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Species diversity and systematics of the *Leptodactylus melanonotus* group (Anura, Leptodactylidae): review of diagnostic traits and a new species from the Eastern Guiana Shield

Thiago Carvalho, Antoine Fouquet, Mariana L. Lyra, Ariovaldo A. Giaretta, C. Eduardo Costa-Campos, Miguel T. Rodrigues, Célio F. B. Haddad, Santiago R. Ron

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Species diversity and systematics of the *Leptodactylus melanonotus* group (Anura, Leptodactylidae): review of diagnostic traits and a new species from the Eastern Guiana Shield

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3 **Species diversity and systematics of the *Leptodactylus melanonotus* group (Anura,**
4 **Leptodactylidae): review of diagnostic traits and a new species from the Eastern Guiana**
5 **Shield**
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12 Thiago R. Carvalho¹, Antoine Fouquet², Mariana L. Lyra¹, Ariovaldo A. Giaretta³, C. Eduardo
13
14 Costa-Campos⁴, Miguel T. Rodrigues⁵, Célio F. B. Haddad¹, Santiago R. Ron⁶
15
16
17
18

19 ¹Laboratório de Herpetologia, Departamento de Biodiversidade e Centro de Aquicultura
20 (CAUNESP), Universidade Estadual Paulista, Rio Claro, SP, Brazil
21
22

23 ²Laboratoire Evolution et Diversité Biologique, Université Paul Sabatier, Toulouse, France
24
25

26 ³Laboratório de Taxonomia e Evolução de Anuros Neotropicais, Instituto de Ciências Exatas e
27 Naturais do Pontal, Universidade Federal de Uberlândia, Ituiutaba, MG, Brazil
28
29

30 ⁴Laboratório de Herpetologia, Departamento de Ciências Biológicas e da Saúde, Universidade
31 Federal do Amapá, Macapá, AP, Brazil
32
33

34 ⁵Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP,
35 Brazil
36
37
38

39 ⁶Museo de Zoología, Escuela de Biología, Pontificia Universidad Católica del Ecuador, Quito,
40 Ecuador
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47 **Corresponding author:** Thiago R. Carvalho. E-mail carvalho.thiagoribeiro@gmail.com;
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49 ORCID: 0000-0003-0910-2583
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53 **Running title:** Systematic review of *Leptodactylus* frogs
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1 **Abstract**

2 The *Leptodactylus melanonotus* species group is an anuran clade widely distributed in the
3 Neotropics. This clade harbours many species that are difficult to identify because of
4 incomplete taxonomic knowledge, ambiguous species boundaries and distribution. Here,
5 we expand the understanding of species diversity of this *Leptodactylus* clade by analysing
6 mtDNA sequences for over 600 individuals, delimiting operational taxonomic units
7 (OTUs), and updating species identifications and distributions by linking sequences to
8 morphotypes and calls. Also, we review the morphological and acoustic traits traditionally
9 used as diagnostic characters of species within this group. The DNA-based species
10 delimitation analyses yielded 57 OTUs. Given that only 19 taxa are currently recognised as
11 valid species, our results suggest the existence of many unnamed species within the *L.*
12 *melanonotus* group. After reassessing morphological traits in the group, we concluded that
13 the combined use of dorsolateral fold, upper lip stripe, and belly colouration is sufficiently
14 informative for species identification in most cases, especially when associated with data
15 on geographic distribution and habitat use. Regarding advertisement calls, the patterns of
16 amplitude and frequency modulation, calling rate, dominant frequency, and frequency
17 modulation were also informative for species discrimination. Furthermore, we designate a
18 neotype for *L. wagneri*, for which we also describe the advertisement call, make
19 comparisons with congeners of the *L. melanonotus* group, especially with the partially
20 sympatric *L. leptodactyloides*. Lastly, we name and describe a new species endemic to the
21 Eastern Guiana Shield. Patterns of distribution and habitat use in the *L. melanonotus* group
22 revealed that sympatric occurrences are more commonly found among distantly related
23 species, whereas allopatric occurrences correspond to closely related ones. Speciation

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4 24 between closely related species of the group seems to be related to ecological divergence
5
6 25 (open vs. forest habitats) in parallel with clear morphological and acoustic differentiation.
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10
11 27 **Keywords:** Advertisement calls, Amazonia, biodiversity, calling habitat, integrative
12
13 28 taxonomy, Leptodactylinae, Neotropics, Phylogeny
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32 **Introduction**

33 With more than 8,400 currently recognised extant species (Frost, 2022), amphibians are a
34 species-rich group of terrestrial vertebrates, whose species discovery rate has increased
35 dramatically over the past decades (e.g., Köhler et al., 2005; Tapley et al., 2018; Streicher
36 et al., 2020) compared to other vertebrate groups (Miralles et al., 2020). This is particularly
37 true in South America, with no less than 1,410 species of amphibians described over the
38 past two decades (Rivera-Correa et al., 2021). Despite this acceleration in the number of
39 new species descriptions, there is a large number of amphibian species in the Neotropics
40 that remain undescribed, notably in Amazonia (Vacher et al., 2020). The rising rate of new
41 species descriptions has been leveraged mainly by the increased use of DNA-sequence data
42 in concert with morphology and, at least for anurans, bioacoustics (Rivera-Correa et al.,
43 2021). This practice has allowed species delimitations within groups that have been
44 taxonomically neglected for a long time, in many cases because of their overall
45 conservative morphology, which was traditionally considered too complex to analyse. This
46 was for example the case of the anuran genus *Adenomera*, containing 29 species of which
47 half of its species richness being described in the last decade. The taxonomy of *Adenomera*
48 frogs has benefited from the combined use of multiple sources of information (Fouquet et
49 al., 2014; Carvalho et al., 2021).

50 Another example of taxonomically neglected anuran clade with notoriously difficult
51 morphological identification is the *Leptodactylus melanonotus* species group. It contains 19
52 currently recognised species with considerable uncertainties in species boundaries and
53 distribution, and thus, in total species richness (Vacher et al., 2020; Gazoni et al., 2021).

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4 54 Members of the *L. melanonotus* group are semi-aquatic frogs distributed from the Pacific
5
6 55 lowlands of Mexico [*L. melanonotus* (Hallowell, 1861)] to central north Argentina [*L.*
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8 56 *podicipinus* (Cope, 1862)]; see Heyer (1994) for details on distribution and natural history.
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11 57 The taxonomy of this *Leptodactylus* species group has been considered challenging due to
12
13 58 the high degree of intraspecific variation in morphological traits and the taxonomic
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15 59 ambiguities of several nominal taxa. Since the phylogenetic study of *Leptodactylus*
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17 60 published by de Sá et al. (2014), the phylogenetic relationships of species within the *L.*
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19 61 *melanonotus* group and the taxonomic identity of the Amazonian *L. petersii* (Steindachner,
20
21 62 1864) were addressed, with the revalidation of its junior synonyms, *L. brevipes* Cope, 1887
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23 63 and *L. intermedius* Lutz, 1930 (Gazoni et al., 2021). Nevertheless, many species of the *L.*
24
25 64 *melanonotus* group still lack an objective definition by linking morphological and acoustic
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27 65 variation to molecular lineages.
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32 66 Of particular taxonomic relevance are the species names assigned to populations of
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34 67 the *L. melanonotus* group distributed in the Eastern Guiana Shield (EGS), north-eastern
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36 68 Amazonia. There are four distinct morphotypes recognised in the EGS and associated with
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38 69 species names: *L. intermedius*, *L. nesiotus* Heyer, 1994, *L. petersii*, and *L. validus* Garman,
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40 70 1888 (Heyer, 1994; Jairam & Fouquet, 2018). In addition to these, a candidate new species
41
42 71 has been repeatedly reported from the EGS, referred to as several combinations: *L.*
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44 72 *leptodactyloides* (Lescure & Marty, 2000; Ouboter & Jairam, 2012), *L. aff. leptodactyloides*
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46 73 (*L. gr. podicipinus* C (Dewynter et al., 2008), *L. gr. podicipinus* C (Dewynter et al., 2020), *L. gr. wagneri* C
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48 74 (Fouquet et al., 2012), *L. gr. wagneri* G-E-F (Fouquet et al., 2007), *L. gr. podicipinus* 2
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50 75 (Fouquet et al., 2015), *L. sp. gr. podicipinus* (Fouquet et al., 2019), *Leptodactylus* sp.
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52 76 Guiana (Vacher et al., 2020). Even though the names *L. leptodactyloides* (Andersson, 1945)
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4 77 and *L. wagneri* (Peters, 1862) have also been applied to populations in the region (see
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7 78 Lescure & Marty, 2000; Ouboter & Jairam, 2012), these two species were described from
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9 79 Ecuador. The only type specimen linked to the name *L. wagneri* by Peters (1862) was
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11 80 collected from the west side of the Andes of Ecuador, according to the original description.
12
13 81 Heyer (1970, 1994) reported this holotype as lost and changed, tentatively, the type locality
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15 82 to ‘Pastassa’ (= Pastaza) in Amazonian Ecuador. In the original description of *L.*
16
17 83 *leptodactyloides*, its type locality was vaguely stated as ‘Río Pastaza’ in Ecuador
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19 84 (Andersson, 1945). Because the Pastaza River stretches in Ecuador along 250 km, with an
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21 85 elevation range from 1,900 m to 250 m, the exact location of the type locality of both *L.*
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23 86 *wagneri* and *L. leptodactyloides* remain uncertain. *Leptodactylus leptodactyloides* was
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25 87 synonymised with *L. wagneri* by Heyer (1970), but revalidated by Heyer (1994) when he
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27 88 noted that these two names were originally associated with two distinct morphotypes in
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29 89 western Amazonia.
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34 90 In this review, we delimit Operational Taxonomic Units (OTUs) based on a
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36 91 mitochondrial DNA dataset and re-evaluate species boundaries and distribution patterns of
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38 92 the *L. melanonotus* species group based on congruence between the mtDNA-based species
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40 93 delimitation and morphological and acoustic characters for 16 of 19 nominal species, plus
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42 94 the putative new species from the EGS. Additionally, we reassess the taxonomic status and
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44 95 geographic range of *L. wagneri* and *L. leptodactyloides* based on data from the type locality
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46 96 region, the Pastaza Valley in Ecuador, and several other populations across Amazonia,
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48 97 including the designation of a neotype for *L. wagneri*. In elucidating the taxonomic status
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50 98 of nominal species in Amazonia, we confirm that populations from the EGS represent a
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52 99 separate species, which is named and described herein as a new species.
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101 **Materials and methods**

102 **Field data collection**

103 Extensive fieldwork focusing on the collection of specimens, tissue samples, and
104 advertisement calls of members of the *L. melanonotus* group has been conducted
105 throughout South America since the early 2000s by some of us and complementary
106 information was obtained from species housed in many herpetological collections and
107 sound archive repositories (see Fig. 1 and Tables S1–S2 for localities).

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109 **Species delimitation, genetic diversity, and phylogenetic analysis**

110 We first delimited all major mtDNA lineages using a total of 624 partial sequences of the
111 16S rRNA gene, essentially comprising the entire geographic range of the *L. melanonotus*
112 group (see Table S1 for the molecular dataset and Appendix S1 for molecular data
113 acquisition). We obtained new 16S sequences for 181 specimens of the *L. melanonotus*
114 species group (Table S1), obtained through fieldwork and loans from collaborators. We
115 also retrieved homologous sequences from GenBank assigned to species of the *L.*
116 *melanonotus* group (441 accessions; Table S1). We added two terminals as outgroups: a
117 representative of the *L. latrans* group (*L. macrosternum* Miranda-Ribeiro, 1926), the sister
118 clade of the *L. melanonotus* group; and a representative of the *L. fuscus* group (*L.*
119 *notoaktites* Heyer, 1978), the sister clade of the other *Leptodactylus* species groups (de Sá
120 et al., 2014). All but five occurrence records were georeferenced (five NCBI sequences
121 lacked spatial information which could not be traced back) and used to create distribution

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4 122 maps with convex polygons using QGIS 2.14. DNA sequence alignment was conducted on
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6 123 the MAFFT online server under the E-INS-i option with default parameters (Katoh &
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8 124 Standley, 2013; Katoh et al., 2019). The final alignment was 1,727 bp long, but was
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10 125 trimmed at both ends down to 613 bp for which more than 50% of the sequences were
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12 126 complete (Appendix S2).

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15 127 We applied three DNA-based single-locus species delimitation approaches: (a) a
16
17 128 distance-based method, the Automated Barcode Gap Discovery (ABGD; Puillandre et al.,
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19 129 2012); (b) a single-threshold coalescent-based method, the Generalized Mixed Yule
20
21 130 Coalescent approach (single threshold GMYC; Monaghan et al., 2009; Pons et al., 2006);
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23 131 and (c) a Poisson Tree Processes model approach (PTP; Zhang et al., 2013). The ABGD
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25 132 delimitation was performed with a prior of intraspecific divergence P between 0.001 and
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27 133 0.1, a proxy for minimum relative gap width, X , of 1, and a number of steps n equal to 30.
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29 134 We kept the partition such that $P = 0.0129$, because it corresponded to the end of a plateau
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31 135 for group number and it is close to the 1% threshold of intraspecific divergence proposed in
32
33 136 other vertebrates' delimitation studies using 16S barcodes (Puillandre et al., 2012).
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35 137 Moreover, lower thresholds suggested an unreasonable number of OTUs and higher
36
37 138 thresholds clustered together well-diagnosable described species. For PTP delimitation we
38
39 139 first reconstructed a ML tree with RAxML v.8.2.4 (Stamatakis, 2014) using the GTR + Γ
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41 140 model. The PTP delimitation was undertaken on the rooted tree, with 5 million Markov
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43 141 chain Monte Carlo (MCMC) iterations, sampling every 1,000th iteration and discarding the
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45 142 initial 20% iterations as burn-in. For the GMYC delimitation, we reconstructed a time-
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47 143 calibrated phylogeny using BEAST 2.5.2 (Bouckaert et al., 2014). We used a birth and
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49 144 death population model to account for extinction processes and incomplete sampling,
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4 145 including the same out-groups used in the RAXML reconstruction. We used a single
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6 146 partition with a GTR + Γ + I substitution model, with an uncorrelated relaxed lognormal
7
8 147 clock model of rate variation among branches (Drummond et al., 2006). The root age,
9
10 148 corresponding to the common ancestor of *Leptodactylus*, was estimated based on the time-
11
12 149 calibrated phylogeny of Feng et al. (2017) and was consequently constrained with a normal
13
14 150 prior distribution (Mean = 25.7 mya, SD = 2). We consider it the best prior because Feng et
15
16 151 al. (2017) included an extensive dataset of nuclear loci for a large set of anurans and used
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18 152 many reliable fossils as calibration points. For the MCMC parameters, we used four
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20 153 independent chains of 100 million iterations, recording every 1,000th iteration and
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22 154 discarding the first 10% iterations as burn-in.
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27 155 We combined the log and the tree files of the independent runs using LogCombiner
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29 156 2.5 discarding the first 20% iterations as burn-in (Bouckaert et al., 2014) and checked the
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31 157 convergence of our parameters, confirmed by all ESS being above 100. Then, we extracted
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33 158 the maximum clade credibility tree using Tree annotator 2.5 (Bouckaert et al., 2014)
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35 159 reducing the number of trees ten times. We performed a GMYC delimitation on the
36
37 160 ultrametric tree using the GMYC function of the R package ‘splits’, version 1.0-11/r29
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39 161 (Ezard et al., 2009), with a threshold interval between 0 and 10 mya and by using the single
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41 162 threshold method. The OTUs were defined manually by a majority-rule consensus from the
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43 163 results of the three methods, i.e., a lineage is considered as being an OTU if supported by at
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45 164 least two of the three methods. The genetic divergences among OTUs and more
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47 165 conservative definitions of species were estimated using uncorrected *p*-distances, calculated
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49 166 in MEGA 10 using partial 16S (613 bp) mtDNA sequences (Table 1).
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4 167 The 16S sequences alone were not sufficiently informative to investigate deep
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6 168 relationships within the *L. melanonotus* group. We completed the 1,727 bp 16S alignment
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9 169 of 624 terminals with 143 partial sequences of the mitochondrially encoded cytochrome c
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11 170 oxidase I gene (COI; 128 newly produced and 15 from GenBank; 648–658 bp). Sequences
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13 171 were obtained as in Gazoni et al. (2021). The COI sequences were aligned using MAFFT,
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15 172 and concatenated with the 16S alignment, leading to a 2,428 bp alignment (Appendix S3).
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18 173 We reconstructed an ML tree with RAxML v.8.2.4 (Stamatakis, 2014) using the GTR + Γ
19
20 174 model and 1,000 pseudobootstrap replicates. We used *L. macrosternum* (*L. latrans* group)
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22 175 and *L. notoaktites* (*L. fuscus* group) as out-groups.
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27 177 **Morphology**

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29 178 We examined specimens belonging to almost all currently recognised species of the *L.*
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31 179 *melanonotus* group, including type specimens and/or topotypes, except for *L. wagneri* and
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33 180 *L. leptodactyloides*, whose type localities are ambiguous (see Introduction), and an
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36 181 additional species from the EGS unassigned to any currently valid taxon (see results;
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38 182 Appendix S4). However, we examined specimens from the Pastaza River basin for both *L.*
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40 183 *wagneri* and *L. leptodactyloides* (same region). We did not examine specimens of *L.*
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42 184 *colombiensis* Heyer, 1994, *L. magistris* Mijares-Urrutia, 1997, and *L. pascoensis* Heyer,
43
44 185 1994, for which morphological traits were obtained from their original descriptions. In the
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46 186 case of *L. sabanensis* Heyer, 1994, we had access to a single specimen (Appendix S4) not
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48 187 linked to a DNA sequence but reported as a call voucher (see Taxonomic accounts).
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50 188 Institutional acronyms of natural history collections follow Sabaj et al. (2020).
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4 189 We determined the sex of examined specimens by the presence of vocal slits and
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6 190 thumb spines in males, and through body size in females (usually larger than males) and
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8 191 gonad examination. Small specimens were excluded from the morphological analyses. We
9
10 192 measured the following morphometric traits using digital callipers (± 0.1 mm): snout–vent
11
12 193 length (SVL), thigh length (THL), tibia length (TL), foot length (FL), hand length (HAL),
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14 194 head length (HL), and head width (HW). Other morphometric traits were measured using
15
16 195 an ocular micrometre (± 0.1 mm) fitted to a stereomicroscope: eye diameter (ED),
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18 196 tympanum diameter (TD), eye–nostril distance (EN), internarial distance (IND), length of
19
20 197 the internal metatarsal tubercle (IMT), length of the outer metatarsal tubercle (OMT),
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22 198 Finger III disc (or unexpanded tip) width (Fin3DW), and Toe IV disc (or unexpanded tip)
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24 199 width (Toe4DW). Some of these morphometric traits (IND, IMT, OMT, Fin3DW, and
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26 200 Toe4DW) were not assessed for specimens of *L. wagneri*, because they were analysed a
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28 201 few years before specimens of other species, and those five traits were not considered at
29
30 202 that time. We followed the definitions and terminology of Watters et al. (2016) for the
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32 203 morphometric analysis.
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41 205 **Acoustic data acquisition and analysis**

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43 206 We recorded calls in the field and obtained additional calls from sound repositories of 16 of
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45 207 17 species of the *L. melanonotus* group with described calls, of which ten species recorded
46
47 208 in the field had associated 16S and/or COI sequences (Tables S1–S2). The exception is *L.*
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49 209 *colombiensis*, whose call was briefly described by de Sá et al. (2014), but the description
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51 210 was not linked to a sound file or specific locality (presumably in Colombia). Besides,
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4 211 digital copies of the original (analogue) sound recording are not available in the
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6 212 Smithsonian Institution (A. Wynn pers. comm. to T.R.C.).
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9 213 Calls were recorded in the field using digital recorders adjusted to sampling rates of
10
11 214 44.1 or 48.0 kHz and sample size of 16 bits, and unidirectional microphones. Recordings
12
13 215 were stored as uncompressed wave files. Sound files are housed in acoustic repositories
14
15 216 (see Table S2). In addition, some of the calls published in the most comprehensive review
16
17 217 of the *L. melanonotus* group (Heyer, 1994) were reanalysed. These were obtained either
18
19 218 from the Smithsonian Institution (USNM; Washington, DC, USA) or the Macaulay Library
20
21 219 collection (ML; Cornell Lab of Ornithology, Ithaca, NY, USA). Additional calls were
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23 220 obtained from Fonoteca Tropical Jacques Vielliard (FNJV; Unicamp, Campinas, SP,
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25 221 Brazil) and Fonoteca Zoologica de Madrid (FonoZoo; Madrid, Spain), or made available by
26
27 222 colleagues. The acoustic analysis was conducted in Soundruler 0.9.6.1 (Gridi-Papp, 2007),
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29 223 built as a package interfacing with Matlab 6.5.2 scripts through automated procedures that
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31 224 allow for unbiased quantification of acoustic traits among species. The main results of the
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33 225 quantitative analysis are presented as minimum–maximum (mean \pm standard deviation).
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35 226 Soundruler settings were: fast Fourier transform (FFT) size = 1024 samples, FFT overlap =
36
37 227 90%, window type = Hann, contrast = 70%. Note rate (per minute) was quantified manually
38
39 228 in Audacity 2.1.1 (Audacity Team, 2020). Descriptive statistics of acoustic traits are
40
41 229 presented as mean \pm standard deviation, and ranges include the span of values from the raw
42
43 230 dataset. Sound figures were produced using seewave 2.1.0 (Sueur et al., 2008) and tuneR
44
45 231 1.3.2 (Ligges et al., 2017) in R 3.5.0 (R Core Team, 2018). Settings for these were: window
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47 232 = Hann, FFT size = 256 or 512 samples, FFT overlap = 90%; the intensity of frequency
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4 233 components is indicated by their darkness in a relative 30-dB scale. Acoustic definitions
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6 234 and terminology follow Carvalho et al. (2019).
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11 236 **Results**

14 237 **Diversity of mtDNA lineages and species delimitation**

16 238 The phylogenetic tree obtained from the ML analysis of COI + 16S mtDNA dataset
17
18 239 recovered the *L. melanonotus* group as a single clade, even though *L. riveroi* Heyer &
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20 240 Pyburn, 1983 is weakly supported (BT = 69%) as sister to the remaining species of the
21
22 241 group (Fig. 1). All other species of the *L. melanonotus* group form a strongly supported
23
24 242 clade (BT = 98%), with *L. pustulatus* (Peters, 1870) in the South American Dry Diagonal
25
26 243 and *L. diedrus* Heyer, 1994 in western Amazonia as early diverging lineages (not shown in
27
28 244 Fig. 1, but see de Sá et al., 2014 for distributions), and the remaining species forming a
29
30 245 nested clade (BT = 95%). We considered five main subclades within the latter group: (#1)
31
32 246 *L. colombiensis*, *L. melanonotus*, *L. validus*, *L. wagneri*, and a putative new species referred
33
34 247 to as *Leptodactylus* sp. from Colombia are distributed in lowland and highland forests in
35
36 248 the northern part of the distribution of the group; (#2) *L. brevipes*, *L. intermedius*, and *L.*
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38 249 *podicipinus* occupy open habitats in the eastern part of the distribution of the group; (#3) *L.*
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40 250 *discodactylus* Boulenger, 1884 and *L. griseigularis* (Henle, 1981) inhabit western
41
42 251 Amazonian forests; (#4) *L. leptodactyloides*, *L. natalensis* Lutz, 1930, *L. nesiotus*, and the
43
44 252 putative new species referred to as *Leptodactylus* sp. from the EGS, widely distributed in
45
46 253 forest and open habitats east of the Andes; (#5) and a subclade formed by no less than 18
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48 254 major mtDNA lineages throughout Amazonia, which are assigned to *L. petersii*. Each of
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4 255 these lineages harbours spectacular diversity on mtDNA and corresponds to a separate
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6 256 OTU.

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9 257 Of the three species delimitation methods, ABGD was found to be the most
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11 258 conservative, delimiting 49 OTUs. By contrast, PTP and GMYC delimited 70 and 59
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13 259 OTUs, respectively (Fig. 1). The consensus of the results obtained from the three methods
14
15 260 resulted in the delimitation of 57 DNA-based OTUs, of which six (*L. diedrus*, *L.*
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17 261 *intermedius*, *L. melanonotus*, *L. nesiotus*, *L. riveroi*, and *Leptodactylus* sp. from Colombia)
18
19 262 are represented by single OTUs. All other species are subdivided into several OTUs,
20
21 263 notably *L. petersii* which harbours an impressive diversity (maximum *p*-distance = 8.3% in
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23 264 16S) and contains at least 18 OTUs. Mean interspecific *p*-distances among *L. petersii*
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25 265 OTUs reach a minimum value of 3.0% in three instances (Table S3).

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29 266 The OTU corresponding to *Leptodactylus* sp. from Andean Colombia (previously
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31 267 identified as *L. colombiensis*) comprises a single terminal that is sister to a clade formed by
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33 268 two OTUs of *L. colombiensis* (Andean Colombia) and *L. wagneri* (western Amazonia). In
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35 269 principle, the two latter species have distinct morphotypes and do not occupy the same
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37 270 habitat (Heyer, 1994), which is congruent with the distinct distributions of these OTUs
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39 271 (Fig. 1). Regarding *Leptodactylus* sp., morphological and acoustic data remain unknown,
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41 272 thus hampering a taxonomic evaluation.

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45 273 One clade formed by EGS populations is highly divergent from *L. nesiotus* (also
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47 274 from the Guiana Shield), altogether forming a moderately supported clade (BT = 74%).
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49 275 Because these populations could not be linked to any known taxon and because
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51 276 corresponding calling males exhibited a distinct vocalisation, we name and describe them
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53 277 as a new species (see Taxonomic accounts). This clade from the EGS is formed by three
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4 278 OTUs: one from the Brazilian state of Amapá and French Guiana, closely related to a
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6 279 second OTU from eastern Suriname and northern Pará in Brazil (mean p -distance = 2.9% in
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8 280 16S), and a third OTU from western and southern Suriname that is sister to the other two
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11 281 OTUs (mean p -distance = 5.3% in 16S).
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15 283 **Morphology**

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18 284 The major taxonomic review of the *L. melanonotus* group (Heyer, 1994) and subsequent
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20 285 studies have focused on several morphological characters of taxonomic relevance. Below,
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22 286 we comment on their usefulness in species discrimination and their variation within and
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24 287 among species of the group. It is important to highlight that distinct colour patterns can be
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26 288 assessed more accurately either from live or preserved individuals, notably the upper lip
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28 289 stripe and ventral colouration. In general, the upper lip stripe is easier to be observed
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30 290 (outline and extension) from live frogs, whereas the belly colour patterns have better pale-
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32 291 dark contrasts in preserved specimens. The exception is when specimens have been through
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34 292 colour fading, making belly patterns unclear or completely immaculate.
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41 294 **Snout-vent length (SVL).** Body size of adults is highly variable within and among species
42
43 295 and largely overlaps between sexes, but females are generally larger and more robust than
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45 296 males. Although most species of the group can be classified into different categories of
46
47 297 body size (i.e., small, medium, and large species based on mean SVL; sensu Heyer, 1994),
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49 298 the majority of species overlap in SVL ranges (see Species Accounts in Heyer, 1994). One
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51 299 point to consider is the possibility that younger and older males can be reproductive (based
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53 300 on thumb spines) synchronically. Therefore, SVL ranges may vary to a great extent in a
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4 301 certain population throughout the breeding season. See below Taxonomic Accounts for
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6 302 SVL variation among sympatric species of the *L. melanonotus* group.
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11 304 **Dorsolateral fold.** A dorsolateral skin fold is present in most species of the *L. melanonotus*
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13 305 group, but completely absent in *L. diedrus* (Fig. 2A) and *L. magistris*. The fold is also
14
15 306 absent in some specimens of *L. discodactylus*, *L. pascoensis*, and *L. pustulatus*. The
16
17 307 assessment of the dorsolateral fold can be biased in poorly preserved specimens, where it is
18
19 308 sometimes flattened. The dorsolateral fold can also be interrupted in one or more parts
20
21 309 along its length, forming a longitudinal glandular row. When present, this morphological
22
23 310 character usually generally varies within species from indistinct (i.e., the indication of a
24
25 311 glandular crest behind the upper eyelid, sometimes fragmented and barely visible; Fig. 2B),
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27 312 and short (extending to the anterior third of the body; Fig. 2C) to moderate length
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29 313 (extending to the anterior half of the body; Fig. 2D). The presence of long (extending to the
30
31 314 posterior third of the body, often interrupted; Fig. 2E) or complete (uninterrupted,
32
33 315 extending from behind the upper eyelid to the groin; Fig. 2F) folds is limited to a few
34
35 316 species. *Leptodactylus wagneri* has a distinctively long dorsolateral fold (Fig. 2E) and *L.*
36
37 317 *riveroi* is the only species of the group with a complete dorsolateral fold (Fig. 2F). Many
38
39 318 species generally have indistinct to short dorsolateral folds, especially *L. griseigularius*, *L.*
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41 319 *leptodactyloides* (Fig. 2B), *L. nesiotus*, *L. sabanensis*, *L. validus*, and *Leptodactylus* sp.
42
43 320 from the EGS, whereas other species generally have short to moderate-length folds, notably
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45 321 *L. brevipes*, *L. colombiensis*, *L. natalensis* (Fig. 2C), and *L. petersii*. However, the
46
47 322 extension of the dorsolateral fold is highly variable in some species. In addition to *L.*
48
49 323 *wagneri*, other species may exhibit intermediate- to long-length folds, notably *L.*

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4 324 *intermedius*, *L. melanonotus*, and *L. podicipinus* (Fig. 2D). Overall, the extension of the
5
6 325 dorsolateral fold contributes to a certain extent to species discrimination in the *L.*
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8 326 *melanonotus* group, but, given its high intraspecific variation, this character should
9
10 327 preferably be used in combination with other morphological and acoustic features, and
11
12 328 linked to locality data and habitat use (see below).
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18 330 **Upper lip stripe.** Heyer (1994) described three states for this character (states A–C),
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20 331 defined as (A) indistinct, as a lighter area below the eye, but the upper and lower limits of
21
22 332 the stripe are weakly defined (Fig. 3A); (B) extending from the posterior corner of the eye
23
24 333 towards the base of the arm (Fig. 3B); and (C) extending from under the mid-eye or
25
26 334 anterior to the eye towards the base of the arm (Fig. 3C). Colour contrasts of the upper lip
27
28 335 stripe may vary between sides of the body, sometimes making character states difficult to
29
30 336 determine, although it was possible in most cases to assign the specimen to one of the
31
32 337 character states based on one of the sides of the head. A few specimens among the species
33
34 338 scored for character states B or C may have an indistinct upper lip stripe (= A) or
35
36 339 completely lack the stripe on one side or both sides of the head. On the other hand, the
37
38 340 states B and C are mutually exclusive among species. Character state C is present in all
39
40 341 three species of the *L. podicipinus* clade (i.e., *L. brevipes*, *L. intermedius*, and *L.*
41
42 342 *podicipinus*; Gazoni et al., 2021), plus *L. melanonotus*, *L. nesiotus*, *L. pustulatus*, and *L.*
43
44 343 *riveroi* (Fig. 3C), even though two of them (*L. melanonotus* and *L. pustulatus*) often have a
45
46 344 fragmented or indistinct upper lip stripe. In the majority of examined specimens, state B is
47
48 345 present in *L. discodactylus*, *L. griseigularis*, *L. natalensis* (Fig. 3B), *L. petersii*, *L. validus*
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50 346 (classified mostly as state A by Heyer, 1994), *L. wagneri*, and *Leptodactylus* sp. from the
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4 347 EGS. Most specimens of *L. colombiensis*, *L. diedrus*, *L. leptodactyloides* (Fig. 3A), and *L.*
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6 348 *sabanensis* are assigned to state A. *Leptodactylus pascoensis* is unique in lacking an upper
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8 349 lip stripe. Based on the colour of the holotype of *L. magistris*, the species is classified as
9
10 350 state B. The upper lip stripe is a useful character for species discrimination in the *L.*
11
12 351 *melanonotus* group and can be assessed from both live and preserved specimens. However,
13
14 352 it is best used in combination with other morphological and acoustic traits, and also locality
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16 353 data and habitat use, given the high levels of intraspecific variation, especially in cases of
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18 354 sympatric occurrence among species of the group (Fig. 1).
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25 356 **Toe tip morphology.** Almost all species of the group have toe tips unexpanded (Fig. 3D)
26
27 357 or slightly expanded (knob-shaped swollen; Fig. 3E). These character states (unexpanded or
28
29 358 slightly expanded) are variable within species. However, two species (*L. diedrus* and *L.*
30
31 359 *discodactylus*) have toe tips expanded into small discs compressed dorsolaterally with
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33 360 grooves on the dorsal surface of the toe disc. There is one central longitudinal groove in *L.*
34
35 361 *diedrus* (Fig. 3F) and three to five longitudinal grooves (curved in the distal portion) in *L.*
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37 362 *discodactylus* (Fig. 3G). The presence of toe discs is diagnostic for these two species in
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39 363 comparison with congeners of the group, and the number of longitudinal grooves on toes
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41 364 distinguishes the two species.
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48 366 **Ventral colouration.** In adult males, the throat can be darkened or not, and such
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50 367 colouration may extend posteriorly to the chest (Fig. 4). Also, the lower jaw is sometimes
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52 368 covered with white spots (Fig. 4B). Within-species variation associated with these colour
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54 369 patterns of the throat is extensive and, as such, did not contribute to species discrimination.
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4 370 Major patterns of belly colouration of the *L. melanonotus* group were classified into
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6 371 different types by Heyer (1994). Although intraspecific variation exists among the character
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8 372 states proposed, most specimens fell mainly within one of them, which are: immaculate;
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10 373 mottling (fine, moderate, or heavy)—the latter can form a peculiar anastomotic or
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12 374 labyrinthine pattern; spotting (pale spots on a dark background). Also, colour patterns can
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14 375 extend throughout the belly or fade away towards the hind limbs, so that the posterior belly
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16 376 tends to be almost or completely immaculate. Three species (*L. petersii*, *L. riveroi*, and *L.*
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18 377 *wagneri*) have a distinctive anastomotic pattern throughout the belly (Fig. 4C). Light to
19
20 378 heavy mottling throughout the belly, but generally not forming an anastomotic pattern (Fig.
21
22 379 4B), is present in *L. brevipes*, *L. discodactylus*, *L. melanonotus*, *L. natalensis*, and *L.*
23
24 380 *nesiotus*. A distinct pattern of mottling concentrated on the anterior portion of the belly and
25
26 381 chest, fading progressively towards the hind limbs (making the posterior belly almost or
27
28 382 completely immaculate; Fig. 4A), is present in *L. colombiensis*, *L. griseigularis*, *L.*
29
30 383 *leptodactyloides*, *L. pascoensis*, *L. sabanensis*, *L. validus*, *Leptodactylus* sp. from EGS, and
31
32 384 possibly *L. magistris* based on the colour characterisation of the holotype. Three species (*L.*
33
34 385 *intermedius*, *L. podicipinus*, and *L. pustulatus*) have a distinctive pale-spotted belly (Fig.
35
36 386 4D) and *L. diedrus* is unique in having an immaculate belly. Species of the *L. melanonotus*
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38 387 group also may have the groin, posterior belly, and/or the ventral surface of hind limbs
39
40 388 bright yellow in life, such as *L. diedrus*, *L. griseigularis*, *L. leptodactyloides*, *L. nesiotus*, *L.*
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42 389 *validus*, and *Leptodactylus* sp. from the EGS (see supplemental figures for life colours).
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44 390 Bright yellow colouration in live frogs is likely present in additional species of the group
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46 391 and, as such, we did not include it as a diagnostic character among species of the *L.*
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48 392 *melanonotus* group.

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6 394 **Thumb spine.** Adult males of almost all species of the *L. melanonotus* group have a pair of
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8 395 black (keratinised) thumb spines at the base of the thumb (Fig. 4A, B, D), which is absent
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10 396 in adult females (Fig. 4C). Keratinised spines can come off easily while examining
11
12 397 preserved specimens (and come off naturally in nature after the breeding season), but the
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14 398 dermal base can still be observed. However, males of two species (*L. discodactylus* and *L.*
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16 399 *pustulatus*) lack thumb spines. Such absence serves as a diagnostic trait of both species in
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18 400 comparison with the other 17 species of the group.
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25 402 **Posterior surface of the thigh.** Heyer (1994) described two character states: (i) a pale-
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27 403 coloured stripe running along the posterior thigh length on a dark brown or black
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29 404 background or (ii) a mottling pattern of pale spots and blotches intervening with a dark
30
31 405 brown or black background. Besides being highly variable within species, there are at least
32
33 406 a few intermediate states for the thigh stripe, which can be irregular and/or interrupted,
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35 407 straight or sinuous, well-marked or weakly outlined in some portions. As an example, *L.*
36
37 408 *leptodactyloides* has been distinguished from other members of the *L. melanonotus* group
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39 409 by the presence of a longitudinal stripe on the posterior surface of the thigh (Heyer, 1994;
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41 410 de Sá et al., 2014), but most specimens of *L. leptodactyloides* morphologically examined by
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43 411 us lack such stripes (see supplemental figures for life colours).
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50 413 **Advertisement calls**

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52 414 Members of the *L. melanonotus* group are well-known for their extended vocal repertoires
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54 415 when compared to the other three *Leptodactylus* groups. Field observations made by us and
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4 416 available data in the literature (e.g., Heyer, 1994; Prado et al., 2007) confirmed that some
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6 417 species have complex intraspecific vocal interactions (male-male and male-female), which
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8 418 might explain the multiple note types in their repertoires. However, the most frequent call
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10 419 types produced, assumedly functioning as advertisement calls, tend to be relatively
11
12 420 stereotyped in structure and composed of a single note type (but see Gazoni et al., 2021 for
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14 421 *L. petersii*). Major patterns in the temporal and spectral dimensions of advertisement calls
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16 422 are presented in this section.
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22 424 **Amplitude modulation (AM).** Most species of the group do not have regular AM patterns
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24 425 (i.e., pulsing) in their calls (Figs. 5A, 6A–F). Five species of the *L. melanonotus* group have
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26 426 amplitude-modulated calls (Figs. 5B–D, 6G–I), of which *L. riveroi* is unique in producing
27
28 427 calls with complete pulses (i.e., AM cycles separated by silent intervals; Fig. 5C). The call
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30 428 of *L. riveroi* is composed of a series of two-pulse notes (Fig. 5C). Three species produce
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32 429 calls with incomplete pulses (i.e., AM cycles not separated by silent intervals; Fig. 5B): *L.*
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34 430 *petersii* call type 1 (sensu Gazoni et al., 2021; Fig. 6G), *L. wagneri* (Fig. 6I), and
35
36 431 *Leptodactylus* sp. from the EGS (Figs. 5B, 6H). The fifth species, *L. pustulatus*, also has a
37
38 432 unique call consisting of a complex combination of complete and incomplete AM patterns
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40 433 (Fig. 5D, H).
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48 435 **Calling rate.** Species that produce the shortest calls (note duration < 30 ms on average)
49
50 436 generally call at the fastest repetition rates (highest repetition rate > 200 notes/min), such as
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52 437 *L. brevipes*, *L. leptodactyloides*, *L. natalensis*, and *L. nesiotus* (Table 2). Exceptions are *L.*
53
54 438 *griseigularis* and *L. melanonotus*, both having short notes and lower repetition rates (Table
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4 439 2), and *Leptodactylus* sp. from the EGS which produces a long note (86 ms on average) at a
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6 440 high repetition rate (highest repetition rate = 211 notes/min). We observed that species of
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8 441 the group producing rapidly repetitive calls can call at a much slower rate depending on
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10 442 motivation (intraspecific interactions), but species typically producing calls at slower rates
11
12 443 never call at such high rates (i.e., highest repetition rate > 200 notes/min). Therefore, the
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14 444 repetition rate of calls was found to be a useful diagnostic trait among species of the *L.*
15
16 445 *melanonotus* group (Table 3).
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22 447 **Frequency modulation (FM).** FM is prevalent in the calls of most species. The FM is
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24 448 always upward and varies in the extent of modulation throughout the call. The dominant
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26 449 frequency always coincides with the fundamental harmonic in *Leptodactylus* calls, from
27
28 450 which the FM was quantified. Species having the highest levels of FM can be visually
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30 451 described in the spectrogram as an S-shaped spectral structure (Fig. 5G). The dominant
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32 452 frequency is usually associated with the highest frequencies in the final portion of upsweep,
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34 453 but can also coincide with lower frequencies in the first third/half in some calls. Calls with
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36 454 pronounced upward modulation (FM > 1 kHz on average; Fig. 5G) are present in *L.*
37
38 455 *brevipes*, *L. discodactylus*, *L. griseigularis*, *L. intermedius*, *L. melanonotus*, *L. petersii* call
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40 456 type 2 (sensu Gazoni et al., 2021), *L. podicipinus*, *L. sabanensis*, *L. validus*, and *L.*
41
42 457 *wagneri*, whereas *L. diedrus*, *L. leptodactyloides*, *L. natalensis*, *L. nesiotus*, *L. pustulatus*,
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44 458 *L. riveroi*, and *Leptodactylus* sp. from the EGS have weak (FM < 100 Hz on average; Fig.
45
46 459 5E) or modest (FM < 600 Hz on average; Fig. 5F) upward modulation in their calls (Tables
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462 **Summary of phenotypic characters with taxonomic relevance**

463 After assessing the morphological and acoustic characters (previous two sections), next we
464 present the combination of those that are especially useful in species discrimination in the
465 *L. melanonotus* group (summarised in Table 3). The combined use of dorsolateral fold,
466 upper lip stripe, and belly colouration are the most reliable suite of characters for species
467 discrimination in the group and can be straightforwardly assessed because of their presence
468 among adult and juvenile specimens. Moreover, the association of morphological and
469 colour traits with locality data and habitat use is of great help in identifying species of the
470 group. To facilitate species discrimination among the species of the *L. melanonotus* group
471 based on advertisement call patterns, we classified them into three major ‘acoustic groups’,
472 as follows: (1) the ‘water drop’ pattern (Fig. 6A–C) is defined as a non-pulsed note with a
473 pronounced FM. This pattern occurs in six species: *L. intermedius*, *L. melanonotus* (Fig.
474 6A), *L. petersii* call type 2 (Fig. 6B), *L. podicipinus*, *L. sabanensis*, and *L. validus* (Fig.
475 6C); (2) the ‘bubbling’ pattern (Fig. 6D–F) is defined as a non-pulsed note with the shortest
476 durations (note duration < 30 ms on average) and the fastest repetition rates (highest
477 repetition rate > 200 notes/min, except *L. griseigularis*; Table 2). This pattern occurs in five
478 other species of the group: *L. brevipes*, *L. griseigularis* (Fig. 6D), *L. leptodactyloides* (Fig.
479 6E), *L. natalensis* (Fig. 6F), and *L. nesiotus*; (3) the ‘grunt’ pattern (Fig. 6G, H) is defined
480 as a note formed by incomplete pulses and with negligible to modest FM. This pattern
481 occurs in two species: *L. petersii* call type 1 (Fig. 6G) and *Leptodactylus* sp. from the EGS
482 (Fig. 6H). In addition to these three major patterns, the following species have unique calls
483 in the *L. melanonotus* group: *L. diedrus*, whose call consists of a non-pulsed note with long
484 duration and weak FM (Fig. 5E; Table 2); *L. discodactylus*, whose call consists of a non-

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4 485 pulsed note with long duration and pronounced FM, which makes it sound like a whistle
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6 486 (Fig. 5G; Table 2); *L. pustulatus*, whose call consists of a note with a complex amplitude-
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8 487 modulated structure formed by both incomplete and complete AM (Fig. 5D, H; see also
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10 488 Brandão & Heyer, 2005); *L. riveroi*, whose call is formed by a series of two-pulse notes
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12 489 (Fig. 5C; see also Heyer & Pyburn, 1983); and *L. wagneri*, whose call consists of a single
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14 490 note formed by incomplete pulses and with modest to pronounced FM (Fig. 6I).
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18 491 We present next the taxonomic results derived from the review of phenotypic
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20 492 characters used in the taxonomy of the *L. melanonotus* group linked to the DNA-based
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22 493 phylogeny and species delimitation analysis. In summary, we (1) designate a neotype for *L.*
23
24 494 *wagneri* and provide the first quantitative analysis of its advertisement call; (2) update the
25
26 495 diagnosis and distribution of the sympatric *L. leptodactyloides* and allopatric *L.*
27
28 496 *griseigularis*; (3) reanalyse the advertisement calls of these two species and other ten
29
30 497 species of the group; and (4) name and describe *Leptodactylus* sp. from the EGS as a new
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32 498 species. Along the taxonomic sections, we also highlight sympatric and allopatric species of
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34 499 the group without a clear phenotypic diagnosis.
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40 41 501 **Taxonomic accounts**

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45 503 *Leptodactylus wagneri* (Peters, 1862)

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47 504 (Tables 1, 2, 4; Figs. 1, 2E, 6I, 7)

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51 506 **Type series.** A single specimen (the holotype), by original designation (Peters, 1862),
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53 507 housed at the Zoologische Staatssammlung München (ZSM), the Bavarian State Collection
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4 508 of Zoology in Munich: ZSM 1080/0. This specimen was destroyed in World War II (see
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6 509 Heyer, 1970; Glaw & Frazen, 2006). Heyer (1970) tentatively corrected the type locality
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8 510 from ‘west of the Andes’ in Peters (1862) to the ‘Pastassa’ (= Pastaza) in Ecuador (ZSM
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10 511 catalogue information), which most likely corresponds to a wide swath of territory
11
12 512 associated with the Pastaza River drainage. The Pastaza River in Ecuador extends along
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14 513 ~250 km from the eastern Andean slopes (1,900 m elevation) to the border with Peru (250
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16 514 m elevation). Peters (1862) describes that type specimen as an adult male (presence of
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18 515 thumb spines) with 68 mm SVL. We agree with Heyer’s (1970) change because the only
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20 516 species of *Leptodactylus* bearing thumb spines in western Ecuador are *L. melanonotus*, *L.*
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22 517 *peritoaktites*, and *L. rhodomerus*. These three species are discriminated from *L. wagneri* in
23
24 518 the size range of adult males. Males of the two species of the *L. pentadactylus* group (*L.*
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26 519 *peritoaktites*: SVL = 124–146 mm; *L. rhodomerus*: SVL = 112–144 mm; Heyer, 2005) are
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28 520 much larger than those of *L. wagneri* (SVL = 46–60 mm), whereas males of *L.*
29
30 521 *melanonotus* are much smaller than the other species (SVL = 32–43 mm; de Sá et al.,
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32 522 2014). In our sample, adult males of *L. wagneri* (SVL = 46–60 mm) do not reach the size of
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34 523 the holotype (SVL = 68 mm), but it falls within the SVL range of the species, with females
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36 524 larger than 80 mm. The other three species have SVL ranges far above or below the SVL of
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38 525 the *L. wagneri* holotype.

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41 526 Heyer (1970) designated the holotype of the sympatric *L. leptodactyloides* as the
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43 527 neotype for *L. wagneri* because he regarded *L. leptodactyloides* as a junior synonym of *L.*
44
45 528 *wagneri*. The neotype designation was later invalidated by Heyer (1994), who considered
46
47 529 that *L. leptodactyloides* was a separate species from *L. wagneri*. The type locality of *L.*
48
49 530 *leptodactyloides* is ‘Río Pastaza’, Ecuador (Andersson, 1945). Our results indicate that
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4 531 specimens from the Pastaza River and surroundings, in Ecuador, belong to two separate
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6 532 species, characterised by distinct phylogenetic positions within the *L. melanonotus* group,
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8 533 as well as substantial differences in morphology and calls. In addition to these, two other
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10 534 species of the group are known to occur in Ecuador: *L. discodactylus*, inhabiting western
11
12 535 Amazonia, and *L. melanonotus*, distributed across the Pacific lowlands from Ecuador to
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14 536 Mexico. *Leptodactylus petersii* was also reported in Ecuador (Ron, 2002), but, based on
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16 537 their morphology (long dorsolateral fold) and DNA sequences (genetic distance between
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18 538 QCAZ-A 20244, GenBank accession #ON564909, and *L. wagneri* from Pastaza, e.g.,
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20 539 USNM 320988, ($\leq 1\%$ in 16S), we concluded that those specimens (QCAZ-A 20242–7) are
21
22 540 instead conspecific with *L. wagneri*. To our knowledge, there are three distinct
23
24 541 morphotypes in Ecuador's province of Pastaza: (1) a large species (specimens from
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26 542 Pastaza: male SVL 46–60 mm, mean = 53.3, $n = 19$; female SVL 62–70 mm, mean = 66.4,
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28 543 $n = 5$; Table 4) with the upper lip stripe extending from the posterior corner of the eye and
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30 544 anastomotic belly pattern, corresponding to *L. wagneri*; (2) a medium species (specimens
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32 545 from Ecuador and Brazil: male SVL 35–45 mm, mean = 39.7, $n = 23$; female SVL 41–52
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34 546 mm, mean = 45.5, $n = 9$) with the upper lip stripe usually indistinct and belly pattern
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36 547 consisting of lightly mottling concentrated anteriorly (tending to immaculate posteriorly),
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38 548 corresponding to *L. leptodactyloides*; and (3) a small species (specimens from Ecuador:
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40 549 male SVL 27–29 mm, mean = 28.1, $n = 4$; female SVL 28–35 mm, mean = 32.7, $n = 3$)
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42 550 with toe discs and with adult males lacking thumb spines, corresponding to *L.*
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44 551 *discodactylus*. The latter two species are distinguished acoustically from each other (Figs.
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46 552 5–6)—the call of *L. wagneri* from Ecuador is described in the present study and also differs
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48 553 from those of the other two species (see Fig. 6I, and Diagnosis and Comparisons below).
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4 554 Although Peters' description of *L. wagneri* is brief, it is possible to associate the holotype
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6 555 with the first morphotype presented earlier in this paragraph based on body size, as
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9 556 previously stated by Heyer (1994). Given that the neotype designated for *L. wagneri* by
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11 557 Heyer (1970) was later invalidated by the same author (Heyer, 1994), the name *L. wagneri*
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13 558 is yet to be linked to a new name-bearing type specimen. Next, we update the diagnosis of
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16 559 *L. wagneri*, designate and describe a neotype for the species, and provide the first
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18 560 quantitative description of its advertisement call. The rationale for the *L. wagneri* neotype
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21 561 designation is threefold: (i) define the nominal taxon objectively, (ii) clarify its taxonomic
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23 562 status relative to congeners distributed in western Amazonia and Andean slopes, including
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25 563 putatively new species, and (iii) circumscribe its type locality within the wide swath of
26
27 564 territory stretching across the Pastaza River drainage in Ecuador and adjacent Peru.
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32 566 **Diagnosis.** The species is recognised in the *L. melanonotus* group by the following
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34 567 combination of character states: (1) large size (male SVL 46–60 mm); (2) long dorsolateral
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36 568 fold; (3) toe tips unexpanded; (4) upper lip stripe extending from the posterior corner of the
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38 569 eye; (5) belly heavily mottled, forming an anastomotic pattern; (6) two keratinised spines
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41 570 on the base of the thumb in adult males; (7) single-note advertisement call; (8) call formed
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43 571 by incomplete pulses; (9) call with modest to pronounced FM.
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48 573 **Comparisons with congeners of the *L. melanonotus* group.** *Leptodactylus wagneri* is
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50 574 distinguished from all other species by the combination of large SVL (male SVL 46–60
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52 575 mm; Table 4) and long dorsolateral fold (Figs. 2E, 7A). The species is also distinguished
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55 576 from *L. diedrus* and *L. discodactylus* by having toe tips unexpanded (toe discs in the other
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577 two species; Fig. 3F, G). *Leptodactylus wagneri* is distinguished by an upper lip stripe
578 extending from the posterior corner of the eye (Fig. 7A); extending from under the mid-eye
579 or over the snout in *L. brevipes*, *L. intermedius*, *L. melanonotus*, *L. nesiotus*, *L. podicipinus*,
580 *L. pustulatus*, and *L. riveroi*; absent in *L. pascoensis*. *Leptodactylus wagneri* has an
581 anastomotic belly pattern (Fig. 7B, D), differing from the ventral colouration of almost all
582 species of the group, except *L. petersii* and *L. riveroi*. *Leptodactylus wagneri* is also
583 distinguished by the presence of keratinised thumb spines in adult males (Fig. 7B, D);
584 absent in *L. discodactylus* and *L. pustulatus*. The advertisement call of *L. wagneri* is
585 frequency modulated and formed by incomplete pulses (Fig. 6I; Table 2). When combined,
586 these two acoustic traits distinguish *L. wagneri* from all other species of the *L. melanonotus*
587 group (Figs. 5–6; Tables 2–3).

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589 **Neotype of *Leptodactylus wagneri*.** QCAZ-A 26219 (field number SC 14012; Fig. 7), an
590 adult male from the outskirts of Puyo (1.443070°S, 77.996660°W; 954 m elevation), in the
591 Province of Pastaza, central Ecuador, collected on 9 January 2004 by S. R. Ron. This
592 specimen is linked to a COI sequence (GenBank accession #MW284682).

593
594 **Description of neotype.** Adult male, SVL 57.2 mm, THL 28.8 mm, TL 29.4 mm, FL 27.5
595 mm, HAL 13.1 mm, HL 20.8 mm, HW 19.5 mm, ED 5.4 mm, TD 4.3 mm, EN 5.3 mm.
596 Snout sub-oval in dorsal view, rounded to acuminate in lateral view. Canthus rostralis
597 rounded; loreal region slightly concave; tympanic annulus well-defined, mostly circular
598 (TD = 80% ED), and partially covered by supratympanic fold; tympanic membrane
599 partially translucent; supratympanic fold from the posterior corner of the eye, over the

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4 600 dorsal edge of the tympanic annulus, to the base of the arm; vocal sac subgular with a fold
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6 601 from jaw extending to arm; vocal slits present; vomerine teeth in two nearly straight rows
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8 602 medial and posterior to choanae and almost parallel to sagittal plane. Tongue elongated,
9
10 603 free from the posterior third. Two keratinised spines at the base of Finger I. Relative finger
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12 604 lengths $IV = II < I < III$; fingers fringed laterally, especially in outer side of Finger I, and
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14 605 inner side of Fingers II–III; finger tips rounded, slightly swollen in Fingers I and IV; inner
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16 606 metacarpal tubercle mostly ovoid; outer metacarpal tubercle elongated. Subarticular
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18 607 tubercles rounded; supernumerary tubercles absent. Dorsal surfaces of body and limbs
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20 608 covered with brown-tipped (keratinised) tubercles, especially in the posterior half of body
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22 609 length and hind limbs. Dorsolateral fold extending from behind the upper eyelid to $2/3$ of
23
24 610 body length, interrupted. Flank shagreened and glandular. Ventral surface of body and
25
26 611 limbs smooth, underside of thigh glandular. Relative toe lengths $I < II < V < III < IV$; toes
27
28 612 extensively fringed; toe tips rounded, unexpanded. Inner metatarsal tubercle elongated;
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30 613 outer metatarsal tubercle nearly rounded. Tarsal fold extending $2/3$ of tarsus length, from
31
32 614 the inner metatarsal tubercle towards the heel. Subarticular tubercles nearly rounded to
33
34 615 oval; supernumerary tubercles absent. Sole of foot and tarsus covered with brown-tipped
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36 616 tubercles.

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39 617 In preservative, dorsal surfaces brown with darker brown blotches. Interorbital bar
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41 618 light brown and grey; another bar of same colour extending obliquely from behind the
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43 619 upper eyelid towards scapula. Upper lip stripe light brown; upper and lower lips with a few
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45 620 scattered white spots. Flank light grey. Posterior surface of thigh pale and dark mottled
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47 621 (contrast of brown shades). Throat faded brown, darker brown surrounding the lower jaw,
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49 622 with white spots and blotches. Chest and especially belly heavily mottled, forming an

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4 623 anastomotic pattern. Ventral surface of arms with an almost solid brown colour extending
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6 624 from the elbow to the hand; hind limbs mottled. Ventral surface of hand, foot, and tarsus
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9 625 dark brown and grey, except tubercles, and finger and toe tips, which vary from cream to a
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11 626 light grey. Thumb spines solid black. Life colours are consistent with colour description in
12
13 627 preservative, but exhibiting well-defined colour contrasts, with reddish contrasts along the
14
15 628 dorsolateral fold and flank. Iris golden on the upper side, silvery white on the lower side.
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18 629 Life colours of the neotype are available at BioWeb Ecuador (access through this link:
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20 630 <<https://bit.ly/2ViPn1V>>).

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25 632 **Variation.** Variation in life colours (photographs of the neotype and additional adult and
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27 633 juvenile specimens) is available at Bioweb Ecuador (link: <<https://bit.ly/2ViPn1V>>).
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29 634 Intraspecific variation was also characterised previously by Heyer (1994). The largest adult
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31 635 specimen examined of *L. wagneri* is a female (QCAZ-A 56554: SVL = 84.3 mm),
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33 636 rendering *L. wagneri* the largest species of the *L. melanonotus* group. Among the
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35 637 specimens examined by us, dorsolateral fold was found to be shorter in specimens from the
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37 638 eastern range of the known distribution of *L. wagneri* (e.g., INPA-H 15789; see Appendix
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39 639 S4 for locality data). Specimens from the upper Amazon Basin in Brazilian Amazonia can
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41 640 be assigned to *L. wagneri* by having a large SVL and an anastomotic belly pattern, but
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43 641 some specimens have a shorter dorsolateral fold than the typically long fold present among
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45 642 Ecuadorian specimens. Despite the morphological variation, we tentatively assign those
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47 643 specimens to *L. wagneri*, but the acquisition of additional morphological and acoustic data
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49 644 would help elucidate the patterns of geographical variation among *L. wagneri* populations
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51 645 occurring in the eastern limit of its distribution range.
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647 **Advertisement call.** The description is based on 12 calls of one male from the province of
648 Napo in Ecuador, and additional nine calls of a second male from the Eastern Andean
649 slopes in Peru (see Table S2 for details). The call (Fig. 6I) consists of a single, partly pulsed
650 note given at a rate of 50 to 55 (52.7 ± 3.8) per minute. Notes last 64 to 136 (103.2 ± 20.1)
651 ms, the rise time varies from 31 to 61 (46.4 ± 0.8) % of note duration. Notes are formed by
652 6 to 11 (7.9 ± 1.5) incomplete pulses with duration varying from 9 to 18 (13.1 ± 0.6) ms,
653 emitted at a rate of 63 to 118 (86.4 ± 1.9) per second. The dominant frequency varies from
654 1,572 to 1,898 ($1,722.1 \pm 22.9$) Hz and coincides with the fundamental harmonic. Notes
655 have a modest to pronounced frequency upsweep, ranging from 656 to 1,172 (962.0 ± 20.6)
656 Hz.

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658 **Geographic distribution.** Based on the genotyped individuals plus specimens
659 morphologically assigned to the species, *L. wagneri* is circumscribed to western Amazonia,
660 distributed in Andean foothills (up to ~1,500 m elevation) and lowland Amazonian forests
661 of north-western Brazil, northern Peru, Ecuador, and Colombia, extending westward to the
662 Eastern Cordillera of Ecuador and Peru (Fig. 1).

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664 **Notes on natural history.** Ecological and reproductive aspects were described in several
665 studies for a large-sized species of the *L. melanonotus* group from western Amazonia,
666 which we consider to represent *L. wagneri*. Main publications include Heyer and Peters
667 (1971), Heyer and Bellin (1973), Crump (1974), Duellman (1978), Heyer (1994), and
668 Rodríguez and Duellman (1994). According to these publications and field observations by

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4 669 some of us, *L. wagneri* occurs in a wide variety of habitats, including river edges, forests,
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6 670 forest clearings, and shallow swamps.
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11 672 **Remarks.** A quantitative acoustic analysis of nominal *L. wagneri* was provided for the first
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13 673 time in our study, but anecdotal descriptions had already been provided from Ecuadorian
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15 674 and Peruvian Amazonia (Duellman, 1978; Rodríguez & Duellman, 1994). It is possible,
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17 675 however, that morphological and acoustic characterisations might have contained both *L.*
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19 676 *wagneri* and *L. leptodactyloides*, sympatric in western Amazonia. Other call descriptions
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21 677 assigned to *L. wagneri* correspond to other species of the *L. melanonotus* group. The call of
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23 678 *L. wagneri* described in the present study consists of a pulsed and frequency-modulated
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25 679 note (Fig. 6I), whereas those described as consisting of a non-pulsed, frequency-modulated
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27 680 note or a pulsed note without frequency modulation (Schlüter, 1980) should probably
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29 681 correspond to the two call types of *L. petersii* or the call of *L. intermedius* (see Gazoni et
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31 682 al., 2021 for further discussion). A quantitative analysis of calls of *L. wagneri* from four
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33 683 different localities was provided by Straughan and Heyer (1976), but none of them could be
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35 684 assigned to *L. wagneri* when compared to our data. The correct association between call
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37 685 patterns and species is often not possible without complementary information on calling
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39 686 habitat and morphological and/or colour patterns of the recorded males, but we tentatively
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41 687 reassigned those calls to species, based on the currently available data on calls and
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43 688 distribution of the *L. melanonotus* group. Calls described by Straughan and Heyer (1976)
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45 689 from Belém, Pará (Eastern Brazilian Amazonia) and Aragua, Venezuela, are beyond the
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47 690 known distribution range of *L. wagneri*. By combining dominant frequency and locality,
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49 691 those calls could correspond to *L. intermedius* and *L. validus*, respectively (Table 2). Calls
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4 692 described by the same authors of other two populations assigned to *L. wagneri* are from the
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6 693 Province of Sucumbíos in Ecuador. Based on the illustrated spectrogram for the calls from
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8 694 Limoncocha (Straughan & Heyer, 1976: fig. 8) and quantified call traits (note duration and
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10 695 dominant frequency), those calls most likely correspond to *L. leptodactyloides*. In contrast,
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12 696 calls from Santa Cecilia do not match well the acoustic traits quantified for any of the three
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14 697 species of the *L. melanonotus* group recorded in Amazonian Ecuador (i.e., *L. discodactylus*,
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16 698 *L. leptodactyloides*, and *L. wagneri*), but they are closest in note duration, calling rate, and
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18 699 dominant frequency to those of *L. discodactylus*.
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22 700 We did not have access to original sound recordings of *L. colombiensis* to allow us
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24 701 to reanalyse calls under the same analytical procedures and make direct comparisons with
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26 702 the calls of *L. wagneri* described in our study. According to personal communication of
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28 703 Addison Wynn (Smithsonian Institution) to one of us (TRC), the original (analogue) tape
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30 704 recordings of *L. colombiensis* might have been lost due to sticky tape syndrome and a
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32 705 digital copy of them is no longer accessible. It is possible that these closely related species
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34 706 diverged phenotypically in morphology, but share a peculiar call pattern for the *L.*
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36 707 *melanonotus* group consisting of a frequency-modulated note formed by incomplete pulses
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38 708 (Fig. 6I; de Sá et al., 2014: fig. 104). The two species are geographically and ecologically
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40 709 separated, being allopatric in lowland forests of western Amazonia (*L. wagneri*) and in
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42 710 Andean Colombia (*L. colombiensis*), although the existence of a contact zone in
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44 711 Colombia's Putumayo and Caquetá provinces is possible.
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52 713 *Leptodactylus leptodactyloides* (Andersson, 1945)

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54 714 (Tables 1, 2; Figs. 1, 2B, 3A, 6E, Fig. S1)

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6 716 **Type series.** An unnumbered specimen housed at the Naturhistoriska riksmuseet (NRM),
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9 717 the Swedish Museum of Natural History—Heyer (1970, 1994) adopted the obsolete
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11 718 acronym NHRM; see Sabaj (2020) for details—by original designation (Andersson, 1945).
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13 719 Heyer (1970) linked the type specimen to NRM 1945. NRM catalogue information links
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15 720 the holotype to the Río Pastaza, specifically between the Río Puyo and Río Copotaza (Fig.
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17 721 S1). In the same study, Heyer synonymised *L. leptodactyloides* with *L. wagneri*, two
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19 722 sympatric species at the Pastaza Valley, their type locality. Later, Heyer (1994) revalidated
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21 723 the species based on morphological data. Species of the *L. melanonotus* group recorded at
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23 724 the Pastaza Valley are *L. discodactylus*, *L. leptodactyloides*, and *L. wagneri*. These three
24
25 725 species are easily distinguished from each other based on morphological and acoustic data
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27 726 (Table 3) and are also distantly related to each other (Fig. 1). *Leptodactylus*
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29 727 *leptodactyloides* (see Fig. S1 for the holotype) is a medium species distinguished by
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31 728 lacking toe discs (present in *L. discodactylus*), and an indistinct or short dorsolateral fold
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33 729 (long fold in *L. wagneri*), two keratinised thumb spines in adult males (absent in *L.*
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35 730 *discodactylus*), anterior belly mottled, posterior belly tending to immaculate (mottling
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37 731 throughout the belly in *L. discodactylus*; anastomotic pattern in *L. wagneri*). The
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39 732 morphotype of *L. leptodactyloides* has been linked to a bubbling call pattern (Fig. 6E) with
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41 733 occurrence in lowland Amazonian forests (but see Geographic distribution below; Fig. 1).

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43 734 Three allopatric OTUs (mean *p*-distance = 2.9–3.2% in 16S; Table S3) have been
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45 735 delimited and considered herein as *L. leptodactyloides* in the broad sense. One of them
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47 736 (OTU #3, Fig. 1) is widespread throughout Amazonia and encompasses the type locality in
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49 737 Ecuador. One of the two other OTUs (#50; Fig. 1) occupies south-western Amazonia,
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4 738 whereas the other OTU (#49; Fig. 1) occupies an Amazonian region south of the Amazon
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6 739 River and extends southward outside Amazonia. Additional data are required to investigate
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9 740 the variation among those groups of populations. Nevertheless, our preliminary analysis of
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11 741 the morphology and calls associated with all three OTUs could not reveal consistent
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13 742 differences. We thus consider the populations of all three OTUs as conspecific. In the
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15 743 following sections, we update the diagnosis and distribution of *L. leptodactyloides*. Also,
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17 744 we redescribe its advertisement call and those of two morphologically similar species of
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19 745 the group (*L. griseigularius* and *L. sabanensis*) to allow direct interspecific comparisons.
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25 747 **Diagnosis.** The species is recognised in the *L. melanonotus* group by the following
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27 748 combination of character states: (1) moderate size (male SVL 35–45 mm); (2) indistinct to
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29 749 short dorsolateral fold; (3) toe tips unexpanded; (4) upper lip stripe generally indistinct; (5)
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31 750 anterior belly mottled, fading progressively towards hind limbs, posterior belly tending to
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33 751 immaculate; (6) two keratinised spines on the base of the thumb in adult males; (7) single-
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35 752 note advertisement call; (8) call non-pulsed; (9) short note duration (10–26 ms); (10) fast
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37 753 repetition rate (highest repetition rate = 236 notes/min); (11) call frequency modulated; (12)
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39 754 low dominant frequency (904–1,593 Hz).
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45 756 **Comparisons with congeners of the *L. melanonotus* group.** *Leptodactylus*
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47 757 *leptodactyloides* (male SVL 35–45 mm) is distinguished from the partially sympatric *L.*
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49 758 *discodactylus* (male SVL 27–29 mm) and *L. petersii* (male SVL 26–32 mm; Gazoni et al.,
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51 759 2021: table 3) by a larger body size, and from the partially sympatric *L. wagneri* (male SVL
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53 760 46–60 mm) by a smaller body size. *Leptodactylus leptodactyloides* is also distinguished by
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4 761 the combination of indistinct or short dorsolateral fold (Fig. 2B, Fig. S1), long in *L.*
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6 762 *wagneri* (Fig. 2E), complete in *L. riveroi* (Fig. 2F), and absent in *L. diedrus* (Fig. 2A) and
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9 763 *L. magistris*; absence of toe discs (present in *L. diedrus* and *L. discodactylus*; Fig. 3F, G);
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11 764 anterior belly mottled, fading progressively towards hind limbs, posterior belly tending to
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13 765 immaculate (Fig. S1), mottling throughout the belly in *L. brevipes* (Fig. 4B), *L.*
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15 766 *discodactylus*, *L. melanonotus*, *L. natalensis*, *L. nesiotus*, *L. petersii* (Fig. 4C), *L. riveroi*,
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17 767 and *L. wagneri* (Fig. 7B, D); spotted pattern in *L. intermedius* (Fig. 4D), *L. podicipinus*, and
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19 768 *L. pustulatus*, immaculate in *L. diedrus*; upper lip stripe generally indistinct (Fig. 3A, Fig.
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21 769 S1), upper lip stripe from under the mid-eye or over the snout in *L. brevipes*, *L.*
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23 770 *intermedius*, *L. melanonotus*, *L. nesiotus*, *L. podicipinus*, *L. pustulatus*, and *L. riveroi* (Fig.
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25 771 3C), and absent in *L. pascoensis*; presence of keratinised thumb spines in adult males (Fig.
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27 772 S1), absent in *L. discodactylus* and *L. pustulatus*. All six adult specimens of *L. griseigularis*
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29 773 examined by us have the upper lip stripe from the posterior corner of the eye, whereas it is
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31 774 generally indistinct in *L. leptodactyloides*. Still, *L. leptodactyloides* is not easily
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33 775 distinguished morphologically from *L. griseigularis* and *L. sabanensis*. Acoustic data
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35 776 effectively distinguish the three species (see below for call redescrptions of the three
36
37 777 species). Despite being morphologically similar to each other, *L. leptodactyloides* and *L.*
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39 778 *griseigularis* are distantly related to each other (Fig. 1); the phylogenetic position of *L.*
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41 779 *sabanensis* has not been assessed.

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43 780 The advertisement call of *L. leptodactyloides* (Fig. 5E) is formed by a non-pulsed
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45 781 note with short duration (10–26 ms) emitted at a fast rate (highest repetition rate = 236
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47 782 notes/min), a low dominant frequency (904–1,593 Hz), and a modest FM (345–689 Hz).
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49 783 When combined, these acoustic characteristics distinguish *L. leptodactyloides* from all
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4 784 members of the *L. melanonotus* group occurring in Amazonia (Tables 2–3). From the two
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6 785 morphologically most similar species, *L. leptodactyloides* is distinguished from *L.*
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8 786 *griseigularis* by a lower dominant frequency (*L. leptodactyloides*: 904–1,593 Hz vs. *L.*
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10 787 *griseigularis*: 1,938–2,864 Hz), a weaker FM (*L. leptodactyloides*: 345–689 Hz vs. *L.*
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12 788 *griseigularis*: 1,120–1,723 Hz), and a faster repetition rate (*L. leptodactyloides*: 110–236
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14 789 notes per minute vs. *L. griseigularis*: 90–104 notes per minute); from *L. sabanensis*, *L.*
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16 790 *leptodactyloides* is mainly distinguished by a shorter note duration (*L. leptodactyloides*:
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18 791 10–26 ms vs. *L. sabanensis*: 29–44 ms) and a faster repetition rate (*L. leptodactyloides*:
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20 792 110–236 notes/min vs. *L. sabanensis*: 76 notes/min).
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27 794 **Advertisement call of *L. leptodactyloides*.** The description is based on 681 calls of seven
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29 795 males, obtained from multiple localities in Amazonia of Ecuador, Peru, and Brazil (see
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31 796 Table S2 for details). The call (Fig. 5E) consists of a single, non-pulsed note given at a fast
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33 797 rate of 110 to 236 (163.1 ± 42.7) per minute. Notes last 10 to 26 (18.9 ± 2.3) ms, the rise
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35 798 time varies from 17 to 64 (31.0 ± 7.4) % of note duration. The dominant frequency varies
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37 799 from 904 to 1,593 ($1,273.0 \pm 162.1$) Hz and coincides with the fundamental harmonic.
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39 800 Notes have a modest frequency upsweep, ranging from 345 to 689 (496.2 ± 80.7) Hz.
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45 802 **Advertisement call of *L. griseigularis*.** The description is based on 60 calls of three males
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47 803 from the eastern Andean slopes in central and northern Peru (see Table S2 for details),
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49 804 including the reanalysis of the recording analysed for the first acoustic description of the
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51 805 species from Tingo María (type locality) by Heyer and Morales (1995). Because of the low
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53 806 sound input, we could not accurately quantify the frequency modulation in the toptypical
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4 807 calls. The call (Fig. 5D) consists of a single, non-pulsed note given at a rate of 90 to 104
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6 808 (96.1 ± 7.5) per minute. Notes last 10 to 30 (18.5 ± 3.5) ms, the rise time varies from 18 to
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8
9 809 $69 (42.7 \pm 10.9)$ % of note duration. The dominant frequency varies from 1,938 to 2,864
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11 810 $(2,525.5 \pm 296.1)$ Hz and coincides with the fundamental harmonic. Notes have a well-
12
13 811 marked frequency upsweep, ranging from 1,120 to 1,723 $(1,479.4 \pm 100.4)$ Hz.
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18 813 **Advertisement call of *L. sabanensis*.** The description is based on the reanalysis of 95 calls
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20 814 from one male previously described from the Gran Sabana, in the Venezuelan state of
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22 815 Bolívar (Heyer, 1994). The call (Fig. S2) consists of a single, non-pulsed note given at a
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24
25 816 rate of 76 per minute. Notes last 29 to 45 (35.3 ± 3.4) ms, the rise time varies from 49 to 73
26
27 817 (62.0 ± 4.1) % of note duration. The dominant frequency varies from 1,529 to 1,873
28
29 818 $(1,678.5 \pm 54.7)$ Hz and coincides with the fundamental harmonic. Notes usually have a
30
31 819 modest or well-marked frequency upsweep, ranging from 474 to 1,163 (927.1 ± 116.5) Hz.
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36 821 **Geographic distribution.** Based on the genotyped individuals plus specimens
37
38 822 morphologically assigned to the species, *L. leptodactyloides* is widely distributed in
39
40 823 lowland Amazonian forests from Ecuador to eastern Brazilian Amazonia. The species also
41
42 824 occurs in the savannah area close to the mouth of the Amazon River in the Brazilian state
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44 825 of Amapá and in the Pantanal floodplains in the Brazilian state of Mato Grosso, as well as
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46 826 other humid habitats in the open formations in adjacent Bolivia (distinct OTUs; see Fig. 1).
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52 828 **Notes on natural history.** In south-western Amazonia of the Brazilian state of Acre, we
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54 829 observed males calling from temporary rain pools in a human-altered area covered with
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4 830 exotic grasses, located ~100 m from the closest forest fragment. Individuals recorded and
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6 831 collected by us in San Martin, Peru (Pongo-Barranquita and Pucallpa; see Tables S1–S2)
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8
9 832 were found in shallow flooded areas near slow-flowing streams in lowland Amazonian
10
11 833 forest. There were nearby clearings and the forest had some degree of human disturbance in
12
13 834 both cases. In the Pongo-Barranquita area, *L. discodactylus* was sympatric with *L.*
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15 835 *leptodactyloides*, whereas *L. griseigularis*, also recorded and collected in the area, was not
16
17 836 collected in sympatry with *L. leptodactyloides*. In Ecuador, the species occurs in artificial
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19 837 open areas, and secondary and primary forests. Vegetation types include *Terra Firme* forest
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21 838 (forests with well-drained soil), *Várzea* forest (seasonally flooded forests), and swamps.
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25 839 They are commonly found next to lakes and rivers.
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27 840

29 841 **Remarks.** We examined a male specimen (ZUEC-AMP 9407) collected from the same
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31 842 locality (Bolívar, Venezuela's Gran Sabana) where the calls (recording FNJV 31079;
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33 843 deposited also in the Smithsonian under the accession USNM 225 and field code AJC 346)
34
35 844 assigned to *L. sabanensis* by W. R. Heyer were recorded by Adão J. Cardoso (AJC).
36
37 845 However, there is a mismatch between the dates of the recording and specimen collection.
38
39 846 It is relevant to mention that AJC himself did not link this specimen as a call voucher of
40
41 847 that recording. The collection date of this specimen is registered in the ZUEC catalogue as
42
43 848 19 June 1990, whereas the corresponding recording was made on 18 or 19 January in the
44
45 849 same year (registered by voice in the original recording by AJC). We cannot trace back if
46
47 850 the divergence between months, but the coincidence on the day of collection and recording,
48
49 851 might have been a typographical error, which would indicate that ZUEC-AMP 9407 could
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51 852 be the call voucher of the recording FNJV 31079. During his narration at the end of the
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4 853 recording, AJC mentioned that he was recording a *Leptodactylus* species with a horizontal
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6 854 stripe under the eye. This favours the idea that ZUEC-AMP 9407 is not a call voucher
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8
9 855 because this specimen has an upper lip stripe extending from the posterior corner of the eye
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11 856 (i.e., character state B); such character state is also present in the adult female of *L.*
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13 857 *sabanensis* in Figure 11 of Duellman (1997). We would expect that, by linking the recorded
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16 858 call pattern from the Gran Sabana to a morphotype with a horizontal upper lip stripe, AJC
17
18 859 could have referred to (1) a species of the *L. fuscus* group (commonly known as white-
19
20 860 lipped frogs; see fig. 5 of Silva et al., 2020 for examples), (2) a species of the *L. bolivianus*
21
22 861 complex (also known as white-lipped frogs; Heyer & de Sá, 2011), or (3) another species of
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24
25 862 the *L. melanonotus* group having the character state C of upper lip stripe (see Fig. 3C).
26
27 863 After reanalysing the recording FNJV 31079, we could discount all *Leptodactylus* species
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29 864 with confirmed or potential occurrence in the Gran Sabana (Fig. 1; Heyer, 1994; Duellman,
30
31
32 865 1997; de Sá et al., 2014; Barrio-Amorós et al., 2019), except *L. longirostris* Boulenger,
33
34 866 1882, a terrestrial species (*L. fuscus* group) with a similar call, sympatric distribution, but
35
36 867 morphologically distinct from all species of the *L. melanonotus* group (see an adult male of
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39 868 *L. longirostris* from the Gran Sabana in Fig. 208 of Barrio-Amorós et al. 2019; referred
40
41 869 therein as *L. sabanensis*). Then, we conducted an acoustic analysis ($n = 12$ males; 389
42
43 870 quantified notes) of *L. longirostris* (Fig. S2, Table 2; see Table S2 for locality data) and
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45
46 871 found that the calls recorded from the Gran Sabana, originally assigned to *L. sabanensis*,
47
48 872 and those of *L. longirostris* overlap in all analysed traits. *Leptodactylus longirostris* is
49
50 873 reported as an abundant species throughout the Gran Sabana (Duellman, 1997). We
51
52 874 conclude that the calls recorded in the Gran Sabana could be conspecific with those of *L.*
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55 875 *longirostris*, but assigned to *L. sabanensis* by Heyer (1994) in error. Perhaps Heyer

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4 876 implicitly assumed that the male ZUEC-AMP 9407 should correspond to a call voucher
5
6 877 because of locality data. In this case, the advertisement call of *L. sabanensis* remains
7
8 878 unknown. We would require the collection of males linked to calls and DNA sequences to
9
10 879 confirm either possibility, focusing on both the morphotypes of the *L. melanonotus* group
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12 880 (i.e., *L. sabanensis*) and *L. fuscus* group (i.e., *L. longirostris*) occurring in Venezuela's
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14 881 Gran Sabana.
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20 883 *Leptodactylus fremitus* sp. nov. (Tables 1, 2, 4; Figs. 1, 5B, 6H, 8, Fig. S3)

21
22 884 *Leptodactylus leptodactyloides* (Heyer, 1994; Lescure & Marty, 2000; Ouboter & Jairam,
23
24 885 2012)

25
26 886 *Leptodactylus* aff. *leptodactyloides* (Dewynter et al., 2008)

27
28 887 *Leptodactylus* gr. *podicipinus* C (Dewynter et al., 2020)

29
30 888 *Leptodactylus* gr. *wagneri* G-E-F (Fouquet et al., 2007)

31
32 889 *Leptodactylus* sp. gr. *wagneri* C (Fouquet et al., 2012)

33
34 890 *Leptodactylus* sp. 2 gr. *podicipinus* (Fouquet et al., 2015)

35
36 891 *Leptodactylus* sp. gr. *podicipinus* (Fouquet et al., 2019)

37
38 892 *Leptodactylus* sp. Guiana (Vacher et al., 2020)

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42 894 **Zoobank:** urn:lsid:zoobank.org:act:7718B9CF-4C40-49F4-ADDC-1E74D0E89CDE

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46 896 **Holotype.** CFBH 43258 (field number TRC 181), an adult male from Parque Municipal do
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48 897 Cancão (0.911290°N, 52.003870°W; 108 m elevation), in Serra do Navio, state of Amapá,
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4 898 northern Brazil, collected on 30 March 2018 by T. R. Carvalho, C. E. Costa-Campos, J. C.
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6 899 de Sousa, P. Sanches, and M. R. D. Souza.
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11 901 **Paratypes.** Six adult males (CFBH 45576–80 and 45583; field numbers CECC 3277–8,
12
13 902 3281–2, 3316, and 3697, respectively) and two adult females (CFBH 45581–2; field
14
15 903 numbers CECC 3276 and 3317, respectively) from Reserva Extrativista Beija-Flor Brilho
16
17 904 de Fogo (0.826528°N, 52.189333°W), in Pedra Branca do Amapari, state of Amapá, Brazil,
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19 905 collected in 2019 and 2021 by C. E. Costa-Campos. Twenty-five adult specimens (18 males
20
21 906 and 7 females) from French Guiana, collected from 2009 to 2015: one male (MNHN-RA-
22
23 907 2021.0063; field number AF 0520) from Cisame camp, left margin of the Approuagues
24
25 908 (4.195265°N, 52.372028°W), collected by A. Fouquet; one male (MNHN-RA-2021.0064;
26
27 909 field number CAAM 40) from Montagne Cacao (2.349128°N, 53.215985°W) by O.
28
29 910 Chaline and M. Dewynter; one female (MNHN-RA-2021.0065; field number PG 784), by
30
31 911 A. Fouquet and E. Courtois, and one male (MNHN-RA-2021.0069; field number AF 0735),
32
33 912 by A. Fouquet, from St. Georges (3.811159–3.967639°N, 51.872250–51.889644°W); one
34
35 913 female (MNHN-RA-2021.0066; field number AF 0570) from Le Galion (4.766144°N,
36
37 914 52.432684°W) by M. Dewynter and K. Pineau; two males (MNHN-RA-2021-0067 and
38
39 915 MNHN-RA-2021-0068; field numbers AF 0702 and AF 0724, respectively) from Paracou
40
41 916 (5.275400°N, 52.923600°W) by A. Fouquet and P. Gaucher; one male (MNHN-RA-
42
43 917 2021.0070; field number AF 0810) from Savane Virgine (4.195900°N, 52.149000°W) by
44
45 918 A. Fouquet, E. Courtois, and M. Dewynter; one female (MNHN-RA-2021.0071; field
46
47 919 number AF 0885), by A. Fouquet, and one male (MNHN-RA-2021.0078; field number AF
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49 920 1550), by A. Fouquet, A. Baglan, and M. Dewynter, from Matoury (4.857080–4.863239°N,
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4 921 52.339175–52.349432°W); two males (MNHN-RA-2021.0072 and MNHN-RA-2021.0073;
5
6 922 field numbers AF 0898 and AF 0914, respectively) from Pic Coudreau du Sud
7
8 923 (2.253400°N, 54.353400°W) by M. Blanc; one male (MNHN-RA-2021.0074; field number
9
10 924 AF 0954) from Route Nationale 2 (4.063933°N, 52.041607°W) by M. Blanc and M.
11
12 925 Dewynter; one female (MNHN-RA-2021.0075; field number AF 1201) from Trinité
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14 926 (4.602500°N, 53.414300°W) by E. Courtois and A. Fouquet; one male (MNHN-RA-
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16 927 2021.0076; field number AF 1374) from Bagne des Annamites (4.818210°N,
17
18 928 52.522123°W) by A. Baglan; one male (MNHN-RA-2021.0077; field number AF 1432)
19
20 929 from Saut Taconet (4.032490°N, 52.526188°W) by M. Dewynter; two males (MNHN-RA-
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22 930 2021.0079 and MNHN-RA-2021.0080; field numbers AF 1609 and AF 1697, respectively)
23
24 931 from Saul (3.562580–3.573170°N, 53.198510–53.210460°W) by A. Fouquet, E. Courtois,
25
26 932 and J. P. Vacher; one female (MNHN-RA-2021.0081; field number AF 1733) from Chutes
27
28 933 Voltaire (5.032550°N, 54.086890°W) by A. Fouquet and J. P. Vacher; one female
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30 934 (MNHN-RA-2021.0082; field number AF 1946) from Flat de la Waki (3.083610°N,
31
32 935 53.412100°W) by J. P. Vacher; one male (MNHN-RA-2021.0083; field number AF 2338)
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34 936 from Ekini (4.050000°N, 52.466700°W) by A. Baglan; two males (MNHN-RA-2021.0086
35
36 937 and MNHN-RA-2021.0088; field numbers AF 2763 and AF 2798, respectively) and one
37
38 938 female (MNHN-RA-2021.0087; field number AF 2802) from Mitaraka (2.235770°N,
39
40 939 54.449280°W) by A. Fouquet, M. Dewynter, and N. Vidal; one male (MNHN-RA-
41
42 940 2021.0089; field number AF 3702) from Itoupé (3.014980°N, 53.132860°W) by A.
43
44 941 Fouquet, E. Courtois, B. Villette, and M. Dewynter. Two adult males (MNHN-RA-
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46 942 2021.0084 and MNHN-RA-2021.0085; field numbers AF 2446 and AF 2478, respectively)
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4 943 from Nassau (4.802620–4.804120°N, 54.555500–54.615020°W), eastern Suriname,
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6 944 collected on 16–18 Dec 2014 by A. Fouquet and R. Jairam.
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11 946 **Additional specimens.** Six adult specimens (four males and two females) from western
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13 947 and southern Suriname, collected from 2014 to 2015: four males (MNHN-RA-2021.0090,
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15 948 MNHN-RA-2021.0091, MNHN-RA-2021.0093, and MNHN-RA-2021.0094; field
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17 949 numbers AF 1966, AF 1967, AF 2069, and AF2224, respectively) and one female (MNHN-
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19 950 RA-2021.0092; field number AF 2058) from Sipaliwini (2.024390–2.179650°N,
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21 951 56.085210–56.125080°W), collected by A. Fouquet and J. P. Vacher; one female (MNHN-
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23 952 RA-2021.0095; field number AF 3369) from Bakhuis (4.762840°N, 56.779110°W) by A.
24
25 953 Fouquet, R. Jairam, and S. Cally. These six specimens, which form a distinct OTU
26
27 954 distributed in western and southern Suriname, were not included in the type series, given
28
29 955 the high genetic divergence displayed in comparison with the two other two OTUs assigned
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31 956 to *L. fremitus* sp. nov. (mean *p*-distance = 5.3% in 16S). The low number of specimens and
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33 957 recorded calls available for the divergent OTU from Suriname prevents us from evaluating
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35 958 phenotypic variation and its taxonomic significance.
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43 960 **Etymology.** The Latin word ‘fremitus’ can refer to a vibration transmitted through the body
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45 961 (medical usage of the term), or a dull humming or roaring sound, among other kinds of
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47 962 sounds. The epithet is related to the peculiar grunt sound produced by the new species.
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52 964 **Diagnosis.** *Leptodactylus fremitus* is recognised in the *L. melanonotus* group by the
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54 965 following combination of character states: (1) moderate size (male SVL = 34.1–47.5 mm);
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4 966 (2) dorsolateral fold indistinct or short; (3) toe tips unexpanded; (4) upper lip stripe
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6 967 extending from the posterior corner of the eye; (4) anterior belly mottled, fading
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8 968 progressively towards hind limbs, posterior belly tending to immaculate; (5) two
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10 969 keratinised spines at the base of the thumb in adult males; (6) single-note advertisement
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12 970 call; (7) call formed by incomplete pulses; (8) fast repetition rate (highest repetition rate =
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14 971 211 notes/min); (9) low dominant frequency (1078–1,443 Hz).
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20 973 **Comparisons with congeners of the *L. melanonotus* group.** *Leptodactylus fremitus* (male
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22 974 SVL = 34.1–47.5 mm; Table 4) can be distinguished from four of five sympatric species in
23
24 975 the EGS by a larger body size: *L. intermedius* (male SVL = 27.9–36.2 mm; Gazoni et al.,
25
26 976 2021), *L. nesiotus* (male SVL = 32.0–33.0 mm; Heyer, 1994), *L. petersii* (male SVL 26.4–
27
28 977 31.8 mm; Gazoni et al., 2021), and *L. validus* (male SVL = 30.6–35.6 mm; Appendix S4)—
29
30 978 the new species is mainly distinguished from the fifth sympatric (but not syntopic) species
31
32 979 in the EGS, *L. leptodactyloides*, in acoustic characteristics (see next paragraph; Table 2).
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34 980 *Leptodactylus fremitus* is mainly distinguished from the other 19 species of the *L.*
35
36 981 *melanonotus* group by an indistinct or short dorsolateral fold (Figs. 8A–B, S3); long in *L.*
37
38 982 *wagneri* (Fig. 2E), complete in *L. riveroi* (Fig. 2F), and absent in *L. diedrus* (Fig. 2A) and
39
40 983 *L. magistris*. The new species is distinguished by an upper lip stripe extending from the
41
42 984 posterior corner of the eye (Figs. 8A–B, S3); extending from under the mid-eye or over the
43
44 985 snout in *L. brevipes*, *L. intermedius*, *L. melanonotus*, *L. nesiotus*, *L. podicipinus*, *L.*
45
46 986 *pustulatus*, and *L. riveroi* (Fig. 3C), generally indistinct in *L. leptodactyloides* (Fig. 3A),
47
48 987 and absent in *L. pascoensis*. *Leptodactylus fremitus* has the anterior belly mottled, fading
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50 988 progressively towards hind limbs, and posterior belly tending to immaculate (Fig. 8F);
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4 989 mottling throughout the belly in *L. brevipes* (Fig. 4B), *L. discodactylus*, *L. melanonotus*, *L.*
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6 990 *natalensis*, *L. nesiotus*, *L. petersii* (Fig. 4C), *L. riveroi*, and *L. wagneri* (Fig. 7D); spotted
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8 991 pattern in *L. intermedius* (Fig. 4D), *L. podicipinus*, and *L. pustulatus*, immaculate in *L.*
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10 992 *diedrus*. The new species is distinguished from *L. diedrus* (Fig. 3F) and *L. discodactylus*
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12 993 (Fig. 3G) by lacking toe tips developed into discs (Fig. 8E–F). *Leptodactylus fremitus* is
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14 994 distinguished from *L. discodactylus* and *L. pustulatus* by the presence of two keratinised
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16 995 thumb spines at the base of the thumb in adult males (Fig. 8D–F), absent in the other two
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18 996 species.

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22 997 *Leptodactylus fremitus* (endemic to the EGS) is more similar morphologically to the
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24 998 allopatric *L. colombiensis* (Andean Colombia), *L. griseigularius* (endemic to Eastern
25
26 999 Andean slopes of Peru and Bolivia), and *L. sabanensis* (endemic to Venezuela's Gran
27
28 1000 Sabana), and the partially sympatric *L. leptodactyloides* (Fig. 1). In contrast, these species
29
30 1001 have distinct advertisement calls. *Leptodactylus fremitus* has a single-note call formed by
31
32 1002 incomplete pulses (Figs. 5B, 6H), differing from the non-pulsed calls of *L. griseigularis*
33
34 1003 (Fig. 6D), *L. leptodactyloides* (Fig. 6E), and *L. sabanensis* (Fig. S2). We did not conduct a
35
36 1004 quantitative acoustic analysis of *L. colombiensis*, yet it is possible to observe a noticeable
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38 1005 frequency upsweep in the spectrogram provided in the original call description (de Sá et al.,
39
40 1006 2014: fig. 104), whereas the call of *L. fremitus* has a negligible or modest FM at the end of
41
42 1007 the call (Fig. 6H; Table 2). The irregular AM pattern in the call of *L. colombiensis* (de Sá et
43
44 1008 al., 2014: fig. 104) also differs from the regular AM pattern (incomplete pulses) in the call
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46 1009 of *L. fremitus* (Figs. 5B, 6H). The call of *L. wagneri* (Fig. 6I) and the call type 1 of *L.*
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48 1010 *petersii* (Fig. 6G) are also formed by incomplete pulses. From *L. wagneri*, the new species
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50 1011 is distinguished by a weaker FM or no modulation at all (*L. wagneri*: 656–1172 Hz vs. *L.*
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4 1012 *fremitus*: 0–431 Hz). From *L. petersii*, the new species is distinguished by a greater number
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6 1013 of pulses per note (*L. petersii*: 3–5 vs. *L. fremitus*: 5–10) and longer note duration (*L.*
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8 1014 *petersii*: 31–50 ms vs. *L. fremitus*: 59–105 ms). The call of *L. fremitus* is composed of a
9
10 1015 single note, whereas that of *L. riveroi* is formed by series of two-pulse notes (Fig. 5C). The
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12 1016 temporal envelope of *L. pustulatus* calls consists of a series of both complete and
13
14 1017 incomplete AM (Fig. 5D), whereas that of *L. fremitus* consists of incomplete pulses
15
16 1018 regularly distributed throughout the calls (Fig. 5B). Along with the call description of *L.*
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18 1019 *fremitus*, we redescribe the advertisement calls of the partially sympatric *L. nesiotus* and *L.*
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20 1020 *validus* to allow direct interspecific comparisons.
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27 1022 **Description of holotype (Fig. 8).** Adult male, SVL 40.4 mm, THL 20.3 mm, TL 20.4 mm,
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29 1023 FL 21.6 mm, HAL 10.0 mm, HL 15.6 mm, HW 15.4 mm, ED 3.9 mm, TD 3.3 mm, EN 4.5
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31 1024 mm, IND 3.6 mm, IMT 1.9 mm, OMT 0.9 mm, Fin3DW 0.9 mm, Toe4DW 1.0 mm. Snout
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33 1025 sub-oval in dorsal view, rounded to acuminate in lateral view. Canthus rostralis rounded;
34
35 1026 loreal region slightly concave; tympanic annulus well-defined, mostly circular (TD/ED =
36
37 1027 85%), covered by supratympanic fold above and posteriorly; tympanic membrane partially
38
39 1028 translucent; supratympanic fold from the posterior corner of the eye, over the dorsal edge of
40
41 1029 the tympanic annulus, to the base of the arm; vocal sac subgular; vocal slits present;
42
43 1030 vomerine teeth in two nearly straight rows medial and posterior to choanae and almost
44
45 1031 parallel to sagittal plane. Tongue elongated, free from the posterior third. Two keratinised
46
47 1032 spines at the base of Finger I, and a small keratinised area more distally. Relative finger
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49 1033 lengths IV < II < I < III; fingers fringed laterally, especially in outer side of Finger I, and
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51 1034 inner side of Fingers II–III; finger tips rounded, tip of Finger I slightly swollen; inner
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4 1035 metacarpal tubercle cordiform; outer metacarpal tubercle ovoid (Fig. 3D). Subarticular
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6 1036 tubercles rounded; supernumerary tubercles absent. Dorsal surfaces of body and limbs
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8 1037 covered with white-tipped tubercles (some keratinised), especially on the posterior half of
9
10 1038 the body and hind limbs. Flank shagreened and glandular. Dorsolateral fold indistinct, with
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12 1039 an indication behind the eyelids as a row of tubercles. Ventral surface of body and limbs
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14 1040 smooth, underside of thigh glandular. Relative toe lengths $I < II < V < III < IV$; toes
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16 1041 extensively fringed; toe tips rounded; tip of Toe II slightly swollen. Inner metatarsal
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18 1042 tubercle elongated; outer metatarsal tubercle conical. Inner tarsal fold extending $2/3$ of
19
20 1043 tarsus length, from the base of the inner metatarsal tubercle towards the heel. Fringe along
21
22 1044 the outer side of Toe V extending to outer metatarsal tubercle. Subarticular tubercles nearly
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24 1045 rounded to oval; supernumerary tubercles absent. Sole of foot and tarsus covered with
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26 1046 brown-tipped tubercles (keratinised).

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32 1047 In preservative, dorsal surfaces (body and limbs) brown with lighter and darker
33
34 1048 brown blotches in the background. Interorbital blotch poorly delimited posteriorly,
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36 1049 anteriorly bordered by a silvery horizontal bar. Upper lip stripe light grey; upper and lower
37
38 1050 lips white spotted. Flank light grey. Throat darkened (brown) with pale spots and dots.
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40 1051 Chest and anterior belly brown mottled on a pale background; posterior belly immaculate.
41
42 1052 Underside of thigh finely mottled on a partially translucent, yellow background. Posterior
43
44 1053 surface of thigh black with a light grey mottling and an irregular, longitudinal stripe (on the
45
46 1054 right side). Palm of hand and sole of foot dark brown, except tubercles and finger and toe
47
48 1055 tips, which vary from cream to grey. Thumb spines solid black. In life, dorsal surfaces with
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50 1056 different shades of brown. Upper side of the iris reddish brown, the lower side grey and
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52 1057 dark brown. Upper lip stripe light brown; upper and lower lips with white spots and
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4 1058 blotches. Flank with a gradient of light brown, red, and yellow towards the belly. Dorsal
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6 1059 surface of thigh with dark brown transverse bars. Posterior surface of thigh black with a
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9 1060 yellow mottling and an irregular, longitudinal stripe (on the right side). Throat light grey
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11 1061 and light cream, belly and underside of thigh with a yellow mottling. Ventral surfaces of
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13 1062 hand and foot dark brown, tarsus dark mottled on a light grey and yellow background.

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15 1063 Thumb spines solid black.

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20 1065 **Variation in the type series.** Dorsolateral fold is mostly indistinct, but can be short,
21
22 1066 interrupted. Upper lip stripe is poorly outlined in CFBH 45580. This specimen also has its
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24 1067 ventral colouration partially faded. Five specimens from Amapá (CFBH 45577–8, 45581–
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26 1068 3) do not have any indication of longitudinal stripe on the posterior surface of the thigh.
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28 1069 Dorsal colouration (especially in life) varies from light grey/brown to dark brown. Dark
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30 1070 brown and black blotches can be present. In life, some specimens have a reddish
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32 1071 colouration on the scapular region (MNHN-RA-2021.0072; Fig. S3). Mottling in life is
33
34 1072 usually formed by contrasts of black and bright yellow. Populations assigned to *L. fremitus*
35
36 1073 form two distinct OTUs (mean *p*-distance = 2.9% in 16S), one of them (OTU #6; Fig. 1)
37
38 1074 occupying French Guiana and Amapá (Brazil), the other (OTU #41; Fig. 1) occupying
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40 1075 eastern Suriname and northern Pará (Brazil). Morphological and acoustic variation of these
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42 1076 two groups of populations overlaps to each other, thus suggesting that the genetic
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44 1077 divergence can be considered intraspecific variation.

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52 1079 **Advertisement call of *L. fremitus*.** The description is based on 312 calls of seven males,
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54 1080 including the holotype and one paratype, from the Eastern Guiana Shield (Brazil, French

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4 1081 Guiana, and Suriname; see Table S2 for details). The call (Figs. 5B, 6H) consists of a single
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6 1082 note formed by incomplete pulses. Notes are given at a rate of 63 to 211 (124.2 ± 62.2) per
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8 1083 minute. Notes last 59 to 105 (85.6 ± 7.6) ms, the rise time varies from 41 to 71 (56.7 ± 3.3)
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10 1084 % of note duration. Notes are formed by 5 to 10 (7.6 ± 0.9) incomplete pulses with duration
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12 1085 varying from 8 to 16 (11.3 ± 1.2) ms, emitted at a rate of 92 to 140 (117.9 ± 8.6) per
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14 1086 second. The dominant frequency varies from 1,078 to 1,443 ($1,232.0 \pm 72.5$) Hz and
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16 1087 coincides with the fundamental harmonic. Notes have a modest frequency upsweep or no
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18 1088 modulation, ranging from 0 to 431 (173.1 ± 60.6) Hz.
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25 1090 **Advertisement call of *L. nesiotus*.** The description is based on the reanalysis of 30 calls of
26
27 1091 one male from the Trinidad Island (type locality), recorded by J. R. Downie and described
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29 1092 by Heyer (1994), plus 48 calls of one male from French Guiana (see Table S2 for details).
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31 1093 The call (Fig. S4) consists of a single, non-pulsed note given at a fast rate of 264 to 288
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33 1094 (276.1 ± 17.3) per minute. Notes last 25 to 38 (29.4 ± 0.2) ms, the rise time varies from 16
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35 1095 to 69 (47.9 ± 13.6) % of note duration. The dominant frequency varies from 1,421 to 1,938
36
37 1096 ($1,877.9 \pm 44.4$) Hz and coincides with the fundamental harmonic. Notes usually have a
38
39 1097 weak to modest frequency upsweep, ranging from 86 to 603 (539.2 ± 31.7) Hz.
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45 1099 **Advertisement call of *L. validus*.** The description is based on 456 calls of 11 males from
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47 1100 Brazil, including lowland Amazonian forests (Amazonas State) and the savannah
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49 1101 ecosystem in Roraima State, as well as Trinidad Island (see Table S2 for details). The call
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51 1102 (Fig. 6C) consists of a single, non-pulsed note given at a rate of 62 to 161 (124.8 ± 31.1)
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53 1103 per minute. Notes last 26 to 63 (45.9 ± 7.0) ms, the rise time varies from 16 to 66 ($38.8 \pm$
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4 1104 10.5) % of note duration. The dominant frequency varies from 2,541 to 3,230 ($2,972.9 \pm$
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6 1105 141.8) Hz and coincides with the fundamental harmonic. Notes usually have a pronounced
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9 1106 frequency upsweep, ranging from 861 to 1,938 ($1,360.3 \pm 180.3$) Hz.
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13 1108 **Geographic distribution.** *Leptodactylus fremitus* is endemic to the EGS in north-western
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15 1109 Pará (Brazil), French Guiana, and eastern Suriname. In French Guiana, *L. fremitus* is
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17 1110 distributed across the entire territory, including the coastal forests. However, the species
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19 1111 has not been recorded from Guyana, or the Brazilian states of Roraima and Amazonas,
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21 1112 which indicates either a western range boundary in Suriname and the Brazilian state of Pará
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23 1113 north of the Amazon River (Fig. 1) or sampling gaps, but in any case, the species is
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25 1114 unambiguously circumscribed to the EGS. It is noteworthy that the westernmost
26
27 1115 populations in Suriname (Bakhuis and Sipaliwini) harbour a distinct mtDNA lineage,
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29 1116 indicating the possible existence of an additional species. This distribution pattern (i.e.,
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31 1117 endemic to the EGS) is shared many species in the region (Vacher et al., 2020) and the
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33 1118 genetic break along the Maroni River strikingly mirrors those observed in other anuran
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35 1119 species (Fouquet et al., 2012), such as *Allobates granti* (Kok et al., 2006), *Anomaloglossus*
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37 1120 *surinamensis* Ouboter & Jairam, 2012, and *Pristimantis chiastonotus* (Lynch & Hoogmoed,
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39 1121 1977).
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48 1123 **Habitat and natural history.** The species occupies marshy areas between 0 and 400 m
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50 1124 elevation of primary and secondary forests, but is sometimes found also at sites under a
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52 1125 certain degree of human disturbance near urbanised areas, notably flooded areas, such as
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54 1126 ponds forming on the bed of streams and rivers. *Leptodactylus fremitus* occurs syntopically
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4 1127 throughout its distribution range with *L. petersii* and syntopically in Suriname with *L.*
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6 1128 *validus*. Groups of several juveniles of *L. fremitus* can sometimes be observed on the
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8 1129 muddy banks. Breeding occurs throughout the rainy season. According to our field
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10 1130 observations, males generally call at night from a cavity excavated at the water level on the
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12 1131 wetland bank or beneath the leaves nearby. They are generally isolated, calling at a long
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14 1132 distance from one another, but can sometimes form small choruses of 2–4 males. The foam
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16 1133 nest protecting the egg clutch is produced in a previously excavated chamber, where it
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18 1134 floats on the accumulated water (reproductive mode 13 of Haddad & Prado, 2005). When a
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20 1135 female joins a male inside the chamber, the male emits a courtship vocalisation and
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22 1136 performs particular courtship movements that have not yet been observed in detail. Another
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24 1137 type of vocalisation is emitted during interactions between males. Once freely swimming,
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26 1138 the tadpoles remain grouped (schooling behaviour) and at short distances from the female.
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28 1139 Adult individuals, when manipulated, secrete a toxic substance from their skin that causes
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30 1140 irritation to human skin and mainly when the secretion comes into contact with the mucosa.
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36 1141 At the type locality (Serra do Navio, Amapá, Brazil), the holotype of *L. fremitus*
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38 1142 was heard calling from inside a previously excavated underground chamber (partially filled
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40 1143 with water) half a metre from the water course of a rocky-bottom rivulet. The chamber was
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42 1144 excavated from underneath a thin layer of leaf litter so that one broad leaf protected it as the
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44 1145 chamber's roof. As the leaf was pulled off the ground, the male was observed with only his
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46 1146 head above the water, which he quickly submerged into the accumulated water inside the
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48 1147 chamber. *Leptodactylus petersii* is the only sympatric species of the group at the type
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50 1148 locality of *L. fremitus*.
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4 1150 **Remarks.** The advertisement and aggressive calls of *L. nesiotus* were recently
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6 1151 characterised by Borzée et al. (2020). Those authors analysed advertisement calls of one
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8 1152 male recorded in the field and two other males recorded in the laboratory. This call type
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10 1153 was described as composed of two note types (named as pulses A and B). Our sample of *L.*
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12 1154 *nesiotus* calls from Trinidad Island and French Guiana consisted of a single type of non-
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14 1155 pulsed note emitted at a fast repetition rate as a typical bubbling call pattern, which is
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16 1156 consistent with the original description (see Heyer, 1994: fig. 30). We reinterpret the
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18 1157 second type of note (= pulse B) described in Borzée et al. (2020) as background calls of an
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20 1158 antiphonal calling male, which is commonly observed among species of the *L. melanonotus*
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22 1159 group with bubbling calls (see Fig. S4).
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31 1161 **Final comments on *Leptodactylus* taxa.** Information on two species (*L. magistris* and *L.*
32 1162 *pascoensis*) is limited to their original descriptions (Heyer, 1994; Mijares-Urrutia et al.,
33 1163 1997). Until now, their calls remain unknown and DNA sequences have not been linked to
34 1164 their morphotypes either. Besides these two species, *L. sabanensis* does not have any
35 1165 available DNA sequence and the calls originally assigned to the species might have been
36 1166 erroneously confused with calls of another *Leptodactylus* species, as stated earlier in our
37 1167 study. Therefore, future efforts in data collection should concentrate on these three species.
38 1168 Moreover, a better characterisation of intraspecific variation of populations currently
39 1169 assigned to *L. colombiensis* and *L. melanonotus* could shed light on potential cryptic
40 1170 diversity in the *L. melanonotus* group.
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1172 **Discussion**

1173 The high diversity of mtDNA lineages within the *L. melanonotus* group indicates that
1174 species richness in the group might still be underestimated. Our DNA-based species
1175 delimitation resulted in 57 OTUs and included 16 nominal species out of 19 (84%). This
1176 figure matches the numerous studies focusing on other groups of Neotropical anurans,
1177 suggesting vast underestimations of species diversity (e.g., *Allobates* Réjaud et al., 2020;
1178 *Synapturanus* Fouquet et al., 2021; *Amazophrynella* Moraes et al., 2022). It is interesting to
1179 note, however, that some species of the group comprise several geographically structured
1180 lineages that could indicate population genetic structure rather than species boundaries
1181 (false positives). For example, *L. natalensis* displays genetic structure among populations
1182 distributed in the Atlantic Forest and Cerrado but without phenotypic disparity (i.e.,
1183 conservative morphology and calls). On the other hand, *L. petersii* displays a remarkable
1184 geographic structure and genetic divergence among populations throughout Amazonia and
1185 also exhibits pronounced phenotypic variation, which could indicate that multiple species
1186 are subsumed under *L. petersii*. In the case of *L. colombiensis*, there is one lineage in
1187 Andean Colombia (referred to herein as *Leptodactylus* sp. from Colombia) that was
1188 recovered as a putative new species. This is a region with limited phenotypic data (i.e.,
1189 morphological and acoustic data of taxonomic relevance) that can actually be linked to
1190 DNA sequences, which hampers an appropriate evaluation of its taxonomic status. Another
1191 limitation is the geographically restricted molecular sampling of *L. melanonotus*,
1192 particularly for Central American populations. Based on our results and sampling gaps,

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4 1193 additional candidate new lineages within the *L. melanonotus* group are expected to be
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6 1194 present in the Andes, Amazonia, and Central America.

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8 1195 The currently available molecular data of *Leptodactylus* is essentially represented
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10 1196 by fragments of mitochondrial DNA genes (16S, 12S, and COI), and the only nuclear DNA
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12 1197 gene comprehensively sampled across the genus (rhodopsin) is not informative enough to
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14 1198 investigate species relationships within the genus (e.g., Carvalho et al., 2021; Gazoni et al.,
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16 1199 2021). The reduced number of sampled genes for *Leptodactylus* taxa may compromise our
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18 1200 understanding of the phylogenetic relationships within the genus and the acquisition of
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20 1201 additional molecular markers for more than 80 species distributed across the Neotropics
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22 1202 remains necessary but a challenging task. However, our phylogenetic tree of the *L.*
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24 1203 *melanonotus* group represents the most geographically and taxonomically complete until
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26 1204 now. We acknowledge that the limited genetic data supporting our phylogenetic hypothesis
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28 1205 might bias a broader understanding of the evolutionary history of this *Leptodactylus* group,
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30 1206 and, as such, prevent us from conducting formal biogeographic analyses (e.g., ancestral
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32 1207 area reconstruction). Nevertheless, in the next paragraph we offer a speculative
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34 1208 interpretation of the diversification of the *L. melanonotus* group. We understand that such a
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36 1209 discussion would serve as ground for future research on the historical biogeography of the
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38 1210 *L. melanonotus* group and, more broadly, the entire genus *Leptodactylus*.

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40 1211 Our phylogenetic hypothesis suggests that the *L. melanonotus* group might have
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42 1212 originated in lowland Amazonian forests, where most diversification within this
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44 1213 *Leptodactylus* group took place, a scenario shared by other co-distributed anuran groups
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46 1214 (e.g., *Adenomera*: Fouquet et al., 2014; *Allobates*: Réjaud et al., 2020; *Pipa*: Fouquet et al.,
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48 1215 2022). Assuming an Amazonian origin for the clade, subsequent diversification within the
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4 1216 *L. melanonotus* group would involve at least five dispersal events. *Leptodactylus pustulatus*
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7 1217 may represent the first dispersal event outside Amazonia by occupying a vast area in the
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9 1218 South American Dry Diagonal (not shown in Fig. 1, but can be visualised in fig. 126 of de
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11 1219 Sá et al., 2014). Another possible dispersal event is related to a clade that occupied Andean
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13 1220 Colombia (*L. colombiensis* and a second lineage reported herein as *Leptodactylus* sp. from
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15 1221 Colombia, possibly endemic to that region; see Fig. 1), the Guiana Shield (*L. validus*,
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17 1222 widely distributed across the region; Fig. 1), and the Pacific lowlands (Ecuadorian
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19 1223 population of *L. melanonotus*; Fig. 1). In the case of *L. melanonotus*, assuming that this
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21 1224 name represents a single taxonomic unit across its geographic range (but see a discussion
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23 1225 on sequences assigned to the species in Gazoni et al., 2021), the species could have
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25 1226 expanded northward into the Caribbean drainage of Colombia and Venezuela, and across
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27 1227 Central America, and Mexico. This clade also contains the Amazonian endemic *L. wagneri*,
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29 1228 which could have occupied lowland Amazonian forests secondarily. A possible third
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31 1229 dispersal event is associated with the *L. podicipinus* clade, in which one species (*L.*
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33 1230 *intermedius*) is widespread in Amazonia, whereas *L. brevipes* and *L. podicipinus* occupied
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35 1231 open formations in central South America (Fig. 1). In the clade formed by *L. nesiotus* and
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37 1232 *L. fremitus*, the geographic range of both species coincides with Amazonia. *Leptodactylus*
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39 1233 *nesiotus* could have expanded towards coastal areas in northern South America and
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41 1234 Trinidad Island, reaching an eastern limit in French Guiana (not occurring in the
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43 1235 easternmost coastal area in French Guiana and also absent in adjacent Amapá, Brazil; Fig.
44
45 1236 1). In contrast, *L. fremitus* is a forest-dwelling species mostly associated with Amazonia but
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47 1237 also occurs in coastal French Guiana. The latter species is endemic to the EGS (Fig. 1).
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49 1238 Lastly, in the clade formed by *L. leptodactyloides* and *L. natalensis*, the first species has a
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4 1239 discontinuous distribution within Amazonia, possibly biased by misidentifications and
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6 1240 insufficient sampling efforts, and is also distributed in the Chiquitano dry forests (Bolivia
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8 1241 and Brazil), reaching Pantanal floodplains and Cerrado ecotone in Brazil (Fig. 1).
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11 1242 *Leptodactylus natalensis* occupied a vast region of coastal Atlantic Forest and humid areas
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13 1243 in the Cerrado and Caatinga (Fig. 1).

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15 1244 Species of the *L. melanonotus* group use a wide variety of aquatic habitats as calling
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17 1245 and breeding sites, such as rain water accumulated in puddles, areas seasonally flooded by
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19 1246 rivers caused by water regimes, or flowing water systems (e.g., Heyer & Bellin, 1973;
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21 1247 Heyer, 1994; Rodrigues et al., 2011). These environments are generated and maintained by
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23 1248 hydrological dynamics (e.g., river seepages) or human activity in completely altered areas
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25 1249 (e.g., uncovered sewage systems in urban perimeter). Calling and breeding habitats often
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27 1250 indicate the occurrence of certain species in a region, but do not reflect phylogenetic
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29 1251 relatedness. Pairs of closely related species of the *L. melanonotus* groups are generally
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31 1252 allopatric and also diverge in phenotypic traits, such as *L. colombiensis* and *L. wagneri*, and
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33 1253 *L. leptodactyloides* and *L. natalensis* (see Fig. 1). Most species of the group are forest
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35 1254 dwellers widely distributed in lowland Amazonian forests, which use temporary pools and
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37 1255 rivulets inside the forest, or seasonally flooded forests (Heyer, 1994). These include *L.*
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39 1256 *diedrus*, *L. discodactylus*, *L. fremitus*, *L. petersii*, and *L. riveroi*—*L. petersii* being
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41 1257 sympatric with all other five species in different parts of Amazonia. In contrast, *L.*
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43 1258 *intermedius* is an Amazonian endemic species that occupies open habitats, including
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45 1259 temporary rain pools in human-altered areas and floating meadows. *Leptodactylus*
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47 1260 *leptodactyloides*, *L. validus*, and *L. wagneri* are species that have been reported to use both
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49 1261 open and forest habitats. Populations of *L. leptodactyloides* and *L. validus* sampled by us in
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4 1262 the field generally prefer open habitats over forests as calling sites, whereas *L. wagneri* is
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6 1263 more commonly found in forest habitats, being the distantly related *L. leptodactyloides* and
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8 1264 *L. wagneri* sympatric in western Amazonia. *Leptodactylus nesiotus*, *L. podicipinus*, and *L.*
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10 1265 *pustulatus* typically use open habitats. An intermediate pattern is observed across the
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12 1266 geographic range of *L. brevipes* and *L. natalensis*. These two species exhibit plasticity in
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14 1267 the range of preferred habitats, occurring predominantly in open formations or forests
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16 1268 depending on the occurrence area. In some localities, shadowy habitats are usually
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18 1269 preferred, such as forest borders, dense groves of Buriti palm (*Mauritia flexuosa*), and
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20 1270 swampy areas inside the forest, often in forest clearings. In other localities, calling males
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22 1271 are more often found in temporary rain pools in pastures, marshes, and artificial ponds.
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24 1272 Interestingly, *L. podicipinus* does not occur syntopically either with *L. brevipes* or *L.*
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26 1273 *natalensis*, even though *L. podicipinus* has a distinct call pattern (water drop call) in
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28 1274 comparison with the bubbling calls of the other two, partially sympatric, species.
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34 1275 The combination of geographical, ecological, and phylogenetic data of the *L.*
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36 1276 *melanonotus* group suggests phylogenetic overdispersion, i.e., the most closely related
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38 1277 species are often ecologically distinct and spatially distant from each other. Together, the
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40 1278 reassessments provided in the present study highlight this widely distributed anuran clade
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42 1279 as a future opportunity of understanding the evolution of ecological niche partitioning, as
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44 1280 well as major morphological and acoustic patterns in the context of sympatric and allopatric
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46 1281 species co-occurrence in open formations and forests across the Neotropics.
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Table 1. Mean interspecific genetic distances (uncorrected *p*-distances) estimated from partial 16S mtDNA fragments in the *Leptodactylus melanonotus* group. Abbreviations: mel (*L. melanonotus*), val (*L. validus*), sp. (*Leptodactylus* sp. from Colombia), col (*L. colombiensis*), wag (*L. wagneri*), bre (*L. brevipes*), int (*L. intermedius*), pod (*L. podicipinus*), dis (*L. discodactylus*), gri (*L. griseigularis*), nes (*L. nesiotus*), fre1 (*L. fremitus* sp. nov.; type series), fre2 (*L. fremitus*; additional specimens from Suriname), lep (*L. leptodactyloides*), nat (*L. natalensis*), pet (*L. petersii*), die (*L. diedrus*), pus (*L. pustulatus*), riv (*L. riveroi*).

	mel	val	sp.	col	wag	bre	int	pod	dis	gri	nes	fre1	fre2	lep	nat	pet	die	pus
val	7.7																	
sp.	6.6	4.4																
col	6.4	4.6	2.1															
wag	7.2	5.0	2.1	2.1														
bre	10.7	10.9	9.9	10.1	10.8													
int	11.0	11.5	10.0	10.4	11.4	6.1												
pod	10.8	10.8	9.3	10.2	10.5	5.8	3.7											
dis	11.7	12.1	11.1	11.3	11.4	11.7	12.0	11.5										
gri	11.0	10.5	9.0	9.4	10.0	10.2	10.3	10.0	8.3									
nes	13.4	11.5	12.4	11.1	11.3	12.3	13.1	12.6	13.5	9.2								
fre1	12.8	13.9	12.4	11.9	12.6	11.6	12.8	12.2	12.4	10.8	10.3							
fre2	13.4	13.4	12.9	12.1	12.7	12.5	13.4	13.2	13.5	11.8	10.6	5.5						
lep	11.0	10.0	9.1	9.0	9.1	11.0	11.9	10.4	11.8	9.1	8.0	10.6	10.1					
nat	13.7	11.5	12.3	12.6	13.0	11.9	13.7	12.2	14.2	11.6	10.0	10.5	11.5	8.8				
pet	13.0	13.4	12.7	12.9	13.0	14.1	14.3	14.6	13.6	12.5	13.0	13.0	14.0	12.2	13.9			
die	9.5	9.7	9.0	9.7	9.7	11.1	11.4	10.0	12.6	11.6	12.8	14.3	14.9	11.3	12.3	15.3		
pus	10.0	9.9	9.4	9.9	10.3	12.5	12.2	11.7	15.1	13.8	13.8	15.4	14.4	12.6	11.9	16.9	9.7	
riv	14.0	12.9	13.0	12.5	13.2	15.1	14.0	14.7	15.5	16.3	17.2	16.6	17.1	14.0	16.6	16.9	15.9	14.5

Table 2. Summary of the quantitative acoustic analysis of the *Leptodactylus melanonotus* group: advertisement call (= note) duration (ND) in milliseconds (except *L. riveroi* with a multi-note call), note repetition rate (NR) per minute, pulses per note (PP; N = non-pulsed), and dominant frequency (DF) and frequency modulation (FM) in Hertz. The same acoustic traits are presented for *L. longirostris* (*L. fuscus* group), sympatric with *L. sabanensis* (see text for details). Sample sizes: numbers of recorded males / analysed notes. * Data extracted from Gazoni et al. (2021), except for the note repetition rate (this study). Locality data of recorded males are provided in Table S2.

Species	ND (ms)	NR (min)	PP	DF (Hz)	FM (Hz)	Sample sizes
<i>L. brevipes</i> *	6–20	150–330	N	1,078–1,172 and 2,016–2,953	938–1,969	7 / 258
<i>L. diedrus</i>	131–217	25–44	N	797–926	0–172	2 / 70
<i>L. discodactylus</i>	103–147	72	N	2,476–2,562	1,206–1,378	1 / 92
<i>L. fremitus</i> sp. nov.	59–105	63–211	5–10	1,078–1,443	0–431	7 / 312
<i>L. griseigularis</i>	10–30	90–104	N	1,938–2,864	1,120–1,723	3 / 60
<i>L. intermedius</i> *	14–23	51–283	N	2,692–3,381	991–1,680	8 / 422
<i>L. leptodactyloides</i>	10–26	110–236	N	904–1,593	345–689	7 / 681
<i>L. melanonotus</i>	28–48	11–89	N	2,132–3,141	904–2,063	4 / 43
<i>L. natalensis</i>	10–26	163–296	N	703–1,453	94–861	16 / 806
<i>L. nesiotus</i>	25–38	264–288	N	1,421–1,938	86–603	2 / 78
<i>L. petersii</i> (call type 1)*	31–50	63–182	3–5	797–1,289	–93 to 328	5 / 251
<i>L. petersii</i> (call type 2)*	43–72	33–50	N	2,304–2,692	1,313–1,809	4 / 66
<i>L. podicipinus</i> *	20–45	73–244	N	2,218–3,258	844–1,641	12 / 420
<i>L. pustulatus</i>	56–85	19–39	5–9	1,400–2,133	–94 to 1,359	5 / 105
<i>L. riveroi</i>	615–2,293	46	15–56	452–624	–43 to 215	1 / 19
<i>L. sabanensis</i>	29–45	76	N	1,529–1,873	474–1,163	1 / 95
<i>L. validus</i>	26–63	62–161	N	2,541–3,230	861–1,938	11 / 456
<i>L. wagneri</i>	64–136	50–55	6–11	1,572–1,898 1,615–1,960	656–1,172	2 / 21
<i>L. longirostris</i>	32–68	65–168	N	and 2,175–3,122	517–2,067	12 / 389

Table 3. Summary of morphological and acoustic characters of taxonomic relevance in the *Leptodactylus melanonotus* group. In characters that display high intraspecific variation (e.g., dorsolateral fold), the most frequent state was considered. Codes for character states: dorsolateral fold (abs: absent; i-s: indistinct to short; s-m: short to moderate; m-l: moderate to long; lon: long; com: complete); upper lip stripe (A: indistinct; B: from posterior eye corner; C: under the eye); belly pattern (ima: immaculate; mot1: mottling concentrated anteriorly; mot2: mottling throughout; ana: anastomotic; spot: spotted); toe tip (u-s: unexpanded to slightly swollen; disc1: developed into discs with a central longitudinal groove; disc3: developed into discs with at least three grooves); thumb spines (abs: absent; pre: present); amplitude modulation (abs: absent; inc: incomplete; com: complete); frequency modulation (wea: weak; mod: modest; pro: pronounced); calling rate (low; high). The definition of character states is detailed in the text. Character states of *L. petersii*'s call type 1 and 2 are presented in this order, separated by a slash.

Characters	bre	die	dis	fre	gri	int	lep	mel	nat	nes	pet	pod	pus	riv	val	wag
Morphology																
Dorsolateral fold	s-m	abs	abs	i-s	i-s	m-l	i-s	m-l	s-m	i-s	s-m	m-l	abs	com	i-s	lon
Upper lip stripe	C	A	B	B	B	C	A	C	B	C	B	C	C	C	B	B
Belly pattern	mot2	ima	mot2	mot1	mot1	spot	mot1	mot2	mot2	mot2	ana	spot	spot	ana	mot1	ana
Toe tip	u-s	disc1	disc3	u-s	u-s	u-s	u-s	u-s	u-s	u-s	u-s	u-s	u-s	u-s	u-s	u-s
Thumb spines	pre	pre	abs	pre	pre	pre	pre	pre	pre	pre	pre	pre	abs	pre	pre	pre
Advertisement call																
Amplitude modulation	abs	abs	abs	inc	abs	abs	abs	abs	abs	abs	inc/abs	abs	inc+com	com	abs	inc
Frequency modulation	pro	wea	pro	mod	pro	pro	mod	pro	mod	mod	wea/pro	pro	mod	wea	pro	pro
Calling rate	high	low	low	high	low	high	high	low	high	high	high/low	high	low	low	high	low

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4 Abbreviations: bre (*L. brevipes*), die (*L. diedrus*), dis (*L. discodactylus*), fre (*L. fremitus* sp. nov.), gri (*L. griseigularis*), int (*L.*
5 *intermedius*), lep (*L. leptodactyloides*), mel (*L. melanonotus*), nat (*L. natalensis*), nes (*L. nesiotus*), pet (*L. petersii*), pod (*L.*
6 *podicipinus*), pus (*L. pustulatus*), riv (*L. riveroi*), val (*L. validus*), wag (*L. wagneri*).
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Table 4. Morphometric data (in mm) of *Leptodactylus wagneri* from the Province of Pastaza in Amazonian Ecuador, including the neotype (QCAZ-A 26219), and the type series of *L. fremitus* sp. nov. from the Eastern Guiana Shield (Brazil, French Guiana, and Suriname). Measurements are presented as mean \pm SD (range). Abbreviations are defined in the Materials and methods.

Trait	<i>Leptodactylus wagneri</i>		<i>Leptodactylus fremitus</i> sp. nov.	
	Males <i>n</i> = 19	Females <i>n</i> = 4	Males <i>n</i> = 27	Females <i>n</i> = 9
SVL	53.3 \pm 3.7 (46.1–60.0)	66.4 \pm 3.3 (62.4–70.3)	39.3 \pm 3.0 (34.1–47.5)	46.3 \pm 1.2 (44.6–48.2)
HL	20.9 \pm 1.4 (17.9–23.5)	25.0 \pm 1.7 (23.2–27.2)	14.6 \pm 1.2 (12.7–18.5)	16.5 \pm 1.1 (14.6–18.2)
HW	19.3 \pm 1.2 (16.7–21.2)	23.8 \pm 1.5 (22.7–26.0)	14.8 \pm 1.0 (12.9–17.3)	17.0 \pm 0.8 (15.8–18.0)
ED	4.9 \pm 0.4 (4.0–5.4)	5.3 \pm 0.4 (5.0–5.9)	4.3 \pm 0.6 (2.8–5.4)	4.9 \pm 0.7 (3.7–5.7)
TD	3.9 \pm 0.3 (3.2–4.5)	4.4 \pm 0.4 (4.0–4.9)	3.4 \pm 0.2 (3.1–4.0)	3.6 \pm 0.3 (3.3–4.1)
EN	5.3 \pm 0.3 (4.7–5.8)	6.7 \pm 0.8 (5.7–7.3)	4.1 \pm 0.3 (3.3–4.6)	4.6 \pm 0.3 (4.1–5.0)
HAL	13.4 \pm 0.8 (11.0–15.0)	16.5 \pm 1.1 (15.4–17.7)	10.0 \pm 0.7 (8.7–11.8)	11.2 \pm 0.8 (10.0–12.5)
THL	26.7 \pm 1.8 (22.9–29.5)	33.3 \pm 1.4 (31.7–35.1)	19.4 \pm 1.4 (17.8–24.0)	21.3 \pm 1.2 (19.5–22.7)
TL	28.1 \pm 1.7 (23.6–30.6)	36.1 \pm 2.4 (33.8–39.4)	19.8 \pm 1.5 (17.1–24.7)	22.2 \pm 1.0 (21.0–23.2)
FL	28.5 \pm 1.7 (24.3–31.1)	36.5 \pm 2.0 (35.0–39.5)	21.5 \pm 1.6 (18.2–26.5)	23.4 \pm 0.8 (21.9–24.8)
IND	—	—	3.4 \pm 0.2 (3.0–3.9)	3.8 \pm 0.2 (3.5–4.0)
IMT	—	—	1.8 \pm 0.2 (1.5–2.5)	2.0 \pm 0.2 (1.7–2.3)
OMT	—	—	1.0 \pm 0.2 (0.7–1.2)	1.0 \pm 0.2 (0.8–1.3)
Fin3DW	—	—	0.8 \pm 0.1 (0.6–1.0)	0.9 \pm 0.1 (0.8–1.0)
Toe4DW	—	—	0.8 \pm 0.1 (0.6–1.1)	0.9 \pm 0.1 (0.7–1.0)

Figure captions

Fig. 1. Maximum Likelihood tree obtained from the analysis of 2,428 bp (16S + COI) with branches collapsed according to the consensus of the results of the three species delimitation methods (based on 613 bp of 16S). Posterior probabilities are indicated at the internal branches. An asterisk indicates a posterior probability of 1.0. OTU numbers resulting from the consensus of the delimitation methods are shown along the vertical axis.

Fig. 2. Variation of the dorsolateral fold (A–E) in the *Leptodactylus melanonotus* group. (A) absent, *L. diedrus* (field number AF 4064); (B), indistinct or fragmented, *L. leptodactyloides* (AAG-UFU 5868); (C) short, *L. natalensis* (AAG-UFU 4984); (D) moderate to long (fragmented posteriorly), *L. podicipinus* (AAG-UFU 0098); (E) long, *L. wagneri* (QCAZ-A 38775); and (F) complete, *L. riveroi* (INPA-H 37253; photo by Leandro J. C. L. Moraes).

Fig. 3. Character states of the upper lip stripe (A–C) and toe tips (D–G) in the *Leptodactylus melanonotus* group. (A) Indistinct, *L. leptodactyloides* (AAG-UFU 5868); (B) from posterior eye corner, *L. natalensis* (AAG-UFU 4984); and (C) under the eye, *L. riveroi* (INPA-H 37253; photo by Leandro J. C. L. Moraes). (D) Unexpanded, *L. petersii* (AAG-UFU 6605); (E) slightly swollen, *L. validus* (AAG-UFU 3887); (F) toe discs with one central longitudinal groove, *L. diedrus* (AAG-UFU 3890); and (G) toe discs with four longitudinal grooves, *L. discodactylus* (ZUEC-AMP 11109).

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7 **Fig. 4.** Variation of belly colour patterns (A–D) in the *Leptodactylus melanonotus* group.

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9 (A) Mottling fading posteriorly, *L. validus* (AAG-UFU 3887); (F) mottling throughout the
10 belly, *L. brevipes* (UFMT-A 12014); (G) anastomotic mottling, *L. petersii* (AAG-UFU
11 6605); and (H) pale spotted, *L. intermedius* (CFBH 43137).
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18 **Fig. 5.** Advertisement calls in the *Leptodactylus melanonotus* group. Patterns of amplitude

19 modulation, AM: oscillograms (focusing on the temporal envelope; not to scale) showing
20 (A) no AM (= non-pulsed call), *L. natalensis*; (B) incomplete AM, *L. fremitus* sp. nov.; (C)
21 complete AM, *L. riveroi*; and (D) incomplete + complete AM, *L. pustulatus*. Patterns of
22 frequency modulation, FM: spectrograms (produced at a 3-kHz scale) showing (E) no/weak
23 FM, *L. diedrus*; (F) modest FM, *L. nesiotus*; (G) pronounced FM, *L. discodactylus*; and (H)
24 upward + downward FM, *L. pustulatus*.
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36 **Fig. 6.** Representatives of the three main ‘acoustic groups’ in the *Leptodactylus*

37 *melanonotus* group. (A–C) ‘Water drop’ pattern: *L. melanonotus*, *L. petersii* (call type 2),
38 and *L. validus*, respectively. (D–F) ‘Bubbling’ pattern: *L. griseigularis*, *L. leptodactyloides*,
39 and *L. natalensis*, respectively. (G–H) ‘Grunt’ pattern: *L. petersii* (call type 1) and *L.*
40 *fremitus* sp. nov., respectively. (I) Unique pattern of *L. wagneri*, a frequency-modulated call
41 formed by incomplete pulses. Scales = 10 ms.
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4 **Fig. 7.** Life colours (A–B), and dorsal and ventral views in preservative (C–D) of the
5 neotype of *Leptodactylus wagneri* (QCAZ-A 26219, adult male: SVL = 57.2 mm) from the
6 Province of Pastaza, Amazonian Ecuador.
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13 **Fig. 8.** Life colours (A–D), and dorsal and ventral views in preservative (E–F) of the
14 holotype of *Leptodactylus fremitus* sp. nov. (CFBH 43258, adult male: SVL = 40.4 mm)
15 from Serra do Navio, Brazilian state of Amapá, in the Eastern Guiana Shield.
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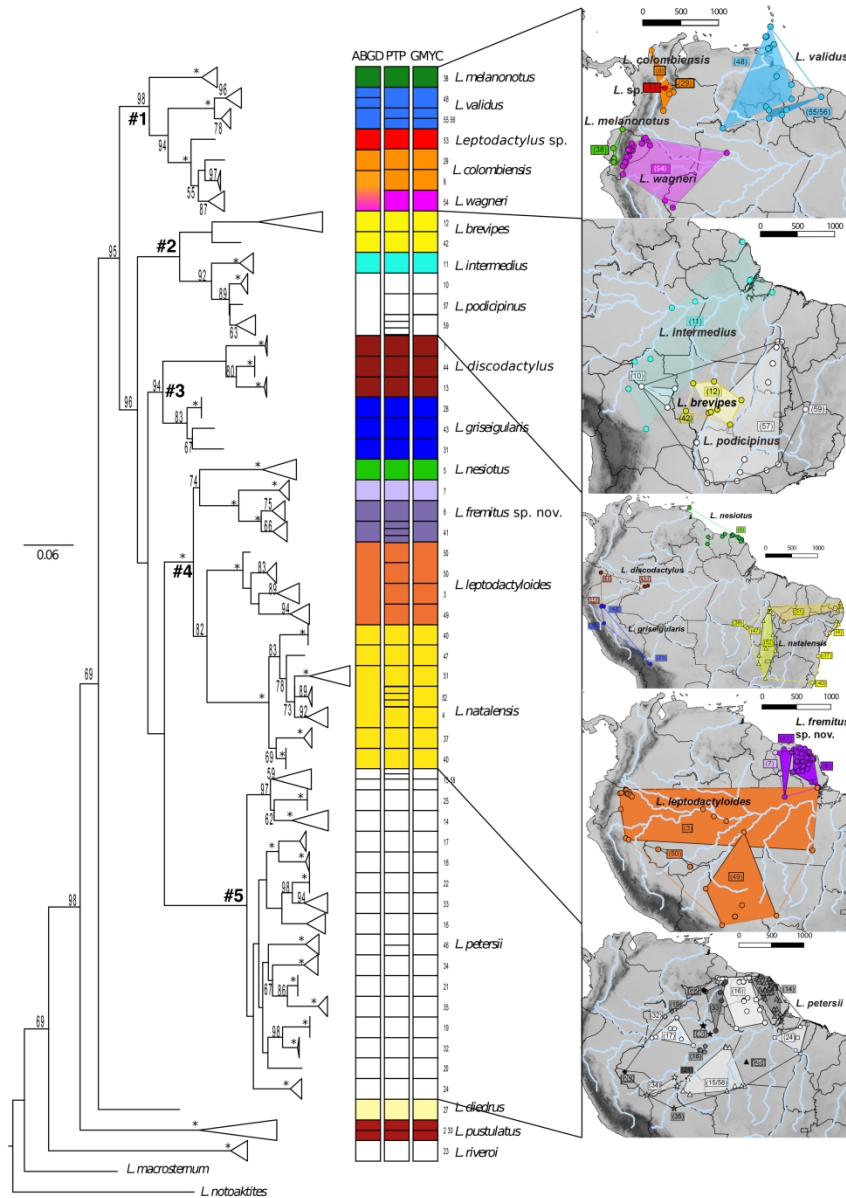


Fig. 1. Maximum Likelihood tree obtained from the analysis of 2,428 bp (16S + COI) with branches collapsed according to the consensus of the results of the three species delimitation methods (based on 613 bp of 16S). Posterior probabilities are indicated at the internal branches. An asterisk indicates a posterior probability of 1.0. OTU numbers resulting from the consensus of the delimitation methods are shown along the vertical axis.

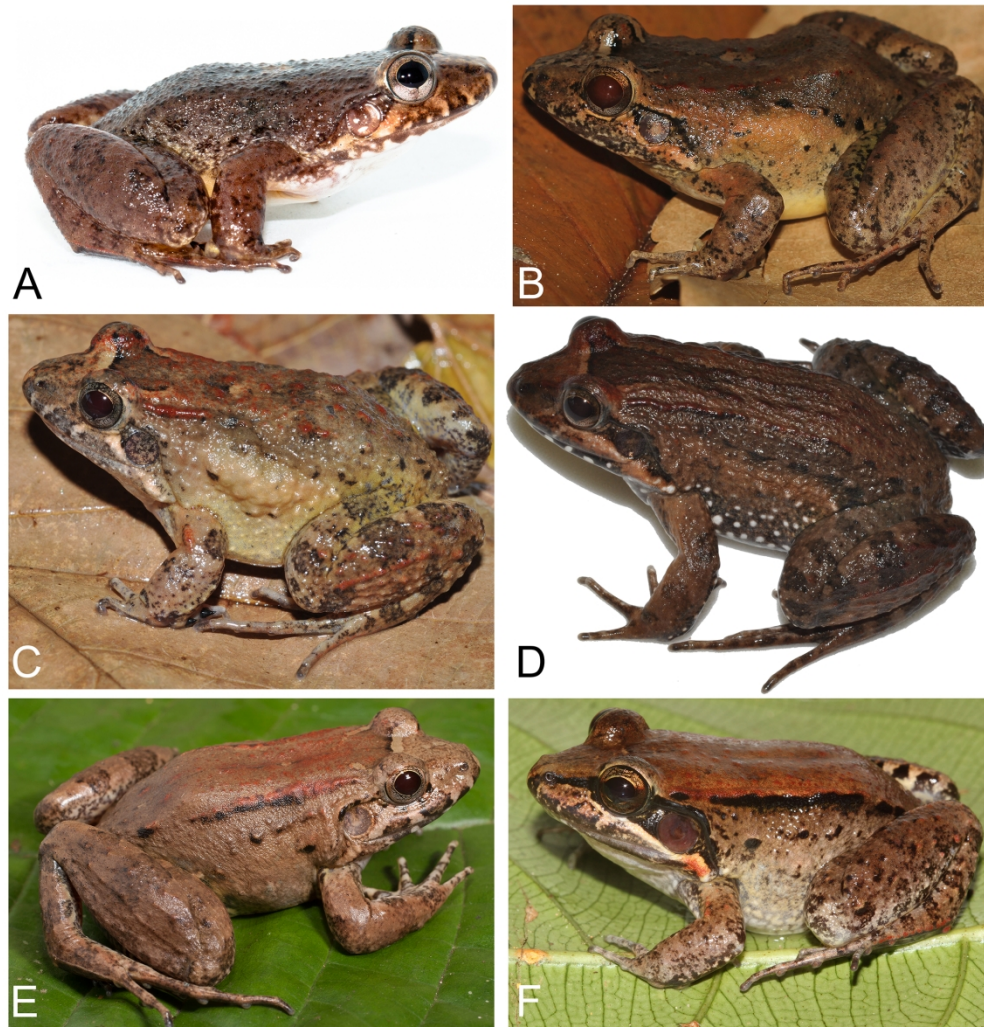


Fig. 2. Variation of the dorsolateral fold (A–E) in the *Leptodactylus melanonotus* group. (A) absent, *L. diedrus* (field number AF 4064); (B), indistinct or fragmented, *L. leptodactyloides* (AAG-UFU 5868); (C) short, *L. natalensis* (AAG-UFU 4984); (D) moderate to long (fragmented posteriorly), *L. podicipinus* (AAG-UFU 0098); (E) long, *L. wagneri* (QCAZ-A 38775); and (F) complete, *L. riveroi* (INPA-H 37253; photo by Leandro J. C. L. Moraes).

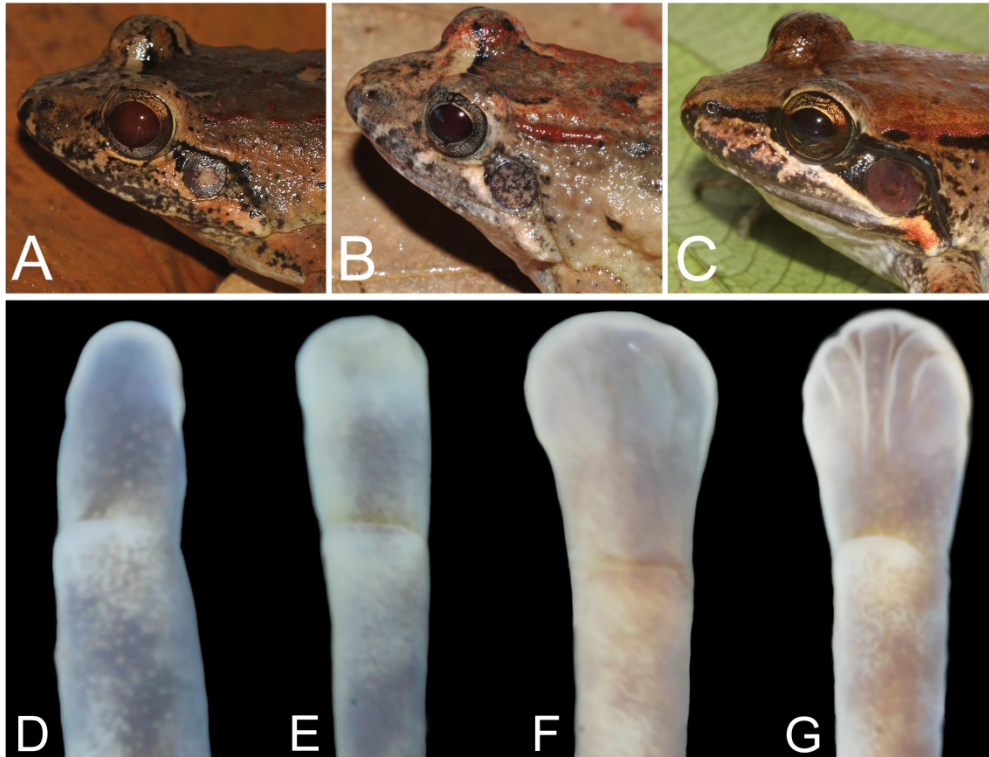


Fig. 3. Character states of the upper lip stripe (A–C) and toe tips (D–G) in the *Leptodactylus melanonotus* group. (A) Indistinct, *L. leptodactyloides* (AAG-UFU 5868); (B) from posterior eye corner, *L. natalensis* (AAG-UFU 4984); and (C) under the eye, *L. riveroi* (INPA-H 37253; photo by Leandro J. C. L. Moraes). (D) Unexpanded, *L. petersii* (AAG-UFU 6605); (E) slightly swollen, *L. validus* (AAG-UFU 3887); (F) toe discs with one central longitudinal groove, *L. diedrus* (AAG-UFU 3890); and (D) toe discs with four longitudinal grooves, *L. discodactylus* (ZUEC-AMP 11109).

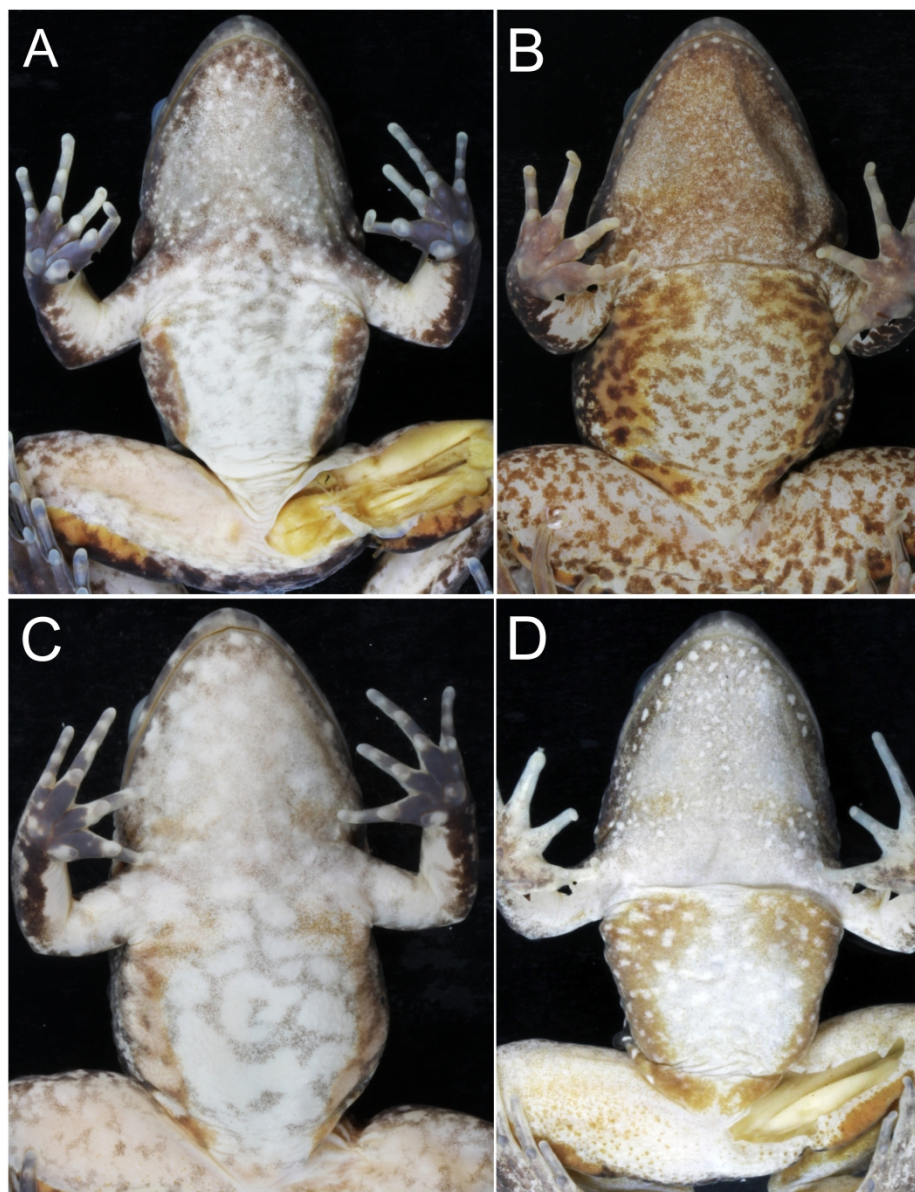


Fig. 4. Variation of belly colour patterns (A–D) in the *Leptodactylus melanonotus* group. (A) Mottling fading posteriorly, *L. validus* (AAG-UFU 3887); (F) mottling throughout the belly, *L. brevipes* (UFMT-A 12014); (G) anastomotic mottling, *L. petersii* (AAG-UFU 6605); and (H) pale spotted, *L. intermedius* (CFBH 43137).

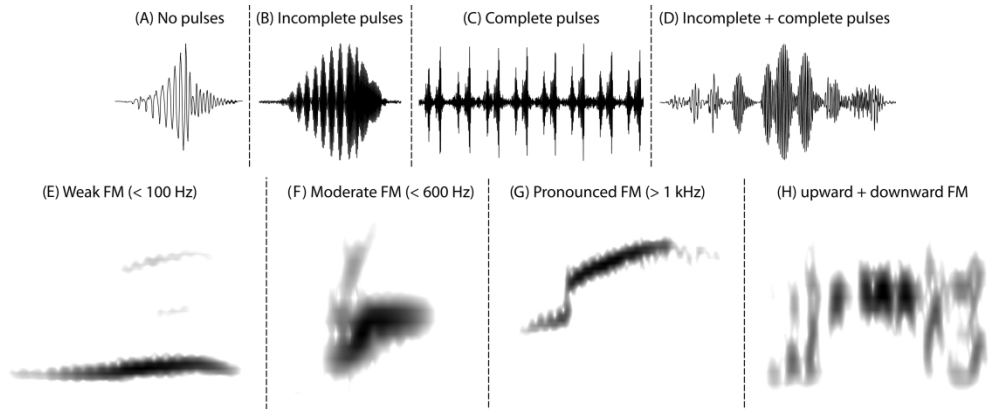
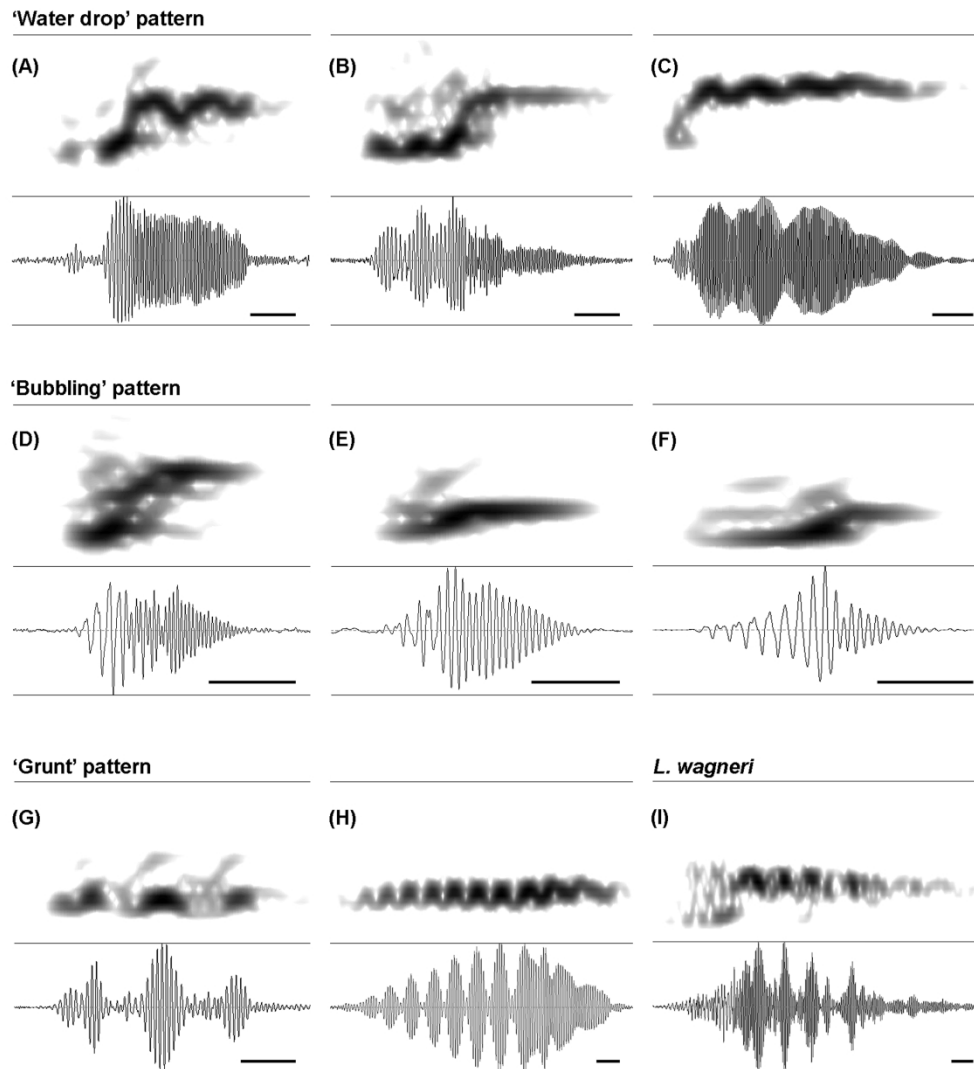


Fig. 5. Advertisement calls in the *Leptodactylus melanonotus* group. Patterns of amplitude modulation, AM: oscillograms (focusing on the temporal envelope; not to scale) showing (A) no AM (= non-pulsed call), *L. natalensis*; (B) incomplete AM, *L. fremitus* sp. nov.; (C) complete AM, *L. riveroi*; and (D) incomplete + complete AM, *L. pustulatus*. Patterns of frequency modulation, FM: spectrograms (produced at a 3-kHz scale) showing (E) no/weak FM, *L. diedrus*; (F) modest FM, *L. nesiotus*; (G) pronounced FM, *L. discodactylus*; and (H) upward + downward FM, *L. pustulatus*.



41 Fig. 6. Representatives of the three main 'acoustic groups' in the *Leptodactylus melanonotus* group. (A–C)
42 'Water drop' pattern: *L. melanonotus*, *L. petersii* (call type 2), and *L. validus*, respectively. (D–F) 'Bubbling'
43 pattern: *L. griseigularis*, *L. leptodactyloides*, and *L. natalensis*, respectively. (G–H) 'Grunt' pattern: *L.*
44 *petersii* (call type 1) and *Leptodactylus* sp. from the EGS, respectively. (I) Unique pattern of *L. wagneri*, a
45 frequency-modulated call formed by incomplete pulses. Scales = 10 ms.

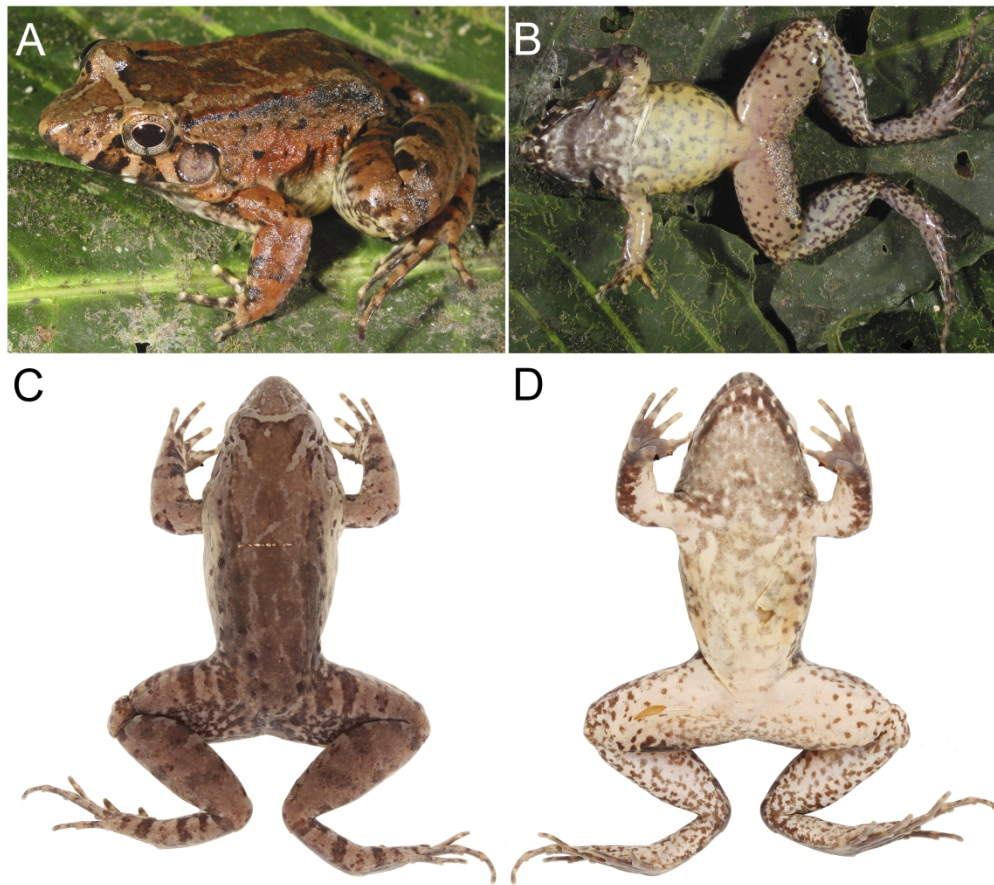


Fig. 7. Life colours (A–B), and dorsal and ventral views in preservative (C–D) of the neotype of *Leptodactylus wagneri* (QCAZ-A 26219, adult male: SVL = 57.2 mm) from the Province of Pastaza, Amazonian Ecuador.

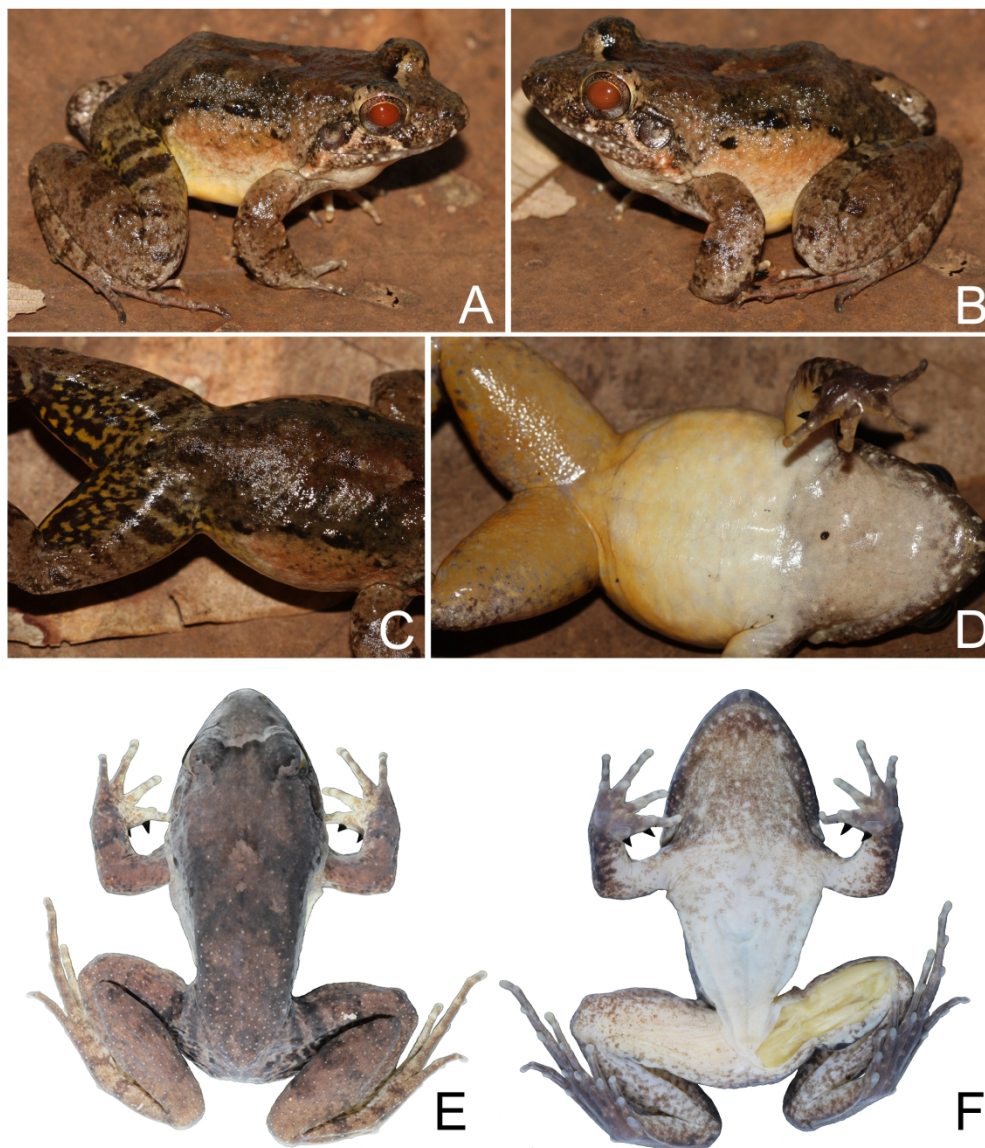


Fig. 8. Life colours (A–D), and dorsal and ventral views in preservative (E–F) of the holotype of *Leptodactylus fremitus* sp. nov. (CFBH 43258, adult male: SVL = 40.4 mm) from Serra do Navio, Brazilian state of Amapá, in the Eastern Guiana Shield.

299x346mm (300 x 300 DPI)

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3 *Systematics and Biodiversity*
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8 **Supplemental material**

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12 Species diversity and systematics of the *Leptodactylus melanonotus* group (Anura,
13 Leptodactylidae): review of diagnostic traits and a new species from the Eastern Guiana
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26 * Corresponding author: carvalho.thiagoribeiro@gmail.com
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30 **Supplementary tables**
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Table S1. List of voucher specimens (*Leptodactylus melanonotus* species group) with their associated locality data and GenBank accession numbers of the sequences included in the phylogenetic and delimitation analyses. New sequences produced in this study are highlighted in bold.

Museum#	Field#	COI	16S	Species	bPTP	ABGD	GMYC	CON	Locality (State)	Country	Latitude	Longitude
	MTR05426		JN691217	brevipes	16	12	41	12	APM Manso (MT)	Brazil	-15.15	-55.066667
	MTR05492		JN691218	brevipes	16	12	41	12	APM Manso (MT)	Brazil	-15.15	-55.066667
AAG-UFU5719		MW284619	ON585883	brevipes	16	12	41	12	Alto Garças (MT)	Brazil	-16.946490	-53.528242
CFBH36740	TG171	MW284710	MW291414	brevipes	16	12	41	12	Brassnorte (MT)	Brazil	-12.102	-57.981
CFBH36743	TG181	MW284712	MW291416	brevipes	16	12	41	12	Sinop (MT)	Brazil	-11.866	-55.461
CFBH36732	TG186	MW284714	MW291418	brevipes	16	12	41	12	Cuiabá (MT)	Brazil	-15.578	-56.104
CFBH36737	TG256	MW284718	MW291421	brevipes	17	36	61	12	Chapada dos Guimarães (MT)	Brazil	-15.451	-55.843
CFBH36738	TG258	MW284720	MW291423	brevipes	16	12	41	12	Chapada dos Guimarães (MT)	Brazil	-15.451	-55.843
	AF0749		KDQF01001482	brevipes	16	12	41	12	APM Manso (MT)	Brazil	-15.15	-55.066667
	AF0750	ON568754	KDQF01001483	brevipes	16	12	41	12	APM Manso (MT)	Brazil	-15.15	-55.066667
	PHV2553		KDQF01003971	brevipes	16	12	41	12	Água Boa (MT)	Brazil	-14.057105	-52.15893
	RGA5340		KDQF01004195	brevipes	13	42	64	42	UHE Guaporé (MT)	Brazil	-15.333333	-58.85
	AJC4000	KP149106	KP149302	colombiensis	40	8	44	8	Caserio Miraflores	Colombia	3.228	-73.852
	AJC3981	KP149198	KP149403	colombiensis	40	8	44	8		Colombia	5.1953	-73.1462
	AJC3986	KP149237	KP149444	colombiensis	40	8	44	8		Colombia	5.1953	-73.1462
	LSB378	KP149249	KP149459	colombiensis	40	8	44	8		Colombia	5.4108	-72.6710
	AJC3978	KP149257	KP149468	colombiensis	40	8	44	8	Miraflores	Colombia	5.1953	-73.1462
	AJC5035		MG030714	colombiensis	40	8	44	8	Tubara	Colombia	10.893	-75.002
	MVJ1618		KM091579	colombiensis	41	29	53	29	Santander; Charalá, Virolín	Colombia	6.13	-73.05
	AJC3848	KP149122	KP149318	sp.	59	8	42	53	Santander, Puente Nacional	Colombia	5.903	-73.695
USNM30715			AY943230	diedrus	3	27	49	27	Río Mawarinuma	Venezuela	0.830556	-66.161111
QCAZA16788			AY943239	discodactylus	9	1	34	1		Ecuador		
	RdeSá		DQ283433	discodactylus	9	1	34	1		Ecuador		
QCAZA16625			EU342502	discodactylus	9	1	34	1	Parque Nacional Yasuni	Ecuador	-0.677167	-76.40117

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4		MTR36335	ON585943	discodactylus	14	13	36	13 Aterradinho, Rio Içá (AM)	Brazil	-2.89187	-68.35518
5		MTR36562	ON585945	discodactylus	14	13	36	13 São Pedro, Rio Içá (AM)	Brazil	-3.03741	-68.88163
6		MTR36588	ON568773 ON585946	discodactylus	14	13	36	13 São Pedro, Rio Içá (AM)	Brazil	-3.03728	-68.88165
7		AF4466	ON585908	discodactylus	15	44	35	44 Pongo-Barranquita	Peru	-6.28639	-76.23164
8		AF4488	ON585912	discodactylus	15	44	35	44 Pongo-Barranquita	Peru	-6.28639	-76.23164
9		CM215	EU201129	fremitus sp. nov.	71	6	14	6 Apatou	French Guiana	5.166667	-54.333333
10		AG056	EU201130	fremitus sp. nov.	71	6	14	6 Trinite, Mont Tabulaire	French Guiana	4.6061	-53.3527
11		MTR13809	JN691205	fremitus sp. nov.	71	6	14	6 Serra do Navio (AP)	Brazil	0.918056	-52.002778
12		AF0040	JN691206	fremitus sp. nov.	71	6	14	6 Saul, galbao	French Guiana	3.6	-53.283333
13		AG263	JN691207	fremitus sp. nov.	71	6	14	6 Lucifer	French Guiana	4.7774	-53.9475
14		AG014	JN691208	fremitus sp. nov.	71	6	14	6 Guyane	French Guiana		
15		AG208	JN691209	fremitus sp. nov.	71	6	14	6 Trinite, Crique Grand Leblond	French Guiana	4.583333	-53.35
16		AF0091	JN691210	fremitus sp. nov.	71	6	14	6 St Georges, armee	French Guiana	3.888232	-51.807804
17	MNHN-RA-2021.0070	AF0810	KR811150	fremitus sp. nov.	71	6	14	6 Savane virginie	French Guiana	4.1959	-52.149
18		PG783	KR811151	fremitus sp. nov.	71	6	14	6 St Georges, Savane 14 juillet	French Guiana	3.967639	-51.87225
19	MNHN-RA-2021.0069	AF0735	KR811152	fremitus sp. nov.	71	6	14	6 St Georges, Saut Maripa	French Guiana	3.811159	-51.889644
20		AM002	ON585920	fremitus sp. nov.	71	6	14	6 Inini Tolenga	French Guiana	3.663159	-53.928308
21	MNHN-RA-2021.0064	CAAM40	ON585925	fremitus sp. nov.	71	6	14	6 Montagne cacao	French Guiana	2.349128	-53.215985
22	CFBH43258	TRC181	ON585928	fremitus sp. nov.	71	6	14	6 Serra do Navio (AP)	Brazil	0.911290	-52.003870
23	MNHN-RA-2021.0063	AF0520	KDQF01000126	fremitus sp. nov.	71	6	14	6 CisameG	French Guiana	4.195265	-52.372028
24	MNHN-RA-2021.0066	AF0570	KDQF01000146	fremitus sp. nov.	71	6	14	6 Le Galion	French Guiana	4.766144	-52.432684
25	MNHN-RA-2021.0067	AF0702	KDQF01000211	fremitus sp. nov.	71	6	14	6 Paracou	French Guiana	5.2754	-52.9236
26	MNHN-RA-2021.0068	AF0724	KDQF01000225	fremitus sp. nov.	71	6	14	6 Paracou	French Guiana	5.2754	-52.9236
27	MNHN-RA-2021.0071	AF0885	KDQF01000296	fremitus sp. nov.	71	6	14	6 Matoury, Mirande	French Guiana	4.863239	-52.349432
28	MNHN-RA-2021.0072	AF0898	KDQF01000304	fremitus sp. nov.	71	6	14	6 Pic Coudreau du Sud	French Guiana	2.2534	-54.3534
29	MNHN-RA-2021.0073	AF0914	KDQF01000320	fremitus sp. nov.	71	6	14	6 Pic Coudreau du Sud	French Guiana	2.2534	-54.3534
30		AF0947	KDQF01000343	fremitus sp. nov.	71	6	14	6 Matoury , Lac des Americains	French Guiana	4.852891	-52.352092
31		AF0948	KDQF01000344	fremitus sp. nov.	71	6	14	6 Matoury , Lac des Americains	French Guiana	4.852891	-52.352092
32	MNHN-RA-2021.0074	AF0954	KDQF01000347	fremitus sp. nov.	71	6	14	6 RN2	French Guiana	4.063933	-52.041607
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4		AF1072		KDQF01000387	fremitus sp. nov.	71	6	14	6 Oiapoque, derriere inselberg (AP)	Brazil	3.859566	-51.759514
5	MNHN-RA-2021.0075	AF1201		KDQF01000444	fremitus sp. nov.	71	6	14	6 Trinite, aya	French Guiana	4.6025	-53.4143
6		AF1280		KDQF01000482	fremitus sp. nov.	71	6	14	6 Nouragues	French Guiana	4.08479	-52.68063
7												
8	MNHN-RA-2021.0076	AF1374		KDQF01000509	fremitus sp. nov.	71	6	14	6 Bagne des annamites	French Guiana	4.81821	-52.522123
9	MNHN-RA-2021.0077	AF1432		KDQF01000533	fremitus sp. nov.	71	6	14	6 Saut Taconet	French Guiana	4.03249	-52.526188
10	MNHN-RA-2021.0078	AF1550		KDQF01000588	fremitus sp. nov.	71	6	14	6 Matoury, crique manceliere	French Guiana	4.85708	-52.339175
11	MNHN-RA-2021.0079	AF1609		KDQF01000602	fremitus sp. nov.	71	6	14	6 Saul, Limonade	French Guiana	3.57317	-53.19851
12	MNHN-RA-2021.0080	AF1697		KDQF01000638	fremitus sp. nov.	71	6	14	6 Saul, Limonade	French Guiana	3.56258	-53.21046
13	MNHN-RA-2021.0081	AF1733		KDQF01000651	fremitus sp. nov.	71	6	14	6 Chutes Voltaire	French Guiana	5.03255	-54.08689
14	MNHN-RA-2021.0082	AF1946		KDQF01000757	fremitus sp. nov.	71	6	14	6 Flat de la Waki	French Guiana	3.08361	-53.4121
15	MNHN-RA-2021.0083	AF2338		KDQF01000905	fremitus sp. nov.	71	6	14	6 Ekini	French Guiana	4.05	-52.4667
16		AF2618		KDQF01001022	fremitus sp. nov.	71	6	14	6 Atachi Bakka, camp1	French Guiana	3.5671	-53.96164
17		AF2696		KDQF01001064	fremitus sp. nov.	71	6	14	6 Alikene, camp polissoir	French Guiana	3.21792	-52.39747
18		AF2738	ON568755	KDQF01001081	fremitus sp. nov.	71	6	14	6 Mitaraka	French Guiana	2.23577	-54.44928
19	MNHN-RA-2021.0087	AF2802		KDQF01001110	fremitus sp. nov.	71	6	14	6 Mitaraka	French Guiana	2.23577	-54.44928
20		AF3190		KDQF01001296	fremitus sp. nov.	71	6	14	6 Mitan G	French Guiana	2.6284	-52.55404
21	MNHN-RA-2021.0089	AF3702		KDQF01001459	fremitus sp. nov.	71	6	14	6 Itoupe	French Guiana	3.01498	-53.13286
22		AF3709		KDQF01001461	fremitus sp. nov.	71	6	14	6 Itoupe	French Guiana	3.01498	-53.13286
23		AG206		KDQF01001516	fremitus sp. nov.	71	6	14	6 Trinite, Crique Grand Leblond	French Guiana	4.583333	-53.35
24		AG426		KDQF01001597	fremitus sp. nov.	71	6	14	6 Atachi Bakka	French Guiana	3.6553	-53.844
25		AG427		KDQF01001598	fremitus sp. nov.	71	6	14	6 Atachi Bakka	French Guiana	3.6553	-53.844
26		AG465		KDQF01001630	fremitus sp. nov.	71	6	14	6 Alikene	French Guiana	3.220044	-52.37855
27		AP079		KDQF01001769	fremitus sp. nov.	71	6	14	6 Plote PPBIO, Porto Grande (AP)	Brazil	0.979331	-51.614895
28		BOAM062		KDQF01001894	fremitus sp. nov.	71	6	14	6 Borne 4	French Guiana	2.3709	-53.7728
29		BOAM064		KDQF01001896	fremitus sp. nov.	71	6	14	6 Borne 4	French Guiana	2.3709	-53.7728
30		CM415		KDQF01002331	fremitus sp. nov.	71	6	14	6 Lucifer	French Guiana	4.77774	-53.9475
31		MTR24131		KDQF01003576	fremitus sp. nov.	71	6	14	6 Oiapoque (AP)	Brazil	3.879417	-51.770972
32		MTR24141		KDQF01003579	fremitus sp. nov.	71	6	14	6 Oiapoque (AP)	Brazil	3.879417	-51.770972
33		PG689		KDQF01003937	fremitus sp. nov.	71	6	14	6 Nouragues , ParareG	French Guiana	4.08585	-52.68132
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4	MNHN-RA-2021.0065	PG784	KDQF01003963	fremitus sp. nov.	71	6	14	6 St Georges, Savane 14 juillet	French Guiana	3.967639	-51.87225	
5		QM390	KDQF01004097	fremitus sp. nov.	71	6	14	6 Montagne de fer	French Guiana	5.4074	-53.5548	
6		QM405	KDQF01004104	fremitus sp. nov.	71	6	14	6 Montagne de fer	French Guiana	5.4074	-53.5548	
7		AF0183	EU201131	fremitus sp. nov.	69	41	15	41 Road to Apura	Suriname	5.183333	-55.616667	
8		AF0179	JN691211	fremitus sp. nov.	69	41	15	41 Road to Apura	Suriname	5.183333	-55.616667	
9		AF2407	ON585894	fremitus sp. nov.	70	41	15	41 Nassau	Suriname	4.81701	-54.60373	
10		AF3810	ON585898	fremitus sp. nov.	69	41	15	41 Voltzberg	Suriname	4.68169	-56.18568	
11	MNHN-RA-2021.0084	AF2446	KDQF01000961	fremitus sp. nov.	70	41	15	41 Nassau, trail 11	Suriname	4.80412	-54.5555	
12		AF2477	KDQF01000969	fremitus sp. nov.	70	41	15	41 Nassau, trail camp	Suriname	4.80262	-54.61502	
13	MNHN-RA-2021.0085	AF2478	KDQF01000970	fremitus sp. nov.	70	41	15	41 Nassau	Suriname	4.80262	-54.61502	
14		AF2514	KDQF01000977	fremitus sp. nov.	70	41	15	41 Nassau	Suriname	4.80262	-54.61502	
15	MPEG29422		KDQF01002845	fremitus sp. nov.	68	41	15	41 Trombetas, FLOTA (PA)	Brazil	-0.962769	-55.5223	
16	MNHN-RA-2021.0090	AF1966	KDQF01000769	cf. fremitus	45	7	16	7 Sipaliwini	Suriname	2.02439	-56.12508	
17	MNHN-RA-2021.0091	AF1967	KDQF01000770	cf. fremitus	45	7	16	7 Sipaliwini	Suriname	2.02439	-56.12508	
18	MNHN-RA-2021.0092	AF2058	KDQF01000817	cf. fremitus	45	7	16	7 Sipaliwini, Apalagadi	Suriname	2.17965	-56.09078	
19	MNHN-RA-2021.0093	AF2069	KDQF01000820	cf. fremitus	45	7	16	7 Sipaliwini, Apalagadi	Suriname	2.17816	-56.08521	
20	MNHN-RA-2021.0094	AF2224	KDQF01000882	cf. fremitus	45	7	16	7 Sipaliwini	Suriname	2.03253	-56.11449	
21	MNHN-RA-2021.0095	AF3369	ON568757	KDQF01001390	cf. fremitus	45	7	16	7 Bakhuis, Low creek	Suriname	4.76284	-56.77911
22		SBH171130	KM091588	griseigularis	22	28	54	28 Potanischer Garten in Tingo Maria	Peru	-9.309626	-76.003509	
23	MNCN43541		EU368907	griseigularis	21	31	50	31 La Paz, Serrania Bellavista	Bolivia	-16.212074	-67.912572	
24		AF4392	ON585902	griseigularis	23	43	37	43 URKU	Peru	-6.46487	-76.35185	
25		AF4394	ON585903	griseigularis	23	43	37	43 URKU	Peru	-6.46487	-76.35185	
26		AF4396	ON585904	griseigularis	23	43	37	43 URKU	Peru	-6.46487	-76.35185	
27		AF4434	ON585905	griseigularis	23	43	37	43 San José	Peru	-6.421372	-76.298029	
28		AF4439	ON585906	griseigularis	23	43	37	43 San José	Peru	-6.421372	-76.298029	
29		AF4441	ON585907	griseigularis	23	43	37	43 San José	Peru	-6.421372	-76.298029	
30		AF4533	ON585914	griseigularis	23	43	37	43 URKU	Peru	-6.46487	-76.35185	
31		AF4535	ON585915	griseigularis	23	43	37	43 URKU	Peru	-6.46487	-76.35185	
32		AF4539	ON585916	griseigularis	23	43	37	43 URKU	Peru	-6.46487	-76.35185	
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4		AF4589	ON585917	griseigularis	23	43	37	43 Leticia	Peru	-6.43773	-75.88458		
5		CM155	EU201132	intermedius	24	11	40	11 Kawl	French Guiana	4.496938	-52.050233		
6		MJ1303	JF789917	intermedius	24	11	40	11 Sara, Buenavista	Bolivia	-17.481683	-63.684867		
7		MJ1304	JF789918	intermedius	24	11	40	11 Sara, Buenavista	Bolivia	-17.481683	-63.684867		
8		MJ1306	JF789919	intermedius	24	11	40	11 Sara, Buenavista	Bolivia	-17.481683	-63.684867		
9		MJ1324	JF789920	intermedius	24	11	40	11 Yucuma, Los Lagos	Bolivia	-12.771967	-65.810933		
10		AS0464	JF789921	intermedius	24	11	40	11 Yucuma, Los Lagos	Bolivia	-12.772	-65.8109		
11		MJ1365	JF789922	intermedius	24	11	40	11 Yucuma, Los Lagos	Bolivia	-12.771967	-65.810933		
12		MTR13985	JN691171	intermedius	24	11	40	11 Macapá (AP)	Brazil	0.045833	-51.05		
13		MTR13986	JN691172	intermedius	24	11	40	11 Macapá (AP)	Brazil	0.045833	-51.05		
14		CMC	JN691173	intermedius	24	11	40	11 Kawl	French Guiana	4.516105	-52.10053		
15		CMD	JN691174	intermedius	24	11	40	11 Kawl	French Guiana	4.516105	-52.10053		
16		CME	JN691175	intermedius	24	11	40	11 Kawl	French Guiana	4.516105	-52.10053		
17	AAG-UFU5807		MW284621	MW291352	intermedius	24	11	40	11 Itapuã do Oeste (RO)	Brazil	-9.279782	-63.157741	
18	AAG-UFU5808		MW284622	MW291353	intermedius	24	11	40	11 Itapuã do Oeste (RO)	Brazil	-9.279782	-63.157741	
19		AF2585	ON585895	intermedius	24	11	40	11 Santana (AP)	Brazil	-0.040816	-51.186018		
20		AF3930	ON568759	ON585901	intermedius	24	11	40	11 Kaw	French Guiana	4.486415	-52.037191	
21	CFBH39692	TG222	MW284715	MW291419	intermedius	24	11	40	11 Urucará (AM)	Brazil	-2.522	-57.754	
22	CFBH39668	TG295	MW284721	MW291424	intermedius	24	11	40	11 Belém (PA)	Brazil	-1.447	-48.441	
23	CFBH39669	TG296	MW284722	MW291425	intermedius	24	11	40	11 Belém (PA)	Brazil	-1.447	-48.441	
24	CFBH39728	TG388	MW284726	MW291428	intermedius	24	11	40	11 Manacapuru (AM)	Brazil	-3.254	-60.578	
25	CFBH39729	TG389	MW284727	MW291429	intermedius	24	11	40	11 Manacapuru (AM)	Brazil	-3.254	-60.578	
26		HJ522		KDQF01002662	intermedius	24	11	40	11 UHE Jirau, Mutum (RO)	Brazil	-9.591318	-65.049181	
27	MZUSP70969		AY943236	leptodactyloides	42	3	3	3 Serra do Kukoinhokren (PA)	Brazil	-7.833333	-51.916667		
28	KU218194		KM091608	leptodactyloides	43	3	3	3 Sucumbios	Ecuador				
29		AF4477	ON585909	leptodactyloides	43	3	3	3 Pongo-Barranquita	Peru	-6.28639	-76.23164		
30		AF4478	ON585910	leptodactyloides	43	3	3	3 Pongo-Barranquita	Peru	-6.28639	-76.23164		
31		AF4485	ON585911	leptodactyloides	43	3	3	3 Pongo-Barranquita	Peru	-6.28639	-76.23164		
32		AF4499	ON585913	leptodactyloides	43	3	3	3 Pongo-Barranquita	Peru	-6.28639	-76.23164		
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4		AF4618	ON585918	leptodactyloides	43	3	3	3 Pucallpa	Peru	-6.47275	-75.83630
5		MTR33844	ON585938	leptodactyloides	43	3	3	3 Tefé, Estrada do Abial (AM)	Brazil	-3.459441	-64.750900
6		MTR36845	ON585947	leptodactyloides	43	3	3	3 Fonte Boa (AM)	Brazil	-2.52904	-66.16221
7		MTR37043	ON568774 ON585949	leptodactyloides	43	3	3	3 Coari (AM)	Brazil	-4.0821	-63.14366
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9	QCAZA19173	MW284675	MW291367	leptodactyloides	43	3	3	3 Sucumbíos	Ecuador	-0.000515	-76.174921
10	QCAZA25549	MW284680	MW291376	leptodactyloides	43	3	3	3 Pastaza	Ecuador	-2.538667	-76.858333
11	QCAZA27911	MW284685	MW291381	leptodactyloides	43	3	3	3 Sucumbíos	Ecuador	-0.088599	-76.142033
12	QCAZA27941		MW291382	leptodactyloides	43	3	3	3 Sucumbíos	Ecuador	-0.318133	-75.766250
13	QCAZA27942	MW284686	MW291383	leptodactyloides	43	3	3	3 Sucumbíos	Ecuador	-0.318133	-75.766250
14	QCAZA28303	MW284687	MW291384	leptodactyloides	43	3	3	3 Sucumbíos	Ecuador	-0.208222	-76.236860
15	QCAZA28304	MW284688	MW291385	leptodactyloides	43	3	3	3 Sucumbíos	Ecuador	-0.208222	-76.236860
16	QCAZA28309		MW291386	leptodactyloides	43	3	3	3 Sucumbíos	Ecuador	-0.088599	-76.142030
17	QCAZA43737	MW284693	MW291395	leptodactyloides	43	3	3	3 Orellana	Ecuador	-0.485010	-76.984850
18	QCAZA43787	MW284694	MW291396	leptodactyloides	43	3	3	3 Orellana	Ecuador	-0.49986	-77.008280
19	QCAZA43893	MW284695	MW291397	leptodactyloides	43	3	3	3 Orellana	Ecuador	-0.431000	-76.786480
20	QCAZA44238		MW291398	leptodactyloides	43	3	3	3 Orellana	Ecuador	-0.498330	-76.071120
21	QCAZA44242	MW284696	MW291399	leptodactyloides	43	3	3	3 Orellana	Ecuador	-0.498330	-76.071120
22	QCAZA44326	MW284697	MW291400	leptodactyloides	43	3	3	3 Orellana	Ecuador	-0.579970	-75.917690
23	QCAZA44327	MW284698	MW291401	leptodactyloides	43	3	3	3 Orellana	Ecuador	-0.579970	-75.917690
24	QCAZA44619	MW284699	MW291402	leptodactyloides	43	3	3	3 Orellana	Ecuador	-0.711630	-75.623950
25	QCAZA44838	MW284700	MW291403	leptodactyloides	43	3	3	3 Orellana	Ecuador	-0.916510	-75.423060
26	CFBH43255	TRC175	ON585926	leptodactyloides	43	3	3	3 Comunidade Ariri, Macapá (AP)	Brazil	0.299306	-51.129889
27	CFBH43256	TRC176	ON585927	leptodactyloides	43	3	3	3 Comunidade Ariri, Macapá (AP)	Brazil	0.299306	-51.129889
28	AAG-UFU6408	TRC177	ON585889	leptodactyloides	43	3	3	3 Comunidade Ariri, Macapá (AP)	Brazil	0.299306	-51.129889
29	AAG-UFU6409	TRC178	ON585890	leptodactyloides	43	3	3	3 Comunidade Ariri, Macapá (AP)	Brazil	0.299306	-51.129889
30	AAG-UFU6410	TRC179	ON585891	leptodactyloides	43	3	3	3 Comunidade Ariri, Macapá (AP)	Brazil	0.299306	-51.129889
31		MTR36303	KDQF01003742	leptodactyloides	42	3	3	3 Serra do Kukoinhokren (PA)	Brazil	-7.833333	-51.916667
32		AS0017	JF789893	leptodactyloides	44	3	5	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
33		AS0185	JF789894	leptodactyloides	44	3	6	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
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	AS0186		JF789895	leptodactyloides	44	3	6	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
	AS0240		JF789896	leptodactyloides	44	3	6	49 Velasco, Caparu	Bolivia	-14.912117	-61.082467
	AS0547		JF789897	leptodactyloides	44	3	6	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
	AS0551		JF789898	leptodactyloides	44	3	5	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
	AS0556		JF789899	leptodactyloides	44	3	6	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
	MJ1263		JF789900	leptodactyloides	44	3	5	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
	MJ1275		JF789901	leptodactyloides	44	3	6	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
	MJ1276		JF789902	leptodactyloides	44	3	5	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
	MJ1282		JF789903	leptodactyloides	44	3	5	49 nuflo de Chavez, San Sebastian	Bolivia	-16.359633	-62.000050
	MJ1305		JF789904	leptodactyloides	44	3	5	49 Sara, Buenavista	Bolivia	-17.481683	-63.684867
	VOGT2172		JN691219	leptodactyloides	44	3	5	49 Cachoeirinha (AM	Brazil	-5.4944444	-60.823056
	MNKA9505		KF723177	leptodactyloides	44	3	6	49 San Sebastian	Bolivia	-16.3596	-62.0001
	SMF94137		KF723178	leptodactyloides	44	3	6	49 San Sebastian	Bolivia	-16.3596	-62.0001
	MNKA9729		KF723179	leptodactyloides	44	3	6	49 San Sebastian	Bolivia	-16.3596	-62.0001
	SMF94193		KF723180	leptodactyloides	44	3	6	49 San Sebastian	Bolivia	-16.3596	-62.0001
	MNKA10357		KF723181	leptodactyloides	44	3	5	49 San Sebastian	Bolivia	-16.3596	-62.0001
	AS410		KF723182	leptodactyloides	44	3	6	49 San Sebastian	Bolivia	-16.3596	-62.0001
	AS483		KF723183	leptodactyloides	44	3	6	49 Yucuma, Los Lagos	Bolivia	-12.772	-65.8109
	MJ1235		ON585935	leptodactyloides	44	3	6	49 Ñuflo de Chavez, San Sebastián	Bolivia	-16.359633	-62.000050
	CFBH36739	TG257	MW284719 MW291422	leptodactyloides	44	3	5	49 Poconé (MT)	Brazil	-16.259516	-56.604485
	AAG-UFU4199		KC477247	leptodactyloides	61	3	4	50 UFAC, Rio Branco (AC)	Brazil	-9.944835	-67.800339
	AAG-UFU5868		MW284623 MW291354	leptodactyloides	62	3	4	50 UFAC, Rio Branco (AC)	Brazil	-9.955971	-67.867064
	AAG-UFU5869		MW284624 MW291355	leptodactyloides	62	3	4	50 UFAC, Rio Branco (AC)	Brazil	-9.955971	-67.867064
		TG2658	ON586009	leptodactyloides	62	3	4	50 Igarapé Esperanca (AC)	Brazil	-7.712039	-72.003719
		TG2659	KDQF01004327	leptodactyloides	62	3	4	50 Igarapé Esperanca (AC)	Brazil	-7.712039	-72.003719
	QCAZA22694		MW291370	melanonotus	8	38	47	38 Durango, Esmeraldas	Ecuador	1.064320	-78.644320
	QCAZA23592		MW291371	melanonotus	8	38	47	38 Naranjal, Guayas	Ecuador	-2.765849	-79.691800
	QCAZA23657		MW291372	melanonotus	8	38	47	38 Carretera Naranjal-El Guabo, Guayas	Ecuador	-2.823519	-79.700850
	QCAZA26859		MW291379	melanonotus	8	38	47	38 El Empalme, Esmeraldas	Ecuador	-1.180070	-79.751550

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4		ESTR0787	KDQF01002468	natalensis	34	4	11	51 Faz. Florence, Estreito (MA)	Brazil	-6.560556	-47.451111	
5	AAG-UFU1967	MW284599	MW291337	natalensis	35	4	10	52 Guarani de Goiás (GO)	Brazil	-13.925235	-46.472289	
6	AAG-UFU2780	MW284600	MW291338	natalensis	35	4	10	52 Carolina (MA)	Brazil	-7.275815	-47.435107	
7	AAG-UFU2781	MW284601	MW291339	natalensis	35	4	10	52 Carolina (MA)	Brazil	-7.275815	-47.435107	
8	AAG-UFU0983	MW284596	MW291336	natalensis	35	4	10	52 Uruaçu (GO)	Brazil	-14.716821	-49.250724	
9	AAG-UFU4984	MW284593	MW291333	natalensis	35	4	10	52 Araguari (MG)	Brazil	-18.458932	-48.529679	
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11		ESTR0077	KDQF01002447	natalensis	35	4	10	52 Carolina (MA)	Brazil	-7.22941	-47.26147	
12		ESTR0313	KDQF01002453	natalensis	35	4	10	52 Filadélfia (TO)	Brazil	-7.345868	-47.50627	
13		ESTR2026	KDQF01002482	natalensis	35	4	10	52 Estreito (MA)	Brazil	-6.560556	-47.451111	
14		MTR07465	ON568765	KDQF01003144	natalensis	35	4	10	52 Guaraí (TO)	Brazil	-8.83416666	-48.510278
15		MTR08221	KDQF01003159	natalensis	35	4	10	52 Petrolina de Goiás (GO)	Brazil	-16.144938	-49.316454	
16		MTR14331	KDQF01003317	natalensis	35	4	10	52 ESEC Serra Geral do Tocantins (TO)	Brazil	-11.220833	-46.88556	
17		SAMA8573	KDQF01004208	natalensis	35	4	10	52 Minaçu (GO)	Brazil	-13.540833	-48.090278	
18		CM081	EU201128	nesiotus	7	5	7	5 Cayenne, Montjoly	French Guiana	4.916667	-52.266667	
19		AF0011	JN691212	nesiotus	7	5	7	5 Cayenne, Montjoly jardin CM	French Guiana	4.912925	-52.269562	
20	SMNS12525		JN691213	nesiotus	7	5	7	5 Bamboo landing	Guyana	5.325	-58.045556	
21	SMNS12526		JN691214	nesiotus	7	5	7	5 Bamboo landing	Guyana	5.325	-58.045556	
22		Voucher#3	KM091603	nesiotus	7	5	7	5 Bonasse Swamp, Trinidad	Trinidad	10.089947	-61.858351	
23		AF1577	ON585892	nesiotus	7	5	7	5 Awala	French Guiana	5.723319	-53.889484	
24		AF1578	ON585893	nesiotus	7	5	7	5 Awala	French Guiana	5.723319	-53.889484	
25		UFRJK043	ON586013	nesiotus	7	5	7	5 Paramaribo, Paramaribo	Suriname	5.859249	-55.160341	
26		AF0003	KDQF01000014	nesiotus	7	5	7	5 Cayenne, Montjoly jardin CM	French Guiana	4.912925	-52.269562	
27		AF0194	KDQF01000082	nesiotus	7	5	7	5 Mana	French Guiana	5.616667	-53.7	
28		AF0237	KDQF01000100	nesiotus	7	5	7	5 Montagne des singes	French Guiana	5.066667	-52.716667	
29		AF1533	KDQF01000579	nesiotus	7	5	7	5 Macouria, Savane Marivat	French Guiana	4.95	-52.45	
30		AF1575	KDQF01000596	nesiotus	7	5	7	5 Mana	French Guiana	5.595278	-53.88903	
31		AF1576	KDQF01000597	nesiotus	7	5	7	5 Mana, dir awala	French Guiana	5.699515	-53.841993	
32		AF2360	KDQF01000919	nesiotus	7	5	7	5 St Laurent	French Guiana	5.497204	-54.023926	
33		AF2894	KDQF01001131	nesiotus	7	5	7	5 Mana, Route d'Awala	French Guiana	5.6982	-53.8407	
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4		AF2895	ON568756	KDQF01001132	nesiotus	7	5	7	5 Mana, Route d'Awala	French Guiana	5.6982	-53.8407
5		AG009		KDQF01001492	nesiotus	7	5	7	5 Cayenne, Montjoly	French Guiana	4.916667	-52.266667
6		AG151		KDQF01001513	nesiotus	7	5	7	5 Mana	French Guiana	5.6727	-53.7913
7		AG166		KDQF01001514	nesiotus	7	5	7	5 Comte, Terrain michel	French Guiana	4.691667	-52.4
8		AG279		KDQF01001533	nesiotus	7	5	7	5 Comte, Terrain michel	French Guiana	4.691667	-52.4
9		AG364		KDQF01001560	nesiotus	7	5	7	5 Marais Yiyi	French Guiana	5.389198	-52.989272
10		AG366		KDQF01001561	nesiotus	7	5	7	5 Marais Yiyi	French Guiana	5.389198	-52.989272
11		AG515		KDQF01001658	nesiotus	7	5	7	5 Cayenne, degrad des cannes	French Guiana	4.854240	-52.270592
12		AMS456		KDQF01001744	nesiotus	7	5	7	5 Berbice River Camp	Guyana	4.154100	-58.177317
13		CM150		KDQF01002240	nesiotus	7	5	7	5 Guatemala	French Guiana	5.15	-52.633333
14		CM173		KDQF01002245	nesiotus	7	5	7	5 Guatemala	French Guiana	5.15	-52.633333
15		CM261		KDQF01002265	nesiotus	7	5	7	5 Montsinery	French Guiana	4.883333	-52.483333
16	MTD47756			KDQF01003036	nesiotus	7	5	7	5 Kabo forestry consession	Suriname	5.378132	-55.621491
17	MTD48109			KDQF01003087	nesiotus	7	5	7	5 Paramaribo	Suriname	5.838515	-55.196521
18		PG796		KDQF01003968	nesiotus	7	5	7	5 Matoury, villa	French Guiana	4.882599	-52.333247
19		QM009		KDQF01004057	nesiotus	7	5	7	5 Cayenne, noyade remire	French Guiana	4.886085	-52.284275
20		QM063		KDQF01004064	nesiotus	7	5	7	5 Guatemala	French Guiana	5.15	-52.633333
21		QM100		KDQF01004069	nesiotus	7	5	7	5 Guatemala	French Guiana	5.15	-52.633333
22		QM309		KDQF01004083	nesiotus	7	5	7	5 Cacao	French Guiana	4.566667	-52.466667
23		AG010		EU201125	petersii	10	14	17	14 Montagne de Kaw3	French Guiana	4.548056	-52.151944
24		CM170		EU201126	petersii	10	14	17	14 St Laurent	French Guiana	5.497204	-54.023926
25		AG098		EU201127	petersii	10	14	18	14 Mont Arawa	French Guiana	2.816389	-53.366389
26		CM132		JN691176	petersii	10	14	17	14 crique Margot	French Guiana	5.443190	-53.972344
27		CM197		JN691177	petersii	10	14	17	14 Apatou	French Guiana	5.166667	-54.333333
28		CM408		JN691178	petersii	10	14	17	14 Lucifer	French Guiana	4.7774	-53.9475
29		AG207		JN691179	petersii	10	14	17	14 Trinite, Crique Grand Leblond	French Guiana	4.583333	-53.35
30		AG209		JN691180	petersii	10	14	17	14 Trinite, Crique Grand Leblond	French Guiana	4.583333	-53.35
31		AG012		JN691181	petersii	10	14	18	14 Matoury, Lac des Americains	French Guiana	4.85	-52.35
32		AF0199		JN691182	petersii	10	14	17	14 Montagne des singes	French Guiana	5.066667	-52.716667
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	AG055	JN691183	petersii	10	14	18	14 Kaw3, CD6/PK 36	French Guiana	4.548056	-52.151944
	AG054	JN691184	petersii	10	14	18	14 Kaw3, CD6/PK 36	French Guiana	4.548056	-52.151944
	AG057	JN691185	petersii	10	14	18	14 Kaw3, CD6/PK 20	French Guiana	4.548056	-52.151944
	CM293	JN691186	petersii	10	14	17	14 Pont Nancibo	French Guiana	4.666667	-52.5
	AG251	JN691187	petersii	10	14	17	14 Kaw, Canal de	French Guiana	4.516105	-52.10053
	AF0008	JN691188	petersii	10	14	18	14 Kaw3, Asarco	French Guiana	4.568211	-52.217774
	AF0010	JN691189	petersii	10	14	18	14 Kaw3, arlesienne	French Guiana	4.548404	-52.152064
	AF938	JN691190	petersii	10	14	18	14 Igarapé Camaipi, Rio Maracá (AP)	Brazil	-0.0241667	-51.8972222
	MTR13775	JN691191	petersii	10	14	18	14 Serra do Navio (AP)	Brazil	0.9180556	-52.0027778
	BPN0890	JN691192	petersii	10	14	18	14 Brownsberg	Suriname	4.936527	-55.194826
	BPN1684	JN691193	petersii	10	14	18	14 Saul	French Guiana	3.625556	-53.207222
	AF3924	ON585900	petersii	10	14	18	14 Montagne de fer	French Guiana	5.407607	-53.554662
	AP049	ON585921	petersii	10	14	18	14 Plote PPBIO, Porto Grande (AP)	Brazil	0.979331	-51.614895
	AP098	ON585922	petersii	10	14	18	14 Plote PPBIO, Porto Grande (AP)	Brazil	0.979331	-51.614895
	AG013	ON585919	petersii	10	14	17	14	French Guiana		
CFBH43264	TRC190	MW284741	ON585929	petersii	10	14	18 14 Serra do Navio (AP)	Brazil	0.906282	-52.013349
	AF0743		KDQF01000231	petersii	10	14	17 14 St Georges, savane	French Guiana	3.925482	-51.788964
	AF0789		KDQF01000243	petersii	10	14	17 14 Le Galion	French Guiana	4.766144	-52.432684
	AF0790		KDQF01000244	petersii	10	14	17 14 Le Galion	French Guiana	4.766144	-52.432684
	AF0849		KDQF01000278	petersii	10	14	17 14 Chutes Voltaire, camp	French Guiana	5.052639	-54.088444
	AF0850		KDQF01000279	petersii	10	14	17 14 Chutes Voltaire, camp	French Guiana	5.052639	-54.088444
	AF1017		KDQF01000369	petersii	10	14	18 14 Saul, Galbao crique	French Guiana	3.63592	-53.272562
	AF1327		KDQF01000493	petersii	10	14	17 14 Saut Grand Machicou	French Guiana	3.897416	-52.583565
	AF1391		KDQF01000515	petersii	10	14	17 14 Aratai	French Guiana	3.9909	-52.5902
	AF1407		KDQF01000520	petersii	10	14	17 14 Aratai	French Guiana	3.9909	-52.5902
	AF1611		KDQF01000604	petersii	10	14	18 14 Saul, Limonade	French Guiana	3.57317	-53.19851
	AF1648		KDQF01000620	petersii	10	14	18 14 Saul, Limonade	French Guiana	3.56258	-53.21046
	AF1754		KDQF01000660	petersii	10	14	17 14 Chutes Voltaire, camp Voltaire	French Guiana	5.05226	-54.08909
	AF1860		KDQF01000722	petersii	10	14	18 14 Flat de la Waki	French Guiana	3.08364	-53.41185

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4	AF1945	KDQF01000756 petersii	10	14	18	14 Flat de la Waki	French Guiana	3.08361	-53.4121	
5	AF2336	KDQF01000903 petersii	10	14	17	14 Machicou	French Guiana	3.890031	-52.573535	
6	AF2353	KDQF01000915 petersii	10	14	17	14 Mapaou	French Guiana	4.189842	-52.314725	
7	AF2561	KDQF01000985 petersii	10	14	17	14 RN2 PK65 mare	French Guiana	4.487368	-52.347811	
8	AF2586	KDQF01001003 petersii	10	14	18	14 Pedra Branca do Amapari (AP)	Brazil	0.772972	-51.94571	
9	AF2892	KDQF01001130 petersii	10	14	18	14 Roura	French Guiana	4.733772	-52.324499	
10	AF3044	KDQF01001203 petersii	10	14	17	14 Memora G	French Guiana	3.31774	-52.19329	
11	AF3283	KDQF01001349 petersii	10	14	17	14 Taparabo, Oiapoque (AP)	Brazil	4.016066	-51.693802	
12	AF3482	KDQF01001433 petersii	10	14	18	14 St Georges, RN2 pk 185	French Guiana	3.918717	-51.843853	
13	AF3482	KDQF01001433 petersii	10	14	18	14 St Georges, RN2 pk 185	French Guiana	3.918717	-51.843853	
14	AG333	KDQF01001548 petersii	10	14	17	14 Petit Laussat	French Guiana	5.449738	-53.883405	
15	AG339	KDQF01001551 petersii	10	14	17	14 Macouria, La Cesaree	French Guiana	5.03255	-52.533717	
16	AG340	KDQF01001552 petersii	10	14	17	14 Macouria, La Cesaree	French Guiana	5.03255	-52.533717	
17	AG382	KDQF01001572 petersii	10	14	18	14 St Pierre	French Guiana	3.154571	-52.662821	
18	AG390	KDQF01001576 petersii	10	14	17	14 Dekou dekou	French Guiana	4.696879	-53.959808	
19	AG403	KDQF01001583 petersii	10	14	17	14 Chutes Voltaire	French Guiana	5.031222	-54.087778	
20	AG438	KDQF01001607 petersii	10	14	18	14 Alikene	French Guiana	3.220044	-52.37855	
21	AG442	KDQF01001610 petersii	10	14	18	14 Alikene	French Guiana	3.220044	-52.37855	
22	AL120414G1	KDQF01001679 petersii	10	14	18	14 Roura	French Guiana	4.736741	-52.327724	
23	AL120414G2	KDQF01001680 petersii	10	14	18	14 Roura	French Guiana	4.736741	-52.327724	
24	AM011	KDQF01001688 petersii	10	14	18	14 Inini Tolenga	French Guiana	3.663159	-53.928308	
25	AM025	KDQF01001696 petersii	10	14	18	14 Inini Tolenga	French Guiana	3.663159	-53.928308	
26	BPN1385	KDQF01001982 petersii	10	14	17	14 Kaw2	French Guiana	4.516105	-52.10053	
27	CAAM18	KDQF01002131 petersii	10	14	18	14 Montagne cacao	French Guiana	2.349128	-53.215985	
28	DAN001	KDQF01002389 petersii	10	14	18	14 St Georges	French Guiana	3.894655	-51.799943	
29	DAN005	KDQF01002390 petersii	10	14	17	14 St Georges	French Guiana	3.894655	-51.799943	
30	DAN006	KDQF01002391 petersii	10	14	17	14 St Georges	French Guiana	3.894655	-51.799943	
31	DAN007	KDQF01002392 petersii	10	14	18	14 St Georges	French Guiana	3.894655	-51.799943	
32	DAN017	KDQF01002396 petersii	10	14	18	14 St Georges	French Guiana	3.888232	-51.807804	
33	DAN033	KDQF01002400 petersii	10	14	17	14 St Georges, RN 2 PK168	French Guiana	4.00126	-51.931057	
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4		DAN035	KDQF01002401 petersii	10	14	17	14 St Georges, piste Saut Maripa	French Guiana	3.862884	-51.863422
5		DSM136	KDQF01002429 petersii	10	14	18	14 Monsinery	French Guiana	4.80338	-52.47466
6		DSM138	KDQF01002430 petersii	10	14	18	14 Monsinery	French Guiana	4.80338	-52.47466
7		FTA293	KDQF01002552 petersii	10	14	18	14 Rio Amapá Grande, Calcoene (AP)	Brazil	2.127111	-51.191333
8		MTR06305	KDQF01003140 petersii	10	14	18	14 Igarapé Camaipi, Rio Maracá (AP)	Brazil	-0.0241667	-51.8972222
9		MTR13810	KDQF01003266 petersii	10	14	18	14 Serra do Navio (AP)	Brazil	0.9180556	-52.0027778
10		MTR13811	KDQF01003267 petersii	10	14	18	14 Serra do Navio (AP)	Brazil	0.9180556	-52.0027778
11		MTR13812	KDQF01003268 petersii	10	14	18	14 Serra do Navio (AP)	Brazil	0.9180556	-52.0027778
12		MTR24193	KDQF01003588 petersii	10	14	18	14 Lourenço (AP)	Brazil	2.3526389	-51.6152222
13		NZCS82	KDQF01003789 petersii	10	14	18	14 Brownsberg	Suriname	4.936527	-55.194826
14		QM020	KDQF01004060 petersii	10	14	17	14 Matiti	French Guiana	5.050249	-52.571622
15		QM070	KDQF01004065 petersii	10	14	18	14 Guatemala	French Guiana	5.15	-52.633333
16		WAAM18	KDQF01004469 petersii	10	14	18	14 Flat de la waki	French Guiana	3.18341	-53.4775
17		WAAM19	KDQF01004470 petersii	10	14	18	14 Flat de la waki	French Guiana	3.18341	-53.4775
18		MTR12652	KDQF01003199 petersii	49	15	20	15 Igarapé Jacundá, Rio Abacaxis (AM)	Brazil	-4.174831	-58.703241
19		MTR12746	ON568767 KDQF01003217 petersii	49	15	20	15 Igarapé Açu, Rio Abacaxis (AM)	Brazil	-4.34416666	-58.635
20		MTR13214	KDQF01003238 petersii	49	15	20	15 Pacamiri, Rio Abacaxis (AM)	Brazil	-4.33333333	-58.1333333
21		MTR13332	KDQF01003240 petersii	49	15	20	15 Palhalzinho, Rio Abacaxis (AM)	Brazil	-4.33333333	-58.1333333
22	SMNS12040		JN691194 petersii	52	16	27	16 Mabura hill forest reserve	Guyana	5.1552778	-58.6997222
23	SMNS12041		JN691195 petersii	52	16	27	16 Mabura hill forest reserve	Guyana	5.1552778	-58.6997222
24	SMNS12042		JN691196 petersii	52	16	27	16 Mabura hill forest reserve	Guyana	5.1552778	-58.6997222
25	SMNS12043		JN691197 petersii	52	16	27	16 Mabura hill forest reserve	Guyana	5.1552778	-58.6997222
26	SMNS12044		JN691198 petersii	52	16	27	16 Mabura hill forest reserve	Guyana	5.1552778	-58.6997222
27	SMNS12045		JN691199 petersii	52	16	27	16 Mabura hill forest reserve	Guyana	5.1552778	-58.6997222
28	SMNS12079		JN691200 petersii	52	16	27	16 Iwokrama	Guyana	4.6713889	-58.685
29	SMNS12046		JN691201 petersii	52	16	27	16 Mabura hill forest reserve	Guyana	5.1552778	-58.6997222
30	SMNS12047		JN691202 petersii	52	16	27	16 Mabura hill forest reserve	Guyana	5.1552778	-58.6997222
31		PK1506	JN691203 petersii	52	16	27	16 Kaieteur NP	Guyana	5.2686111	-59.7686111
32		PK1664	JN691204 petersii	52	16	27	16 Kaieteur NP	Guyana	5.2686111	-59.7686111
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4		AF3745	ON585896	petersii	52	16	27	16 Voltzberg	Suriname	4.68169	-56.18568	
5		AF3754	ON585897	petersii	52	16	27	16 Voltzberg	Suriname	4.68169	-56.18568	
6		AF3829	ON568758	ON585899	petersii	52	16	27	16 Voltzberg	Suriname	4.71578	-56.21116
7												
8		BPN1746	ON585923	petersii	52	16	27	16 Saramacca River Bridge	Suriname	5.38974	-55.36955	
9		BPN2958	ON585924	petersii	52	16	27	16 RAP Basecamp 2	Suriname	2.47881	-55.63161	
10		PK1516	ON585958	petersii	52	16	27	16 Kaieteur NP	Guyana	5.167199	-59.500294	
11		TJC1262	ON586012	petersii	52	16	27	16 NARIL	Guyana	5.12295	-59.10673	
12		AF2018	KDQF01000794	petersii	52	16	27	16 Sipaliwini, Apalagadi	Suriname	2.1728	-56.0969	
13		AF2126	KDQF01000853	petersii	52	16	27	16 Sipaliwini, camp1 to Apalagadi	Suriname	2.09753	-56.1472	
14		AF2133	KDQF01000855	petersii	52	16	27	16 Sipaliwini	Suriname	2.02682	-56.12564	
15		AF2795	KDQF01001108	petersii	52	16	27	16 Mitaraka, Layon A	French Guiana	2.23577	-54.44928	
16		AF3304	KDQF01001359	petersii	52	16	27	16 Bakhuis, near camp	Suriname	4.72462	-56.7638	
17		AF3346	KDQF01001379	petersii	52	16	27	16 Bakhuis, Creek 10k	Suriname	4.65616	-56.78649	
18		AF3446	KDQF01001422	petersii	52	16	27	16 Spari Creek	Suriname	5.23285	-55.80462	
19		AF3464	KDQF01001430	petersii	52	16	27	16 Spari Creek	Suriname	5.23285	-55.80462	
20		AF3467	KDQF01001432	petersii	52	16	27	16 Spari Creek	Suriname	5.23285	-55.80462	
21		BPN2817	KDQF01002011	petersii	52	16	27	16 RAP Basecamp 1, nr camp	Suriname	2.477	-55.62941	
22												
23												
24	MPEG23260	KDQF01002839	petersii	52	16	27	16 Faro, FLOTA (PA)	Brazil	-1.714011	-57.213300		
25	MPEG23261	KDQF01002840	petersii	52	16	27	16 Faro, FLOTA (PA)	Brazil	-1.714011	-57.213300		
26	MPEG23262	KDQF01002841	petersii	52	16	27	16 Faro, FLOTA (PA)	Brazil	-1.714011	-57.213300		
27	MPEG29675	KDQF01002864	petersii	52	16	27	16 ESEC Grão-Pará (PA)	Brazil	0.630281	-55.7285		
28	MPEG30373	KDQF01002911	petersii	52	16	27	16 REBIO Maicuru (PA)	Brazil	0.828619	-53.931200		
29	MPEG30376	KDQF01002912	petersii	52	16	27	16 REBIO Maicuru (PA)	Brazil	0.828619	-53.931200		
30	MPEG30377	KDQF01002913	petersii	52	16	27	16 REBIO Maicuru (PA)	Brazil	0.828619	-53.931200		
31	MPEG30506	KDQF01002919	petersii	52	16	27	16 Paru (PA)	Brazil	-0.943969	-53.236300		
32	MPEG30507	KDQF01002920	petersii	52	16	27	16 Paru (PA)	Brazil	-0.943969	-53.236300		
33	MPEG30511	KDQF01002921	petersii	52	16	27	16 Paru (PA)	Brazil	-0.943969	-53.236300		
34	MPEG30515	KDQF01002922	petersii	52	16	27	16 Paru (PA)	Brazil	-0.943969	-53.236300		
35	MTD47781	KDQF01003044	petersii	52	16	27	16 Mabura hill forest reserve	Guyana	5.155278	-58.699722		
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4	NZCS42		KDQF01003770 petersii	52	16	27	16 maripaston, caught on transect 1	Suriname	5.268728	-55.435886
5		PK3688	KDQF01004019 petersii	52	16	27	16 Close to Iwokrama field station	Guyana	4.672190	-58.684733
6		TJC1276	KDQF01004367 petersii	52	16	27	16 NARIL	Guyana	5.12757	-59.11460
7		MTR35690	ON585941 petersii	55	17	32	17 Alvarães (AM)	Brazil	-3.21026	-64.8053
8		MTR36069	ON585942 petersii	55	17	32	17 Açaí, Rio Içá (AM)	Brazil	-2.90378	-68.33864
9		MTR36546	ON585944 petersii	55	17	32	17 São Pedro, Rio Içá (AM)	Brazil	-3.03611	-68.88238
10		MTR36973	ON585948 petersii	55	17	32	17 Coari (AM)	Brazil	-4.0821	-63.14366
11		MTR40972	ON585956 petersii	55	17	32	17 Boa Vista (AM)	Brazil	-0.343457	-65.408344
12		MTR41361	ON585957 petersii	55	17	32	17 Rio Inhambú (AM)	Brazil	-0.231949	-65.416147
13		MTR33583	KDQF01003727 petersii	55	17	32	17 Maraa, Trilha da Capoeira (AM)	Brazil	-1.7591878	-65.748269
14		MTR33653	ON568771 KDQF01003734 petersii	55	17	32	17 Japurá, Trilha de Santa Fé (AM)	Brazil	-1.7533947	-66.338219
15	INPA-H152		KDQF01002685 petersii	54	18	31	18 BR-319 (AM)	Brazil	-4.986944	-61.567222
16		MTR18764	KDQF01003391 petersii	54	18	31	18 Rio Purus (AM)	Brazil	-4.18314	-61.48801
17		MTR18955	KDQF01003411 petersii	54	18	31	18 Rio Purus, Lago Chavian (AM)	Brazil	-4.18314	-61.48801
18		MTR19027	KDQF01003413 petersii	54	18	31	18 Rio Purus, Moiobamba (AM)	Brazil	-4.720095	-62.133036
19		MTR19221	ON568768 KDQF01003429 petersii	54	18	31	18 Rio Purus (AM)	Brazil	-4.702148	-62.309074
20		MTR19322	KDQF01003437 petersii	54	18	31	18 Rio Purus (AM)	Brazil	-4.702148	-62.309074
21		MTR19378	KDQF01003440 petersii	54	18	31	18 Rio Purus, Moiobamba (AM)	Brazil	-4.720095	-62.133036
22		MTR39719	ON585951 petersii	38	19	26	19 Maturacá (AM)	Brazil	0.621452	-66.120803
23		MTR40007	ON568776 ON585953 petersii	38	19	26	19 Maturacá (AM)	Brazil	0.625169	-66.117435
24		TG2844	ON568777 KDQF01004330 petersii	53	20	62	20 Igarapé Esperança (AC)	Brazil	-7.720152	-72.636981
25		HJ056	ON568762 KDQF01002630 petersii	18	21	23	21 UHE Jirau, Mutum (RO)	Brazil	-8.748483	-63.903465
26		HJ645	KDQF01002671 petersii	18	21	23	21 Caiçara, Porto Velho (RO)	Brazil	-8.696257	-63.912477
27		MTR20418	KDQF01003456 petersii	56	22	29	22 ESEC Maracá (RR)	Brazil	3.36977	-61.44177
28		MTR20419	ON568769 KDQF01003457 petersii	56	22	29	22 ESEC Maracá (RR)	Brazil	3.36977	-61.44177
29	CFBH16742	MW284636	MW291358 petersii	12	24	30	24 Belém (PA)	Brazil	-1.447	-48.241
30		MTR33862	ON585939 petersii	12	24	30	24 Peixe-Boi (PA)	Brazil	-1.143941	-47.288139
31		MTR33863	ON585940 petersii	12	24	30	24 Peixe-Boi (PA)	Brazil	-1.143941	-47.288139
32	CHUNB56789		KDQF01000011 petersii	12	24	30	24 Tailândia (PA)	Brazil	-2.920212	-48.899459
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	MJ1333		JF789911	petersii	19	35	22	35 Yucuma, Los Lagos	Bolivia	-12.771967	-65.810933
	HJ057		KDQF01002631	petersii	48	45	60	45 UHE Jirau, Mutum (RO)	Brazil	-8.748483	-63.903465
	MSH10374		JN691220	petersii	63	46	33	46 E.E. Anavilhanas, Base 2 (AM)	Brazil	-2.534444	-60.836667
	MTR40433		ON585954	petersii	64	46	33	46 Santa Helena, Barcelos (AM)	Brazil	-1.418088	-61.779996
	MTR40622		ON585955	petersii	63	46	33	46 Curirú, Rorainópolis (RR)	Brazil	-1.32165	-61.78059
	LZUMSH17425		ON585934	petersii	50	14	19	58 Guajará-Mirim, Rio Formoso (RO)	Brazil	-10.321389	-64.563333
CFBH36707	TG172	MW284711	MW291415	petersii	51	14	19	58 Alta Floresta (MT)	Brazil	-9.663	-56.054
CFBH36582	TG185	MW284713	MW291417	petersii	51	14	19	58 Paranaíta (MT)	Brazil	-9.671	-56.482
	TG226.1	MW284716	MW291420	petersii	51	14	19	58 Paranaíta (MT)	Brazil	-9.671	-56.482
	AF191		KDQF01000743	petersii	51	14	19	58 Apiacás (MT)	Brazil	-9.650846	-57.393665
	HJ003		KDQF01002621	petersii	50	14	19	58 UHE Jirau (RO)	Brazil	-8.748483	-63.903465
	MTR25620	ON568770	KDQF01003625	petersii	50	14	19	58 Pacaás Novos (RO)	Brazil	-10.792625	-63.629707
	MTR25740		KDQF01003696	petersii	50	14	19	58 Pacaás Novos (RO)	Brazil	-10.799614	-63.627189
	MTR25799		KDQF01003706	petersii	50	14	19	58 Pacaás Novos (RO)	Brazil	-10.786979	-63.627305
	MTR976856		KDQF01003755	petersii	51	14	19	58 Juruena (MT)	Brazil	-10.323611	-58.492778
	MTR976857		KDQF01003756	petersii	51	14	19	58 Juruena (MT)	Brazil	-10.323611	-58.492778
	AS0216		JF789912	podicipinus	25	10	39	10 Velasco, Caparu	Bolivia	-14.912117	-61.082467
	AS0275		JF789913	podicipinus	25	10	39	10 Velasco, Caparu	Bolivia	-14.912117	-61.082467
	AS0276		JF789914	podicipinus	25	10	39	10 Velasco, Caparu	Bolivia	-14.912117	-61.082467
	AS0277		JF789915	podicipinus	25	10	39	10 Velasco, Caparu	Bolivia	-14.912117	-61.082467
	AS0278		JF789916	podicipinus	25	10	39	10 Velasco, Caparu	Bolivia	-14.912117	-61.082467
SMF94320			KF723184	podicipinus	25	10	39	10 Velasco, Caparu	Bolivia	-14.912117	-61.082467
MNKA9638			KF723185	podicipinus	25	10	39	10 Velasco, Caparu	Bolivia	-14.912117	-61.082467
	AS286		KF723186	podicipinus	25	10	39	10 Velasco, Caparu	Bolivia	-14.912117	-61.082467
AAG-UFU5267		MW284611	MW291349	podicipinus	25	10	39	10 Vilhena (RO)	Brazil	-12.715336	-60.190196
AAG-UFU5280		MW284612	MW291350	podicipinus	25	10	39	10 Costa Marques (RO)	Brazil	-12.077912	-64.035155
	UC243		EF632048	podicipinus	28	10	38	57 Estância Mimosa, Bonito (MS)	Brazil	-21.1211	-56.4819
	UC244		EF632049	podicipinus	28	10	38	57 Estância Mimosa, Bonito (MS)	Brazil	-21.1211	-56.4819
	UC278		EF632050	podicipinus	28	10	38	57 Chácara Renascer, Bauru (SP)	Brazil	-22.284522	-49.102565

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	MTR39721		ON585952	riveroi	1	23	48	23 Maturacá, Sta. Isabel do Rio Negro (AM) Brazil		0.621452	-66.120803
CFBH39707	TG385	MW284723	MW291426	riveroi	1	23	48	23 São Gabriel da Cachoeira(AM) Brazil		-0.055000	-67.094000
CFBH39708	TG387	MW284725	MW291427	riveroi	1	23	48	23 São Gabriel da Cachoeira(AM) Brazil		-0.055000	-67.094000
USNM314793			EF632000	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314794			EF632001	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314795			EF632002	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314796			EF632003	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314813			EF632004	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314814			EF632005	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314815			EF632006	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314816			EF632007	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314817			EF632008	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314818			EF632009	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314819			EF632010	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314820			EF632011	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314821			EF632012	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314822			EF632013	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314831			EF632014	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314798			EF632015	validus	66	48	45	48 St.George, Grand Anse Bay Grenada		12.021514	-61.766038
USNM314512			EF632016	validus	66	48	45	48 VincentSt.Andrew;nearVermont. St. Vincent		13.248975	-61.189953
USNM314513			EF632017	validus	66	48	45	48 VincentSt.George;ArnosVale. St. Vincent		13.248975	-61.189953
USNM314516			EF632018	validus	66	48	45	48 VincentSt.George;RoseCottage. St. Vincent		13.248975	-61.189953
USNM314517			EF632019	validus	66	48	45	48 VincentSt.George;RoseCottage. St. Vincent		13.248975	-61.189953
USNM314514			EF632020	validus	66	48	45	48 VincentSt.George;ArnosVale. St. Vincent		13.248975	-61.189953
USNM314515			EF632021	validus	66	48	45	48 VincentSt.George;ArnosVale. St. Vincent		13.248975	-61.189953
USNM314718			EF632022	validus	66	48	45	48 VincentSt.George;ArnosVale. St. Vincent		13.248975	-61.189953
USNM314719			EF632023	validus	66	48	45	48 VincentSt.George;ArnosVale. St. Vincent		13.248975	-61.189953
USNM314720			EF632024	validus	66	48	45	48 VincentSt.George;ArnosVale. St. Vincent		13.248975	-61.189953
USNM314721			EF632025	validus	66	48	45	48 VincentSt.George;ArnosVale. St. Vincent		13.248975	-61.189953

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4	USNM314722	EF632026	validus	66	48	45	48 VincentSt.George;ArnosVale.	St. Vincent	13.248975	-61.189953	
5	USNM314723	EF632027	validus	66	48	45	48 VincentSt.George;ArnosVale.	St. Vincent	13.248975	-61.189953	
6	USNM314714	EF632028	validus	66	48	45	48 VincentSt.George;ArnosVale.	St. Vincent	13.248975	-61.189953	
7	USNM523940	EF632029	validus	66	48	45	48 St.Paul;Delafor,Louisd'OrRiver.	Trinidad and Tobago	11.144450	-60.791459	
8	USNM523941	EF632030	validus	66	48	45	48 St.Paul;Delafor,Louisd'OrRiver.	Trinidad and Tobago	11.144450	-60.791459	
9	USNM286948	EF632031	validus	66	48	45	48 St.George;SimlaResearchStation.	Trinidad and Tobago	10.653508	-61.463492	
10	USNM286959	EF632032	validus	66	48	45	48 St.George	Trinidad and Tobago	10.653508	-61.463492	
11	USNM306105	EF632033	validus	66	48	45	48 St.George;nearBrassoSecoVillage.	Trinidad and Tobago	10.746113	-61.264143	
12	USNM314627	EF632034	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
13	USNM314628	EF632035	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
14	USNM314629	EF632036	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
15	USNM314630	EF632037	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
16	USNM314631	EF632038	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
17	USNM314632	EF632039	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
18	USNM314633	EF632040	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
19	USNM314634	EF632041	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
20	USNM314635	EF632042	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
21	USNM314636	EF632043	validus	66	48	45	48 St.Patrick;nearChathamBeach.	Trinidad and Tobago	10.653508	-61.463492	
22	USNM314679	EF632044	validus	66	48	45	48	Trinidad and Tobago			
23	USNM314672	EF632045	validus	66	48	45	48 St.George;westofCarapo.	Trinidad and Tobago	10.653508	-61.463492	
24	USNM302408	EF632046	validus	66	48	45	48 Igarapé Cocal, Tepequém, Amajari (RR)	Brazil	3.750000	-61.733333	
25	USNM535774	EF632047	validus	66	48	45	48 Baramita	Guyana	7.3666	-60.4833	
26		BWMC6881	EF632057	validus	66	48	45 48 St Andrew, Spring Gardens Estate	Grenada	12.110615	-61.667880	
27		BWMC6882	EF632058	validus	66	48	45 48 St Andrew, Birch Grove	Grenada	12.110615	-61.667880	
28		BWMC06883	EF632059	validus	66	48	45 48 St Andrew, Birch Grove	Grenada	12.110615	-61.667880	
29		BWMC6939	EF632060	validus	66	48	45 48 St George, Beausejour	Grenada	12.093280	-61.743904	
30		BPN1092	JN691221	validus	66	48	45 48 Kartabo	Guyana	6.3833333	-58.7	
31	AAG-UFU3885	MW284609	MW291347	validus	66	49	45 48 Cucuí, São Gabriel da Cachoeira (AM)	Brazil	1.191023	-66.834194	
32	AAG-UFU3886	MW284610	MW291348	validus	66	49	45 48 Cucuí, São Gabriel da Cachoeira (AM)	Brazil	1.191023	-66.834194	
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4	MTD47968		KDQF01003066	validus	66	48	45	48 Iwokrama	Guyana	4.6713889	-58.685	
5		MTR20849	KDQF01003524	validus	66	48	45	48 Tepequém, riacho alojamento (RR)	Brazil	3.754780	-61.717448	
6		AF0129	EU201133	validus	65	9	45	55 Brownsberg	Suriname	4.936527	-55.194826	
7		AF0131	KDQF01000053	validus	65	9	45	55 Brownsberg	Suriname	4.936527	-55.194826	
8		BPN3439	KDQF01002039	validus	65	9	45	55 Yupukari	Guyana	3.381367	-59.314533	
9		BPN3666	ON568761 KDQF01002080	validus	67	9	46	56 Kusad Mountain	Guyana	2.795400	-59.846900	
10		MTR20554	KDQF01003478	validus	67	9	46	56 Fazenda Salvamento	Brazil	3.33256	-61.38237	
11		MTR23094	KDQF01003555	validus	67	9	46	56 Serra da Maroquinha	Brazil	2.380344	-61.357627	
12		MTR23124	KDQF01003556	validus	67	9	46	56 Serra da Maroquinha	Brazil	2.380344	-61.357627	
13		MTR23133	KDQF01003557	validus	67	9	46	56 Serra da Maroquinha	Brazil	2.380344	-61.357627	
14	LSUNZ H-12885		EF632052	wagneri	60	8	43	54 Cuyabeno	Ecuador	-0.0886	-76.1419	
15	LSUMZ H-13653		EF632053	wagneri	60	8	43	54 5 km N of Porto Walter (AC)	Brazil	-8.266389	-72.743611	
16	USNM320988		EF632054	wagneri	60	8	43	54 Pastaza, Coca, 1km ENE of Río Tiguino	Ecuador			
17	LSU H-12415		ON585932	wagneri	60	8	43	54				
18		MTR33747	ON568772 ON585937	wagneri	60	8	43	54 Japurá, Trilha da Anta (AM)	Brazil	-1.772073	-66.367929	
19	QCAZA13937	MW284668	MW291360	wagneri	60	8	43	54 Morona Santiago	Ecuador	-2.967000	-78.433000	
20	QCAZA14709	MW284669	MW291361	wagneri	60	8	43	54 Morona Santiago	Ecuador	-3.040651	-77.996064	
21	QCAZA15956	MW284670	MW291362	wagneri	60	8	43	54 Pastaza	Ecuador	-1.411389	-78.000000	
22	QCAZA17024	MW284671	MW291363	wagneri	60	8	43	54 Morona Santiago	Ecuador	-2.892752	-78.385210	
23	QCAZA18192	MW284673	MW291365	wagneri	60	8	43	54 Napo	Ecuador	-1.064716	-77.613430	
24	QCAZA19172	MW284674	MW291366	wagneri	60	8	43	54 Sucumbios	Ecuador	-0.259710	-75.888600	
25	QCAZA20709		MW291368	wagneri	60	8	43	54 Orellana	Ecuador	-0.675639	-76.397083	
26	QCAZA20950	MW284676	MW291369	wagneri	60	8	43	54 Orellana	Ecuador	-0.677167	-76.401167	
27	QCAZA23812	MW284677	MW291373	wagneri	60	8	43	54 Morona Santiago	Ecuador	-2.731199	-78.281800	
28	QCAZA23916	MW284678	MW291374	wagneri	60	8	43	54 Morona Santiago	Ecuador	-3.346620	-78.643900	
29	QCAZA23924	MW284679	MW291375	wagneri	60	8	43	54 Morona Santiago	Ecuador	-3.349899	-78.6431900	
30	QCAZA25639	MW284681	MW291377	wagneri	60	8	43	54 Pastaza	Ecuador	-1.625000	-77.907200	
31	QCAZA26295	MW284683	MW291378	wagneri	60	8	43	54 Morona Santiago	Ecuador	-2.904599	-78.386930	
32	QCAZA29284		MW291387	wagneri	60	8	43	54 Sucumbios	Ecuador	0.0298160	-75.974490	
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QCAZA29301	MW284689	MW291388	wagneri	60	8	43	54 Napo	Ecuador	-0.992033	-77.407910
QCAZA31071	MW284690	MW291390	wagneri	60	8	43	54 Zamora Chinchipe	Ecuador	-4.332731	-78.662960
QCAZA32488		MW291391	wagneri	60	8	43	54 Pastaza	Ecuador	-1.498099	-77.879310
QCAZA38979		MW291392	wagneri	60	8	43	54 Pastaza	Ecuador	-1.510010	-77.514160
QCAZA39315	MW284691	MW291393	wagneri	60	8	43	54 Pastaza	Ecuador	-1.421710	-77.678210
QCAZA39511	MW284692	MW291394	wagneri	60	8	43	54 Orellana	Ecuador	-0.893836	-75.448032
QCAZA46462	MW284701	MW291404	wagneri	60	8	43	54 Morona Santiago	Ecuador	-2.165000	-77.902910
QCAZA46465	MW284702	MW291405	wagneri	60	8	43	54 Morona Santiago	Ecuador	-2.165001	-77.902919
QCAZA48651	MW284703	MW291406	wagneri	60	8	43	54 Pastaza	Ecuador	-1.266360	-77.888073
QCAZA48652		MW291407	wagneri	60	8	43	54 Pastaza	Ecuador	-1.266360	-77.888073
QCAZA48908	MW284704	MW291408	wagneri	60	8	43	54 Napo	Ecuador	-0.682100	-77.602680
QCAZA48909	MW284705	MW291409	wagneri	60	8	43	54 Napo	Ecuador	-0.682100	-77.602680
QCAZA49024	MW284706	MW291410	wagneri	60	8	43	54 Morona Santiago	Ecuador	-2.258333	-78.198333
QCAZA49380	MW284707	MW291411	wagneri	60	8	43	54 Pastaza	Ecuador	-1.411388	-78.000000
	MTR28117	KDQF01003712	wagneri	60	8	43	54 PARNA Serra do Divisor (AC)	Brazil	-7.433993	-73.660945

Table S2. Sound recordings of species the *Leptodactylus melanonotus* group and *L. longirostris* (*L. fuscus* group) analysed in this study. ‘##’ corresponds to occasions when the recorded male was observed but not collected. Sound repositories: AAG-UFU, Universidade Federal de Uberlândia (Ituiutaba, Brazil); FNVJ, Universidade Estadual de Campinas (Brazil); FonoZoo, Fonoteca Zoológica de Madrid (Madrid, Spain); LH, Universidade Federal de Mato Grosso (Cuiabá, Brazil); Macaulay Library (ML), The Cornell Lab of Ornithology (Ithaca, United States); MNHN, Muséum National d'Histoire Naturelle (Paris, France); QCAZA, Pontifica Universidad Catolica del Ecuador (Quito, Ecuador); USNM, Smithsonian Institution (Washington DC, United States).

Sound file	Species	Locality	Voucher	Sound repository	Recordist
TRC1	<i>L. brevipes</i>	Chapada dos Guimarães (MT, Brazil)	AAG-UFU 1462	AAG-UFU	Thiago R. Carvalho
LH16A-11	<i>L. brevipes</i>	Chapada dos Guimarães (MT, Brazil)		LH	Christine Strüssmann
AAG5c	<i>L. brevipes</i>	Barra dos Garças (MT, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
AAG6a	<i>L. brevipes</i>	Barra dos Garças (MT, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
AAG7a	<i>L. brevipes</i>	Barra dos Garças (MT, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
AAG9a	<i>L. brevipes</i>	Barra dos Garças (MT, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
AAG10c	<i>L. brevipes</i>	Barra dos Garças (MT, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
Tape255_track1	<i>L. diedrus</i>	Juruá (AM, Brazil)	INPA-H 5020	USNM	Claude Gascon
MNHN-SO-2021-1574	<i>L. diedrus</i>	Vaupés (Colombia)		MNHN	Antoine Fouquet
Tape254_track13	<i>L. discodactylus</i>	Juruá (AM, Brazil)		USNM	Claude Gascon
cf_wagneriFG	<i>L. fremitus</i>	French Guiana		*	
MNHN-SO-2021-1575	<i>L. fremitus</i>	Sipaliwini (Suriname)	Field# AF2224	MNHN	Antoine Fouquet
MNHN-SO-2021-1576	<i>L. fremitus</i>	French Guiana		MNHN	Antoine Fouquet
L_petersii_20-05-2003_CECC	<i>L. fremitus</i>	Serra do Navio (AP, Brazil)		AAG-UFU	C. Eduardo Costa-Campos
TRC1	<i>L. fremitus</i>	Serra do Navio (AP, Brazil)	CFBH 43258	AAG-UFU	Thiago R. Carvalho
CECC1	<i>L. fremitus</i>	Pedra Branca do Amapari (AP, Brazil)		AAG-UFU	C. Eduardo Costa-Campos
CECC2	<i>L. fremitus</i>	Pedra Branca do Amapari (AP, Brazil)		AAG-UFU	C. Eduardo Costa-Campos
Tape274_track1	<i>L. griseigularis</i>	Tingo María, Huánuco (Peru)	UNMSM 236	USNM	Victor R. Morales
MNHN-SO-2021-1577	<i>L. griseigularis</i>	Pongo-Barranquita, Caynarachi (Peru)		MNHN	Antoine Fouquet

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4	MNHN-SO-2021-1578	<i>L. griseigularis</i>	Urku, Tarapoto (Peru)	Field# AF4392	MNHN	Antoine Fouquet
5	TRC1b	<i>L. intermedius</i>	Manacapuru (AM, Brazil)	CFBH 43132	AAG-UFU	Thiago R. Carvalho
6	TRC2	<i>L. intermedius</i>	Manacapuru (AM, Brazil)		AAG-UFU	Thiago R. Carvalho
7	TRC3	<i>L. intermedius</i>	Manacapuru (AM, Brazil)		AAG-UFU	Thiago R. Carvalho
8	TRC5	<i>L. intermedius</i>	Manacapuru (AM, Brazil)		AAG-UFU	Thiago R. Carvalho
9	TRC6	<i>L. intermedius</i>	Manacapuru (AM, Brazil)		AAG-UFU	Thiago R. Carvalho
10	TRC1	<i>L. intermedius</i>	Santana (AP, Brazil)	CFBH 43251	AAG-UFU	Thiago R. Carvalho
11	TRC2	<i>L. intermedius</i>	Santana (AP, Brazil)	CFBH 43252	AAG-UFU	Thiago R. Carvalho
12	TRC3	<i>L. intermedius</i>	Santana (AP, Brazil)	CFBH 43253	AAG-UFU	Thiago R. Carvalho
13	FZ8319	<i>L. leptodactyloides</i>	Loreto (Peru)		FonoZoo	José M. Padial
14	FZ8321	<i>L. leptodactyloides</i>	Loreto (Peru)		FonoZoo	José M. Padial
15	Tape239_cut1	<i>L. leptodactyloides</i>	Rio Branco (AC, Brazil)	ZUEC-AMP 5639	USNM	Adão J. Cardoso
16	Tape16_track1	<i>L. leptodactyloides</i>	Limoncocha, Napo (Ecuador)		USNM	W. Ronald Heyer
17	Tape17_track1	<i>L. leptodactyloides</i>	Limoncocha, Napo (Ecuador)		USNM	W. Ronald Heyer
18	Tape207B_Tracks1&2	<i>L. leptodactyloides</i>	Tambopata, Madre de Dios (Peru)	USNM 307125	USNM	Reginald B. Cocroft
19	Tape267_track9	<i>L. leptodactyloides</i>	Tambopata, Madre de Dios (Peru)		USNM	Reginald B. Cocroft
20	Tape83_track1	<i>L. melanonotus</i>	Costa Rica		USNM	Roy W. McDiarmid
21	FZ7204	<i>L. melanonotus</i>	Panama	KU 76523	FonoZoo	William E. Duellman
22	FZ7498	<i>L. melanonotus</i>	Panama	KU 115305	FonoZoo	William E. Duellman
23	ML208478	<i>L. melanonotus</i>	Panama	##	ML	Martin J. Fouquette Jr.
24	AAG1c	<i>L. natalensis</i>	Araguari (MG, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
25	AAG5	<i>L. natalensis</i>	Araguari (MG, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
26	AAG8b	<i>L. natalensis</i>	Araguari (MG, Brazil)	AAG-UFU 4667	AAG-UFU	Ariovaldo A. Giaretta
27	AAG9	<i>L. natalensis</i>	Araguari (MG, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
28	AAG10b	<i>L. natalensis</i>	Araguari (MG, Brazil)	AAG-UFU 4984	AAG-UFU	Ariovaldo A. Giaretta
29	AAG11c	<i>L. natalensis</i>	Araguari (MG, Brazil)	AAG-UFU 4985	AAG-UFU	Ariovaldo A. Giaretta
30	AAG12c	<i>L. natalensis</i>	Araguari (MG, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
31	TRC1	<i>L. natalensis</i>	Carolina (MA, Brazil)		AAG-UFU	Thiago R. Carvalho
32	TRC2	<i>L. natalensis</i>	Carolina (MA, Brazil)	AAG-UFU 2780	AAG-UFU	Thiago R. Carvalho
33	TRC3	<i>L. natalensis</i>	Carolina (MA, Brazil)		AAG-UFU	Thiago R. Carvalho
34	AAG1a	<i>L. natalensis</i>	Cumari (GO, Brazil)	AAG-UFU 1181	AAG-UFU	Ariovaldo A. Giaretta
35	AAG2b	<i>L. natalensis</i>	Cumari (GO, Brazil)	AAG-UFU 1182	AAG-UFU	Ariovaldo A. Giaretta
36	TRC1b	<i>L. natalensis</i>	Macaíba (RN, Brazil)	AAG-UFU 3578	AAG-UFU	Thiago R. Carvalho
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4	AAG2a	<i>L. natalensis</i>	Uruaçu (GO, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
5	AAG3a	<i>L. natalensis</i>	Uruaçu (GO, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
6	Tape323_track1	<i>L. natalensis</i>	São Cristóvão (SE, Brazil)	MZUSP 89945	USNM	Celso M. de Carvalho
7	MNHN-SO-2021-1579	<i>L. nesiotus</i>	French Guiana		MNHN	Antoine Fouquet
8	Trinidad1994	<i>L. nesiotus</i>	Trinidad Island		**	J. Roger Downie
9	FNJV31086	<i>L. petersii</i>	Cruzeiro do Sul (AC, Brazil)	ZUEC-AMP 4387	FNJV	Adão J. Cardoso
10	TRC1	<i>L. petersii</i>	São Gabriel da Cachoeira (AM, Brazil)	AAG-UFU 3891	AAG-UFU	Thiago R. Carvalho
11	TRC2	<i>L. petersii</i>	São Gabriel da Cachoeira (AM, Brazil)	AAG-UFU 3892	AAG-UFU	Thiago R. Carvalho
12	AAG1c	<i>L. petersii</i>	São Gabriel da Cachoeira (AM, Brazil)	AAG-UFU 3867	AAG-UFU	Ariovaldo A. Giaretta
13	Tape256_track9	<i>L. petersii</i>	Porongaba, Juruá (AM, Brazil)	INPA-H 4222	USNM	Claude Gascon
14	TRC1b	<i>L. petersii</i>	Cantá (RR, Brazil)	AAG-UFU 5450	AAG-UFU	Thiago R. Carvalho
15	LH341	<i>L. petersii</i>	Primavera (PA, Brazil)		LH)	André Pansonato
16	Tape239_cut2	<i>L. petersii</i>	Carajás (PA, Brazil)		USNM	Adão J. Cardoso
17	Tape239_cut3	<i>L. petersii</i>	Carajás (PA, Brazil)		USNM	Adão J. Cardoso
18	Tape207A_track12	<i>L. petersii</i>	Tambopata, Madre de Dios (Peru)	USNM 307121	USNM	Reginald B. Cocroft
19	LBM1c	<i>L. podicipinus</i>	Limeira do Oeste (MG, Brazil)	AAG-UFU 1240	AAG-UFU	Lucas B. Martins
20	AAG2a	<i>L. podicipinus</i>	Araguari (MG, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
21	LBM1c	<i>L. podicipinus</i>	Araporã (MG, Brazil)		AAG-UFU	Lucas B. Martins
22	AAG3a	<i>L. podicipinus</i>	Costa Marques (RO, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
23	AAG4a	<i>L. podicipinus</i>	Costa Marques (RO, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
24	CBS1c	<i>L. podicipinus</i>	Itaguaçu (BA, Brazil)		AAG-UFU	Cyro S. Bernardes
25	AAG6b	<i>L. podicipinus</i>	Ituiutaba (MG, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
26	AAG7a	<i>L. podicipinus</i>	Ituiutaba (MG, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
27	AAG2c	<i>L. podicipinus</i>	Ituiutaba (MG, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
28	AAG2a	<i>L. podicipinus</i>	Monte Alegre de Minas (MG, Brazil)	AAG-UFU 3149	AAG-UFU	Ariovaldo A. Giaretta
29	AAG1a	<i>L. podicipinus</i>	Uberlândia (MG, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
30	TRC1a	<i>L. podicipinus</i>	Cuiabá (MT, Brazil)	AAG-UFU 5721	AAG-UFU	Thiago R. Carvalho
31	AAG5a	<i>L. pustulatus</i>	Pontal do Araguaia (MT, Brazil)	AAG-UFU 3450	AAG-UFU	Ariovaldo A. Giaretta
32	IAH5e	<i>L. pustulatus</i>	Pontal do Araguaia (MT, Brazil)	AAG-UFU 3451	AAG-UFU	Isabelle A. Haga
33	IAH6c	<i>L. pustulatus</i>	Pontal do Araguaia (MT, Brazil)	AAG-UFU 3452	AAG-UFU	Isabelle A. Haga
34	AAG3b	<i>L. pustulatus</i>	Pontal do Araguaia (MT, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
35	AAG4b	<i>L. pustulatus</i>	Pontal do Araguaia (MT, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
36	Tape128_track2	<i>L. riveroi</i>	Vaupés (Colombia)		USNM	William F. Pyburn
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4	Tape225_track1	<i>L. sabanensis</i>	Gran Sabana, Bolívar (Venezuela)		FNJV	Adão J. Cardoso
5	TRC1c	<i>L. validus</i>	Tepequém (RR, Brazil)	AAG-UFU 5502	AAG-UFU	Thiago R. Carvalho
6	TRC2	<i>L. validus</i>	Tepequém (RR, Brazil)	AAG-UFU 5501	AAG-UFU	Thiago R. Carvalho
7	AAG2	<i>L. validus</i>	Cantá (RR, Brazil)	AAG-UFU 5544	AAG-UFU	Ariovaldo A. Giaretta
8	AAG3	<i>L. validus</i>	Cantá (RR, Brazil)	AAG-UFU 5545	AAG-UFU	Ariovaldo A. Giaretta
9	AAG4	<i>L. validus</i>	Cantá (RR, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
10	AAG6	<i>L. validus</i>	Cantá (RR, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
11	TRC1b	<i>L. validus</i>	São Gabriel da Cachoeira (AM, Brazil)	AAG-UFU 3885	AAG-UFU	Thiago R. Carvalho
12	TRC2	<i>L. validus</i>	São Gabriel da Cachoeira (AM, Brazil)		AAG-UFU	Thiago R. Carvalho
13	TRC3	<i>L. validus</i>	São Gabriel da Cachoeira (AM, Brazil)		AAG-UFU	Thiago R. Carvalho
14	BFVT1a	<i>L. validus</i>	São Gabriel da Cachoeira (AM, Brazil)		AAG-UFU	Bernardo F. V. Teixeira
15	Tape246_Track1	<i>L. validus</i>	Trinidad Island		USNM	Ronald I. Crombie
16	LS100487	<i>L. wagneri</i>	Near Pacto Sumaco, Napo (Ecuador)	##	QCAZA	Santiago R. Ron
17	MNHN-SO-2021-1580	<i>L. wagneri</i>	Ichigkat, Eastern Cordillera (Peru)	Field# AF4856	MNHN	Antoine Fouquet
18	TRC1	<i>L. longirostris</i>	Cantá (RR, Brazil)		AAG-UFU	Thiago R. Carvalho
19	TRC2	<i>L. longirostris</i>	Cantá (RR, Brazil)		AAG-UFU	Thiago R. Carvalho
20	TRC3	<i>L. longirostris</i>	Cantá (RR, Brazil)		AAG-UFU	Thiago R. Carvalho
21	TRC4	<i>L. longirostris</i>	Cantá (RR, Brazil)	AAG-UFU 5438	AAG-UFU	Thiago R. Carvalho
22	Tape53_track4	<i>L. longirostris</i>	Itaituba (PA, Brazil)	USNM 234051	USNM	Ronald I. Crombie
23	TRC1	<i>L. longirostris</i>	Serra do Navio (AP, Brazil)	AAG-UFU 6414	AAG-UFU	Thiago R. Carvalho
24	AAG1a	<i>L. longirostris</i>	Serra do Navio (AP, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
25	AAG2a	<i>L. longirostris</i>	Serra do Navio (AP, Brazil)	AAG-UFU 5990	AAG-UFU	Ariovaldo A. Giaretta
26	AAG3b	<i>L. longirostris</i>	Serra do Navio (AP, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
27	AAG4a	<i>L. longirostris</i>	Serra do Navio (AP, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
28	AAG5a	<i>L. longirostris</i>	Serra do Navio (AP, Brazil)		AAG-UFU	Ariovaldo A. Giaretta
29	AAG7a	<i>L. longirostris</i>	Serra do Navio (AP, Brazil)		AAG-UFU	Ariovaldo A. Giaretta

* Sound guide of amphibians of French Guiana (Marty & Gaucher, 2001)

** Original recording made available by J. Roger Downie

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4 **Table S3.** Mean uncorrected pairwise genetic distances of partial 16S (613 bp) mtDNA sequences among OTUs of the *Leptodactylus*
5 *melanonotus* group. Distances lower than 3% are indicated in grey. Available as a spread sheet file.
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3 *Systematics and Biodiversity*
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8 **Supplemental material**

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12 Species diversity and systematics of the *Leptodactylus melanonotus* group (Anura,
13 Leptodactylidae): review of diagnostic traits and a new species from the Eastern Guiana
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17 Shield
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21 Thiago R. Carvalho *, Antoine Fouquet, Mariana L. Lyra, Ariovaldo A. Giaretta, C. Eduardo
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24 Costa-Campos, Miguel T. Rodrigues, Célio F. B. Haddad & Santiago R. Ron
25

26 * Corresponding author: carvalho.thiagoribeiro@gmail.com
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30 **Supplementary figures**
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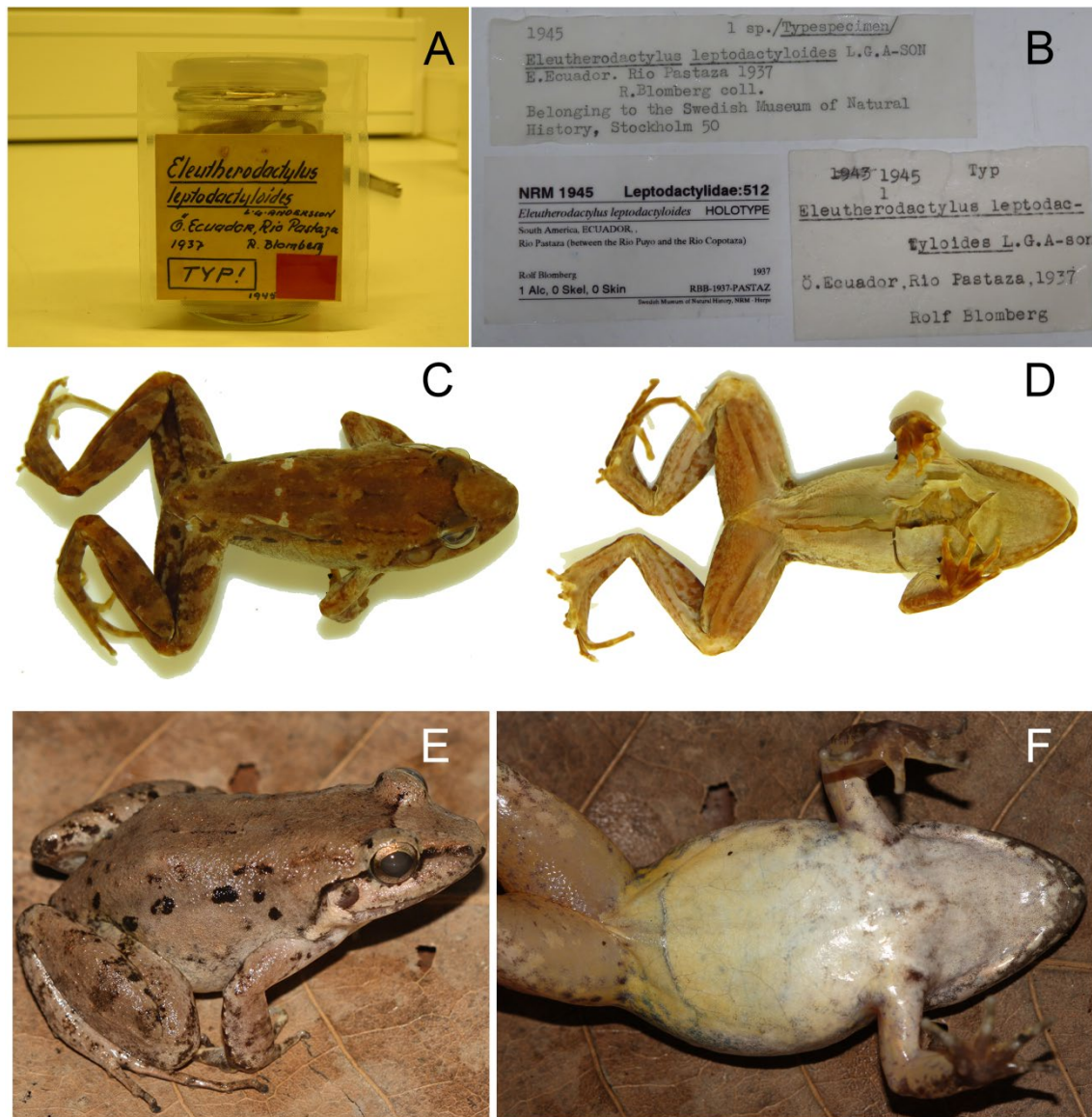


Fig. S1. Holotype of *Leptodactylus leptodactyloides* (NRM 945, adult male: SVL = 44 mm), housed at the Swedish Museum of Natural History. NRM catalogue information (A–B) associated with the holotype, and dorsal (C) and ventral (D) views of the entire specimen. Comparative specimen (E–F) of *L. leptodactyloides* (CFBH 43256, adult female: 43.8 mm). Note the similarity in the dorsolateral fold, spots and glands in the dorsum and flank, and ventral colouration without bold mottling or spotted pattern throughout the belly.

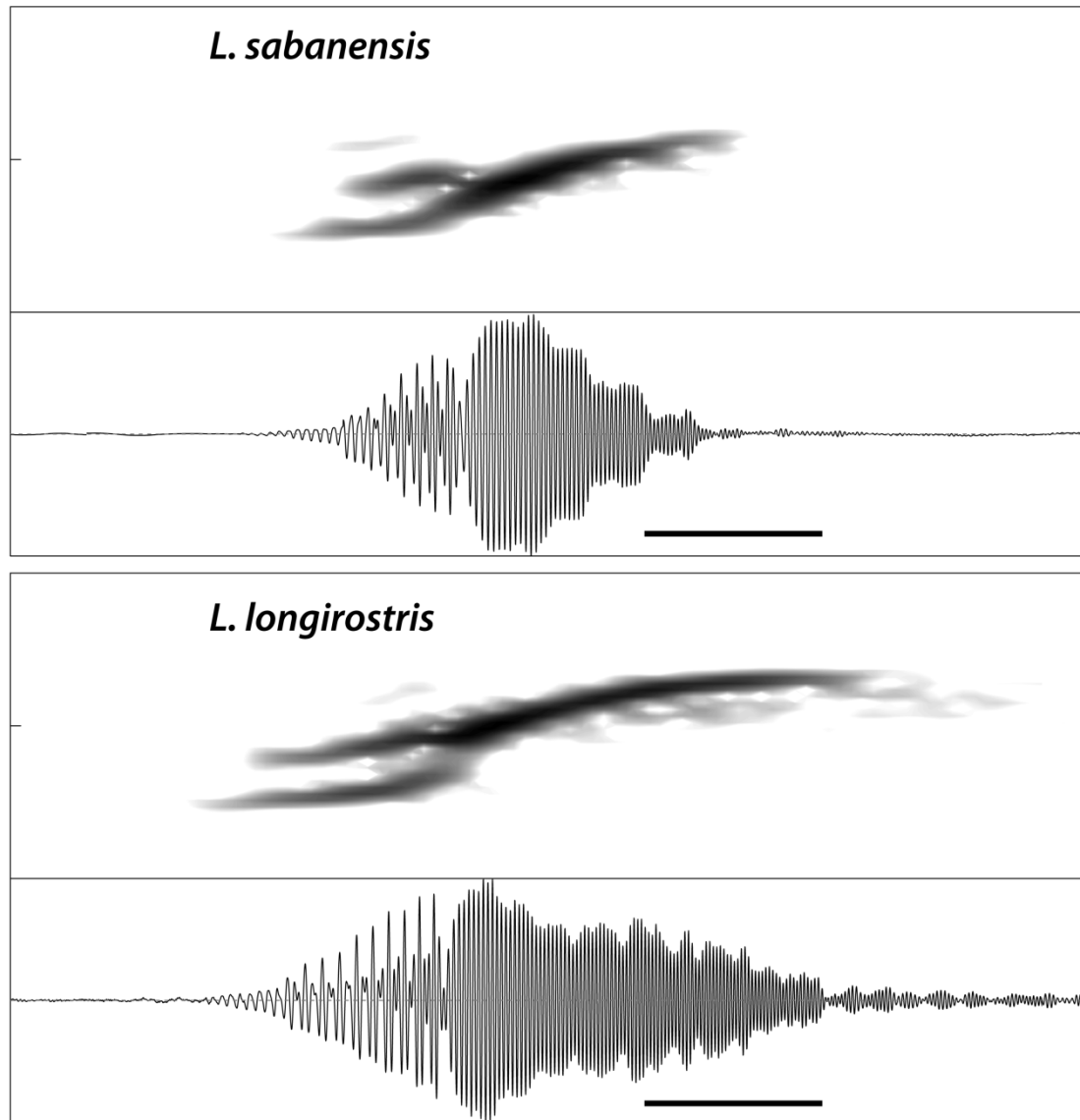


Fig. S2. Advertisement calls of *Leptodactylus sabanensis* from the Gran Sabana in Venezuela and the sympatric *L. longirostris*, a species of the *L. fuscus* group, from adjacent Brazil (Roraima). Spectrograms produced at a 4-kHz scale. For oscillograms, scale bars = 20 ms. See Supplemental Appendix 2 for detailed information.

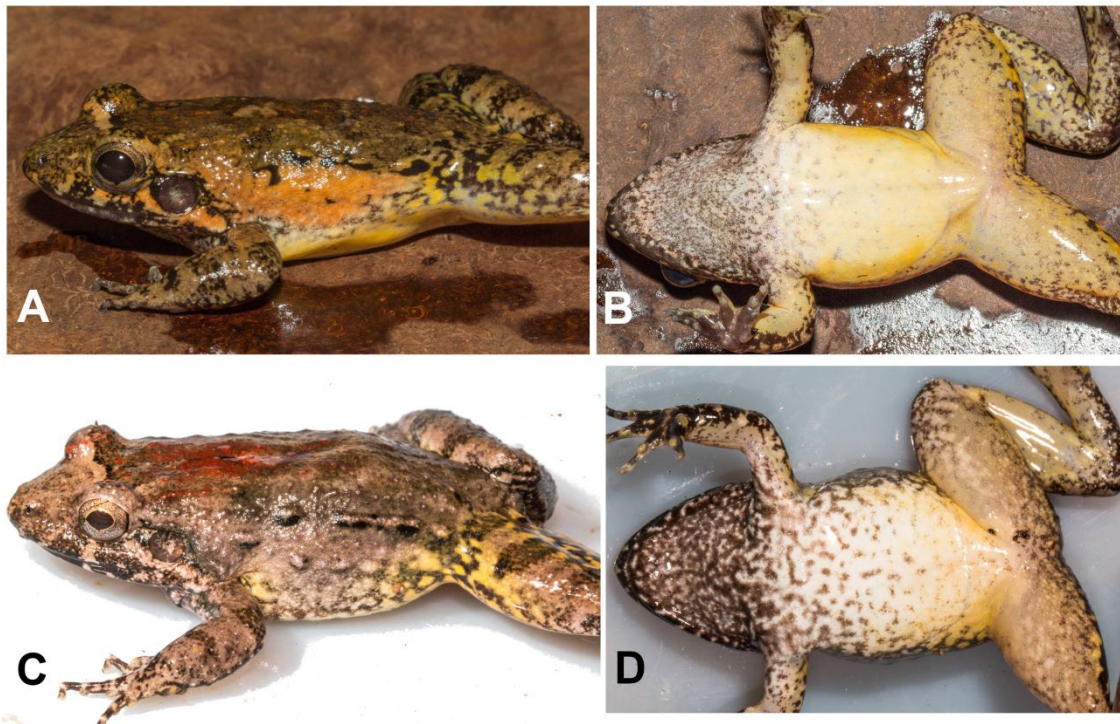


Fig. S3. Variation in life colours of *Leptodactylus fremitus* sp. nov. (A–B) Paratype from French Guiana (MNHN-RA-2021.0072, adult male: SVL = 39.1 mm). (C–D) Non-type specimen from western Suriname (field number AF 2058, adult female: SVL = 42.4 mm).

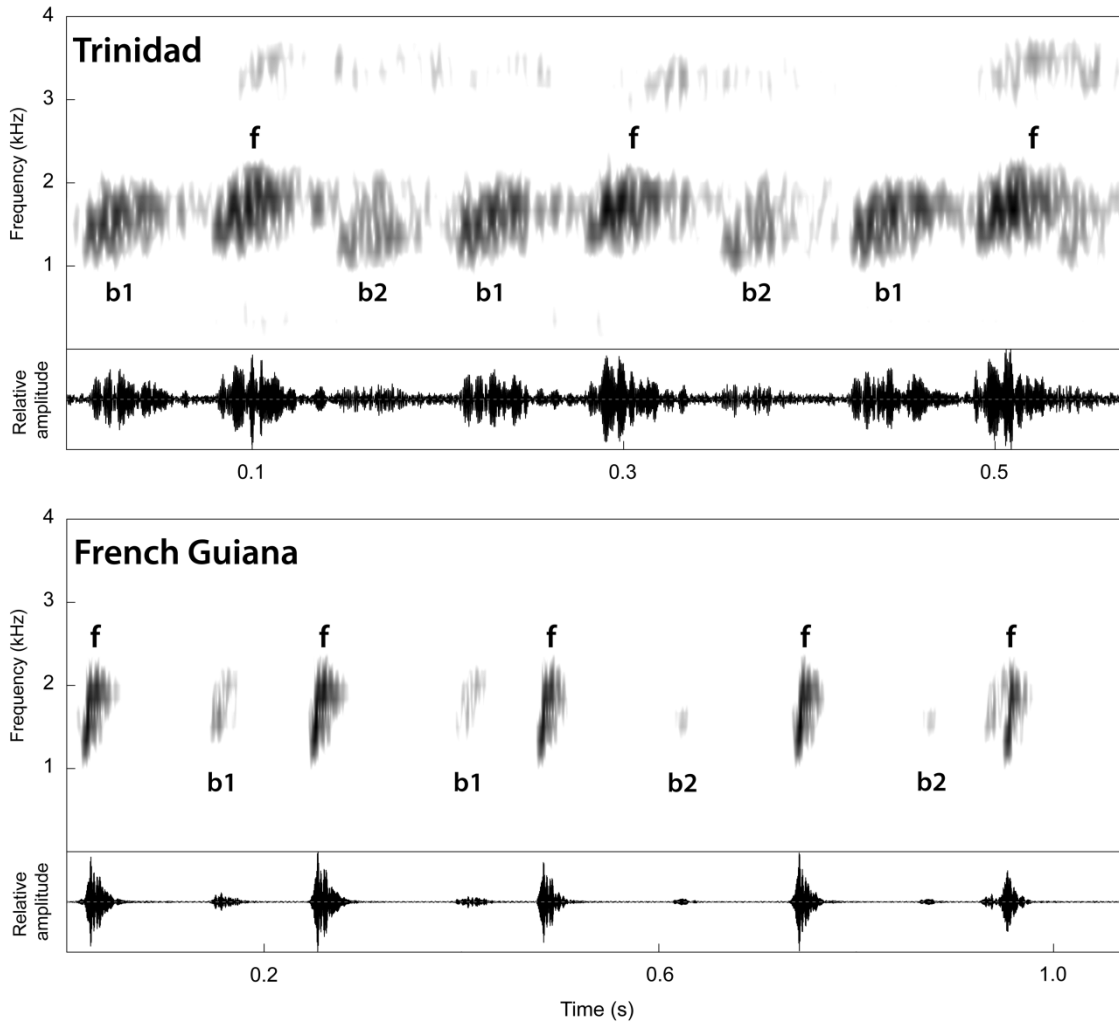


Fig. S4. Antiphonal calling in *Leptodactylus nesiotus* recorded from Trinidad Island and French Guiana. On both occasions, advertisement calls of the focal male (f) and antiphonal calling of two conspecific males in the background (b1 and b2).

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4 *Systematics and Biodiversity*
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8 9 **Supplemental material**

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14 Species diversity and systematics of the *Leptodactylus melanonotus* group (Anura,
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16 Leptodactylidae): review of diagnostic traits and a new species from the Eastern Guiana
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23 Thiago R. Carvalho*, Antoine Fouquet, Mariana L. Lyra, Ariovaldo A. Giaretta, C. Eduardo Costa-
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25 Campos, Miguel T. Rodrigues, Célio F. B. Haddad & Santiago R. Ron
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27 * Corresponding author: carvalho.thiagoribeiro@gmail.com
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31 **Supplementary text**

32 33 34 35 36 **Appendix S1.** Molecular data acquisition.

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41 We extracted DNA from liver or muscle tissue samples (thigh or toe-clip) using the Wizard
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43 Genomic extraction protocol (Promega; Madison, WI, USA) or ammonium acetate
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45 precipitation method. We sequenced partial sequences of the 16S ribosomal RNA gene
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47 (16S) using two approaches: (i) we amplified a 16S fragment using primers 16Sar-L and
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49 16Sbr-H (Palumbi et al., 1991) and sanger sequenced these fragments as in Gazoni et al.
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51 (2021); and (ii) we amplified a 16S fragment with primers N16R and N16F (Salducci et al.,
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53 2005), and sequenced fragments in a Miseq Illumina sequencer. For that, primers N16R and
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4 N16F were brcoded by adding NNN + 8-nucleotide labels (hereafter designated as “tags”)
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6 for sample identification as all resulting PCR products were mixed into single libraries: 32
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8 tags for forward primer (N16R) and 36 tags for reverse primer (N16F).
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11 The final volume of PCRs was 20 μ l and contained 2 μ l of DNA extract diluted 10
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13 fold, 10 μ l of Amplitaq Gold® 360 Master Mix (Life Technologies, Carlsbad, CA, USA),
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15 5.84 μ l of Nuclease Free Water Ambion (Thermo Fisher Scientific, Massachusetts, USA),
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17 0.25 μ M of each primer and 3.2 μ g of Bovine Serum Albumin (Roche Diagnostic, Basel,
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19 Switzerland). We ran the PCR in duplicate for each sample, and we included blank PCR
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21 controls in the analysis using nuclease-free water as template. First, the mixture was
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23 denatured at 95°C for 10 minutes, followed by 40 cycles of 30 seconds at 95°C, 30 seconds
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25 at 55°C, and 1 minute at 72°C, followed by a final step of 7 minutes at 72°C. Libraries of
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27 mixed PCR products were sequenced using 2 x 250 paired-end reads sequencing
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29 technology through MiSeq high throughput sequencing (Illumina) at the Génopole
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31 (Toulouse, France). The resulting outputs were analysed with the OBITOOLS software
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33 suite. Paired-end reads were assembled and merged, and we used the tag attached to the
34
35 primer to assign each read to its label. Then we removed low-quality reads (alignment
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37 scores < 50, containing Ns or shorter than 50 bp). The resulting batch of reads was
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39 dereplicated while keeping the coverage information (number of reads merged). All
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41 sequences <300 bp were discarded. Eventually, every sequence that we included in our
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43 dataset was all >380 bp long.
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52 **References**

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4 Palumbi, S. R., Martins, A., Romano, S., McMillan, W. O., Stice, L., & Grabowski, G.
5
6 (1991). *The Simple Fool's Guide to PCR* (version 2.0). Privately published, compiled
7
8 by S. Palumbi, Honolulu, University of Hawaii.
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11 Salducci, M.-D., Marty, C., Fouquet, A., & Gilles, A. (2005). Phylogenetic relationships
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13 and biodiversity in hylids (Anura: Hylidae) from French Guiana. *Comptes Rendus*
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15 *Biologies*, 328(10–11), 1009–1024. <https://doi.org/10.1016/j.crv.2005.07.005>
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4 **Appendix 2.** Alignment file (fasta format) of partial sequences of the 16S rDNA gene (613
5 bp) used in the mtDNA delimitation analysis of the *Leptodactylus melanonotus* group. See
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7 Table S1 for associated information on voucher specimens (museum accession numbers of
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9 field codes) and locality data.
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4 **Appendix 3.** Alignment file (fasta format) of partial sequences of the 16S rDNA and COI
5 genes (2,428 bp) used in the phylogenetic analysis of the *Leptodactylus melanonotus* group.
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7 See Table S1 for associated information on voucher specimens (museum accession
8 numbers of field codes) and locality data.
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4 **Appendix 4.** Specimens of the *Leptodactylus melanonotus* species group morphologically
5 examined.
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9 *Leptodactylus brevipes*.—BRAZIL: Mato Grosso: Alto Garças (male: AAG-UFU
10 5719). Barra do Garças (males: AAG-UFU 1046–53, 3500; females: AAG-UFU 1054–7).
11 Chapada dos Guimarães (males: UFMT-A 12002–5, 12010–4, 12016, 12018; females:
12 UFMT-A 11983, 11998–9, 12001, 12009). Cuiabá (male: AAG-UFU 1462; female: AAG-
13 UFU 1463). Pontal do Araguaia (female: AAG-UFU 3123).
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21 *Leptodactylus cf. colombiensis*.—COLOMBIA: Valle del Cauca: Cali (male:
22 MZUSP 69913).
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26 *Leptodactylus diedrus*.—BRAZIL: Amazonas: Rio Juruá (males: INPA-H 3591,
27 5020). São Gabriel da Cachoeira: Cucuí (male: AAG-UFU 3890).
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31 *Leptodactylus discodactylus*.—BRAZIL: Acre: Cruzeiro do Sul (males: ZUEC-
32 AMP 10606, 11108–9). Parque Nacional da Serra do Divisor (male: INPA-H 41956).
33 ECUADOR: Morona Santiago: Tukupi (females: QCAZ-A 53242, 53244). Pastaza:
34 Juyuintza (female: QCAZ-A 53525). Sucumbíos: La Selva Amazon Ecolodge (males:
35 QCAZ-A 12112, 44068). Playas de Cuyabeno (males: QCAZ-A 28271, 28276).
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43 *Leptodactylus griseigularis*.—PERU: San Martín: Leticia (female: field number AF
44 4589). San José (female: field number AF 4441; juveniles: field number AF 4434, 4439).
45 Tarapoto (male: field number AF 4396, 4535, 4539; female: field number AF 4392;
46 juvenile: field number AF 4394).
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4 *Leptodactylus intermedius*.—BRAZIL: Amapá: Santana (males: AAG-UFU 6406–
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6 7, CFBH 43251–3; female: AAG-UFU 6405). Amazonas: Manacapuru (males: CFBH
7
8 43132–8). Rondônia: Itapuã do Oeste (males: AAG-UFU 5807–8).

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11 *Leptodactylus leptodactyloides*.—BRAZIL: Acre: Cruzeiro do Sul (males: ZUEC-
12
13 AMP 11020, 11027–8). Marechal Thaumaturgo: Restauração (males: ZUEC-AMP 8466,
14
15 8481–2). Rio Branco (males: AAG-UFU 5868–9; ZUEC-AMP 5407, 5409, 5637, 5639–42;
16
17 female: ZUEC-AMP 5638). Xapuri (males: ZUEC-AMP 5725–7; female: ZUEC-AMP
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19 5676). Amapá: Macapá: Ariri (males: CFBH 43254–5; females: AAG-UFU 6408–10;
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21 CFBH 43256). Mato Grosso: Poconé (male: CFBH 36739). Pará: Serra do Krukoinhoken
22
23 (male: MZUSP 69323; females: MZUSP 69324, 69327–8). ECUADOR: Orellana:
24
25 Comunidad el Descanso (female: QCAZ-A 43893). La Joya de los Sachas (male: QCAZ-A
26
27 20446, 20098, 20100; females: QCAZ-A 20096–7). Puerto Francisco de Orellana (females:
28
29 QCAZ-A 43660, 43737, 43776, 43785, 43787). Comunidad El Edén (male: QCAZ-A
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31 44242; female: QCAZ-A 44240). Pastaza: Montalvo (female: QCAZ-A 20955).
32
33 Sucumbíos: La Selva Amazon Ecolodge (male: QCAZ-A 4378). Puerto Bolívar (females:
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35 QCAZ-A 27911, 27952, 28343). Río Cuyabeno (male: QCAZ-A 8003; females: QCAZ-A
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37 8004–5, 8007).

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39 *Leptodactylus melanonotus*.—ECUADOR: El Oro: El Progreso (males: QCAZ-A
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41 10347–8). Esmeraldas: Durango (males: QCAZ-A 22694, 23368, 23542; female: QCAZ-A
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43 23370). Manabí: Río Ayampe (male: QCAZ-A 9904). MEXICO: Sinaloa: San Ignacio
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45 (males: ZUEC-AMP 18775–6). Chiapas: Las Cruces (female: ZUEC-AMP 18798).
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4 *Leptodactylus natalensis*.—BRAZIL: Bahia: Ilhéus (AAG-UFU 0234–6). Goiás:
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6 Cumari (AAG-UFU 1181–4). Guarani de Goiás (AAG-UFU 1967). Uruaçu (AAG-UFU
7
8 0983–7, 1416–25). Maranhão: Carolina (AAG-UFU 2780–3). Minas Gerais: Araguari
9
10 (AAG-UFU 4658, 4660–1, 4663–4, 4666–8, 4686, 4695, 4749, 4984, 4986). Rio Grande do
11
12 Norte: Canguaretama (AAG-UFU 3851–2). Macaíba (AAG-UFU 3578–9, 3850). Natal
13
14 (CFBH 39748–50). Tocantins: Aragominas (AAG-UFU 6242).
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18 *Leptodactylus nesiotus*.—FRENCH GUIANA: Cayenne (male: field number AF
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20 194; female: field number AF 237).
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23 *Leptodactylus petersii*.—BRAZIL: Acre: Assis Brasil (males: AAG-UFU 5915–6;
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25 female: AAG-UFU 5914). Parque Nacional da Serra do Divisor (males: INPA-H 41959,
26
27 41961). Rio Branco (males: AAG-UFU 5870–2; female: AAG-UFU 5873). Amapá:
28
29 Santana (males: AAG-UFU 6402–3). Serra do Navio (male: CFBH 43264). Amazonas: São
30
31 Gabriel da Cachoeira (neotype, male: CFBH 44102; other males: AAG-UFU 3867, 3891,
32
33 3893–5; female: AAG-UFU 3868). Pará: Santa Bárbara do Pará (female: AAG-UFU 6605).
34
35 Roraima: Cantá (male: AAG-UFU 5450; female: AAG-UFU 5451).
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40 *Leptodactylus podicipinus*.—BRAZIL: Mato Grosso: Cáceres (female: AAG-UFU
41
42 5365). Cuiabá (male: AAG-UFU 5721). Mato Grosso do Sul: Bela Vista (male: AAG-UFU
43
44 0154; female: AAG-UFU 0155). Minas Gerais: Araguari (male: AAG-UFU 4082).
45
46 Ituiutaba (female: AAG-UFU 0098). Uberlândia (male: AAG-UFU 2628). Rondônia: Alta
47
48 Floresta d'Oeste (males: AAG-UFU 6027, 6036–7; females: AAG-UFU 6028–35). Costa
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50 Marques (females: AAG-UFU 5279–80). Vilhena (male: AAG-UFU 5267).
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4 *Leptodactylus pustulatus*.—BRAZIL: Mato Grosso: Pontal do Araguaia (males:
5 AAG-UFU 3450–2, 4876). Tocantins: Brejinho de Nazaré (male: AAG-UFU 0915).
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9 *Leptodactylus riveroi*.—BRAZIL: Amazonas: São Gabriel da Cachoeira (male:
10 CFBH 39707*). Roraima: Parque Nacional da Serra da Mocidade (males: CFBH 43673–4).
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14 * Listed as a female in table S4 of Gazoni et al. (2021).
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17 *Leptodactylus sabanensis*.—VENEZUELA: Bolívar (male: ZUEC-AMP 9407).
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20 *Leptodactylus validus*.—BRAZIL: Amazonas: São Gabriel da Cachoeira: Cucuí
21 (males: AAG-UFU 3885–8; female: AAG-UFU 3889). Roraima: Cantá (males: AAG-UFU
22 5544–5). Serra do Tepequém (males: AAG-UFU 5501–2).
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27 *Leptodactylus wagneri*.—BRAZIL: Acre: Parque Nacional da Serra do Divisor
28 (males: INPA-H 41936, 41940). Amazonas: Parque Nacional do Pico da Neblina (female:
29 INPA-H 15789). ECUADOR: Morona Santiago: Gualaquiza (male: QCAZ-A 23924).
30 Limón (females: QCAZ-A 8567, 26295). Macas (female: QCAZ-A 42460). Méndez
31 (female: QCAZ-A 27419). Nuevo Israel (males: QCAZ-A 46446, 46465–7; female:
32 QCAZ-A 46463). Parque Nacional Sangay (males: QCAZ-A 58799, 59119; females:
33 QCAZ-A 58812–4). Río Yunganza (male: QCAZ-A 17024). Napo: Cotundo (male: QCAZ-
34 A 57177). Estación Biológica Wildsumaco (males: QCAZ-A 53934–5, 57330, 57757).
35 Tena (male: QCAZ-A 36250). Orellana: Parque Nacional Yasuní (males: QCAZ-A 8190,
36 64229; females: QCAZ-A 8303, 8828–9, 51220, 54681). Vía Pompeya Sur (male: QCAZ-
37 A 5194; females: QCAZ-A 8275, 43068). Pastaza: Campo Oglán (male: QCAZ-A 55150).
38 Campo Villano (males: QCAZ-A 54997; females: QCAZ-A 38775, 39292, 56388, 56554).
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4 Canelos (male: QCAZ-A 15958). Centro Ecológico Zanjarajuno (males: QCAZ-A 40894,
5 57796; female: QCAZ-A 40949). Comunidad Kurintza (male: QCAZ-A 38979). Juyuintza
6
7 (male: QCAZ-A 53543). Lorocachi (male: QCAZ-A 55867). Parque Nacional Llanganates
8
9 (males: QCAZ-A 59963, 59967, 59969–71). Pomona (female: QCAZ-A 25639). Puerto
10
11 Canelos (male: QCAZ-A 56593). Puyo (neotype, male: QCAZ-A 26219; other males:
12
13 QCAZ-A 15955–7). Sarayacu (male: QCAZ-A 52738). Shell (male: QCAZ-A 36082;
14
15 female: QCAZ-A 36084). Sucumbíos: Sacha Lodge (male: QCAZ-A 20244; juveniles:
16
17 QCAZ-A 20242–3; undetermined sex: QCAZ-A 20245–7). Zamora Chinchipe:
18
19 Destacamento Militar Shaime (male: QCAZ-A 31072; females: QCAZ-A 31069, 31071).
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25 *Leptodactylus* sp. (*L. melanonotus* group).—VENEZUELA: Mantecal (males:
26
27 ZUEC-AMP 9367–8; undetermined sex: ZUEC-AMP 9366). Santa Bárbara del Zulia
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29 (male: ZUEC-AMP 9391; female: ZUEC-AMP 9390).
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