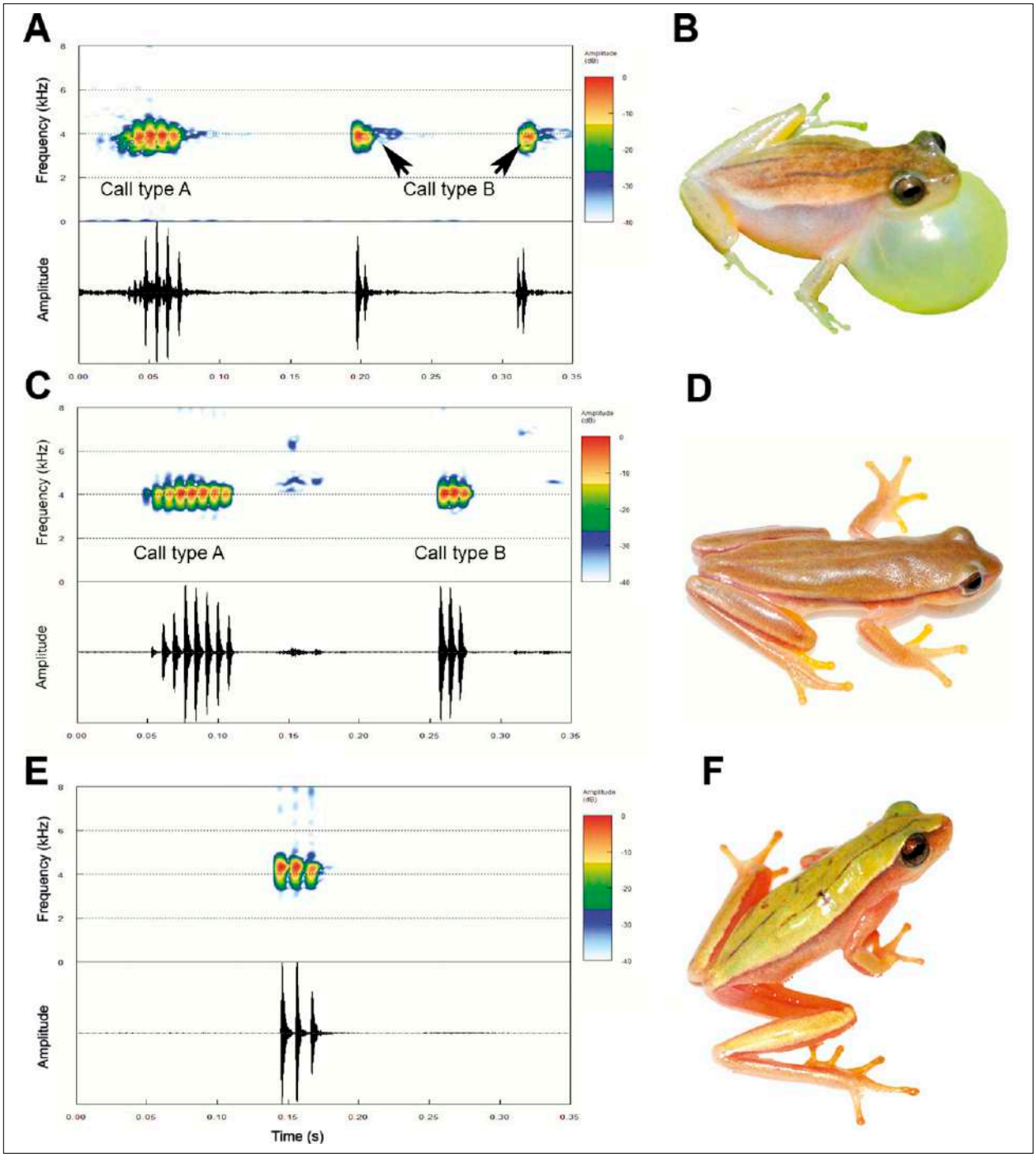

Fig. 6. Audiospectrogram (above) and waveform (below) of advertisement calls and fotos in live of three closely related species of the *D. rubicundulus* group: (A) advertisement call of paratype SMF 88490 *D. rozenmani* sp. nov., recorded on 19 February 2012 by Martin Jansen; air temperature 25.6°C; (B) MNKA 9922 in live; photo: Martin Jansen; (C) topotypical advertisement call of *D. anataliasiasi*, recorded on 26 November 2011 by Bernardo Teixeira; air temperature 28°C (Teixeira *et al*. 2015); (D) *D. anataliasiasi* in live; photo: Ariovaldo A. Giaretta; (E) advertisement call of *D. tritaeniatus*, recorded on 24 November 2012 by Bernardo Teixeira; air temperature 20.5°C (Teixeira *et al*. 2013); (F) *D. tritaeniatus* in live; photo: Thiago R. de Carvalho.

±9.7). The interval between a composite call (e.g., ABBB interval ABB interval ABB) or solely emitted calls of type A was 0.93–8.40 sec (3.06 sec±1.28; n=126 intervals measured from 10 individuals). Numerical call parameters of call type A are as follows (range followed by mean±standard deviation in parentheses): call duration 18–66 ms (42±9; n=159); pulses per call 3–9 (5.45±1.14; n=159); pulse duration 2–10 ms (5 ms; ±1; n=579); pulse rate 82–167 pulses/sec (131± 17; n=159); dominant frequency 3531–4565 Hz (4135± 209; n=159). Numerical call parameters of call B are: call duration 4–23 ms (12±3; n=284); pulses/call 1–3 (1.8±0.5; n=284); pulse duration 2–17 ms (5 ms; ±2; n=253); pulse rate 43–250 pulses/sec (154±41;

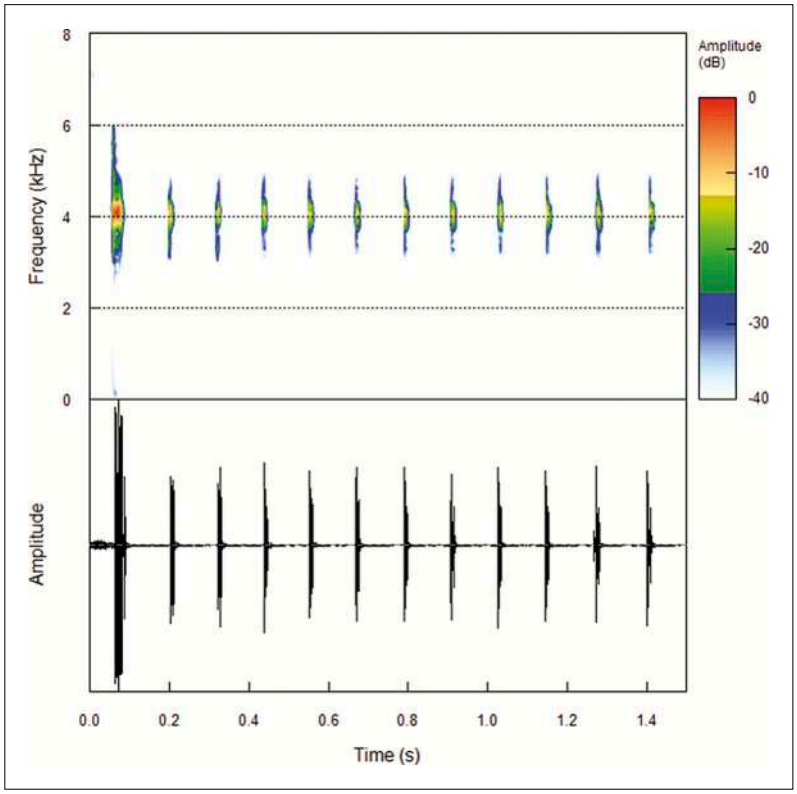

Fig. 7. Audiospectrogram (above) and waveform (below) of a composite advertisement call of *Dendropsophus rozenmani* sp. nov. (paratype SMF 88490). Same data as in Figure 6A.

n=284); dominant frequency 3575–4593 Hz (4136± 211; n=284). Fig. 8 shows the distribution of values in histograms.

Distribution, habitat, and conservation status. *Dendropsophus rozenmani* sp. nov. is known from two localities, one in the Department of Santa Cruz, Bolivia (Caparú Ranch), and a second locality (Los Lagos) in the Department of Beni. However, we assume that other authors refer to *Dendropsophus rozenmani* sp. nov. when reporting recordings of *Hyla tritaeniata* from the Estación Biológica del Beni (EBB) (REICHLE & KÖHLER, 1996; REICHLE, 1997; REICHLE & KÖHLER, 1998; DE LA RIVA *et al*., 2000; MÁRQUEZ *et al*., 2002).

The type locality (Fig. 5), the cattle ranch Caparú, is situated in the contact zone of the ecoregions Cerrado, Pantanal, Madeira-Tapajós moist forests, and Chiquitano dry forest (sensu DINERSTEIN *et al*., 2017). The average annual precipitation varies between 1100 and 1500 mm, and average annual temperature is 25–30°C. The second locality, Los Lagos, as well as the Estación Biológica del Beni (EBB) is located in the ecoregion Beni savannas i (sensu DINERSTEIN *et al*., 2017) and the dominant vegetation type consists of open Cerrado savannas.

Other hylid species found in sympatry at Caparú Ranch (CAP) and Los Lagos (LL) include *Dendropsophus* cf. *nanus* (CAP, LL), *D. cachimbo* A (CAP; fide JANSEN *et al*., 2011), *D.* cf. *minutus* (CAP: lineage 33 fide GEHARA *et al*., 2014; LL: lineage 30), *Boana raniceps* (CAP, LL), *Scinax fuscomarginatus* (CAP, LL), *S. madeirae* (CAP, LL) and at least two species of the *S. ruber* clade (CAP, LL).

All individuals included in the study herein were found in recently flooded Cerrado savannas (Fig. 4B) or along lakeshores. We assume this species to be associated with the Pantanal Flooded Savannas, Moxos Plain Flooded Savannas, and the Cerrado of Beni and Chiquitano (fide IBISCH & MÉRIDA, 2004) and is, thus, restricted to the these regions in the eastern lowlands of Bolivia. Reproductive mode and larvae are unknown.

Etymology. The specific name is a patronym for JAIME ROZENMAN, one of the owners of Caparú Ranch, Bolivia, in recognition of his long-lasting logistic support of taxonomic research on his property, and in honor of his great effort for conservation of the local flora and fauna.

Discussion

Dendropsophus rozenmani is morphologically most similar to the species of the *D. tritaeniatus* complex, because of its striped dorsal pattern. NAPOLI & CARAMASCHI (1998, 1999a,b) stated that *D. tritaeniatus* should be seen as a complex of species due to large intra- and inter-populational variations (without giving details on variation). The eastern Bolivian lowland populations indeed could be separated by morphology, DNA, their habitat, and also by bioacoustics. Advertisement calls have been described for the following species of the *D. rubicundulus* group: *D. anataliasiasi* (TEIXEIRA & GIARETTA, 2015),

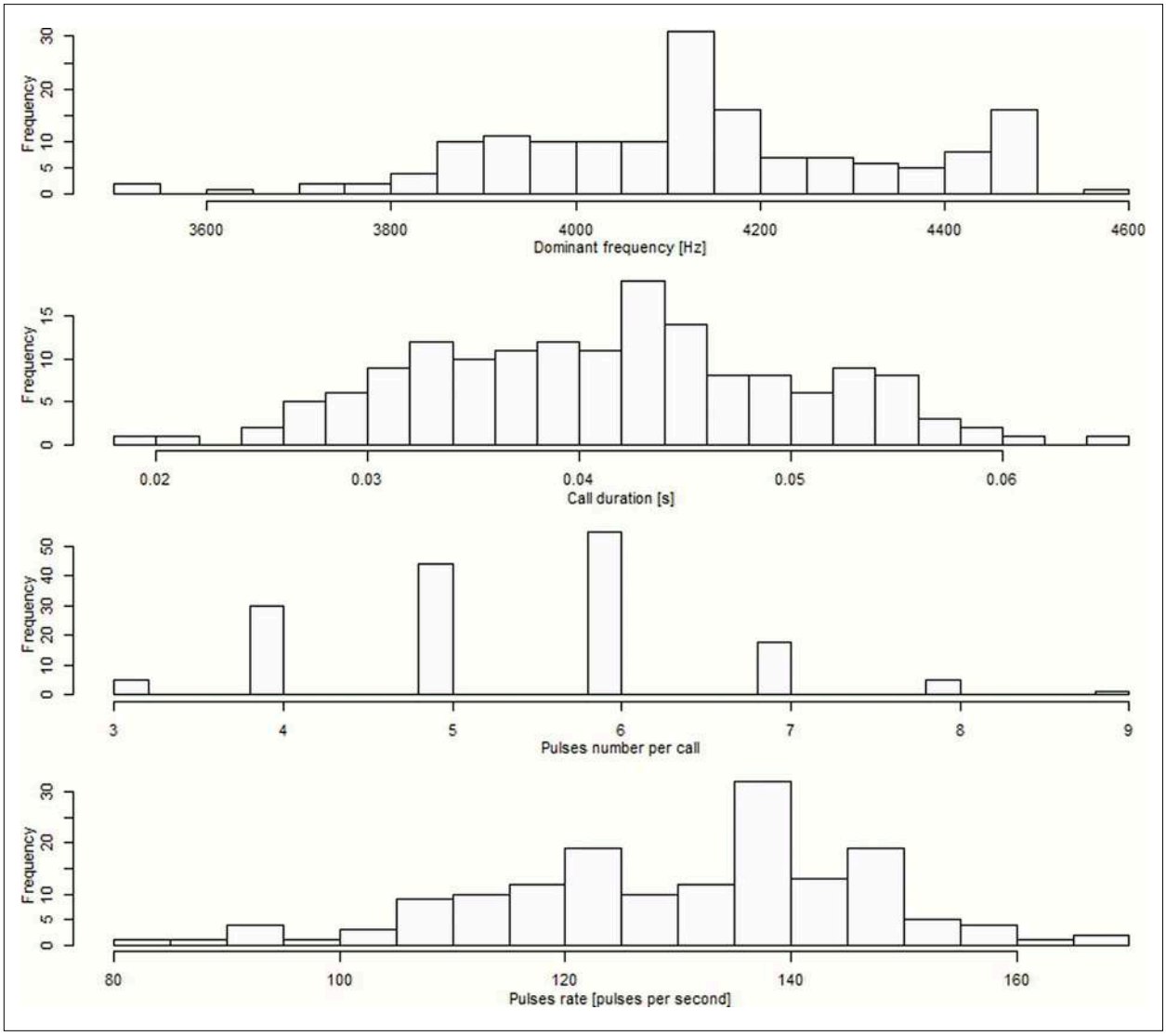

Fig. 8. Histograms showing distribution of values of dominant frequency, call duration, pulses number, and pulse rate of 159 calls type A from 10 individuals of *D. rozenmani*. See text for details.

D. cachimbo (Teixeira & Giaretta, 2015), *D. elianeae* (Martins & Jim, 2004), *D. jimi* (Martins & Jim, 2004), *D. rubicundulus* (Cardoso & Vielliard, 1985; Teixeira & Giaretta, 2015), and *D. tritaeniatus* (Teixeira *et al*., 2013). Among these, *D. anataliasiasi* and *D. rozenmani* sp. nov. are unique by having a composite call consisting of two types of calls (this study, Teixeira & Giaretta, 2015). In their comprehensive review of the use of advertisement calls in anuran taxonomy, Köhler *et al*. (2017) suggested that qualitative call differences, such as number of different call types, are robust indicators in acoustic delimitation of anuran species. Indeed, bioacoustical methods have proven to be very valuable in the delimitation of species (e.g., Teixeira *et al*., 2013; Teixeira & Giaretta 2015; Caminer *et al*., 2017), and especially qualitative acoustic characters clearly evidenced the distinctiveness of *Dendropsophus rozenmani*. Besides, the occurrence of only few species of the *rubicundulus* group with a composite call raises questions on the call evolution within that group. Similar as proposed for species related to *D. elegans* (Forti *et al*., 2017), the respective phylogenetic positions of *D. anataliasiasi* and *D. rozenmani* sp. nov. (not directly related) let assume that the composite call in these two species have independent origins. Regarding the *microcephalus* group, the existence of two call types is known in only few species as noted by Köhler & Lötters (2001; e.g., in *D. juliani*, *D. joannae*, *D. microcephalus*, *D. nanus*, and *D. sanborni*). However, in how far these call types actually present a composite call, i.e., in how far these two call types are actually functionally linked with each other (as they most probably are in *D. rozenmani* sp. nov. and *D. anataliasiasi*), or, alternatively, if they are independently related to different social contexts, remains to be studied. As an example for the latter, *D. nanus* emits longer ("initial") calls as first of a call series that might be skipped as well (Jansen, pers. obs.), probably due to different densities of calling males.

Nevertheless, the methodological potential of bioacoustical analyses for frog species delimitation is still not

yet exploited (KÖHLER *et al*., 2017). However, although studies on individual call variation, as well as descriptions of anuran call repertoires are important for taxonomy, they are still scarce (e.g. BEE *et al*., 2013a, b; JANSEN *et al*., 2016a, b). For example, a trait that is static on the intra-specific level might be informative for species delimitation. Therefore, it would be interesting to assess the variability of call traits in the *D. rubicundulus* group with the aim to test for traits useful for species delimitation, and to further develop the methodology of acoustic species delimitation in frogs.

Comments on the *D. rubicundulus* group

Regarding the species described herein the results of our molecular analyses suggest a nested position within the *Dendropsophus microcephalus* species group. The closeness of the new species to the (morphologically defined) *rubicundulus* group (fide NAPOLI & CARAMASCHI, 1998) is supported by general morphological appearance and overall call structure. The *D. rubicundulus* species group was first defined by NAPOLI & CARAMASCHI (1998) as having the following characters: size small (16–26 mm), thighs immaculate, dorsum predominantly green in life and pink to violet in preservative. Currently, 11 species are recognized as belonging to the *D. rubicundulus* group distributed mainly in open environments in the Cerrado domain (see introduction). FAIVOVICH *et al*. (2005) defined the *Dendropsophus rubicundulus* clade based solely in one sequence of *D. rubicundulus* ("AY843661", most probably belonging to *D. elianeae*, see above). A recent molecular phylogenetic analysis of the micro*cephalus* group (MEDEIROS *et al*., 2013) demonstrated that this species group does not constitute a monophyletic group in respect to *D. sanborni*, although the authors did not further discuss their finding. Our data support the non-monophyly of the *rubicundulus* group (Fig. 1 and 2), particularly because of the position of *D. sanborni*, *D. cruzi* and *D. juliani*. The morphological and molecular definition of the *D. rubicundulus* group fide NAPOLI & CARAMASCHI (1998) and *D. rubicundulus* clade fide FAIVOVICH *et al*. (2005), all remain to be tested.

Our study, next to many other recent studies, shows that the actual amphibian diversity in the Neotropics is still far from being sorted out and completely described, notably in the genus *Dendropsophus* (e.g., JANSEN *et al*., 2011; GEHARA *et al*., 2014; CAMINER *et al*., 2017). More field surveys are needed to cover especially the vast, remote and understudied areas (e.g., in eastern Bolivia the Beni savannas and the Chiquitano region or Chiquitanía). Moreover, studies repeatedly found that "widespread" frog species actually represent complexes of species with often much smaller distribution areas (GEHARA *et al*., 2014). It is obvious that decision makers must react, and that much more protected areas are needed to actual cover the still increasing number of recognized anuran species, including micro-endemics (e.g., PIE *et al*., 2013), in the future.

Acknowledgments

We thank the owners of Caparú Ranch (J. ROZENMAN and G. WEISE) for their invitation to conduct herpetological surveys on their properties and for logistic support. Collecting and export permits were provided by the Ministerio de Medio Ambiente y Aqua, Bolivia (MMAyA-VMABCC-DGBAP 941), and the Instituto Chico Mendes de Conservação da Biodiversidade, Brasil (ICMBio/SISBIO 30059-12 and 02015.008064/02-51). PATRICIA HERRERA and KATHIA RIVERO (Museo Noel Kempff Mercado, Santa Cruz de la Sierra) provided valuable assistance to obtain these permits. For the loan of specimens or access to collections we are indebted to D. RÖDDERS (ZFMK), and R. SOSA (MNK). FRANCISCO BRUSQUETTI provided valuable data on specimens from Paraguay housed in the herpetological collection of the Instituto de Investigación Biológica del Paraguay (IIBP). For field assistance we thank O. BARROSO, Q. VIDOZ, and A. SCHULZE who also provided some sound recordings. MJ received financial support from the Erika and Walter Datz-Stiftung, Bad Homburg v. d. H., and material support from Globetrotter Equipment, Frankfurt a. M. DJS thanks CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for his research fellowship (311492/2017-7). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – that provided a research grant to BFVT – Finance Code 001.

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Appendix 1

Additional specimens examined

Dendropsophus aperomeus: PERU: El Boquerón, ZFMK 39323-41.

Dendropsophus brevifrons: PERU: Andoas, ZFMK 40157-59.

Dendropsophus coffea: BOLIVIA: La Paz: 55 km on road from Caranavi to Palos Blancos, 800 m, MNKA 6538 (holotype), ZFMK 80590 (paratype); 5 km N Río Beni bridge, near Sapecho, 550 m, ZFMK 82182 (paratype).

Dendropsophus cruzi: BOLIVIA: Santa Cruz: P.N. Noel Kempff Mercado, ZFMK 72672–73.

Dendropsophus delarivai: BOLIVIA: Cochabamba: road from Paractito to Cochabamba via El Palmar, ZFMK 67139–142, 70317 (paratypes); La Paz: Colonia Eduardo Avaroa, 1300 m, MNKA 6539, ZFMK 80587–588.

Dendropsophus joannae: BOLIVIA: Pando: Cobija, 250 m, ZFMK 67119–120, 67121–124 (paratypes).

Dendropsophus juliani A (fide Jansen *et al*., 2011): BOLIVIA: Santa Cruz: Caparú, MNKA 9579, 9919.

Dendropsophus leali: BOLIVIA: Beni: Río Ibaré, 300 m, ZFMK 60721–22; Santa Cruz: Buenavista, MNKA 9479–80; Hacienda San Sebastián and Centro de Investigaciones Ecológicas Chiquitos, MNKA 9431, 9434, 9458, 9703–06.

Dendropsophus leali A (fide Jansen *et al*., 2011): BOLIVIA: Santa Cruz: Caparú, MNKA 9575.

Dendropsophus melanargyreus: BOLIVIA: Santa Cruz: Caparú, MNKA 9541.

Dendropsophus meridianus: BRAZIL: Rio de Janeiro: 20 km N of Rio de Janeiro, ZFMK 39499–500.

Dendropsophus "*minutus*" (probably contains more than a single species): BOLIVIA: Chuquisaca: W of Vaca Guzmán, 1360 m, ZFMK 66045; Santa Cruz: Samaipata, 1900 m, ZFMK 60403–407; Laguna de Bermejo, 1130 m, ZFMK 60440; W of Río Seco, 900 m, ZFMK 67053–055; La Hoyada, 1700 m, ZFMK 72634–635; Pando: Cobija, 250 m, ZFMK 66790.

Dendropsophus minutus A (fide Jansen *et al*., 2011): BOLIVIA: Hacienda San Sebastián and Centro de Investigaciones Ecológicas Chiquitos, MNKA 9453–54, 9711–12, 9719–20, 9723.

Dendropsophus minutus B (fide Jansen *et al*., 2011): BOLIVIA: Beni: Los Lagos (Selva Blue), MNKA 9283, 9360;

Dendropsophus "*nanus*" (probably contains more than a single species): BOLIVIA: Beni: Puerto Almacén, ZFMK 60458–462; Santa Cruz: Buenavista, 250 m, ZFMK 80011–014, MNKA 9474, MNKA 9989, SMF 88421, SMF 88420; Campamento, MNKA 9960; Hacienda Caparú, MNKA 9540, 9578, 9586, SMF 88442; Hacienda San Sebastián and Centro de Investigaciones Ecológicas Chiquitos, MNKA 9405, 9408–09, 9424, 9427, 9495, 9667–68, 9675–76, 9784, 9824; San Ramón, ZFMK 60391–392; La Florida, ZFMK 60374–381; Santa Cruz de la Sierra, 400 m, ZFMK 67001; PARAGUAY: Chaco: 23 km S of Filadelfia, ZFMK 53262–266.

Dendropsophus cf. *nanus*: BOLIVIA: Beni: Los Lagos (Selva Blue), MNKA 9305, 9321–22, 9388, 9390; Santa Cruz: Estancia Büchler, MNKA 9802.

Dendropsophus nanus A (fide Jansen *et al*., 2011): BOLIVIA: Campamento, MNKA 9960; Hacienda Caparú, MNKA 9530, 9540, 9578, 9586, SMF 88442; Hacienda San Sebastián and Centro de Investigaciones Ecológicas Chiquitos, MNKA 9405, 9408–09, 9424, 9427, 9495, 9667–68, 9675–76, 9784, 9824.

Dendropsophus sanborni: PARAGUAY: Misiones: Isla Yacyreta: SMF 105080–82.

Appendix 2

Call vouchers, localities, and Animal Sound Archive (http://www.tierstimmenarchiv.de/) accession numbers of some of the recordings used in the analyses.

Species	Voucher	Locality	Animal Sound Archive	Remarks
D. rozenmani sp. nov.	MNKA 9368	Los Lagos, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_01	2 February 2010; 21:15 hrs; 29.2°C
D. rozenmani sp. nov.	SMF 88449	Los Lagos, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_02	6 January 2007; 22:00 hrs
D. rozenmani sp. nov.	MNKA 9922 (paratype)	Caparú Ranch, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_03	18 February 2012; 22:30 hrs; 26.6°C
D. rozenmani sp. nov.	SMF 88450 (paratype)	Caparú Ranch, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_04	18 February 2012; 22:50 hrs; 26.1°C
D. rozenmani sp. nov.	SMF 88490 (paratype)	Caparú Ranch, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_05	19 February 2012; 01:22 hrs; 25.8°C
D. rozenmani sp. nov.	MNKA-11504 (holotype)	Caparú Ranch, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_06	17 February 2006; 02:30 hrs; 24.4°C
D. rozenmani sp. nov.	Not collected #1	Caparú Ranch, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_07	6 January 2007; 22:00 hrs
D. rozenmani sp. nov.	Not collected #2	Caparú Ranch, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_08	02 February 2007; 22:00 hrs
D. rozenmani sp. nov.	Not collected #3	Caparú Ranch, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_09	02 February 2007; 01:30 hrs
D. rozenmani sp. nov.	Not collected #4	Caparú Ranch, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_10	02 February 2007; 01:30 hrs
D. rozenmani sp. nov.	Not collected #5	Caparú Ranch, Department of Santa Cruz, Bolivia	Dendropsophus_rozenmani_DIG0201_11	22 February 2012; 01:50 hrs

Appendix 3

Species, GenBank accession numbers and localities of individuals used in the phylogenetic analyses. For abbreviations of voucher numbers, refer to the publications listed.

species	museum voucher	GenBank accession number	locality	author
D. arndti	MNKA 10349	MK919546	Santa Cruz, Ñuflo de Chavez, San Sebastián, Bolivia	this study
D. melanargyreus	MNKA 10445	MK919556	Santa Cruz, Ñuflo de Chavez, San Sebastián, Bolivia	this study
D. miyatai	JPC 10772	AY843647	Sucumbios, Ecuador	FAIVOVICH *et al.* (2005)
D. parviceps	AMNH A-139315	AY843652	Universidade do Acre, Acre, Brazil	FAIVOVICH *et al.* (2005)
D. minutus B	MNKA 9360	JF790085	Los Lagos, Yucuma, Beni, Bolivia	JANSEN *et al.* (2011)
D. labialis	QULC 97005	AY843635	Parque Natural Nacional Chingaza, Colombia	FAIVOVICH *et al.* (2005)
D. carnifex	DFCH-USFQ 899	AY843616	Pichincha, Tandayapa, Ecuador	FAIVOVICH *et al.* (2005)

Appendix 3 continued.

species	museum voucher	GenBank accession number	locality	author
D. anataliasiasi	AAG-UFU 934	MK919543	Brejinho de Nazaré Tocantins, type locality	this study
D. anataliasiasi	AAG-UFU 936	MK919544	Brejinho de Nazaré Tocantins, Brazil (type locality)	this study
D. anataliasiasi	AAG-UFU 937	MK919545	Brejinho de Nazaré Tocantins, Brazil (type locality)	this study
D. berthalutzae	CFBH 5418	AY843607	Duque de Caxias, Rio de Janeiro, Brazil	Faivovich *et al*. (2005)
D. bipunctatus	MRT5946	AY843608	Serra do Teimoso, Jussari, Bahia, Brazil	Faivovich *et al*. (2005)
D. cachimbo	UFU 1632	MK919550	Vilhena, Mato Grosso, Brazil	this study
D. cachimbo A	SMF 88443	JF790049	San Sebastián, Ñuflo de Chavez, Santa Cruz, Bolivia	Jansen *et al*. (2011)
D. cachimbo A	SMF 88442	JF790048	San Sebastián, Ñuflo de Chavez, Santa Cruz, Bolivia	Jansen *et al*. (2011)
D. cachimbo A	MNKA 9655	JF790046	San Sebastián, Ñuflo de Chavez, Santa Cruz, Bolivia	Jansen *et al*. (2011)
D. cachimbo A	MNKA 9656	JF790047	San Sebastián, Ñuflo de Chavez, Santa Cruz, Bolivia	Jansen *et al*. (2011)
D. cachimbo A	MNKA 9721	MK919547	San Sebastián, Ñuflo de Chavez, Santa Cruz, Bolivia	This study
D. cachimbo A	MNKA 10309	MK919548	San Sebastián, Ñuflo de Chavez, Santa Cruz, Bolivia	This study
D. cachimbo A	MNKA 10417	MK919549	San Sebastián, Ñuflo de Chavez, Santa Cruz, Bolivia	This study
D. coffea	ZFMK 82181	JF790050	near Sapecho, Sur Yungas, La Paz, Bolivia	Jansen *et al*. (2011)
D. cruzi	UFU 1343	MK919551	Silvania, Goiás, Brazil (type locality)	
D. decipiens	CFBHT07254	KU495203	Cananeia, Sao Paulo, Brazil	Lyra et al (2016), direct submission
D. elianeae	IIBPH 1134	MK919555	Estancia Pirá Potrero, Amambay, Paraguay	this study
D. elianeae	IIBPH 550	MK919552	Reserva Natural Privada Cerrados del Tagatiyá, Estancia Garay Kué, Concepción, Paraguay	this study
D. elianeae	IIBPH 561	MK919553	Reserva Natural Privada Cerrados del Tagatiyá, Estancia Garay Kué, Concepción, Paraguay	this study
D. juliani	NMP6V 72799/3	JF790051	Barracón, Madre de Dios, Pando, Bolivia	Jansen *et al*. (2011)
D. leali	MNHM 2005.0013	JN206639	Pidima, French Guiana	Fouquet *et al*. (2011)
D. microcephalus	UTA A-50632	AY843643	Atlántida, Cordillera Nombre de Dios, Honduras	Faivovich *et al*. (2005)
D. nanus	SMF 88421	JX187442	Buenavista, Ichilo, Santa Cruz, Bolivia	this study
D. nanus	MACN 37785	AY549346	Entre Rios, Islas del Ibicuy, Argentina	Faivovich *et al*. (2005)
D. reichlei	EBT2	JF790109	E.B.Tahuamanu, Manuripi, Pando, Bolivia	Jansen *et al*. (2011)
D. rhodopeplus	MHZ 462	AY843658	Jenaro Herrera, Loreto, Peru	Faivovich *et al*. (2005)
D. rubicundulus	IT-H 0653	AY843661	Buri, Sao Paulo, Brazil	Faivovich *et al*. (2005)
D. rubicundulus	UFU 562_AAG	MK919557	Serra do Cipó – MG	
D. sanborni	MACN 38638	AY843663	Islas del Ibicuy, Entre Ríos, Argentina	Faivovich *et al*. (2005)
D. tritaeniatus (*D. rozenmani* sp. nov.)	SMF 88491	JF790113	Los Lagos, Yucuma, Beni, Bolivia	Jansen *et al*. (2011)
D. tritaeniatus (*D. rozenmani* sp. nov.)	SMF 88453	JF790114	Los Lagos, Yucuma, Beni, Bolivia	Jansen *et al*. (2011)

Appendix 3 continued.

species	museum voucher	GenBank accession number	locality	author
D. tritaeniatus (*D. rozenmani* sp. nov.)	MNKA 9368	JF790115	Los Lagos, Yucuma, Beni, Bolivia	JANSEN *et al*. (2011)
D. tritaeniatus (*D. rozenmani* sp. nov.)	MNKA 9531	JF790112	Los Lagos, Yucuma, Beni, Bolivia	JANSEN *et al*. (2011)
D. walfordi	MJH 129	AY843683	Brazil	FAIVOVICH *et al*. (2005)
Xenohyla truncata	—	AY843775	Restinga de Marica, Rio de Janeiro, Brazil	FAIVOVICH *et al*. (2005)

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File 1: App_4_Jansen_et_al.mp4. — DOI: 10.26049/VZ69-3-2019-01/1