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Systematics of the Neotropical Genus *Leptodactylus* Fitzinger, 1826 (Anura: Leptodactylidae): Phylogeny, the Relevance of Non-molecular Evidence, and Species Accounts

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Abstract. A phylogeny of the species-rich clade of the Neotropical frog genus *Leptodactylus* sensu stricto is presented on the basis of a total evidence analysis of molecular (mitochondrial and nuclear markers) and non-molecular (adult and larval morphological and behavioral characters) sampled from > 80% of the 75 currently recognized species. Our results support the monophyly of *Leptodactylus* sensu stricto, with *Hydrolaetare* placed as its sister group. The reciprocal monophyly of *Hydrolaetare* and *Leptodactylus* sensu stricto does not require that we consider *Hydrolaetare* as either a subgenus or synonym of *Leptodactylus* sensu lato. We recognize *Leptodactylus* sensu stricto, *Hydrolaetare, Adenomera,* and *Lithodytes* as valid monophyletic genera. Our results generally support the traditionally recognized *Leptodactylus* species groups, with exceptions involving only a few species that are easily accommodated without proposing new groups or significantly altering contents. The four groups form a pectinate tree, with the *Leptodactylus fuscus* group diverging first, followed by the *L. pentadactylus* group, which is sister to the *L. latrans* and *L. melanonotus* groups. To evaluate the impact of non-molecular evidence on our results, we compared our total evidence results with results obtained from analyses using only molecular data. Although non-molecular evidence comprised only 3.5% of the total evidence matrix, it had a strong impact on our total evidence results. Only one species group was monophyletic in the molecular-only analysis, and support differed in 86% of the 54 *Leptodactylus* clades that are shared by the results of the two analyses. Even though no non-molecular evidence was included for *Hydrolaetare,* exclusion of that data partition resulted in that genus being nested within *Leptodactylus,* demonstrating that the inclusion of a small amount of non-molecular evidence for a subset of species can alter not only the placement of those species, but also species that were not scored for those data. The evolution of several natural history and reproductive traits is considered in the light of our phylogenic framework. Invasion of rocky outcrops, larval oophagy, and use of underground reproductive chambers are restricted to species of the *Leptodactylus fuscus* and *L. pentadactylus* groups. In contrast, larval schooling, larval attendance, and more complex parental care are restricted to the *L. latrans* and *L. melanonotus* groups. Construction of foam nests is plesiomorphic in *Leptodactylus* but their placement varies extensively (e.g., underground chambers, surface of waterbodies, natural or excavated basins). Information on species synonymy, etymology, adult and larval morphology, advertisement call, and geographic distribution is summarized in species accounts for the 30 species of the *Leptodactylus fuscus* group, 17 species of the *L. pentadactylus* group, eight species of the *L. latrans* group, and 17 species of the *L. melanonotus* group, as well as the three species that are currently unassigned to any species group.

Keywords. Behavior; Distribution; Life history; Morphology; Taxonomy; Vocalization.

Resumen. Se presenta una filogenia del género *Leptodactylus,* un clado neotropical rico en especies, basada en análises combinados de datos moleculares (marcadores nuclear y mitocondriales) y no moleculares (caracteres de la morfología de adultos y larvas así como de comportamiento) se muestrearon > 80% de las 75 especies reconocidas. Los resultados apoyan la monofília de *Leptodactylus* sensu stricto, con *Hydrolaetare* como su grupo hermano. La monofília recíproca de *Hydrolaetare* y *Leptodactylus* no requiere considerar a *Hydrolaetare* como un subgénero o sinónimo de *Leptodactylus* sensu lato. Se reconocen *Leptodactylus* sensu stricto, *Hydrolaetare, Adenomera* y *Lithodytes* como géneros monofiléticos válidos. Los resultados en general resuelven los grupos tradicionalmente reconocidos de *Leptodactylus,* con excepciones de algunas especies que son reasignadas sin la necesidad de proponer nuevos grupos o alterar significativamente el contenido de los grupos tradicionales. Los cuatro grupos de especies forman una topología pectinada donde el grupo de *L. fuscus* tiene una posición basal, seguido por el grupo de *L. pentadactylus* que es el grupo hermano al clado formado por los grupo de *L. latrans* y *L. melanonotus.* Se estimó el impacto de los datos no moleculares en los resultados, comparándose los resultados de evidencia total con los de los análises de datos moleculares solamente. Los datos no moleculares representan un 3.5% de la matriz de evidencia total, pero estos datos tuvieron un impacto significativo en los resultados del análisis de evidencia total. En el análisis estrictamente molecular solamente un grupo de especies resultó monofilético, y el apoyo difirió en 86% de los 54 clados de *Leptodactylus* compartidos entre los dos análises. A pesar que datos no moleculares no fueron incluídos para *Hydrolaetare,* la exclusión de evidencia no molecular resultó en el género estar dentro de *Leptodactylus,* demostrando que la inclusión de evidencia no molecular pequeña para un subgrupo de especies altera no solamente la posición topológica de esas especies, sino tambien de las especies para las cuales dichos datos no fueron codificados. La evolución de patrones de historia natural y reprodución se evalúan en el contexto filogenético. La invasión de afloramientos rocosos y la construción de cámaras de reprodución subterraneas está limitada a los grupos de *Leptodactylus fuscus* y *L. pentadactylus,* mientras que la oofagia larval está restringida al grupo de *L. pentadactylus.* Por otro lado, los cárdumenes larvales, la proteción del cárdumen, y otros comportamientos parentales complejos carecterizan al clado formado por los grupos de especies de *L. latrans* y *L. melanonotus.* Los resúmenes de especies incluyen información de sinonímias, etimología, morfología de adultos y larvas, cantos, y distribución geográfica para las 30 especies del grupo de *Leptodactylus fuscus,* 17 especies del grupo *L. pentadactylus,* ocho especies del grupo de *L. latrans,* 17 especies del grupo de *L. melanonotus,* así como para las tres especies que actualmente no se encuentran asociadas a ninguno de los grupos de especies.

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CONTENTS

INTRODUCTION

The Neotropical genus *Leptodactylus* Fitzinger, 1826 is a species-rich clade of Neotropical frogs ranging in size from medium to very large (relative to most other Neotropical anurans), some species are active foragers in the leaf-litter (e.g., *L. wagneri,* Pough et al., 1992), whereas some of the larger species are sit-and-wait predators found around ponds (e.g., *L. latrans,* Strüssmann et al., 1984) or sit outside burrows they occupy permanently (e.g., *L. savagei,* reported as *L. pentadactylus* in Scott, 1983); *Leptodactylus* species usually consume small invertebrate prey (Rodrigues et al., 2004) but can also predate on anurans as well as other small vertebrates (e.g., *L. chaquensis,* Duré, 1999; *L. labyrinthicus;* Vaz-Silva and da Frota 2003; *L. laticeps,* Scott and Aquino, 2005).

The reproductive behavior of *Leptodactylus* is often complex and has been studied extensively. Species of *Leptodactylus* have conspicuous advertisement calls to attract females (e.g., *L. mystacinus,* Abrunhosa et al., 2001), male aggressive and competitive calls (e.g., *L. albilabris,* Lopez et al., 1988), female defensive calls (e.g., *L. latrans,* Vaz-Ferreira and Gehrau, 1975), and distress calls (e.g., *L. pentadactylus,* Hödl and Gollmann, 1986; *L. chaquensis* and *L. elenae,* Padial et al., 2006); seismic communication has also been reported in the genus (e.g., *L. albilabris,* Lewis and Narins, 1985; *L. syphax* Cardoso and Heyer, 1995). Some species have distinct sexual dimorphism with hypertrophied forelimbs in males, sometimes accompanied by sharp nuptial spines on the thumb (e.g., *L. latrans,* Cei, 1980; *L. bolivianus* complex, Heyer and de Sá, 2011). Complex parental care has been reported in the genus, such as the construction of distinct underground burrows (Arzabe and Prado, 2006) and foam nests in which embryos develop; various forms of protection by the parents of the foam nest and subsequently the larvae, including adults actively attacking predators and emitting unique vocalizations (e.g., *L. latrans,* Vaz-Ferreira and Gehrau, 1975), and tadpole schooling (e.g., *L. chaquensis,* Prado et al., 2000). Furthermore, some species have evolved larval oophagy (e.g., obligatory in *L. fallax,* Gibson and Buley, 2004) and carnivory (e.g., facultative in *L. savagei,* Ruibal and Thomas, 1988), which play important functions in community ecology (Allmon, 1991; Conte and Machado, 2005).

Some *Leptodactylus* species are a source of human food (e.g., *L. chaquensis, L. latrans* [reported as *L. ocellatus*], Gallardo, 1979; *L. fallax,* Krintler, 1986), and the dermal glands of several species are known to produce defensive skin secretions (Cei et al., 1967), including antimicrobial peptides and other protein toxins found in *L. fallax* (Rollins-Smith et al., 2005; King et al., 2005a), *L. labyrinthicus* (Libério et al., 2014), *L. laticeps* (Conlon et al., 2009), *L. latrans* (Nascimento et al., 2004, 2007; Leite et al., 2010), *L. pentadactylus* (Habermehl, 1981; Barlow, 1998; King et al., 2005b; Limaverde et al., 2009; Sousa et al., 2009), *L. syphax* (Dourado et al., 2007). Similarly, the foam nests of *L. vastus* possess a novel surfactant protein (Hissa et al., 2008, 2014).

Leptodactylus is widely distributed across Neotropical lowlands from southern North America to southern South America. The genus extends throughout South America (on both sides of the Andes in northern South America but restricted to the east of the Andes across most of their distribution in South America) and over the West Indies (Fig. 1). *Leptodactylus* is also ecologically diverse, occupying a wide range of environments from lowland dense rainforests (primary and secondary rainforest) to open habitats (including Savanna, Caatinga, Cerrado, Chaco, and Grasslands, Ab'Sáber, 1977; Joly et al., 1999); they are also found in artificial open habitats, previously forested areas, and areas currently used for agriculture and cattle ranching.

Although the clade (and even some species, e.g., *Leptodactylus fuscus*) extends over an impressive latitudinal range, its elevational range is generally more restricted. *Leptodactylus* is a predominantly lowland clade with most species occurring below 2,000 m. A few species occur and reproduce above 1,000 m sea level (e.g., *L. furnarius, L. latrans* in Serra da Bocaina, Rio do Janeiro and São Paulo states, Brazil) or at 1,300–1,600 m (e.g., *L. syphax, L. labyrinthicus, L. latrans, L. jolyi, L. fuscus, L. cunicularius,* and *L. camaquara* in Serra do Cipó, Minas Gerais state, Brazil). However, *L. colombiensis* extends from lowland areas

Figure 1. Geographic distribution of the genus *Leptodactylus* (shown in gray).

to 2600 m in the northern Andes of Colombia, whereas *L. silvanimbus* is restricted to the high altitude cloud forests of Honduras from 1700–1900 m.

Although some *Leptodactylus* species occur at considerable distances from water sources throughout the year, most species are strongly associated with water bodies; some species are associated primarily or exclusively with lotic systems (e.g., streams and creeks of riparian environments) and others associated with lentic systems (e.g., lakes, permanent and annual ponds, smaller ephemeral pools, and artificial water sources). Until recently, the fossil record for the genus was limited to remains of extant or indeterminate species from the Quaternary of Mexico, Bolivia, Brazil, Uruguay, Argentina, and the West Indies (Vergnaud-Grazzini, 1968; Lynch, 1971; Mones, 1975; Pregill, 1981; Van Devender et al., 1985; Lezcano et al., 1993; Sanchiz, 1998). However, the history of the genus was extended back to the early Pliocene of Argentina (Farola Monte Hermoso, Buenos Aires Province) based on fossils remains considered close to *L. latrans* (Gómez et al., 2013).

The systematic documentation of the diversity of the genus *Leptodactylus* began in 1826 when Fitzinger erected the genus, provided a key to the known species, and described three new species (Fitzinger, 1826). Since then and until about the middle of the 20th century, taxonomic activity on the group mainly consisted of species descriptions. The last six decades have seen a rapid rate of discovery and description of new species (including > 40% of the 75 currently known species), as well as the reevaluation of species limits and relationships and numerous nomenclatural synonymies and resurrections.

Current understanding of *Leptodactylus* systematics and diversity is derived primarily from the works of W.R. Heyer and collaborators over the last four decades; a bibliography of the genus was recently published (Heyer et al., 2009a, b). Two papers in particular have influenced the understanding of the genus taxonomy. First, Heyer (1969a) redefined the genus and described the monotypic genus *Barycholos* for *L. pulcher.* Second, Heyer (1969b) clustered *Leptodactylus* species based on their overall ecological characteristics into five species groups, the *L. fuscus, L. marmoratus, L. melanonotus, L. ocellatus* (= *L. latrans;* Lavilla et al., 2010), and *L. pentadactylus* groups.

Subsequent research, much of it by Heyer and collaborators, resulted in taxonomic contributions that documented the diversity of the genus. The 1970s witness the osteological characterization of the genus in the context of all other leptodactyloid frogs (Lynch, 1971), revision of the *L. melanonotus* group (Heyer, 1970a), the *L. pentadactylus* group (Heyer, 1972), and the *L. fuscus* group (Heyer, 1978), and recognition of the monotypic genus *Vanzolinius* to accommodate *L. discodactylus* (Heyer, 1974a), as well as the resurrection of *Adenomera* Steindachner 1867 for the *L. marmoratus* group (Heyer, 1974b). In the 1980s, Heyer and Maxson (1982) and Maxson and Heyer (1988) assessed relationships among the species groups of *Leptodactylus* sensu Heyer (1974a) using immunological distances. In the 1990s, Heyer (1994) revised the *L. podicipinus-wagneri* species complex within the *L. melanonotus* group and Heyer et al. (1996a) analyzed, but did not diagnose, the *L. mystaceus* species complex within the *L. fuscus* group.

In the 21st Century, anuran systematics and taxonomy has progressed rapidly based on both molecular and detailed morphological studies (Haas, 2003; Faivovich et al., 2005; Frost et al., 2006; Grant et al., 2006; Van der Meijen et al., 2007; Pyron and Wiens, 2011; de Sá et al., 2012). *Vanzolinius discodactylus* was returned to *Leptodactylus* (de Sá et al., 2005a; Frost et al., 2006) and Frost et al. (2006) also returned the species of *Adenomera,* along with the monotypic *Lithodytes* Fitzinger, 1843, to *Leptodactylus,* a taxonomic group we refer to as *Leptodactylus* sensu lato. Although that taxonomic arrangement has not been followed universally (e.g., Kwet et al., 2009), it also has not been rejected by phylogenetic analysis. As such, below we refer to the group composed of *Leptodactylus* sensu Heyer (1969a, b), i.e., excluding the *L. marmoratus* group and *L. lineatus* but including *Vanzolinius,* as *Leptodactylus* sensu stricto. Ponssa (2008) performed a cladistic analysis of the *L. fuscus* group and subsequently expanded the morphological matrix by adding data from Heyer et al. (1998) and new evidence from *L. nesiotus* (Ponssa et al., 2010). Heyer and de Sá (2011) revised the *L. bolivianus* species complex. Recently, Miranda et al. (2014) built on Larson and de Sá's (1998) analysis of internal larval morphology and combined it with a subset of the characters from Ponssa (2008) and Ponssa et al. (2010).

Perhaps of greatest importance, over the nearly half-century since Heyer's first contributions, the known diversity of *Leptodactylus* s.s. has grown from the 24 species listed in Heyer (1969a) to 75 species known currently, which has had a profound impact on understanding of the diversity and evolution of this clade.

Although the last 50 years have witnessed an undeniable increase in understanding of the systematics of *Leptodactylus,* information is scattered across numerous articles and is derived from analyses of limited datasets that consider only a fraction of the known diversity of the clade. As such, in this paper we analyze a large dataset composed of mitochondrial and nuclear DNA sequences and morphological and behavioral data for species of *Leptodactylus* s.s. and a large outgroup sample in order to (1) provide a species level phylogeny for *Leptodactylus* s.s., (2) evaluate the monophyly of the traditionally recognized species groups, and (3) determine the closest relatives to *Leptodactylus* s.s. To facilitate future studies of this fascinating clade of Neotropical frogs, we also provide species accounts for all known species of *Leptodactylus* s.s., assess the behavioral evolution in the clade, and evaluate the effects of a modest matrix of non-molecular characters on an analysis dominated by DNA sequence data.

MATERIALS AND METHODS

Ingroup delimitation and outgroup sampling

We defined *Leptodactylus* s.s. as the ingroup for this study and sampled outgroup terminals specifically to test the monophyly of *Leptodactylus* s.s. and the polarity of the states of the ingroup root node. To that end, we targeted taxa previously recovered as closely related to the ingroup (Frost et al., 2006; Grant et al., 2006; Lourenço et al., 2008; Pyron and Wiens, 2011). We included species of *Leptodactylus* s.l., including three (one undescribed) of the 18 species of the *L. marmoratus* group (= *Adenomera*) and *L. lineatus,* the sole member of the *L. lineatus* group (= *Lithodytes*), and representatives of all other leptodactylid genera, including two of the three species of *Hydrolaetare, Scythrophrys sawayae* (the sole representative of the genus), and three of the seven recognized species of *Paratelmatobius,* as well as three more apparently undescribed species of that genus.

The inclusion of Leptodactylidae within Athesphatanura is non-controversial; therefore we restricted our sampling to that clade and included the non-athesphatanuran taxa *Hemiphractus helioi* (Hemiphractidae) and *Craugastor rhodopis* (Terrarana, Craugastoridae) to direct the topology. In contrast, the precise sister-group of Leptodactylidae among athesphatanurans is highly controversial; consequently, we included numerous species of each of the potential sister clades. Grant et al. (2006) found leiuperids and leptodactylids to be distantly related; however, other studies found them to be closely related and treated them as members of the same family (Frost et al., 2006) or subfamily (Pyron and Wiens, 2011). Moreover, we included a large number of leiuperids in our sample of outgroup taxa, including 10 species of *Engystomops* (including two undescribed species), 9 species of *Physalaemus,* and 1 species each of *Edalorhina, Pleurodema,* and *Pseudopaludicola.* Several studies (e.g., Frost et al., 2006; Guayasamin et al., 2009) have found centrolenids and *Allophryne ruthveni* (variably treated as a centrolenid or as a separate family) to be sister to Leptodactylidae whereas others (e.g., Grant et al., 2006; Pyron and Wiens, 2011) recovered different sister-group relationships but still found them to be in the same vicinity as leptodactylids. As such, we included *Allophryne ruthveni* and seven species from across the diversity of centrolenids (including *Centrolene grandisonae, Espadarana prosoblepon, Nymphargus bejaranoi, N. garciae, Vitreorana eurygnatha,* and an unidentified specimen of *Hylalinobatrachium*). Additionally, we included a representative sample of plesiomorphic bufonids (four species), ceratophryids (seven species), cycloramphids (six species), hemiphractids (two species), hylids (two species), hylodids (three species), and one dendrobatid.

Given our objectives, taxon sampling, and evidence (molecular and non-molecular characters), our analyses were intended to test the relationships of *Leptodactylus* s.s. and were not designed to test the relationships among the outgroup taxa proposed in previous studies (e.g., Frost et al., 2006; Grant et al., 2006; Pyron and Wiens, 2011).

Molecular data and sampling

To address the relationships of *Leptodactylus* s.s., we targeted the large (16S) and small (12S) mitochondrial ribosomal subunits and the nuclear gene rhodopsin. Voucher information for molecular data are provided in Appendix 1. DNA sequences were obtained for all included outgroup taxa. Our ingroup included 62 of the 75 currently recognized species (83%) of *Leptodactylus* s.s. We included DNA sequences for all 6 of the 7 species (85%) of the *L. latrans* group (not included *L. guianensis*) 24 of the 28 species (86%) of the *L. fuscus* group (not included: *L. caatingae, L. cupreus, L. oreomantis,* and *L. spixi*), 16 of the 18 species (89%) of the *L. pentadactylus* group (not included: *L. rhodomerus* and *L. turimiquensis*), and 13 of the 16 species (81%) of the *L. melanonotus* group (not included: *L. magistris, L. pascoensis,* and *L. sabanensis*). We also included DNA sequences for *L. lithonaetes, L. riveroi, L. silvanimbus,* and *L. viridis,* which previously were not strongly associated with any species group. We were unable to include *L. lauramiriamae* (not associated with any species group), *L. hylodes* (known only from the lectotype, Heyer, 2000), and *L. ochraceus* (known only from the holotype, Caramaschi, 2008). We included multiple terminals for ingroup taxa known or suspected to be species complexes, as well as conspecifics collected at disparate localities. In total, our ingroup included 81 terminals of *Leptodactylus* s.s. The following species are considered not to belong to the genus *Leptodactylus: Hylodes hallowelli* Cope, 1862 and *Plectomantis rhodostima* Cope, 1874.

Non-molecular data and sampling

Morphological and behavioral characters were taken from Ponssa (2008) and Ponssa et al. (2010) and also include 21 additional characters (characters 8, 29, 30–31, 33, 35–36, 40, 45–49, 51, 56–60, and 69–71; Appendix 2). Unfortunately, our study was already accepted for publication prior to the publication of Miranda et al. (2014), so we were unable to include that data. Locality data and catalog numbers for specimens examined are provided in Appendix 3. These characters were included for 61 of the 62 nominal species (not included: *L. sertanejo* of the *L. fuscus* group).

Non-molecular sampling of the outgroup taxa was limited to *Leptodactylus lineatus* (= *Lithodytes*), *L. hylaedactylus* of the *L. marmoratus* group (= *Adenomera*), *Scythrophrys sawayae* (data from Verdade, 2005), *Paratelmatobius lutzi,* and *Engystomops pustulosus*.

Molecular methods

Total genomic DNA was extracted with DNeasy Tissue Kits (Qiagen, Valencia, CA) from liver or thigh muscle that was preserved in ethanol 95%. Fragments of the 12S ribosomal RNA (rRNA), 16S rRNA, and rhodopsin genes were PCR amplified (Palumbi, 1996) using an MJ Research PTC-200 thermocycler. Double-stranded PCR amplifications were executed with 25 µl of Promega Master Mix (Promega, Madison, WI), 23 µl of purified water, 0.4 µl of forward and reverse primers, and approximately 0.5–2 µl of DNA (depending on strength of DNA isolation). A segment of about 900 base pairs (bp) from the 12S rDNA gene was amplified with primers 12Sa 5'-AAACTGGGATTAGATACCCCACTAT-3', 12Sb 5'-GAGGGTGACGGGCGCTGTGT-3', 12S Tphef 5'-ATAGC(A/G)CTGAA(A/G)A(C/T)GCT(A/G)AGATG-3', and 12S RdS1 5'-GGTACCGTCAAGTCCTTTGGGTT-3' using the following thermal conditions: initial 94°C for 2 min followed by 30 cycles of 94°C for 1, 53°C for 1 min, and 72°C for 1.5 min. A segment of about 800 base pairs (bp) from the 16S rDNA gene was amplified with primers 16S L2A 5'-CCAAACGAGCCTAGTGATAGCTGGTT-3', 16S Ar 5'-CGCCTGTTTACCAAAAACAT-3', and 16S Br 5'-CTCCGGTCTGAACTCAGATCACGTAG-3' under the following thermal conditions: initial denaturation at 94°C for 2 min followed by 34 cycles of 94°C for 1.5 min, 58°C for 1 min, and 72°C for 1.5 min. A segment of about 310 bp from the rhodopsin nuclear gene was amplified with primers Rhod 1A/D (Hoegg et al., 2004) with the following conditions: 94°C for 2 min, 49°C for 1 min, and 72°C for 1 min, followed by 34 cycles of 94°C for 1 min, 49°C for 1 min, 72°C for 1 min, and one final cycle of 72°C for 6 min.

Amplified segments were purified using Exo-Sap (USB) by heating samples at 80°C for 15 min. Purified products were cycle-sequenced with the dideoxy chain termination method using the Sequi-Therm Excel II DNA sequencing kit (Epicentre Technologies). Infrared-labeled sequencing primers (same as amplification primers) were used in sequencing reactions (Li-Cor Biotechnology) under the following thermal conditions: initial denaturation at 95°C for 2.5 min, followed by 30 cycles of 95°C for 30 s, 58°C for 30 s, and 70°C for 30 s. Sequencing products were run in 6% acrylamide, 44 cm in length, gels using a Li-cor DNA 4300 automatic sequencer at the University of Richmond. Sequencing reactions were single stranded; double-stranded PCR fragments were sequenced in both directions. Complementary sequence strands for each sample were first aligned and, using the chromatographs created by BaseImagr software (Li-cor Biotechnology), were inspected visually for mismatches of aligned positions to confirm or manually correct the automatic nucleotide reading. Sequences included in the analyses represent a consensus of both DNA strands.

Locality data for specimens included in the molecular analyses as well as GenBank accession numbers for sequences generated in this study are given in Appendix 1.

Non-molecular characters and methods

Skeletal characters were scored in specimens doubled-stained for cartilage and bone with alcian blue and alizarin red following Wassersug (1976). Prior to staining, specimens were rehydrated, eviscerated, and washed in distilled water; the duration of each step varied due to the size of the specimens. Dry skeletons and digital X-rays also were analyzed. All observations were made with a Carl Zeiss Discovery V8 stereo dissection microscope. Measurements were taken with a digital caliper (Mitutoyo CD-30C and CD-15B; ± 0.01 mm), or with Image Tool software on digital images taken with a 5-megapixel digital camera. Terminology follows Trueb (1973) and Trueb et al. (2000) for cranial and postcranial characters, Maglia et al. (2007) and Pugener and Maglia (2007) for the olfactory region, and Trewavas (1933) for laryngeal morphology.

Behavioral characters were scored based on data from many studies, including Cei (1949a, b, 1980), Gallardo (1958, 1964a), Sexton (1962), Heatwole et al. (1965), Pisanó and Barbieri (1965), Heyer and Silverstone (1969), Lescure (1972, 1979), Barrio (1973), Heyer and Bellin (1973), Heyer (1974a, b; 1978), Philibosian et al. (1974), Muedeking and Heyer (1976), Heyer and Rand (1977), Toft and Duellman (1979), Downie (1984, 1989, 1990, 1994, 1996), Lescure and Letellier (1983), Aichinger (1985), Solano (1987), Martins (1988), Wells and Bard (1988), Caldwell and Lopez (1989), Gascon (1991), Rodriguez (1992), Pisanó et al. (1993), Rodríguez and Duellman (1994), Cardoso and Heyer (1995), De la Riva (1995, 1996), Lamar and Wild (1995), Vaira (1997), Prado et al. (2000), Freitas et al. (2001), Lewis et al. (2001), Ponssa (2001), Almeida and Angulo (2002), Prado et al. (2002), Prado and Haddad (2003), Readin and Jofré (2003), França et al. (2004), Giaretta and Kokubum (2004), Gibson and Buley (2004), Toledo et al (2005), da Silva et al (2005), de Carvalho (2005), Oliveira Filho et al. (2005), Kokubum and Giaretta (2005), Santos and Amorim (2005, 2006), Muniz and da Silva (2005), Prado et al. (2005), Prado and Haddad (2005), Shepard and Caldwell (2005), Tozetti and Toledo (2005), Zina and Haddad

(2005), Arzabe and Prado (2006), Fenolio et al. (2006), Giaretta and Oliveira Filho (2006), Siqueira et al. (2006), Lucas et al. (2008), Ponssa and Barrionuevo (2008), Silva and Giaretta (2008), da Silva and Giaretta (2009), Oliveira Filho and Giaretta (2009), Giaretta and Facure (2009), Kokubum et al. (2009), Schlüter et al. (2009).

Phylogenetic analyses

We performed a total evidence analysis (Kluge, 1989, 2004) of the molecular and non-molecular data under the parsimony optimality criterion, applying equal weights to all transformations. On the basis of the arguments of Padial et al. (2014), we employed tree-alignment (e.g., Sankoff, 1975; Wheeler, 1996; Varón and Wheeler, 2012, 2013) in POY 4.1.3 (Varón et al., 2010), which tests hypotheses of nucleotide homology dynamically by optimizing unaligned DNA sequences directly onto alternative topologies (Kluge and Grant, 2006; Wheeler et al., 2006; Grant and Kluge, 2009) while simultaneously optimizing prealigned transformation series as standard static matrices.

Following the rationale of Grant et al. (2006:56–57), we treated each sequenced individual as a separate terminal and duplicated the non-molecular data coded for the species as a whole for each conspecific terminal ML Comment. Although we maintain that the total evidence analysis of all available evidence identifies the optimal explanation (Kluge, 1989, 2004), we also analyzed the molecular data separately using the same parameters in order to evaluate the effect of a small morphological matrix when combined with a larger DNA sequence dataset (see below).

Analyses were run on the Museu de Zoologia da Universidade de São Paulo's high-performance computing cluster, Ace, which consists of 12 quad-socket AMD Opteron 6376 16-core 2.3-GHz CPU, 16 MB cache, 6.4 GT/s compute nodes (= 768 cores total), eight with 128 GB RAM DDR3 1600 MHz (16 × 8 GB), two with 256 GB (16 × 16 GB), and two with 512 GB (32 × 16 GB), and QDR 4x InfiniBand (32 GB/s) networking. For both the total evidence and molecular-only datasets, we performed the following analyses. First, using the standard direct optimization algorithm (Wheeler, 1996), we ran 10 6-hr searches on 644 CPUs (giving a total of 38,400 CPU-hours) using the command "search", which implements a driven search composed of random addition sequence Wagner builds, Subtree Pruning and Regrafting (SPR) and Tree Bisection and Reconnection (TBR) branch swapping (RAS + swapping; Goloboff, 1996), Parsimony Ratcheting (Nixon, 1999), and Tree Fusing (Goloboff, 1999), storing the shortest trees from each independent run and performing a final round of Tree Fusing on the pooled trees. Next, using the approximate iterative pass algorithm (Wheeler, 2003a), we read the optimal trees found in all of previous analyses and swapped the optimal tree(s) to completion. We then used the exact iterative pass algorithm to calculate the cost of the optimal tree(s) from the approximate iterative pass analysis and generate the matrix version of the tree-alignment (i.e., the implied alignment; Wheeler, 2003b). Finally, we performed 1,280 RAS + TBR of the implied alignment to verify the length reported by POY and search for additional optimal trees.

We estimated clade support (Grant and Kluge, 2008a) using the Goodman-Bremer measure (GB; Goodman et al., 1982; Bremer, 1988; Grant and Kluge, 2008b) by determining the length difference between the optimal tree and all trees visited during a TBR swap of the minimum length tree. To accelerate GB analyses, we calculated tree lengths using the implied alignment of the optimal topology. Although shorter suboptimal trees might be found by calculating the optimal tree-alignment for each visited topology, Padial et al. (2014) found that this approach overestimates GB values significantly less than when GB is calculated using a MAFFT (Katoh et al., 2005) similarity-alignment.

To evaluate the impact of the small non-molecular dataset on our results, we repeated all analyses using only the molecular dataset. We assessed differences by examining clade-by-clade differences and by calculating the pairwise rooted SPR distances between the optimal molecular-only and total evidence topologies using the method of Goloboff (2008; replicates = 50, stratification level = 20) in the program TNT (Goloboff et al., 2008). In order to meaningfully compare the GB values obtained in the two analyses, for selected clades shared by both results we calculated the ratio of explanatory power (REP) value (Grant and Kluge, 2007), which scales the observed support for a given clade relative to its maximum possible support (Grant and Kluge, 2010). We obtained the lengths of least parsimonious trees by conducting 1,152 random addition sequence + TBR searches with all characters assigned a weight of -1 and taking the absolute value of the resulting lengths. To make REP values more manageable, we multiplied them by 10,000 and report them to two significant figures.

Other methods

Institutional acronyms for specimen repositories follow Sabaj Pérez (2010), with the following exceptions. AL-MN, The Adolfo Lutz amphibian collection is maintained separately from the MNRJ herpetology collection within the Museu Nacional, Rio de Janeiro; CHINM, Dr. Avelino Barrio described a new species *Leptodactylus geminus* (currently a synonym of *L. plaumanni;* Kwet et al., 2001) with the holotype given as CHINM 5860. The holotype has since been transferred to the Museo Nacional de

Ciencias Naturales, Buenos Aires, Argentina but retains the original specimen number (J. Faivovich, pers. comm.). EHT: Edward H. Taylor (1937 "1936") described the species *Leptodactylus occidentalis* using his field tag number for the holotype, now deposited in the Field Museum of Natural History and bears the number FMNH 100015 (Marx, 1976). WCAB, Werner C.A. Bokermann amassed an extensive private amphibian collection identified by his initials (WCAB). After Bokermann's death, Paulo E. Vanzolini at the Museu de Zoologia da Universidade de São Paulo (MZUSP) purchased the Bokermann collection and replaced all of the WCAB specimen tags with MZUSP tags.

Species accounts are first arranged according to the species groups as defined in this paper based on our phylogenetic analyses and second in alphabetical order within each species group. Adult size categories (small, medium, large) follow the definitions of Heyer and Thompson (2000). Mean size of adult males and females is not reported for small sample sizes. Several of the characters used in the adult morphology and similar species sections utilize three terms that form a subjectively divided continuum of meaning: (1) distinct: that which may be clearly seen, conspicuous; (2) indistinct: not clear, difficult to distinguish, inconspicuous; (3) indiscernible: not discernible, imperceptible, undistinguishable, apparently absent.

Brief descriptions of external larval morphology are provided for each species, but do not include all available descriptions for the same species. Tadpole stages follow Gosner (1960). Oral disc terminology follows Altig (1970). Additional references on reproduction and tadpole descriptions and anatomy are provided in Heyer et al. (2009a, b). Recordings are housed at the USNM, Department of Vertebrate Zoology, Division of Amphibians and Reptiles (numbers of analyzed cuts are provided in the figure legends). Call waveforms and spectrograms (using 256 point fast Fourier transform) were generated using Raven Pro v.1.4 (Bioacoustics Research Program, 2011).

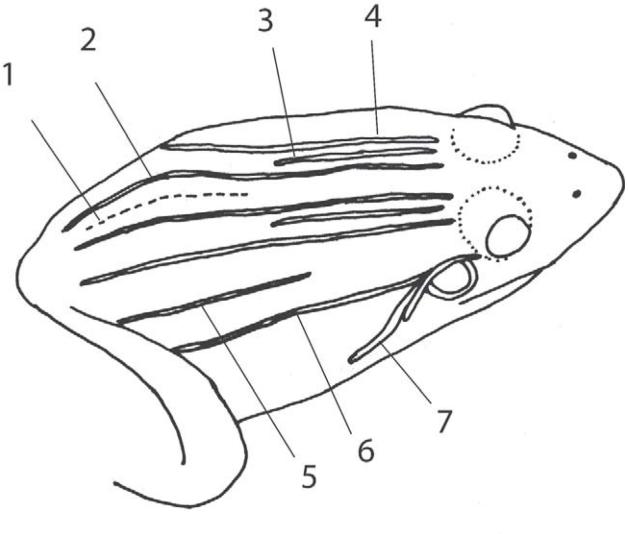


Figure 2. Diagram of skin folds found in *Leptodactylus.* (Illustration by WRH).

Dermal folds vary considerably in species of *Leptodactylus,* which is often useful in species determination. A total of seven fold (or fold-like) structures occur in the genus (Fig. 2). Three of the folds are described in the adult morphology sections of the species accounts: dorsal folds, dorsolateral folds, and lateral folds. Additional fold information is used in the 'Similar Species' sections where the fold information differentiates species. Folds may be complete (= entire), interrupted, or a combination of both complete and interrupted. The mid-dorsal fold we refer to as "dorsal fold 1" is typically a row of small spines or tubercles and is not strictly a dermal fold.

RESULTS AND DISCUSSION

Overview and outgroup relationships

Driven searches using the standard direct optimization algorithm completed 21,428 replicates of random addition sequence builds + branch swapping, 45,530 rounds of tree-fusing, and 8,334 iterations of ratcheting, resulting in a tree of 16,572 steps. Swapping using the approximate iterative pass algorithm further resulted in a tree of 16,517 steps, which was further reduced to 16501 steps using the exact iterative pass algorithm; 1,280 replicates of random addition sequence builds + branch swapping did not identify a shorter tree. The strict consensus of the 27 minimum length trees (Figs. 3A, B) collapses only two ingroup nodes, resulting in the following polytomies (Fig. 3A): (1) three of the *Leptodactylus fuscus* samples and (2) the three *L. labyrinthicus* samples. Goodman-Bremer values were calculated using the 585,173 trees visited during the TBR swap of one of the optimal trees. The least parsimonious tree (used for calculating REP values) was 35,895 steps.

We recovered a monophyletic *Hydrolaetare* Gallardo, 1963 (type species: *Limnomedusa schmidti* Cochran and Goin, 1959, by original designation) nested within *Leptodactylus* s.l. as the sister group of *Leptodactylus* s.s. (Fig. 3A). This placement agrees with the results of Fouquet et al. (2013), although those authors indicated that adequate sampling within *Leptodactylus, Adenomera,* and *Hydrolaetare* was needed to test the monophyly of these genera. Our results also agree with Jansen et al. (2011), although only if their neighbor-joining tree is re-rooted on any leiuperid instead of within *Leptodactylus.* The close relationship between *Hydrolaetare* and *Leptodactylus* is not unexpected. Lynch (1971:177) remarked on the "striking similarity between *Hydrolaetare* and *Leptodactylus* (*ocellatus* [= *latrans*] and *pentadactylus* groups)" and emphasized that the "otic plate of *Hydrolaetare* is small and like that seen in the *melanonotus, ocellatus,* and *pentadactylus*

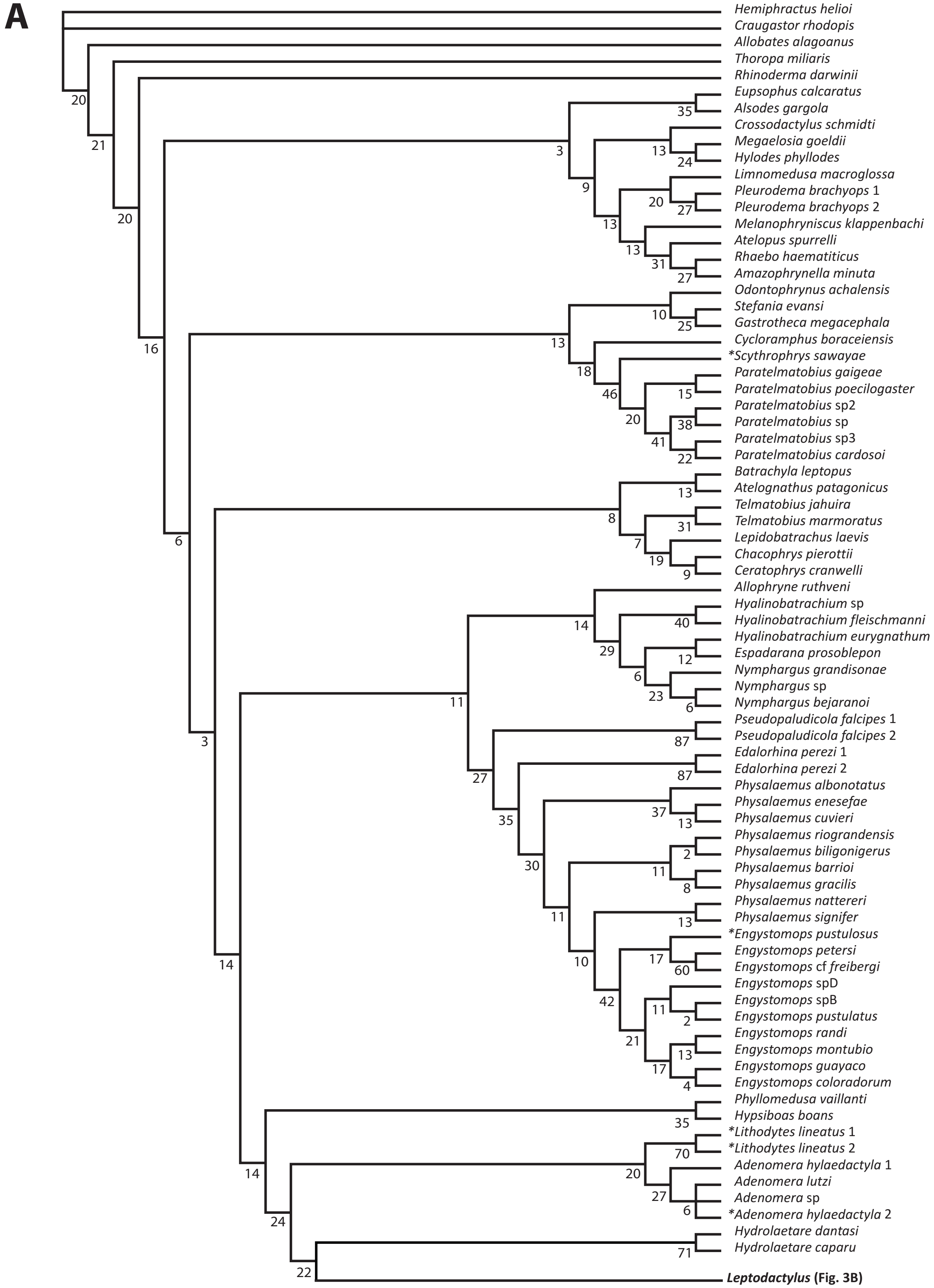
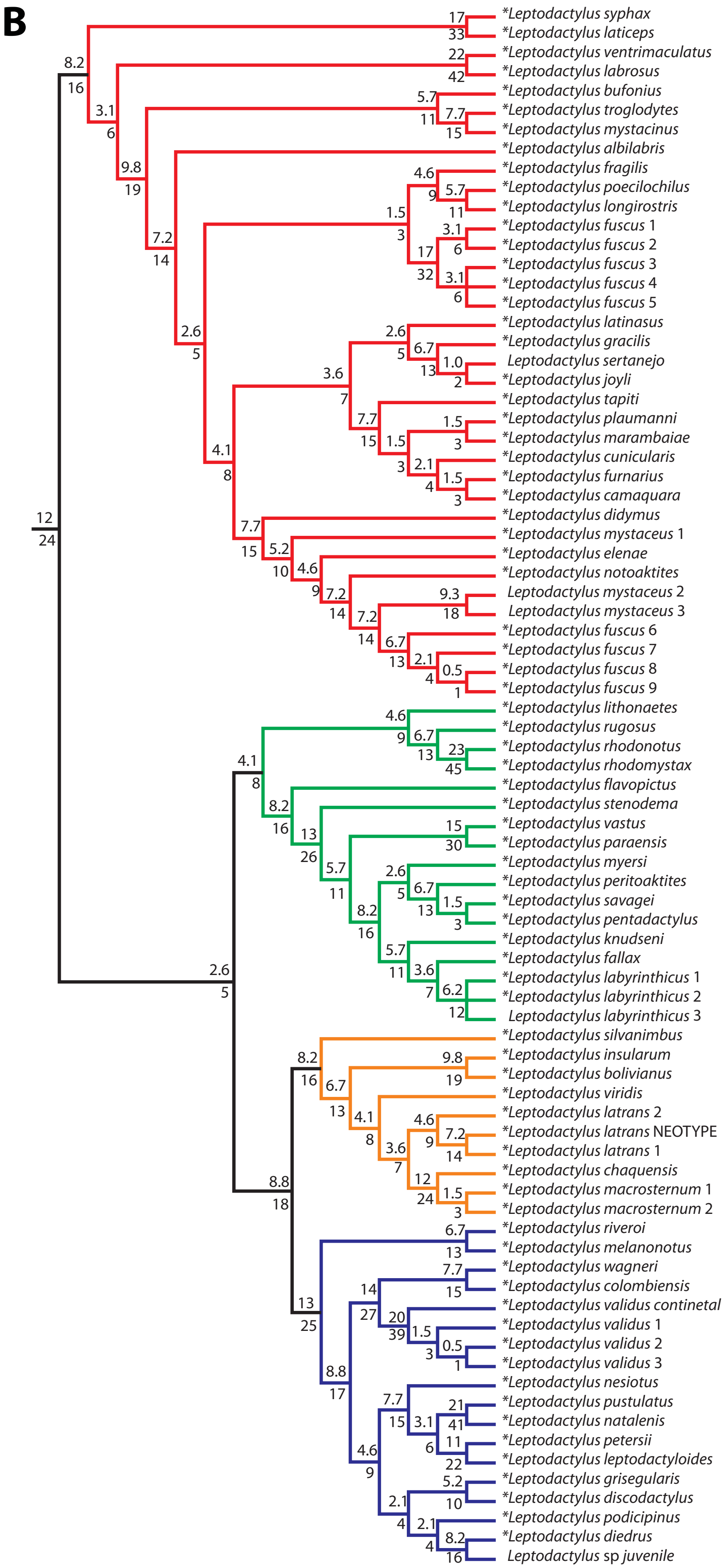


Figure 3. Strict consensus of 27 most parsimonious trees (16,501 steps) from the total evidence analysis. **(A)** Outgroup relationships. **(B)** Ingroup relationships (on following page). Values below branches are Goodman-Bremer support and above branches are REP support. Terminals coded for non-molecular characters are marked with an asterisk (*). Red = *L. fuscus* species group, green = *L. pentadactylus* species group, orange = *L. latrans* species group, blue = *L. melanonotus* species group.


B
*Leptodactylus syphax
*Leptodactylus laticeps
*Leptodactylus ventrimaculatus
*Leptodactylus labrosus
*Leptodactylus bufonius
*Leptodactylus troglodytes
*Leptodactylus mystacinus
*Leptodactylus albilabris
*Leptodactylus fragilis
*Leptodactylus poecilochilus
*Leptodactylus longirostris
*Leptodactylus fuscus 1
*Leptodactylus fuscus 2
*Leptodactylus fuscus 3
*Leptodactylus fuscus 4
*Leptodactylus fuscus 5
*Leptodactylus latinasus
*Leptodactylus gracilis
Leptodactylus sertanejo
*Leptodactylus joyli
*Leptodactylus tapiti
*Leptodactylus plaumanni
*Leptodactylus marambaiae
*Leptodactylus cunicularis
*Leptodactylus furnarius
*Leptodactylus camaquara
*Leptodactylus didymus
*Leptodactylus mystaceus 1
*Leptodactylus elenae
*Leptodactylus notoaktites
Leptodactylus mystaceus 2
Leptodactylus mystaceus 3
*Leptodactylus fuscus 6
*Leptodactylus fuscus 7
*Leptodactylus fuscus 8
*Leptodactylus fuscus 9
*Leptodactylus lithonaetes
*Leptodactylus rugosus
*Leptodactylus rhodonotus
*Leptodactylus rhodomystax
*Leptodactylus flavopictus
*Leptodactylus stenodema
*Leptodactylus vastus
*Leptodactylus paraensis
*Leptodactylus myersi
*Leptodactylus peritoaktites
*Leptodactylus savagei
*Leptodactylus pentadactylus
*Leptodactylus knudseni
*Leptodactylus fallax
*Leptodactylus labyrinthicus 1
*Leptodactylus labyrinthicus 2
Leptodactylus labyrinthicus 3
*Leptodactylus silvanimbus
*Leptodactylus insularum
*Leptodactylus bolivianus
*Leptodactylus viridis
*Leptodactylus latrans 2
*Leptodactylus latrans NEOTYPE
*Leptodactylus latrans 1
*Leptodactylus chaquensis
*Leptodactylus macrosternum 1
*Leptodactylus macrosternum 2
*Leptodactylus riveroi
*Leptodactylus melanonotus
*Leptodactylus wagneri
*Leptodactylus colombiensis
*Leptodactylus validus continetal
*Leptodactylus validus 1
*Leptodactylus validus 2
*Leptodactylus validus 3
*Leptodactylus nesiotus
*Leptodactylus pustulatus
*Leptodactylus natalenis
*Leptodactylus petersii
*Leptodactylus leptodactyloides
*Leptodactylus grisegularis
*Leptodactylus discodactylus
*Leptodactylus podicipinus
*Leptodactylus diedrus
Leptodactylus sp juvenile

groups of *Leptodactylus*." *Hydrolaetare* currently consists of three recognized species; variation on external morphology and coloration was recently reported for the species (Ferrão et al., 2014).

Given the placement of *Hydrolaetare* as the sister of *Leptodactylus* s.s., one alternative is to place *Hydrolaetare* within *Leptodactylus* as either a junior synonym of *Leptodactylus* s.s. or a subgenus within *Leptodactylus* s.l. Insofar as this would require the least perturbation to the current taxonomy, this option is attractive. Furthermore, treating *Hydrolaetare* as a junior synonym of *Leptodactylus* s.s. would be consistent with our analysis of the molecular data (see below). However, *Hydrolaetare* is a morphologically diagnosable (e.g., Lynch, 1971; Souza and Haddad, 2003) genus that has been recognized consistently since it was proposed half a century ago (Gallardo, 1963) and whose monophyly is corroborated in our results. The paraphyly of *Leptodactylus* s.l. with respect to *Hydrolaetare* in our total evidence results owes to recent taxonomic changes to the content of *Leptodactylus* and might, therefore, be better addressed by reverting to the previous content.

Frost et al. (2006) placed *Adenomera* Steindachner, 1867, as a synonym of *Lithodytes* Fitzinger, 1843, and *Lithodytes* as a subgenus of *Leptodactylus* noticing that "Heyer (1998) and Kokubum and Giaretta (2005) also presented evidence that recognizing *Adenomera* renders *Leptodactylus* paraphyletic and that *Lithodytes* is the sister taxon of *Adenomera*." However, this taxonomic action was not required given that in Frost et al.'s (2006) phylogeny none of the genera were rendered paraphyletic. Subsequent morphological analyses also suggested the paraphyly of *Leptodactylus* relative to *Adenomera* and *Lithodytes* (Ponssa 2008; Ponssa et al. 2010). However, the reciprocal monophyly of *Leptodactylus* s.s., *Adenomera* (= *L. marmoratus* group), and *Lithodytes* s.s. was supported in other molecular studies (Pyron and Wiens, 2011; Fouquet et al. 2013), leading a recent study to conclude that "proper sampling within *Leptodactylus* and *Adenomera* as well as the integration of *Hydrolaetare* is still needed to test the monophyly of these groups within Leptodactylinae (Fouquet et al., 2013:447)."

The present analysis is the first to combine both the molecular and non-molecular evidence, and it supports the monophyly of the three groups. These three genera and *Hydrolaetare* (Souza and Haddad, 2003; Fouquet et al., 2013) all produce foam nests, but *Adenomera* differs from *Leptodactylus* s.s. in having facultative endotrophic larvae that complete their development in the nest, whereas the others (except *L. fallax* and *L. pentadactylus,* see below) have free-swimming larvae that leave the nest after hatching (Altig and McDiarmid, 1999). As such, based on our results, and in order to recognize the separate evolutionary trajectory of this lineage based on life history traits we remove *Adenomera* Steindachner, 1867 (type species: *Adenomera marmorata* Steindachner, 1867, by monotypy) from the synonymy of *Lithodytes* and consider it to be a genus corresponding to the clade currently recognized as the *L. marmoratus* group.

Continued recognition of *Hydrolaetare* and resurrection of the genus *Adenomera* necessitate the recognition of *Lithodytes* at the generic level as well. Although *Lithodytes* is currently monotypic, we based our decision on: (1) the placement of *Lithodytes* as sister to *Adenomera* (Fig. 3), (2) *Lithodytes* lacks endotrophic larvae (differentiating it from its sister taxon *Adenomera,* (3) morphology, and (4) the more than 6% divergence of the mitochondrial large ribosomal subunit between samples from Mato Grosso, Brazil and Perú reported by Fouquet et al. (2007) suggests that the widespread taxon *Lithodytes lineatus* consists of at least two species. As such, we anticipate that other species will soon be described given the published evidence. We believe it better serves the needs of working biologists and documentation efforts, taxonomic understanding, and reconciling synonyms (Costello et al., 2013) to recognize *Adenomera* and *Hydrolaetare* now than to await the formal description of additional species of *Lithodytes.* Therefore, herein we remove *Lithodytes* Fitzinger, 1843 as a subgenus of *Leptodactylus* and place it at the genus rank.

Ingroup monophyly and relationships

The monophyly of *Leptodactylus* s.s. is well supported (GB = 24). Due to the lack of morphological evidence for *Hydrolaetare,* the sister group of *Leptodactylus,* no non-molecular character-states optimize to this node under accelerated transformation (Swofford and Maddison, 1992). Nevertheless, 15 phenotypic transformations occur at this node under delayed transformation (Table 1). Assuming the current topology, some of these optimizations remain unaltered when available evidence from *Hydrolaetare* is considered. For example, *Hydrolaetare* lacks nuptial excrescences on the thumb (Lynch, 1971; Souza and Haddad, 2003), so the occurrence of two spines on the thumb in adult males persists as a synapomorphy of *Leptodactylus.* In contrast, both *Leptodactylus* and *Hydrolaetare* share a prominent posterior epiotic eminence (Lynch, 1971), so this character-state originates at the shared *Hydrolaetare* + *Leptodactylus* node.

Our results disagree with recently published hypotheses of the phylogeny of *Leptodactylus.* The analyses of Ponssa (2008) and Ponssa et al. (2010) of adult osteology recovered *Leptodactylus discodactylus* outside *Leptodactylus* in a clade with *Lithodytes* and *Adenomera.* Furthermore, those studies also recovered a sister clade relationship between the *L. latrans* + *L. melanonotus* and *L. pentadactylus* + *L. fuscus* clades. Those species group relationships were previously suggested (Heyer, 1969b) and supported by a study of larval internal anatomy based on

Table 1. Non-molecular transformation events delimiting the major clades of *Leptodactylus*. All transformations are unambiguously optimized except those reported for *Leptodactylus,* which are reported under delayed transformation optimization (see text for explanation).

Clade	Character	Ancestral State	Derived State
Leptodactylus	12: Dark supratympanic stripe	0: Absent	2: Extending dorsad above tympanum and continuing posterolaterad behind the tympanum
	21: Nuptial excrescences on thumb	3: Sandpaper-like nuptial callosities	2: Two lateral keratinized spines
	43: Termination of pars facialis of maxilla	0: Anterior to palatines	1: At level of palatines
	49: Posterior termination of maxillary teeth	0: Anterior to the anterior tip of the quadratojugal	1: Reaching or surpassing the anterior tip of the quadratojugal
	52: Position of tectum nasi	1: At the same level as alary processes of premaxillae	0: Posterior to alary processes of premaxillae
	59: Posterior epiotic eminence	0: Part of the overall shape of the otic capsule, lacking a posterolateral extension beyond the otic capsule body	1: prominent, extending laterally beyond the otic capsule body
	71: Anterior expansion of nasals	0: Absent	1: Present, anterior apex forming a distinct protuberance
	76: Vomerine teeth	0: Arranged in a straight line	1: Arranged in a shallowly arched series
	78: Number of vomerine teeth	1: 2–7	2: > 8
	84: Ridge on ventral surface of palatine	0: Absent	1: Present, superficial and hardly noticeable
	87: Anterior extension of anterior ramus of pterygoid	1: Contacting palatine	0: Not reaching palatine
	94: Anteromedial process of hyoid	1: Present	0: Absent
	96: Depth of hyoglossal sinus	1: Reaching anterior borders of alary processes	2: Deep, extending 2 mm past anterior borders of the alary process
	102: Neural spine of vertebrae I–V	1: Non-imbricate	2: Imbricate
	145: Parental care	0: Absent	1: Present, care of nest
L. fuscus group	18: Toe webbing	1: Present as weak basal fringe and/or web	0: Absent
	64: Nasals	1: Adjacent or in medial contact along the middle or anterior portion	2: Adjacent or in medial contact along entire length
L. pentadactylus group + *L. latrans* group + *L. melanonotus* group	64: Nasals	1: Adjacent or in medial contact along the middle or anterior portion	0: Separated
	104: Position of base of occipital condyles relative to posterior-most points of the skull	0: Posterior	1: Anterior
	145: Parental care	1: Present, care of nest	2: Present, care of nest and larvae
L. pentadactylus group	24: Male chest spines	0: Absent	1: Present
	31: Inguinal gland	0: Absent	1: Present
	96: Depth of hyoglossal sinus	2: Deep, extending 2 mm past anterior borders of the alary processes	3: Very deep, extending > 2 mm past anterior borders of alary processes
L. latrans group + *L. melanonotus* group	18: Toe webbing	1: Present as weak basal fringe and/or web	2: Present, fringes extending along entire length of the toes except tips
	113: Relationship between suprarostral corpus and ala	1: Fused dorsally	2: Fused ventrally
	116: Planum trabeculare anticum width	0: Wide	1: Narrow
	122: Attachment of processus ascendens	1: Intermediate	0: Low
	129: Processus branchialis	0: Open	1: Closed
L. latrans group	16: Color patter of ventral surface of thighs	1: Pigmented, different patterns evident on entire surface: uniformly pigmented, labyrinthine, vermiculate, spotted	0: Immaculate or with spots on the margins
	36: Keratinized male tarsal fold	0: Absent	1: Present
	109: Shape of terminal phalanges	1: Rounded and bifurcated: dilated with a split that defines two lobules	0: Rounded or knobbed
L. melanonotus group	40: Angle between mentomeckelian and angulosplenial	1: Approximately parallel	0: Acute
	52: Position of tectum nasi	0: Posterior to alary processes of premaxillae	1: At the same level as alary processes of premaxillae
	91: Skull proportions	0: Wider than long	1: Width and length subequal or longer than wide
	121: Processus posterolateralis of crista parotica	0: Distinct	1: Reduced
	130: Hyoquadrate process	0: Small, triangular	1: Large, rounded

the analysis of 22 species of *Leptodactylus* (Larson and de Sá, 1998). A histological study of tadpole buccal foam-producing glands of *Adenomera* sp. and two species of *Leptodactylus* (*L. furnarius* and *L. labyrinthicus*) by Giaretta et al. (2011) suggested two characters that were mapped, along with seven other reproductive traits, on Ponssa et al.'s (2010)[1] phylogeny. This study lacks rigorous ingroup and outgroup sampling to place their findings in an evolutionary framework. Subsequently, Fouquet et al.'s (2013) phylogenetic analysis of foam-nest building showed that tadpole buccal foam-producing glands are homoplasic traits in *Adenomera* and the *Leptodactylus fuscus* species group. Consequently, herein we reject Giaretta et al.'s (2011) proposed use of the name *Spumoranuncula* to cluster species of *Adenomera* with the *L. fuscus* and *L. pentadactylus* species groups. Miranda et al. (2014) proposed a phylogenetic hypothesis based on larval characters of 22 *Leptodactylus* species built on previous studies (Larson and de Sá, 1998; de Sá et al., 2007a, b) and coded chondrocranial data for four species (*L. camaquara, L. spixi, L. troglodytes,* and *L. furnarius,* although the chondrocranial morphology was not reported) and internal oral anatomy of larvae. Among recognized species groups, Miranda et al. (2014) recovered only the *L. latrans* group as monophyletic. *Leptodactylus riveroi* was recovered as the sister taxon of the remainder of the genus, which results in a polyphyletic *L. melanonotus* group. Furthermore, the *L. latrans* and most of the *L. melanonotus* species groups were imbedded within the *L. fuscus* group. Finally, *L. rhodomystax,* a member of the *L. pentadactylus* species group, was sister taxa to the all other *Leptodactylus* except *L. riveroi*. The low resolution of the tree based on larval characters (Miranda et al., 2014:6, fig. 4) could be due to the low number of taxa included in the analyses and the high level of homoplasy of larval internal oral anatomy characters (reported previously by Wassersug and Heyer, 1988) as a result of anuran larval caenogensis. However, the trees resulting from the combination of larval and non-molecular adult characters (although different sampling of taxa was utilized) also exhibit poor resolution of *Leptodactylus* relationships (Miranda et al., 2014:7, fig. 5).

At the same time, our results generally support the species groups proposed by Heyer (1969b). Although those groups are not strictly monophyletic, exceptions involve only a few species that are easily accommodated without proposing new groups or significantly changing their contents (see below). The four groups form a pectinate tree, with the *Leptodactylus fuscus* group diverging first, followed by the *L. pentadactylus* group, which is sister to the *L. latrans* and *L. melanonotus* groups (Fig. 3B).

The clade formed by the *Leptodactylus pentadactylus, L. latrans,* and *L. melanonotus* groups has not been proposed previously. Support for the clade is weak (GB = 5), but the clade is diagnosed by three unambiguously optimized transformations, two from osteology and one from behavior (Table 1).

The clade formed by the *Leptodactylus latrans* and *L. melanonotus* groups is well supported (GB = 18) and was recognized previously on the basis of five synapomorphies in the larval chondrocranium (Larson and de Sá, 1998). Among those synapomorphies, a closed *processus branchialis* between ceratobranchials II and III is a synapomorphy distinguishing species of the *L. latrans* group + *L. melanonotus* clade from all other *Leptodactylus*. More recently, an analysis of osteological data to assess the relationships of *L. nesiotus* agreed with the previous study and added two more synapomorphies for this clade (Ponssa et al., 2010). In the present analysis, this clade is delimited by five unambiguously optimized transformations. Beyond the molecular evidence and morphological characters noted above that support the monophyly of the *L. latrans* + *L. melanonotus* clade, the group is unique in the elaborate complex social larval and parental care behaviors that have evolved in this clade.

***Leptodactylus fuscus* group**

We found the traditionally defined *Leptodactylus fuscus* group to be monophyletic. However, we also found two species of the traditionally defined *L. pentadactylus* group, *L. laticeps* and *L. syphax,* to be sister to the *L. fuscus* group, thereby rendering the *L. pentadactylus* group paraphyletic. Consequently, we transfer *L. laticeps* and *L. syphax* to the *L. fuscus* group, thereby rendering both the *L. fuscus* and *L. pentadactylus* groups monophyletic (see below). This expanded *L. fuscus* group is well supported (GB = 16; Fig. 3B) and is diagnosed by two unambiguously optimized non-molecular transformations (Table 1). Within the *L. fuscus* group, we recovered a clade consisting of *L. ventrimaculatus* and *L. labrosus,* which form the sister clade to all other species of the *L. fuscus* group. Next, *L. bufonius* is recovered basal in a clade that also include *L. troglodytes* and *L. mystacinus* as sister taxa; these three species are the sister clade to the remaining species in the *L. fuscus* group.

Although they did not explicitly identify any diagnostic character-states, Heyer et al. (1996a) analyzed the advertisement calls of a group of similar species they referred to as the *Leptodactylus mystaceus* species complex (*L. mystaceus, L. spixi, L. notoaktites, L. elenae,* and *L. didymus*). Caramaschi et al. (2008) described *L. cupreus* as pertaining to this complex and Cassini et al. (2013) suggested that *L. cupreus* is closely related to *L. mystacinus;* our evidence does not support the inclusion of *L. mystacinus* in the *L. mystaceus* species complex.

Species identification within the *Leptodactylus mystaceus* species complex remains problematic and

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[1] Giaretta et al. (2011) refer to Ponssa et al. (2008), but there is no such publication.

challenging. *Leptodactylus didymus* and *L. mystaceus* are morphologically indistinguishable and recognizable only by characteristics of their advertisement calls: non-pulsed in *L. didymus* and pulsed in *L. mystaceus* (Heyer et al., 1996a). Nevertheless, our evidence placed *L. didymus* as sister to the remainder of the *L. mystaceus* species complex, thereby supporting a previous study (de Sá et al., 2005b) based on fewer species that indicated that *L. didymus* and *L. mystaceus* were not sibling species (sensu Mayr, 1942). Similarly, *L. mystaceus* was not monophyletic in our analysis, with one sample recovered as sister to a clade that includes *L. notoaktites* and two other samples of *L. mystaceus,* which are the sister group of four *L. fuscus* samples. This suggests that the nominal *L. mystaceus* includes undescribed cryptic species.

Fouquet et al. (2007) recovered *Leptodactylus longirostris* embedded within *L. fuscus.* In our results, *L. longirostris* is sister to *L. poecilochilus* within a clade that also includes *L. fragilis,* and that clade forms the sister group to a clade of five additional *L. fuscus* samples. Our finding that *L. fuscus* is non-monophyletic is in overall agreement with the previous identification of three geographical lineages within *L. fuscus* (Camargo et al., 2006).

Although *Leptodactylus plaumanni* and *L. gracilis* have been considered a classical example of morphological sibling species in *Leptodactylus* recognized only by their advertisement calls (Heyer, 1978; Cardoso, 1985), our findings reveal that their phylogenetic affinities are actually quite distant. *Leptodactylus plaumanni* and *L. marambaiae* clade are the sister clade to *L. cunicularius, L. furnarius,* and *L. camaquara; L. tapiti* is the sister taxa to these two clades. In contrast, *L. gracilis* is nested within a clade with a basal *L. latinasus* and the sister species *L. sertanejo* and *L. joyli.*

Leptodactylus pentadactylus group

As noted above, we transferred two traditionally *Leptodactylus pentadactylus* group species (*L. laticeps* and *L. syphax*) to the *L. fuscus* group. Further, we found that *L. lithonaetes,* a species previously not assigned to any species group (Heyer, 1995), is recovered within the *L. pentadactylus* group and as sister to a clade that includes *L. rugosus* and the sister pair of *L. rhodonotus* and *L. rhodomystax.* This four-species clade is sister to the remainder of the *L. pentadactylus* group. Consequently, we transfer *L. lithonaetes* to the *L. pentadactylus* group, which is delimited by two externally visible character-states (presence of chest spines in males; presence of a conspicuous inguinal gland) and one from internal anatomy (very deep hyoglossal sinus) and has GB = 8 (Table 1, Fig. 3B).

Our results show that *Leptodactylus labyrinthicus* is sister to *L. fallax* within a clade that also includes *L. knudseni,* whereas *L. paraensis* and *L. vastus,* the latter recognized as distinct from *L. labyrinthicus* by Heyer (2005), are recovered as sister taxa that are not closely related to *L. labyrinthicus.* Recently, Jansen and Shulze (2012) reported that Bolivian populations identified previously as *L. labyrinthicus* (e.g., De la Riva et al., 2000) are genetically similar to *L. vastus* and *L. paraensis;* those authors tentatively assigned the Bolivian populations to *L. vastus,* reporting red coloration of the thighs and groin of Bolivian specimens. The same coloration is found in juvenile–subadult specimens of *L. vastus* from Brazil (see Plate 8E). Red coloration on the groin and posterior and anterior surfaces of the thighs is common in juvenile stages of species in the *L. pentadactylus* species group (e.g., *L. labyrinthicus,* Plates 6C–D; *L. myersi,* Plate 6E; *L. peritoaktites,* Plate 7B). The striking difference in coloration between juveniles and adults is unknown in other *Leptodactylus* species groups and, therefore, might be an additional synapomorphy for the *L. pentadactylus* group. Jansen and Shulze (2012) also noted that Heyer (2005) reported extensive intraspecific variation in morphological characters but did not provide unique diagnostic characters for species identification to differentiate the newly described species.

Our analysis recovered *Leptodactylus myersi* as sister of a clade consisting of *L. peritoaktites* and the sister species *L. pentadactylus* and *L. savagei.* Heyer (2005) recognized *L. peritoaktites* and *L. savagei* as distinct from *L. pentadactylus* based on evidence from morphology and vocalizations. In life, juveniles of *L. peritoaktites* have distinct bright red coloration on thighs and groin (RdS, pers. obs.); this coloration has not been reported for juveniles of either *L. pentadactylus* or *L. savagei.* Recently, a closer relationship between *L. savagei* and *L. pentadactylus* was suggested (Jansen and Shulze, 2012); however, in that analysis the relationships of *L. rhodomerus* were uncertain and *L. peritoaktites* and *L. myersi* were not included.

Leptodactylus latrans group

Our evidence corroborated the monophyly of the *Leptodactylus latrans* group, with *L. silvanimbus* placed as sister to all other species in the group (Fig. 3B). *Leptodactylus silvanimbus* is unique among *Leptodactylus* in that it is restricted to relatively high elevations (1,700–1,900 m) and has 24 chromosomes (Amaro-Ghilardi et al., 2006; all other known *Leptodactylus* have at most 2n = 22; 2n = 20–22 in *L. podicipinus,* Gazoni et al., 2012). This species was first placed in the *L. pentadactylus* species group (McCranie et al., 1980) and was then transferred to the *L. melanonotus* species group based on external larval morphology (McCranie et al., 1986) and call characteristics (Heyer et al., 1996b). On the basis of their analysis of morphological and limited molecular evidence, Heyer et al. (2005a) rejected the association of *L. silvanimbus* with the *L. melanonotus* group and suggested a possible basal position of the species in the genus, but they did not associate it with any of the *Leptodactylus* species groups. *Leptodactylus silvanimbus* was recovered nested within *Leptodactylus* in a polytomy with *L. melanonotus* and a clade consisting of *L. riveroi, L. discodactylus,* and *L. diedrus* by de Sá et al. (2005a). Given its phylogenetic position in our results, we transfer *L. silvanimbus* to the *L. latrans* group and interpret its unique chromosome number as autoapomorphic. This expanded *L. latrans* group is delimited by three unambiguous non-molecular transformations (Table 1) and has a GB value of 16 (Fig. 3B).

The clade formed by *Leptodactylus bolivianus* and *L. insularum* is the sister group to the remaining species in the *L. latrans* species group. Recently, a third species—*L. guianensis*—was described from this species complex (Heyer and de Sá, 2011). This species was not included in our analyses, but according to the original description it is more closely related to *L. bolivianus* (adult males with single thumb spine in both species) than to *L. insularum* (adult males with two thumb spines).

Leptodactylus viridis was first placed in the *L. melanonotus* species group by Jim and Spirandeli Cruz (1973) but was transferred to the *L. latrans* species group by Heyer and Maxson (1982). We recovered *L. viridis* imbedded in the *L. latrans* group and sister to the *L. latrans–L. macrosternum* species complex. Within this species complex, it is interesting to note that *L. chaquensis* is more closely related to *L. macrosternum* than to *L. latrans,* although *L. chaquensis* and *L. latrans* have been considered sibling species since *L. chaquensis* was described (Cei, 1950, 1962).

***Leptodactylus melanonotus* group**

Our results show that *Leptodactylus riveroi,* a species not strongly associated with any species group previously, is part of the *L. melanonotus* group. It is recovered as sister to *L. melanonotus,* which together are sister to all other *L. melanonotus* group species. This result is consistent with previous results by de Sá et al. (2005a) that reported *L. riveroi* to be sister to a clade composed of *L. diedrus* and *Vanzolinius* (= *L. discodactylus*). The relationships of *L. riveroi* have been unclear since its original description suggested that it was morphologically intermediate between the *L. latrans* and *L. melanonotus* species groups (Heyer and Pyburn, 1983). Although we find *L. riveroi* to be nested within the *L. melanonotus* group, its relatively basal position is consistent with previous suggestions by Heyer and Pyburn (1983) and Larson and de Sá (1998). The *L. melanonotus* group (including *L. riveroi*) is delimited by five unambiguous non-molecular transformations (Table 1) and has a GB value of 25 (Fig. 3B).

Leptodactylus colombiensis and *L. wagneri* are sister taxa in a clade with *L. validus.* This clade is sister to all remaining taxa in the *melanonotus* species clade. Our results corroborate previous findings that *L. discodactylus* is nested within *Leptodactylus* (de Sá et al. 2005a; Frost et al. 2006) and, therefore, that its recognition as the monotypic genus *Vanzolinius* would render *Leptodactylus* paraphyletic. Our data decisively place this species within the *L. melanonotus* group, as originally suggested by Heyer (1970a), although he hypothesized *L. discodactylus* to be sister to all other species of the group. Instead, we found *L. discodactylus* to be sister to *L. griseigularis* (GB = 10) and that clade to be sister to *L. podicipinus* + *L. diedrus*. The remaining species of the *L. melanonotus* group form a clade consisting of *L. nesiotus* as sister to two pairs of species, *L. leptodactyloides* + *L. petersii* and *L. natalensis* + *L. pustulatus.*

The relevance of non-molecular evidence

By the end of the 20th century, modern systematics, aided by technological advancements such as Sanger sequencing and PCR technology (Sanger et al. 1977; Mullis, 1990), had become dominated by DNA sequence data. Undoubtedly, this owes largely to the ease and decreasing cost with which large data sets could be assembled—a situation that promises to improve even more with next generation of sequencing methods. In contrast, scoring morphological characters requires time-consuming study to obtain specialized knowledge that ultimately returns only a fraction of the amount of evidence provided by molecular data. In light of this situation, the question faced by practically minded professional scientists, graduate students in training, undergraduates, and funding agencies alike is whether or not it is worthwhile to dedicate the months or even years necessary to obtain a comparatively small number of morphological characters instead of sequencing more loci. That is, in terms of biological knowledge, understanding the evolution of the phenotype is at least as intrinsically important as understanding the evolution of the genotype (Love, 2003; Wake et al., 2011), and epistemologically the increased explanatory power that results from including additional evidence validates total evidence analysis (Grant and Kluge, 2003; Kluge, 2004). However, in practical terms, do non-molecular characters matter?

To evaluate the effect of the non-molecular evidence on our results, we repeated the analyses using only the molecular evidence. Assuming that truly optimal trees were obtained in both heuristic searches, any differences between the results of the two analyses must be due to the morphological evidence. Given our taxon and character sampling, we focus these comparisons on the relationships within *Leptodactylus.*

Analysis of the molecular-only dataset resulted in 12 most parsimonious trees of 15,472 steps (Fig. 4). Goodman-Bremer values were calculated using the 573,183 trees visited during the TBR swap of one of the optimal

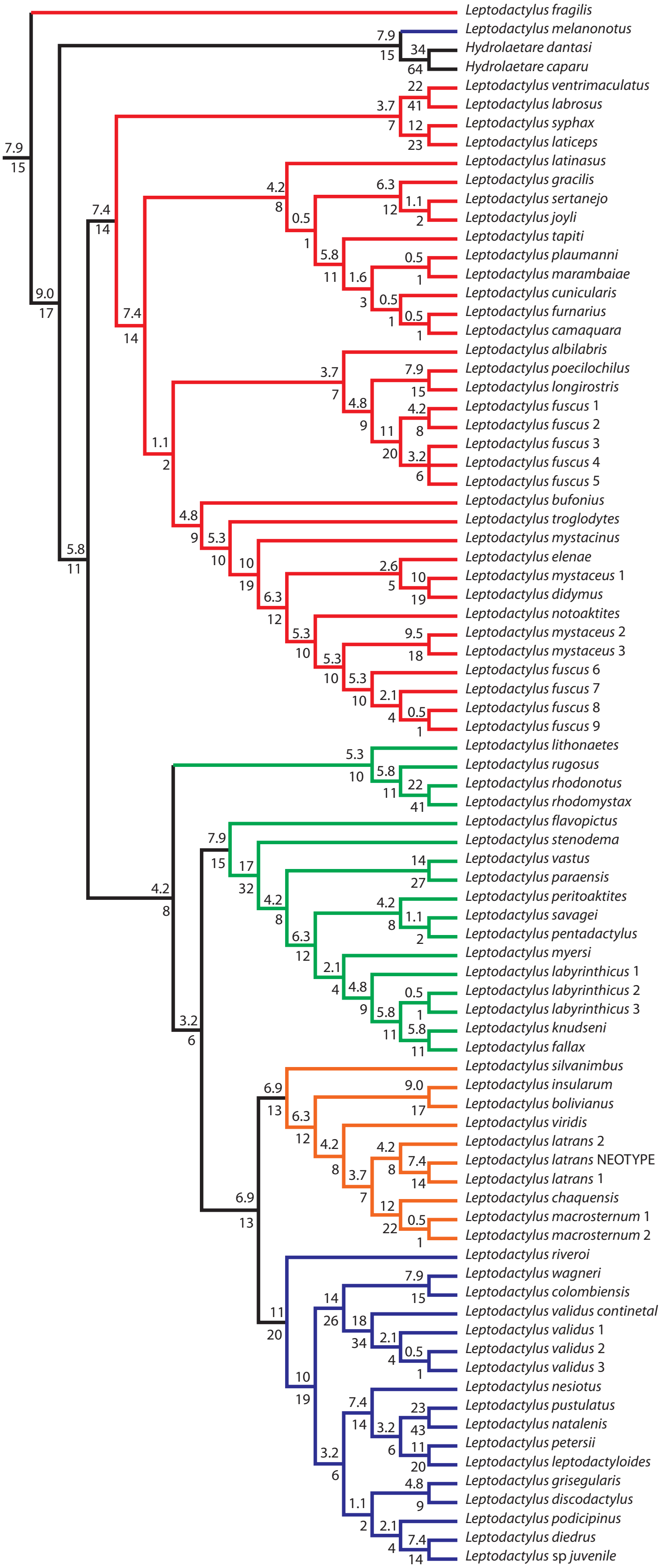

Figure 4. Strict consensus of 12 most parsimonious trees (15,472 steps) from the molecular-only analysis. Values below branches are Goodman-Bremer support and above branches are REP support. Terminals coded for non-molecular characters are marked with an asterisk (*). Red = *L. fuscus* species group, green = *L. pentadactylus* species group, orange = *L. latrans* species group, blue = *L. melanonotus* species group.

trees. The least parsimonious tree was 34,404 steps. Within *Leptodactylus,* relationships in the two analyses are largely congruent, and the pairwise rooted SPR distances between the most parsimonious trees with and without morphology are only 23–25 SPR moves (for comparison, the distances between equally parsimonious trees from the same dataset are only 1–3 SPR moves). Extensive congruence between the topologies is not surprising given that the total evidence dataset is dominated by molecular evidence.

Nevertheless, comparison of REP values within *Leptodactylus* from the two analyses (Figs. 3B, 4) demonstrates that support for most clades increased with the inclusion of morphological evidence (mean REP for total evidence dataset = 6.7; mean REP for molecular-only dataset = 6.3; *Hydrolaetare* not included, see below). For example, REP support for *Leptodactylus* (including *Hydrolaetare*) was 7.9 in the molecular-only analysis and increased to 12 in the total evidence analysis. Among the 54 clades that are shared between the two strict consensus topologies, REP increased for 30 clades (56%), remained the same for eight clades (15%), and decreased for 16 clades (30%). For example, REP support for the *L. latrans* group, which was monophyletic in both analyses, increased from 6.9 in the molecular-only analysis to 8.2 with the inclusion of morphological evidence. Within the *L. fuscus* group, the *L. ventrimaculatus* + *L. labrosus* clade is one of the most strongly supported relationships in both analyses; however, although GB support increased from 41 in the molecular-only analysis to 42 in the total evidence analysis, REP was 22 in both analyses, indicating that the increase in support merely kept pace with the overall increase in evidence in the total evidence analysis (Grant and Kluge, 2009). Also within the *L. fuscus* group, the monophyly of *L. poecilochilus* and *L. longirostris* was supported in both analyses, but REP decreased from 7.9 in the molecular-only analysis to 5.7 in the total evidence analysis.

The only species group that is monophyletic without non-molecular evidence is the *Leptodactylus latrans* group, and the topology of the group is also identical in the two analyses. The monophyly of the *L. fuscus* group is violated by the placement of *L. fragilis* as the sister of all other species of *Leptodactylus*. Within the *L. fuscus* group, *L. bufonius, L. troglodytes,* and *L. mystacinus* form a clade near the root of the group in the total evidence results, but they form a grade that is deeply nested within the *L. fuscus* group in the molecular-only analysis. In contrast, *L. didymus, L. mystaceus,* and *L. elenae* form a grade in the total evidence analysis but are monophyletic in the molecular-only analysis.

The *Leptodactylus pentadactylus* group is paraphyletic in the molecular-only analysis, with most of the group being more closely related to most of the *L. melanonotus* group than to *L. lithonaetes, L. rugosus, L. rhodonotus,* and *L. rhodomystax*. *Leptodactylus myersi* is sister to *L. labyrinthicus, Leptodactylus knudseni,* and *L. fallax* in the molecular-only analysis, but is sister to *L. peritoaktites, L. savagei,* and *L. pentadactylus* in the total evidence analysis. Similarly, *L. knudseni* and *L. fallax* are sister species in the molecular-only results, whereas in the total evidence results *L. knudseni* is sister to *L. fallax* and *L. labyrinthicus*.

Most of the relationships within the *Leptodactylus melanonotus* group are identical in the two analyses. However, in the molecular-only results *L. melanonotus* is placed near the base of *Leptodactylus* as the sister of *Hydrolaetare,* which is sister to *Leptodactylus* in the total evidence results but is placed within *Leptodactylus* in the molecular-only results. The different placement of *Hydrolaetare* in the two analyses was unexpected because neither species of that clade was scored for any non-molecular characters. However, although this result might seem counter-intuitive, it is easily explained and reveals a previously under-appreciated effect of adding even a comparatively small amount of morphology (or any other class of evidence) to a subset of the terminals in a dataset: the inclusion of morphology for a subset of terminals alters the optimal position of those terminals and, in doing so, also alters the respective molecular character optimizations, which alters the optimal placement of terminals for which morphology was not added. In the present case, the morphological characters made it more parsimonious for *L. melanonotus* to be placed with other species of the *L. melanonotus* group, *L. fragilis* to be placed with other species of the *L. fuscus* group, and the two clades of the *L. pentadactylus* group to be placed as sisters, all of which changed the molecular optimizations such that *Hydrolaetare* is optimally placed outside *Leptodactylus*.

In conclusion, even though non-molecular evidence comprises only 3.5% of the total evidence matrix (4,263 aligned nucleotides, 156 morphological characters), our results showed unequivocally that non-molecular evidence had a strong impact on our results. The distance between optimal topologies from the two analyses was 23–25 rooted SPR moves. Among the 54 *Leptodactylus* clades that are shared by the two analyses, support differed in 85% when non-molecular evidence was included, increasing in 56% and decreasing in 30%. More importantly, although monophyly of all four of the traditionally recognized species groups required only minor rearrangements of a few species in the total evidence analysis, only one species group was monophyletic in the molecular-only analysis, with no way of rearranging species to resemble the other groups. Finally, analysis of only DNA sequences without non-molecular data resulted in the inclusion of *Hydrolaetare* within *Leptodactylus,* whereas analysis of the combined molecular and non-molecular dataset placed *Hydrolaetare* outside *Leptodactylus,* even though no morphological evidence was coded for *Hydrolaetare*. Clearly, non-molecular evidence mattered in the present study.

Evolution of *Leptodactylus* traits

In addition to elucidating the pattern of phylogenetic diversification of *Leptodactylus,* our results have implications for the evolution of several aspects of their natural history. Below we discuss the invasion of rocky outcrops, construction of foam nests, parental care, and larval oophagy.

Invasion of rocky outcrops

Species of *Leptodactylus* inhabit a variety of habitats, but only three species of the *L. pentadactylus* species group (viz., *L. lithonaetes, L. rugosus,* and *L. myersi*) and one of the *L. fuscus* species group (viz., *L. syphax*) inhabit and are restricted to rocky outcrops. Based on our phylogeny, speciation related to the invasion and apparent adaptation to this unique habitat occurred three or four times in the evolutionary history of *Leptodactylus,* depending on whether the ancestor of the *L. lithonaetes, L. rugosus, L. rhodonotus,* and *L. rhodomystax* clade in the *L. pentadactylus* group inhabited rocky outcrops or not (both possibilities are equally parsimonious; Fig. 5). The geographic distribution of these rocky outcrop species was modeled and areas that need to be surveyed for the likelihood of occurrence of these, or of yet undescribed, species were identified by Fernández et al. (2009).

Foam nest construction

Construction of foam nests is widespread in Leptodactylidae and some other anuran clades (Faivovich et al., 2012; Fouquet et al., 2013) and enhances the survival of larvae by providing protection against desiccation and at least some predators (Vaz Ferreira and Gehrau, 1975; Downie, 1996). In *Leptodactylus,* the foam nests result from the amplectic pair—but mostly the male—beating with their hind limbs the oviductal secretions released during oviposition (Gallardo 1958, 1964a). A recent study suggested that foam nest construction in Leptodactylidae either evolved once and was subsequently lost in the genus *Pseudopaludicola* or evolved independently in Leptodactylinae and Leiuperinae (Fouquet et al., 2013). Our results confirm that foam nest construction is plesiomorphic in *Leptodactylus.*

Heyer (1969b) surmised that the genus exhibited a tendency to terrestriality with the *Leptodactylus latrans* group + *L. melanonotus* group clade having the most primitive reproductive modes of depositing a foam nest on the surface of water and having exotrophic larvae. The implicit idea of a ‘progression’ towards terrestriality was subsequently embraced by other authors (e.g., Duellman, 1985; Prado et al., 2002). However, our results suggest a more complex evolutionary history of these traits.

In *Leptodactylus* the placement of foam nests in underground chambers is restricted to the *L. fuscus* group and *L. fallax* and *L. vastus* (in the latter species suggested, but unconfirmed; see below) of the *L. pentadactylus* group, with other species characterized by aquatic foam nests. Based on our optimal topology, the occurrence of terrestrial foam nests is unambiguously and independently derived in *L. fallax* and *L. vastus* (if confirmed), because the remainder of the *L. pentadactylus* group possesses aquatic foam nests. However, due to the distribution of aquatic and terrestrial foam nests in close relatives—terrestrial in *Adenomera* (Haddad and Prado, 2005) and probably also in *Lithodytes* (Lamar and Wild, 1995), potentially aquatic or terrestrial in *Hydrolaetare* (Souza and Haddad, 2003)—the ancestral state for *Leptodactylus* is ambiguous. If foam nests in *Hydrolaetare* are found to be terrestrial, then the terrestrial foam nests of the *L. fuscus* group are plesiomorphic and the aquatic foam nests of the *L. pentadactylus, L. latrans,* and *L. melanonotus* groups are a synapomorphic; alternatively, if *Hydrolaetare* has aquatic foam nests, then the ancestral state for *Leptodactylus* will remain ambiguous.

Previous studies have also concluded that the evolution of foam nests is more complex than the preconceived notions of linear, progressive, evolutionary trends (Faivovich et al., 2012; Fouquet et al., 2013), and quantitative studies of other previously assumed progressive scenarios have arrived at similar conclusions. For example, the aquatic, nocturnal species *Aromobates nocturnus* is not the plesiomorphic sister species of all other dendrobatids (Myers et al., 1991) but is instead deeply nested within an otherwise terrestrial, diurnal clade (Grant et al., 2006). Perhaps more dramatically, in both plethodontid salamanders (Chippindale et al., 2004; Chippindale and Wiens, 2005) and *Gastrotheca* (Wassersug and Duellman, 1984; Wiens et al., 2007) some biphasic species appear to have evolved from direct-developing ancestors that, in turn, evolved from biphasic ancestors.

Although the larvae of *Leptodactylus laticeps* (*L. fuscus* group) and *L. myersi* (*L. pentadactylus* group) remain unknown, it would not be surprising for these larvae to develop partially or completely underground; *L. bufonius* (Schalk, 2012) and *L. laticeps* (Cei, 1980) were reported to inhabit the underground caves of *Lagostomus maximus* (Rodentia, Chinchillidae). Based on the phylogeny and considering that *L. myersi* is restricted to rocky outcrops, it is possible that *L. myersi* larvae are oophagous and develop in underground burrows.

Placement of foam nests varies within other clades from being placed on the surface of water bodies to being located in basins, either natural or excavated by the male, at variable distances from the edges of ponds. Furthermore, the larvae of *L. pentadactylus* (and likely associated species *L. savagei,* and *L. peritoaktites*) may or may not complete development in the foam nest as a mechanism to cope with unfavorable environmental conditions (see below). It does not seem that the *L. latrans* group +

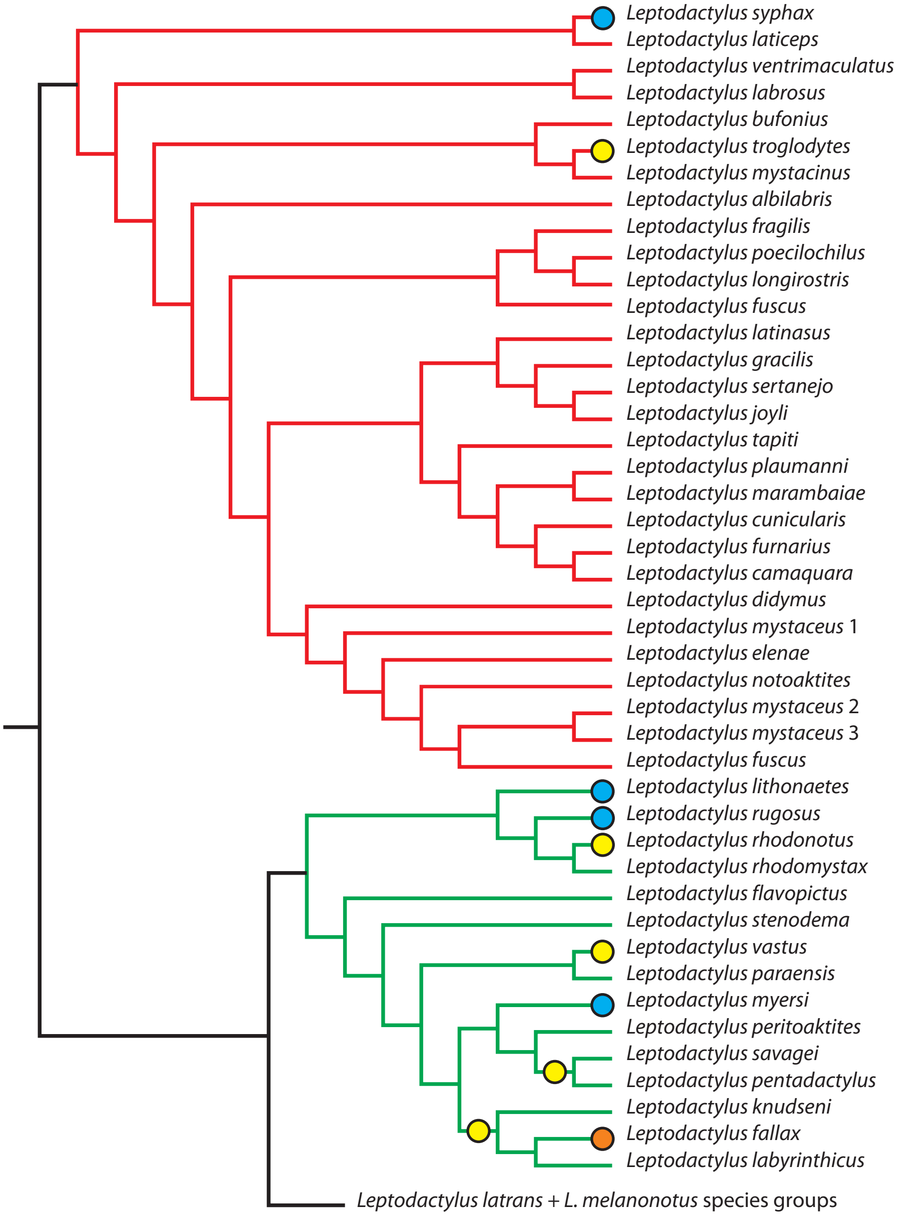

Figure 5. Distribution of some natural history traits reported in *Leptodactylus*. Optimizations are ambiguous due to extensive missing data; states marked on internal nodes are unambiguously present in the respective hypothetical ancestors (although the state might have originated earlier) and are known to occur in all descendant terminals. See text for details. Blue dot = occupation of rocky outcrops; yellow dot = facultative oophagous larvae; orange dot = obligate oophagous larvae.

L. melanonotus group clade has a primitive reproductive mode but one that is characterized by highly specialized and elaborate parental care. The complex behaviors found in the *L. latrans* + *L. melanonotus* clade extend beyond construction of a foam nests and involve elaborate behaviors and interactions between adults and larvae.

Parental care

Eggs attended by at least one of the parents have numerous benefits (reviewed by Crump, 1995). The earliest reports available are for *Leptodactylus latrans* (Fernández and Fernández, 1921; Gallardo, 1964b, 1970), which is also the species that has been most studied. Vaz-Ferreira and Gehrau (1974, 1975) provided the most complete description of the complex behavior in *L. latrans*. These authors documented that: (1) the foam nest is shaped like a 'crown' or 'ring' of foam with a central hole where the female sits; (2) females can leave and re-enter the foam nest through underwater tunnels without disturbing the nests; (3) mostly females, but also males in recently built nests, actively protect the nest against predators with aggressive behaviors that include jumping, biting, and emitting a unique defensive call; (4) after hatching tadpoles form a school that moves together as a relatively compact mass until metamorphosis; (5) females attend and actively protect the tadpoles; (6) tadpoles use their mouths to scrape the dorsal surfaces of the female; (7) frequently the females 'push' the mass of tadpoles toward the edge of the ponds; (8) females rapidly raise the sacral region, producing waves over the water surface; and (9) emission of sounds is correlated with water surface waves produced by the tadpoles and the attending female.

At least part of the complex behavior reported for *Leptodactylus latrans* has been reported subsequently for other species in the *L. latrans* group + *L. melanonotus* group clade. Foam nests with adults (female or male) sitting in its center and attending the eggs were reported in *L. chaquensis* (Prado et al., 2000). A recent analysis of the *L. bolivianus* species complex recognized *L. guianensis* (Heyer and de Sá, 2011). Although not yet reported in the literature, based on our phylogeny is it likely that *L. guianensis, L. macrosternum,* and *L. viridis* also have ring shaped nests and adults with similar behavioral patterns. Larval schooling and parental attendance of eggs and larvae have been reported in all species in the *L. latrans* species group (*L. latrans,* Vaz-Ferreira and Gehrau, 1974; *L. insularum,* Wells and Bard, 1988; *L. macrosternum,* Caldwell, 1992; *L. bolivianus,* Vaira, 1997; *L. chaquensis,* Prado et al., 2000; Martins, 2001; Ponssa, 2001), except the recently described *L. guianensis, L. viridis* (larvae unknown in both species), and *L. silvanimbus*. Herein, we add *L. silvanimbus* to the species with larval schooling. During fieldwork in Honduras, one of us (RdS) observed a school of tadpoles of this species moving through the water column as a ball and rolling on top of each other while an adult remained in close proximity; larvae from this school were used in the larval description of the species (Heyer et al., 2002). Larval schooling has also been reported for *L. riveroi* and *L. validus* (Downie, 1996), *L. leptodactyloides* (Downie, 1996; Rodrigues et al., 2011), *L. podicipinus* (Prado et al., 2000; Martins, 2001), *L. melanonotus* (Hoffman, 2006), *L. natalensis* (Santos and Amorim, 2006), and *L. pustulatus* (de Sá et al., 2007a). Based on our phylogeny and documented reports of larval schooling, this larval behavioral trait is likely an ancestral condition for the entire *L. latrans* + *L. melanonotus* clade; however, additional field observations are still needed for the majority of species in the *melanonotus* species group.

The earlier evolution of egg attendance coupled with post-hatching larval schooling would have facilitated the evolution of more advanced behaviors such as attendance and active defense of larvae. Parental care in the form of attendance of eggs and larvae were reported for *L. validus* (Downie, 1996), *L. podicipinus* (Prado et al., 2000, 2002; Martins, 2001), *L. leptodactyloides* (Downie, 1996 reported as "R. Cocroft and V. Morales, pers. comm."), *L. natalensis* (Santos and Amorim, 2006), and *L. pustulatus* (de Sá et al., 2007a). Only attendance of larvae was reported in *L. chaquensis* (Prado et al., 2000); however, this species also attends eggs and larvae (C. Prado and R. de Sá, pers. obs.). Parental care in these species ranges from tadpoles congregating closely around and/or on top of the attending female (e.g., if the water close to the larval school is disturbed) to active defense of the larvae by adults.

The most complex parental care reported includes attendance and active defense of eggs and larvae in *Leptodactylus latrans* (Fernández and Fernández, 1921; Gallardo, 1964b; Vaz-Ferreira and Gehrau, 1974, 1975, 1986) and *L. insularum* (Wells and Bard, 1988; Vaira, 1997; Ponssa, 2001). Furthermore, several studies have reported the female communicating with the larval school. The first report was on *L. latrans* females where two behaviors were observed: (1) jumping and pushing of the larval school ["… empellón dado por la rana al grupo muy compacto de renacuajos que los desplazo hacia la costa…; Vaz-Ferreira and Gehrau, 1975:8] and (2) female pelvic region maneuvers and tadpole schools following the female ["… oscilación vertical de la zona sacroutistilar y base de los miembros posteriores… este movimiento provoca pequeñas ondulaciones de la superficie del agua… realiza dicho acto y es seguida de inmediato por los renacuajos…; Vaz-Ferreira and Gehrau, 1975:8]. The latter was subsequently described as "pumping" display in *L. insularum* (Wells and Bard, 1988) and as a means for the females to "… communicate with their tadpoles by means of a 'pumping' display in which the rear part of the body was moved up and down in the water, creating a series of concentric waves that moved toward the tadpoles" (Wells, 2007).

Reports of pumping maneuvers are available for other *Leptodactylus* species and sometimes this behavior is associated with observations of the female leading the tadpoles from shallow to deeper areas of the ponds, in some cases pushing or actively digging channels through vegetation and soil (*L. insularum:* Wells and Bard, 1988, Vaira, 1997; *L. validus:* Downie, 1996; *L. podicipinus:* Prado et al., 2000, Martins, 2001, Prado et al., 2002, Rodrigues et al., 2011; *L. melanonotus:* Hoffman, 2006; *L. natalensis:* Santos and Amorim, 2006; *L. pustulatus:* de Sá et al., 2007a; *L. latrans:* Rodrigues et al., 2011, *L. leptodactyloides:* Rodrigues et al., 2011). This guiding or pushing of the larval school in *Leptodactylus* (as well as other anurans) towards deeper areas and specific microhabits within the ponds increases tadpole survival by avoiding desiccation or predation (particularly aquatic predators, as shown by Rodrigues et al., 2011) and/or tapping into available food resources or optimizing developmental temperatures (Kok et al., 1989; Kaminsky et al., 1999; Cook et al., 2001; de Sá et al., 2007a; Rodriguez et al., 2011).

The earliest report on the aggressive behavior of *Leptodactylus* females protecting foam nests and larval schools from approaching predators showed the female attacking, jumping, biting, and emitting a unique call in

L. latrans (Vaz-Ferreira and Gehrau, 1975). These authors observed females attacking approaching predators (birds) and reported that presentation of dead predators and gentle introduction and movement of the observer hand toward the foam nest triggered the same defensive behaviors. Aggressive behaviors toward potential predators were also reported in *L. podicipinus* (Prado et al., 2002); however, another study did not observe aggressive behavior in that species (Rodrigues et al., 2011). The emission of calls during the defensive behavior in *L. latrans* is likely the same as the 'hissing' reported in *L. insularum* that may function to frighten predators (Ponssa, 2001).

Furthermore, the extended parental attendance of eggs and larvae is more elaborate and complex in the *Leptodactylus latrans* group + *L. melanonotus* group clade than in the other species groups. Additional field observations are needed to understand the evolution of these traits; however, we anticipate that some, if not all, will be shown to be ancestral for the entire *L. latrans* group + *L. melanonotus* group clade. The distribution of parental care reported behaviors is summarized in Fig. 6.

Larval oophagy

Among species of *Leptodactylus, L. fallax* is unique in having tadpoles that lack a free-swimming larval stage and obligatorily complete their development within the foam nest deposited in underground chambers constructed by the male at some distance from water sources (Brooks, 1968; Lescure, 1979; Lescure and Letellier, 1983). The eggs are small and clutch size consists of no more than 45 eggs; hatching occur 6–10 days after oviposition, and metamorphosis occurs in about 60 days. Both males and females actively defend the nest and, about every 3–4 days after hatching, the female lays additional unfertilized eggs that serve as the source of nutrients for the developing tadpoles (Davis et al., 2000; Gibson and Buley, 2004). Tadpoles of *L. fallax* become more active and move toward the approaching female when she visits the nest to lay unfertilized eggs (Gibson and Buley, 2004).

Recently, a second case of completion of metamorphosis within the nest was suggested (but not observed) for *Leptodactylus vastus* (Schulze and Jansen, 2012).

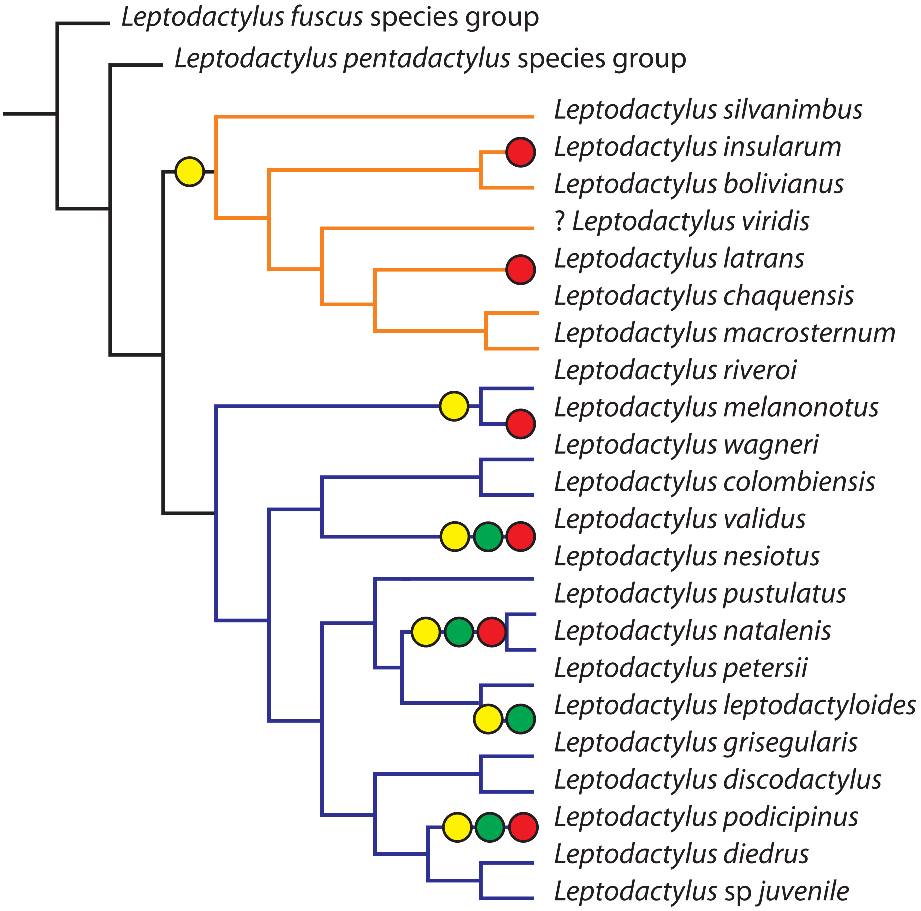

Figure 6. Distribution of some reproductive traits reported in *Leptodactylus*. Optimizations are ambiguous due to extensive missing data; states marked on internal nodes are unambiguously present in the respective hypothetical ancestors (although the state might have originated earlier) and are known to occur in all descendant terminals (reproductive biology and larvae of *L. viridis* have not been documented; = ?). Yellow dot = larval schooling; green dot = larval attendance; red dot = complex parental care. Complex parental care extends beyond attendance and includes such behaviors as active defense against predators, communication with larvae, and guiding larvae through the pond; see text for description.

These authors suggested two reproductive modes for the species: (1) semi-aquatic oviposition (foam nest in burrows or underground chambers, free-swimming larval stage present) and (2) terrestrial oviposition (foam nest underground without unfertilized eggs, free-swimming larval stage absent). Additional observations and studies are needed to fully understand the reproductive biology of *L. vastus*.

In *Leptodactylus labyrinthicus,* from the Cerrado of Brazil, a substantial proportion of the eggs deposited in a foam nest apparently are not fertilized and serve as food for developing tadpoles (da Silva et al., 2005). However, there is no evidence that females return to the nest to provision the tadpoles (Shepard and Caldwell, 2005). Considering, (1) the report of *L. vastus* as possessing terrestrial oviposition and absence of both unfertilized eggs and free swimming stage (at least in some populations) and (2) that endotrophic larvae have not been described for any *Leptodactylus* species, then we should add this species as exhibiting larval oophagy.

Larval oophagy has been reported in *Leptodactylus fallax, L. knudseni, L. labyrinthicus, L. pentadactylus, L. savagei, L. troglodytes,* and *L. vastus.* Opportunistic oophagy on heterospecific eggs was reported in free-swimming tadpoles of *L. syphax* and *L. labyrinthicus* (da Silva and Giaretta, 2009), *L. troglodytes* (Silva and Juncá, 2006), *L. vastus* (Schulze and Jansen, 2012), whereas larvae of *L. rhodomystax* were reported to feed on both intra- and interspecific eggs. It is likely that opportunistic oophagy might also occur in other species of *Leptodactylus.* Conspecific obligate oophagy evolved once in the *L. pentadactylus* group. The larvae of *L. fallax* are obligatorily oophagous and females lay between 10,000–25,000 unfertilized eggs, over a two-month period, to sustain the development of a single clutch of tadpoles (Davis et al., 2000; Gibson and Buley, 2004; Martin et al., 2007). The larvae of other *Leptodactylus* species exhibit facultative oophagy. Species with facultative larval oophagy lay their foam nest in burrows or cavities close to or at variable distances from the edges of water bodies; part of the larval development occurs within the nests but it is completed as free-swimming exotrophic larvae (*L. savagei,* Muedeking and Heyer, 1976; *L. pentadactylus,* Hero and Galatti, 1990; *L. knudseni,* Hero and Galatti, 1990; *L. labyrinthicus,* Agostinho, 1994; Rodriguez and Duellman, 1994).

Larval oophagy in nests was reported for *Leptodactylus savagei* (Muedeking and Heyer, 1976), *L. labyrinthicus,* (Agostinho, 1994; da Silva et al., 2005) and *L. pentadactylus* (Heyer et al., 2011). It is likely that in all of these species the larvae feed on unfertilized eggs deposited along with the fertilized eggs, as reported for *L. labyrinthicus* (da Silva et al., 2005), as supplementary nutrition during their development. There are no reports of the female depositing unfertilized eggs after initial oviposition in any of these species. Additionally, the free-swimming larvae of these species are known to be carnivorous and cannibalistic (Muedeking and Heyer, 1976; Hero and Galatti, 1990; Cardoso and Sazima, 1997; Eterovick and Sazima, 2000; Heyer et al., 2011); based on our phylogeny, we agree with the previous suggestion that larval oophagy may have facilitated the evolution of larval carnivory in this clade (Prado et al., 2005).

The obligate oophagous tadpole is a uniquely derived condition in *Leptodactylus fallax.* The larvae of *L. myersi* and *L. peritoaktites* remain unknown. Recently *L. peritoaktites* was recognized as a separate species from *L. pentadactylus* and *L. paraensis* from *L. labyrinthicus* (Heyer, 2005). We anticipate that this entire subclade of species will have facultative larval oophagy and carnivory (although *L. myersi,* due to its association with rocky outcrops, might have terrestrial development and obligate oophagy). Whereas the construction of underground reproductive chambers characterizes the *L. fuscus* species group, larval oophagy and the invasion of rocky outcrops are traits that overall are more common in the *L. pentadactylus* species group. Distribution of reported oophagy in *Leptodactylus* is summarized in Figure 5.

ACCOUNTS FOR SPECIES OF THE GENUS *LEPTODACTYLUS* FITZINGER, 1826

Leptodactylus Fitzinger, 1826:38. Type species: *Rana typhonia* Latreille *in* Sonnini and Latreille an X, 1801–1802 (= *Rana fusca* Schneider, 1799), by subsequent designation of Fitzinger, 1843:31.

Cystignathus Wagler, 1830:202. Type species: *Cystignathus pachypus* Wagler, 1830 (= *Rana pachypus* Spix, 1824) by subsequent designation of Fitzinger, 1843:31. The subsequent designation of *Rana mystacea* Spix, 1824, by Lynch, 1971:187, is in error. Synonymy by Tschudi, 1838:78 (although using *Cystignathus*); Boulenger, 1882:237.

Gnathophysa Fitzinger, 1843:31. Type species: *Rana labyrinthica* Spix, 1824, by original designation. Synonymy by Jiménez de la Espada, 1875:36; Boulenger, 1882:237.

Sibilatrix Fitzinger, 1843:31. Type species: *Cystignathus gracilis* Duméril and Bibron, 1841, by original designation. Synonymy by Jiménez de la Espada, 1875:44.

Plectromantis Peters, 1862:232. Type species: *Plectromantis wagneri* Peters, 1862, by monotypy. Synonymy by Nieden, 1923:479.

Entomoglossus Peters, 1870:647. Type species: *Entomoglossus pustulatus* Peters, 1870 by monotypy. Synonymy by Boulenger, 1882:237.

Pachypus Lutz, 1930:22. Type species: None designated. Proposed as a subgenus of *Leptodactylus.* Preoccupied by *Pachypus* d'Alton, 1840 (Mammalia) and *Pachypus* Cambridge, 1873 (Arachnida).

Cavicola Lutz, 1930:2, 22. Type species: None designated. Coined as a subgenus of *Leptodactylus*. Preoccupied by *Cavicola* Ancey, 1887 (Mollusca).

Vanzolinius Heyer, 1974a:88. Type species: *Leptodactylus discodactylus* Boulenger, 1884 "1883", by original designation. Synonymy by de Sá, Heyer, and Camargo, 2005a:87–97; Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green, and Wheeler, 2006:207.

Leptodactylus fuscus species group

Leptodactylus albilabris (Günther, 1859a) (Plate 1A)

Cystignathus albilabris Günther, 1859a:217. Type locality: West Indies, St. Thomas. Lectotype: BMNH 1947.2.1760, adult male.

Leptodactylus dominicensis Cochran, 1923:184–185. Type locality: Dominican Republic, El Seibo Province, Las Cañitas. Holotype: USNM 65670, adult male.

Etymology. From the Latin *albi* (white) and *labris* (lip).

Adult morphology. Moderate size, female snout–vent length (SVL) 32.9–48.1 mm ($\overline{X}$ = 41.2 mm), male SVL 30.0–43.1 mm ($\overline{X}$ = 41.2 mm); adult male snout spatulate; males lack thumb spines and chest spines; light lip stripe almost always distinct (94% of specimens); dorsal folds absent; complete pair of dorsolateral folds; lateral folds absent or interrupted; posterior thigh with light stripe; upper shank barred; belly uniform light to lightly mottled or speckled; toes without lateral fringes (Heyer, 1978:37–38; Joglar et al., 2005:74–87).

Similar species. *Leptodactylus albilabris* is the only species of the genus that occurs on the following Antillean islands: Anegada, Dominican Republic, Puerto Rico, St. Croix, St. John, St. Thomas, and Tortola.

Larval morphology. Maximum total length (Gosner 36) 42.6 mm; oral disk anteroventral; tooth row formula 2(2)/3; tail mottled (Heyer, 1978:37–38).

Advertisement call. Dominant (= fundamental) frequency 2,000–2,800 Hz; call duration 0.046–0.050 s; each call with 2 pulses; rising frequency modulations throughout call; call rate 4/s; no harmonic structure (Heyer, 1978:37–38; Joglar et al., 2005:74–87) (Fig. 7).

Distribution. Puerto Rico, Puerto Rican bank islands, Dominican Republic (Fig. 8).

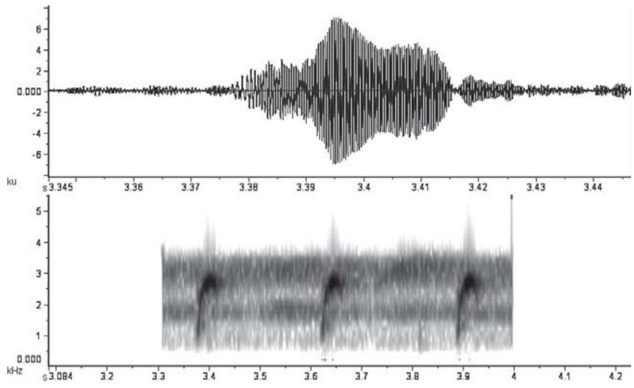

Figure 7. Advertisement call of *Leptodactylus albilabris* (recording USNM 324).

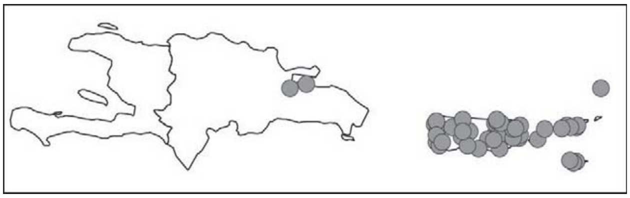

Figure 8. Distribution map of *Leptodactylus albilabris.*

Leptodactylus bufonius Boulenger, 1894 (Plate 1B)

Leptodactylus bufonius Boulenger, 1894:348. Type locality: "Asuncion, Paraguay." Lectotype: BMNH 1947.2.17.72, female.

Etymology. From the Latin *bufo* (toad), *bufonius* (toad-like).

Adult morphology. Moderate size, female SVL 49.0–61.8 mm ($\overline{X}$ = 54.7 mm), male SVL 45.5–59.4 mm ($\overline{X}$ = 52.2 mm); adult male snout spatulate; males lack thumb spines and chest spines; light upper lip stripe absent; dorsal folds absent; dorsolateral folds usually absent, sometimes weak; lateral folds complete; no light stripe on posterior thigh; upper shank barred; belly uniform light; toes without lateral fringes (Heyer, 1978:44–46).

Similar species. *Leptodactylus bufonius* occurs in Argentina, Bolivia, Brazil, and Paraguay. Similar species from these countries that lack toe fringes and dorsal folds are *L. cupreus, L. elenae, L. latinasus, L. mystaceus, L. mystacinus, L. troglodytes* and some individuals of *L. notoaktites* and *L. spixi. Leptodactylus bufonius* lacks a light longitudinal pinstripe on the posterior thigh; *L. cupreus, L. elenae, L. latinasus, L. mystaceus, L. notoaktites,* and *L. spixi* have distinct light stripes on the posterior thigh. *Leptodactylus bufonius* usually lack dorsolateral folds, but some specimens have weak dorsolateral folds; *L. mystacinus* always have well-defined dorsolateral folds. *Leptodactylus bufonius* is morphologically very similar to *L. troglodytes.*

The post-tympanic gland is sometimes pigmented in males of *L. bufonius* and not in *L. troglodytes*. *Leptodactylus troglodytes* (both males and females) have a calcified pseudo-odontoid (Sebben et al., 2007) on the mandibular symphysis that is unique within *Leptodactylus*. *Leptodactylus troglodytes* differ in advertisement calls (dominant frequency range 1,000–2,000 Hz in *L. bufonius,* 2,600–3,200 Hz in *L. troglodytes*) and distribution in Brazil (*L. bufonius* in Mato Grosso, *L. troglodytes* in Bahia, Ceará, Goiás, Minas Gerais, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe).

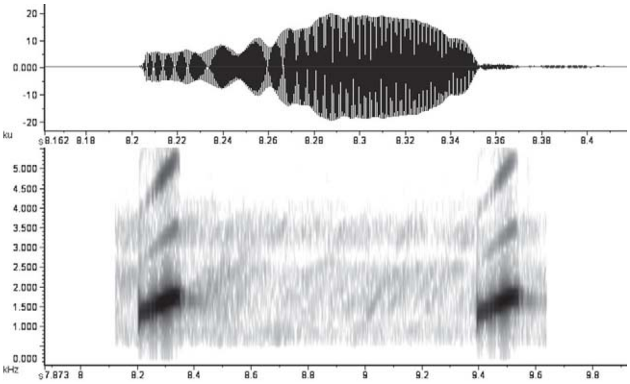

Figure 9. Advertisement call of *Leptodactylus bufonius* (recording USNM 19).

Figure 10. Distribution map of *Leptodactylus bufonius.*

Larval morphology. Total length (Gosner 37) 38.9 mm, oral disk anteroventral, tooth row formula 2(2)/3(1), tail weakly mottled (data from Cei, 1980).

Advertisement call. Dominant (= fundamental) frequency modulated between 1,000–2,000 Hz; call duration 0.2 s; each call comprised of a single note; rising frequencies throughout call; call rate 1.25 calls/s; no harmonic structure (Heyer 1978:44–45) (Fig. 9).

Distribution. Arid habitats in Argentina, Bolivia, Brazil, and Paraguay (Fig. 10).

Leptodactylus caatingae Heyer and Juncá, 2003 (Plate 1C)

Leptodactylus caatingae Heyer and Juncá, 2003:324. Type locality: Brazil, Bahia, Joazeiro. Holotype: ZUEC 8833, adult male.

Etymology. Latinized from the Portuguese word *caatinga,* referring to the characteristic distribution of this species within the Caatinga Morphoclimatic Domain (Ab'Sáber, 1977).

Adult morphology. Small, female SVL 36.2–39.1 mm (*n* = 2), male SVL 32.1–36.9 mm ($\overline{X}$ = 34.7 mm); adult male snout spatulate; males lack thumb spines and chest spines; light lip stripe usually distinct, smoothly or roughly defined; dorsal folds absent; dorsolateral folds absent or interrupted; lateral folds absent; posterior thigh usually with light stripe; upper shank barred; belly with uniform dispersion of melanophores to speckled; distinct white tubercles on outer surface of tarsus and sole of foot; toes lacking fringes (Heyer and Juncá, 2003).

Similar species. *Leptodactylus caatingae* occurs only in Brazil. Other species that occur in Brazil that have a distinct light stripe on the posterior surface of the thigh and distinct white tubercles on the outer surface of the tarsus and sole of foot are *L. elenae, L. latinasus,* and *L. mystaceus*. *Leptodactylus elenae* and *L. mystaceus* have distinct, complete dorsolateral folds (indicated by color pattern in poorly preserved specimens); *L. caatingae* has interrupted, indistinct, or no dorsolateral folds. *Leptodactylus caatingae* and *L. latinasus* have considerable morphological and color pattern overlap and cannot be consistently diagnosed from each other based on these features. The advertisement calls of *L. caatingae* are pulsed, with dominant frequencies ranging from 940–1,620 Hz; the calls of *L. latinasus* are not pulsed and have higher dominant frequencies ranging from 3,000–3,780 Hz. *Leptodactylus caatingae* and *L. latinasus* have completely allopatric distributions in Brazil (the southernmost state in Brazil in which *L. caatingae* occurs is Espírito Santo; the northernmost occurrence of *L. latinasus* is the Brazilian state of Rio Grande do Sul).

Larval morphology. Total length (Gosner 38) 32.1 mm; oral disk ventral; tooth row formula 2(2)/3(1); dorsal tail musculature homogeneously brown, ventral tail musculature light cream with scattered brown spots and markings, fins translucent with scattered brown markings on the edges (Magalhães et al., 2013:205–206).

Advertisement call. Dominant (= fundamental) frequency 1,070–1,120 Hz; call duration 0.06–0.08 s; each call with 7–8 distinct pulses; rapidly rising frequency modulation throughout each call; call rate 2.6/s; no harmonic structure (Heyer and Juncá, 2003) (Fig. 11).

Distribution. Northeast Brazil (Fig. 12).

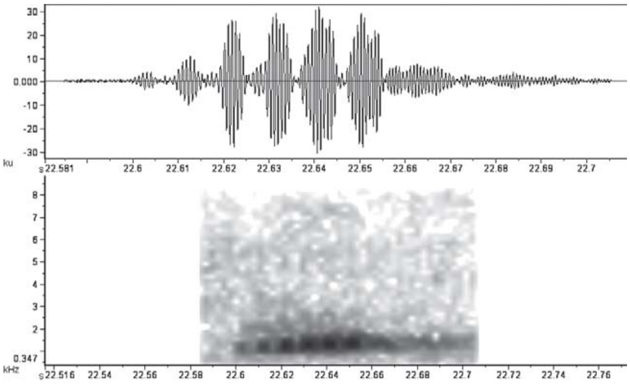

Figure 11. Advertisement call of *Leptodactylus caatingae* (recording USNM 22).

Figure 12. Distribution map of *Leptodactylus caatingae.*

Leptodactylus camaquara Sazima and Bokermann, 1978 (Plate 1D)

Leptodactylus camaquara Sazima and Bokermann, 1978:907. Type locality: "km 132 da Estrada Vespasiano a Conceição do Mato Dentro, Serra do Cipó, [1500 m] Jaboticatubas, Minas Gerais, Brasil." Holotype: MZUSP 73693 [formerly WCAB 48120], adult male.

Etymology. The name *camaquara* is an indigenous term for pond dweller in allusion to the species' habit of making excavations (translated from Sazima and Bokermann, 1978:908).

Adult morphology. Small size, female SVL 31.8–38.3 mm ($\overline{X}$ = 34.8 mm), male SVL 30.7–33.7 mm ($\overline{X}$ = 32.2 mm); males and females with weakly protruding snouts; males lack thumb spines and chest spines; light lip stripes irregular, well to poorly ill-defined; a pair of weakly developed dorsal folds; a pair of weakly developed dorsolateral folds; lateral folds complete; posterior thighs with a series of small light spots in the same field as the continuous light thigh stripes occurring in other species; upper shank barred; belly uniform light; toes without lateral fringes (Sazima and Bokermann, 1978:907–909).

Similar species. All specimens of *Leptodactylus camaquara* have a series of small light spots on the posterior thigh where light stripes occur in many other species of *Leptodactylus. Leptodactylus cunicularius, L. jolyi,* and *L. tapiti* are the only other known species in which some specimens have a series of light spots on the posterior thigh. *Leptodactylus camaquara* lacks a light longitudinal stripe on the dorsal shank surface; *L. jolyi* either has a light stripe or a series of light dots on the dorsal shank surface. *Leptodactylus camaquara* is morphologically similar to *L. cunicularius* and *L. tapiti. Leptodactylus camaquara* is sympatric with *L. cunicularius* at the Serra do Cipó (Minas Gerais, Brazil); *L. tapiti* occurs at the Chapada dos Veadeiros (Goiás, Brazil). The advertisement calls differ between *L. camaquara* (single calls of 0.3 s duration) and *L. cunicularius* (calls organized in bouts of 1–2 s duration, with each call 0.07 s duration).

Larval morphology. Total length (Gosner 39) 37 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Sazima and Bokermann, 1978:908–909).

Advertisement call. Dominant (= fundamental) frequency 2,300–2,800 Hz; call duration 0.3 s; each call a single pulse; rising frequency modulations throughout call; call rate 0.75/s; calls with harmonic structure, third harmonic not quite as intense as dominant frequency (Sazima and Bokermann, 1978:905, 908) (Fig. 13).

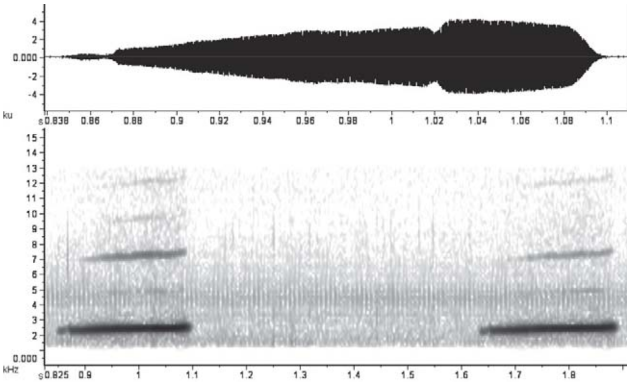

Figure 13. Advertisement call of *Leptodactylus camaquara* (recording USNM 328).

Figure 14. Distribution map of *Leptodactylus camaquara.*

Distribution. Known only from the Serra do Cipó, Minas Gerais, Brazil (Fig. 14).

Leptodactylus cunicularius Sazima and Bokermann, 1978 (Plate 1E)

Leptodactylus cunicularius Sazima and Bokermann, 1978. Type locality: "km 114/115 da Estrada de Vespasiano a Conceição do Mato Dentro, Serra do Cipó, Jaboticatubas, Minas Gerais, Brasil." Holotype: MZUSP 73685 (formerly WCAB 48000), adult male.

Etymology. The Latin word *cunicularius* means miner or burrower and alludes to excavations the frogs create that are similar to those dug by rabbits.

Adult morphology. Small–moderate size, female SVL 43.6–44.9 mm ($\overline{X}$ = 44.2 mm), male SVL 35.5–43.2 mm ($\overline{X}$ = 39.2 mm); adult male snout weakly spatulate; males lack thumb spines and chest spines; light lip stripe distinct; weak pair of sinuous dorsal folds; weak pair of sinuous dorsolateral folds; lateral folds interrupted; posterior thigh with a series of light spots or a light stripe; upper shank barred or with a series of light dots; belly uniform light; toes without lateral fringes (Heyer et al., 2008).

Similar species. *Leptodactylus cunicularius* occurs in Serra do Espinhaço and Serra da Mantiqueira (Minas Gerais, Brazil) and is similar to *L. camaquara, L. furnarius,* and *L. jolyi,* which also occur in the Serra do Cipó. The dorsolateral folds of *L. cunicularius* are sinuous, not straight throughout their length; the dorsolateral folds of *L. furnarius* and *L. jolyi* are slightly curved just behind the tympanum and straight on the rest of the body. *Leptodactylus cunicularius* is very similar to *L. camaquara* morphologically. Some individuals of *L. cunicularius* have a series of light dots where the light posterior thigh stripes occur in other species, whereas all individuals of *L. camaquara* have a series of light dots on

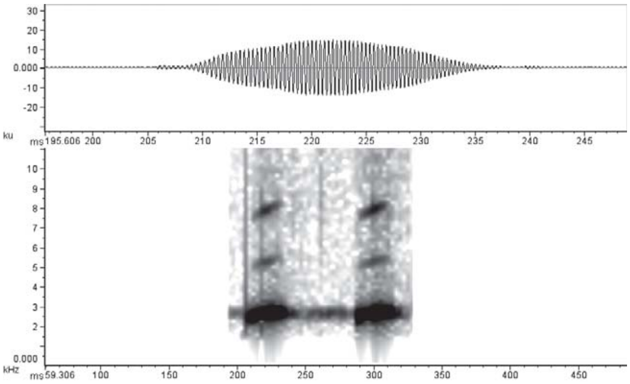

Figure 15. Advertisement call of *Leptodactylus cunicularius* (recording USNM 242).

Figure 16. Distribution map of *Leptodactylus cunicularius.*

the posterior thighs. Some individuals of *L. cunicularius* have a series of light dots on the upper shank; no individuals of *L. camaquara* have a series of light dots on the upper shank. The advertisement calls of *L. cunicularius* and *L. camaquara* are very different. *Leptodactylus cunicularius* produce individual notes at a rate of 12 per second and the duration of each note is about 0.07 s; individual notes of *L. camaquara* occur at a rate of less than 1 per second (0.75/s) and each note duration is about 0.3 s.

Larval morphology. Maximum total length (Gosner 38) 39.0 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Sazima and Bokermann, 1978:905–906).

Advertisement call. Dominant (= fundamental) frequency 2,200–2,700 Hz; call duration 1–2 s with 2–4 s intervals between calls; each call consisting of a single-pulsed note; each note with rising frequency modulations; call = note = pulse rate 3.1/s; call with harmonic structure (Sazima and Bokermann, 1978:905–906) (Fig. 15).

Distribution. Known only from the Serra do Espinhaço and Serra da Mantiqueira, Minas Gerais, Brazil (Fig. 16).

Leptodactylus cupreus Caramaschi, Feio, and São Pedro, 2008 (Plate 1F)

Leptodactylus cupreus Caramaschi, Feio, and São Pedro, 2008:44. Type locality: Lagoa das Bromélias (20°25'S, 43°29~ , 1,227 m above sea level), Parque Estadual da Serra do Brigadeiro, District of Careço, Municipality of Ervália, State of Minas Gerais, Southeastern Brazil. Holotype: MNRJ 47752, adult male.

Etymology. The Latin adjective *cupreus* refers to the copper coloration of the species.

Adult morphology. Moderate size, female SVL 55.7–57.9 mm ($\overline{X}$ = 56.8 mm), male SVL 50.1–57.0 mm ($\overline{X}$ = 52.3 mm); adult male snout spatulate; males lack thumb spines and chest spines; light lip stripe distinct; no dorsal folds; dorsolateral folds thick, from anterior third of body to groin, marked by a lighter coloration than that of flanks and dorsum; lateral folds absent; flanks from bright copper with scattered small markings to solid dark; posterior thigh with light stripe; upper shank indistinctly barred; belly whitish grey with scattered irregular cream markings; toes without lateral fringes (Caramaschi et al., 2008:44–54; Cassini et al., 2013).

Similar species. *Leptodactylus cupreus* is a member of the *L. mystaceus* complex comprising *L. didymus, L. elenae, L. mystaceus, L. notoaktites,* and *L. spixi* that is defined by having two distinct dorsolateral folds (no dorsal or lateral folds), a distinct light upper lip stripe, a distinct longitudinal light stripe on the posterior surface of the thighs and the sole of the foot with prominent white tubercles. *Leptodactylus cupreus* lacks dark markings/spots on the dorsum, the dorsal surfaces of the thighs and shanks are not distinctly barred, and posses a divided outer metacarpal tubercle; all other members of the *L. mystaceus* complex have distinct dorsal patterns of dark marks, the dorsal surfaces of thighs and shanks are distinctly barred, and have entire outer metacarpal tubercles. In addition, the presence of small spines on the dorsal surface of the tibia of *L. cupreus* distinguished it from *L. mystaceus* (spines on tibia absent).

Larval morphology. Maximum total length (Gosner 40) 52.5 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Motta et al., 2010:65–68).

Advertisement call. Dominant (= fundamental) frequency 2,800–3,058 Hz; call groups given irregularly in long

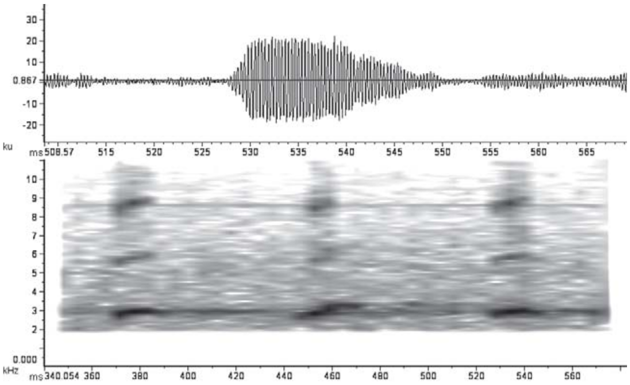

Figure 17. Advertisement call of *Leptodactylus cupreus.*

Figure 18. Distribution map of *Leptodactylus cupreus.*

and fast sequence of notes, note duration 0.16/s; notes not pulsed; rising frequency modulations through most of note with a terminal drop in frequency; note rate about 12/s; two distinct harmonics in addition to fundamental (Caramaschi et al., 2008:50) (Fig. 17).

Distribution. Known from the Brazilian states of Bahía, Espirito Santo, and Minas Gerais (Fig. 18).

Leptodactylus didymus Heyer, García-Lopez, and Cardoso, 1996 (Plate 2A)

Leptodactylus didymus Heyer, García-Lopez, and Cardoso, 1996:25. Type locality: Peru: Madre de Dios; Tambopata Reserved Zone, 12°50'S, 69°17~ . Holotype: USNM 332861, adult male.

Etymology. From the Greek *didymus,* double or twin, referring to the morphological similarity between *Leptodactylus didymus* and *L. mystaceus.*

Adult morphology. Moderate size, female SVL 43.7–53.5 mm ($\overline{X}$ = 49.2 mm), male SVL 45.9–52.2 mm ($\overline{X}$ = 49.0 mm); adult male snout weakly spatulate; males lacking thumb spines and chest spines; muted light upper lip stripe; dorsal folds absent; distinct pair of dorsolateral folds; lateral folds interrupted or absent; posterior thigh with light stripe; upper shank barred; belly uniform light; toes without lateral fringes (Heyer et al., 1996a).

Similar species. *Leptodactylus didymus* is known from the Bolivian departments of Beni, La Paz, Pando, the Brazilian states of Acre, Amazonas, and the Peruvian department of Madre de Dios. The other similar species occurring within the distribution of *L. didymus* are *L. fuscus* and *L. mystaceus. Leptodactylus fuscus* have a pair of longitudinal dorsal folds; *L. didymus* lack dorsal folds. There are no morphological features that distinguish *L. didymus* from *L. mystaceus*. The advertisement call of *L. didymus* exhibits a single or two partial pulses; the call of *L. mystaceus* has 9–17 pulses.

Larval morphology. Unknown.

Advertisement call. Dominant (= fundamental) frequency 510–1,510 Hz; call duration 0.09–0.32 s; each call consists of a single pulse or two partial pulses; rising frequency modulation through entire call or with a brief terminal drop in frequency; call rate 1.4–3.1/s; harmonic structure present (Heyer et al., 1996a, Köhler and Lötters, 2002) (Fig. 19).

Distribution. Bolivian departments of Beni, La Paz, Pando; Brazilian states of Acre, Amazonas; Peruvian department of Madre de Dios (Fig. 20).

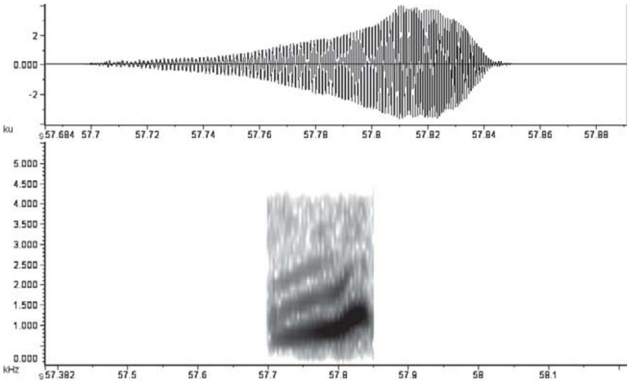

Figure 19. Advertisement call of *Leptodactylus didymus* (recording USNM 205).

Figure 20. Distribution map of *Leptodactylus didymus.*

Leptodactylus elenae Heyer, 1978 (Plate 2B)

Leptodactylus elenae Heyer, 1978:45. Type locality: Argentina, Salta, Embarcación. Holotype: LACM 92096, adult female.

Etymology. Named for W.R. and M.H. Heyer's daughter, Elena.

Adult morphology. Moderate size, female SVL 38.7–48.6 mm ($\overline{X}$ = 43.8 mm), male SVL 37.9–46.4 mm ($\overline{X}$ = 43.2 mm); adult male and female snouts not spatulate nor protruding beyond the lower jaw; males lack thumb spines and chest spines; light upper lip stripe usually (77% of specimens) distinct; dorsal folds absent; distinct pair of dorsolateral folds; lateral folds absent, interrupted, or present; posterior thigh with light stripe; upper shank barred; ventral surface of belly mostly uniformly light with few melanophores or clumps of melanophores on lateral-most areas of the belly; toes without lateral fringes; posterior surfaces of the shank and sole of foot with distinct white tubercles (Heyer, 1978:45–46, Heyer and Heyer, 2002:1–5).

Similar species. *Leptodactylus elenae* occurs in arid regions of northwest Argentina (Jujuy, Salta), Brazil (Mato Grosso, Mato Grosso do Sul), Bolivia (Beni, La Paz, Santa Cruz), and Paraguay. Similar species that occur with *L. elenae* are *L. bufonius, L. fuscus, L. latinasus,* and *L. mystacinus. Leptodactylus bufonius* and *L. mystacinus* lack a light stripe on the posterior thigh, *L. elenae* have a light thigh stripe. *Leptodactylus elenae* lack dorsal folds whereas *L. fuscus* have a pair of dorsal folds. *Leptodactylus elenae* are larger than *L. latinasus* (female SVL 29.1–35.7 mm, male SVL 27.0–37.9 mm) and dorsolateral folds are absent or indistinct in *L. latinasus.*

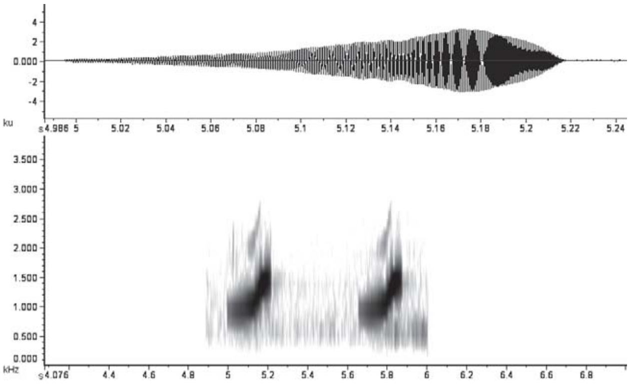

Figure 21. Advertisement call of *Leptodactylus elenae* (recording USNM 180).

Figure 22. Distribution map of *Leptodactylus elenae.*

Larval morphology. Maximum total length (Gosner 36) 24.1 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Prado and d'Heursel, 2006, Vera Candioti et al., 2007).

Advertisement call. Dominant (= fundamental) frequency 700–870 Hz at beginning of call, 1,370–1,500 Hz at end of call; each call a single note, unpulsed or weakly pulsed in mid-call; rising frequency modulations throughout call; call rate 64–120/min; harmonics either absent or present (Barrio, 1965, Heyer and Heyer, 2002) (Fig. 21).

Distribution. Arid regions of Argentina (Jujuy, Salta), Brazil (Mato Grosso, Mato Grosso do Sul), Bolivia (Beni, La Paz, Santa Cruz), and Paraguay (Fig. 22).

Leptodactylus fragilis (Brocchi, 1877) (Plate 2C)

Cystignathus fragilis Brocchi, 1877:182. Type locality: "Cet animal a été envoyé de Tehuantepec [Mexique]." Holotype: MNHN 6316, female.
Leptodactylus fragilis: Brocchi, 1881–1883:19. First usage of *fragilis* with the genus *Leptodactylus.*
Leptodactylus mystaceus labialis: Shreve, 1957:246.

Etymology. The Latin *fragilis* means brittle. It is unclear why Brocchi used this name.

Adult morphology. Small size, female SVL 30.1–43.6 mm ($\overline{X}$ = 36.3 m), male SVL 27.0–43.0 mm ($\overline{X}$ = 34.8 mm); adult male snout spatulate; males without thumb spines and chest spines; indistinct light upper lip stripe (97% of specimens); dorsal folds absent; weak dorsolateral folds; lateral folds interrupted or absent; posterior thigh with light stripe; upper shank barred; belly without pattern or with small spots on lateral and anterior portions of belly; toes without lateral fringes (Heyer et al., 2006).

Similar species. *Leptodactylus fragilis* has been misidentified in the literature as *L. melanonotus. Leptodactylus fragilis* lacks toe fringes; *L. melanonotus* has toe fringes. Otherwise, *L. fragilis* is similar to *L. fuscus* and *L. poecilochilus* with which it co-occurs. *Leptodactylus fuscus* has a pair of dorsal folds; *L. fragilis* lacks dorsal folds. *Leptodactylus poecilochilus* has distinct dorsolateral folds and almost always (93% of specimens) lacks white tubercles on the sole of the foot; *L. fragilis* has indistinct dorsolateral folds and has many white tubercles on the sole of the foot.

Larval morphology. Maximum total length (Gosner 32–34) 32 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Heyer et al., 2006).

Advertisement call. Dominant (= fundamental) frequency 600–2,010 Hz; call duration ranges from 0.11–0.20 s; call consists of one or two notes and may be partially or fully pulsed; call frequency modulated, rising throughout call, sometimes a short drop in frequency at the beginning or end of call; call rate 1.5–150 calls/min; call with harmonic structure (Heyer et al., 2006:2) (Fig. 23).

Distribution. From southernmost Texas (USA) on the Atlantic coast and Colima, Mexico on the Pacific coast through Middle America to northern Colombia including the Cauca and Magdalena valleys, the Río Arauca and Río Apure drainages in Colombia and northern Venezuela extending as far as the Venezuelan State of Sucre (Fig. 24).

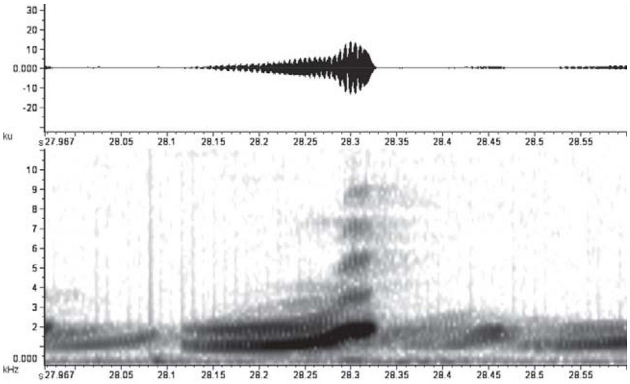

Figure 23. Advertisement call of *Leptodactylus fragilis* (recording USNM 225).

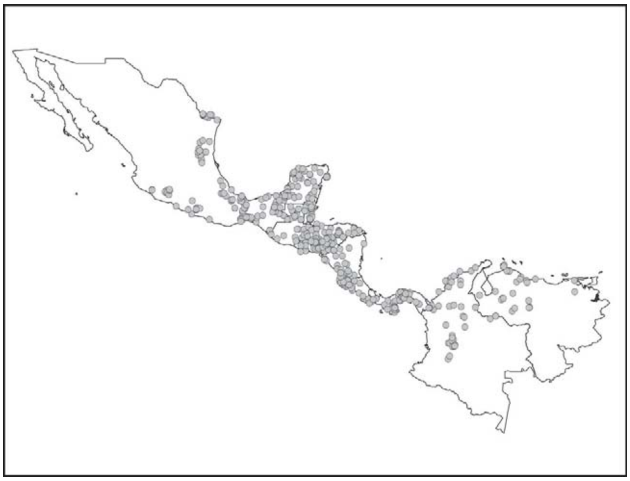

Figure 24. Distribution map of *Leptodactylus fragilis.*

Leptodactylus furnarius **Sazima and Bokermann, 1978 (Plate 2D)**

Leptodactylus furnarius Sazima and Bokermann, 1978:899. Type locality: “Campo Grande, [900 m] Paranapiacaba, São Paulo, Brasil.” Holotype: MZUSP 73678 [formerly WCAB 47949], adult male.

Leptodactylus laurae Heyer, 1978:59. Type locality: Brazil: Minas Gerais; Água Limpa, Juiz de Fora. Holotype: MZUSP 130, adult male. Placed in synonymy of *L. furnarius* by Heyer, 1983:271.

Etymology. Sazima and Bokermann (1978:901) indicated that the Latin *furnarius* was equivalent to the Portuguese word “oleiro” = potter, maker of earthenware vessels. (Jaeger, 1955:106, translates *furnarius* as baker.) The name is in allusion to the species’ construction of incubating chambers, similar to earthen ovens.

Adult morphology. Small–moderate size, female SVL 36.0–49.6 mm SVL ($\overline{X}$ = 42.5 mm SVL), male SVL 30.7–46.4 mm SVL ($\overline{X}$ = 36.6 mm SVL); adult male snout rounded (usually) or weakly spatulate; males lack thumb spines and chest spines; light upper lip stripe present, usually (71% of specimens) distinct or indistinct (29% of specimens); one pair of dorsal folds; one pair of dorsolateral folds; lateral folds complete; posterior thigh with distinct (51% of specimens) or indistinct (49% of specimens) light stripes; upper shanks barred; belly uniform light; toes without lateral fringes (Heyer and Heyer, 2004).

Similar species. *Leptodactylus furnarius* occurs throughout the semi-arid Cerrado and Campo Rupestre morphoclimatic domains and marginally occurs in the Atlantic Forest morphoclimatic domain. Other similar species occurring with *L. furnarius* are *L. elenae, L. fuscus, L. gracilis, L. latinasus, L. mystaceus, L. mystacinus, L. notoaktites,* and *L. plaumanni. Leptodactylus gracilis* and *L. plaumanni* have thin, light longitudinal stripes on the upper shanks; *L. furnarius* lacks light stripes on the upper surface of the shanks. *Leptodactylus elenae, L. latinasus, L. mystaceus, L. mystacinus,* and *L. notoaktites* lack a pair of dorsal folds; *L. furnarius* have a pair of dorsal folds. *Leptodactylus furnarius* have a light mid-dorsal stripe; most individuals (90%) of *L. fuscus* lack light mid-dorsal stripes. The legs of *L. furnarius* are longer than those of *L. fuscus* (e.g., female *L. furnarius* shank/SVL ratios range from 54–63% and males range from 53–66% whereas female *L. fuscus* shank/SVL ratios range from 43–52% and males range from 40–51%).

Larval morphology. Maximum total length (Gosner 38) 41 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Sazima and Bokermann, 1978:901, 909).

Advertisement call. Dominant (= fundamental) frequency 2,600–3,400 Hz; call duration 0.04 s; each call = note with 3–4 pulses; rising frequency modulation throughout call; call rate ca. 200/min to 450/min; no evident harmonic structure (Sazima and Bokermann, 1978:901, 903; Heyer and Heyer, 2004:1) (Fig. 25).

Distribution. Primarily arid habitats in the Brazilian states of Distrito Federal, Goiás, Mato Grosso, Minas Gerais, Paraná, Rio Grande do Sul, São Paulo, and northeastern Uruguay (Fig. 26).

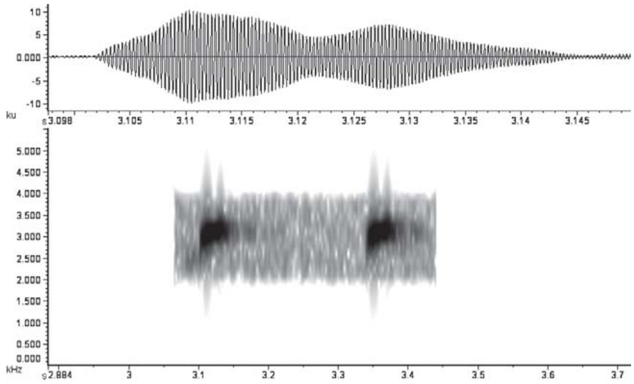

Figure 25. Advertisement call of *Leptodactylus furnarius* (recording AJC33).

Figure 26. Distribution map of *Leptodactylus furnarius.*

Leptodactylus fuscus (Schneider, 1799) (Plate 2E)

Rana virginica Laurenti, 1768:31. Type locality: Not designated. Holotype: Frog illustrated by Seba, 1734, plate 75, fig. 4 by original designation. Considered (as *Rana virginica* Merrem, 1820, a subsequent usage) a synonym of *Cystignathus fuscus* by Günther, 1859b “1858”:28, and (under *Cystignathus typhonius*) by Duméril and Bibron, 1841:402. Junior homonym of *Rana virginica* Laurenti, 1768.

Rana fusca Schneider, 1799:130. Type locality: Implied to be from Surinam. Syntypes: “Museo Lev. Vincentii,” “Museo Lampiano,” presumed lost. MNHN 680, a male, designated Neotype by Heyer, 1968:160–162. Lynch, 1971:186–187 cited W.C.A. Bokermann [pers. comm.] that some of the original syntypes were still extant and without study of these, Heyer’s neotype designation should not be accepted. Syntypes of *Rana fusca* Schneider have not been located.

Rana typhonia Daudin an XI 1802 or 1803:55–56. Type locality: “Amérique meridionale” given as Surinam by Heyer, 1978:50. Syntypes: MNHN 680 (2 specimens) according to Guibé, 1950 “1948”:30. MNHN 680 designated lectotype (and neotype of *Rana fusca* Schneider, 1799) by Heyer, 1968:160–162. Synonymy by Duméril and Bibron, 1841:402; Heyer, 1968:160–162.

Rana sibilatrix Wied-Neuwied, 1824a: Heft 8: plate 47, figure 2. Also published by Wied-Neuwied, 1824b:671. Type locality: “Ostkuste von Brasiliens … Peruhype bei Villa Viçosa vor, am Mucuri, Caravellas …,” Brazil. Restricted to “Villa Viçosa am Peruhype,” Brazil by Müller, 1927:281. Types: Include animal figured on plate 47, figure 2 of the original; specimens otherwise not designated or located according to Heyer, 1978:30. Synonymy [and expressed doubt about restricted type locality] by Heyer, 1978:30. Synonymy with *Rana typhonia* Daudin by Reinhardt and Lütken, 1862 “1861”:164 and Steindachner 1867:24.

Rana pachypus var. 2 Spix, 1824:26. Type locality: “aquis Parae” Brazil. Type(s): Not specifically stated, but including animals figured on pl. 2, figs. 1–2 in the original publication, formerly including ZSM 2503/0, now lost according to Hoogmoed and Gruber, 1983:356. Synonymy by Peters, 1872:199; Hoogmoed and Gruber, 1983:356.

Leptodactylus typhonia: Fitzinger, 1826:64.

Leptodactylus sibilatrix: Fitzinger, 1826:64.

Cystignathus typhonius: Wagler, 1830:203.

Cystignathus sibilatrix: Wagler, 1830:203.

Cystignathus schomburgkii Troschel, 1848:659. Type locality: “Britisch-Guiana.” Types: Not designated and presumed lost, according to Heyer, 1978:30. Synonym of *Leptodactylus typhonius* by Boulenger, 1882:240; tentative synonymy by Heyer, 1978:30.

Cystignathus fuscus: Günther, 1859b “1858”:28.
Leptodactylus typhonius: Boulenger, 1882:240.
Leptodactylus raniformis Werner, 1899:479. Type locality: “Rio Meta, Llanos [Orocué],” Rio Meta, Colombia. Holotype: Originally ZIUG, now ZFMK 28484, male, according to Böhme and Bischoff, 1984:177. Synonymy by Heyer, 1978:29.
Leptodacytlus sibilator: Müller, 1927:281. Incorrect subsequent spelling.
Leptodactylus sybilatrix: Cei, 1950:408. Incorrect subsequent spelling.
Leptodactylus sybilator: Cei, 1956:48. Incorrect subsequent spelling.
Leptodactylus gualambensis Gallardo, 1964a:46. Type locality: “Argentina, Salta, Urundel, 43 km al Oeste de Orán, Río Santa María.” Holotype: MACN 9752, adult male. Synonymy by Heyer, 1968:160–162.
Leptodactylus fuscus: Heyer, 1968:160–162.

Etymology. The Latin word *fuscus* translates to brown, dark, dusky in English.

Adult morphology. Small–moderate size, female SVL 36.5–56.3 mm ($\overline{X}$ = 44.8 mm), male SVL 32.4–55.3 mm ($\overline{X}$ = 43.4 mm); adult male snout spatulate; adult males lacking thumb spines and chest spines; light upper lip stripe usually distinct (81% of specimens); a pair of well-developed dorsal folds; a pair of well-developed dorsolateral folds; lateral folds complete; posterior thigh light stripe distinct; upper shank barred; belly patternless, rarely (< 10% of specimens) with small speckles over entire belly; toes lacking fringes (Heyer, 1978:50–52).

Similar species. *Leptodactylus fuscus* has a broad distributional range from Panamá, throughout the lowlands of South America east of the Andes to about 30° S latitude. *Leptodactylus fuscus* and the following species have a pair of dorsal folds and lack toe fringe: *L. camaquara* (some individuals lack dorsal folds), *L. cunicularius, L. furnarius, L. gracilis, L. jolyi, L. longirostris, L. marambaiae, L. notoaktites, L. plaumanni, L. poecilochilus* (some individuals lack dorsal folds), *L. spixi,* and *L. tapiti.* Of the preceding, only *L. fuscus* individuals usually lack a light mid-dorsal stripe. The upper shank of *L. fuscus* is barred and lacks light longitudinal stripes; all individuals of *L. gracilis, L. marambaiae,* and *L. plaumanni* have a light longitudinal stripe on the upper shank; *L. jolyi* has either a light stripe or a series of light dots on the upper shank. *Leptodactylus fuscus* rarely have distinct white tubercles on the sole of the foot and posterior surface of the tarsus, but small light spots are present on these surfaces indicating the presence of weakly developed tubercles. The posterior surface of the tarsus and sole of the foot are smooth and uniform in coloration in *L. furnarius, L. longirostris,* and *L. poecilochilus.* The posterior surface of the tarsus and sole of the foot of *L. spixi* have distinct white tubercles. *Leptodactylus notoaktites* has a smooth posterior surface of the tarsus. Camargo et al. (2006) suggested that *L. fuscus* consists of three species consisting of three cryptic evolutionary lineages.

Larval morphology. Maximum total length (Gosner 39) 32.0 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Lescure, 1972:96–99; Sazima, 1975:34–35).

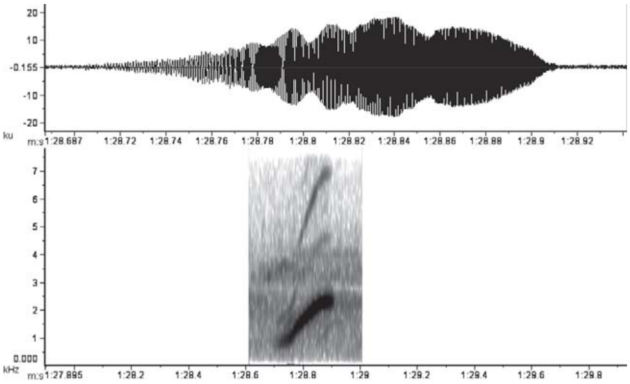

Figure 27. Advertisement call of *Leptodactylus fuscus* (recording USNM 19).

Figure 28. Distribution map of *Leptodactylus fuscus.*

Advertisement call. Dominant (= fundamental) frequency 1,000–2,800 Hz; call = note duration 0.16–0.17 s; notes pulsed or partially pulsed; rising frequency modulations throughout call; call rate 1/s; harmonic structure present or absent (Heyer, 1978:18–19, 50; Marquez et al., 1995:316) (Fig. 27).

Distribution. Lowland regions of Panamá and west of the Andes in South America with a southern limit of about 30° S latitude (Fig. 28).

Leptodactylus gracilis **(Duméril and Bibron, 1840) (Plate 2F)**

Cystignathus gracilis Duméril and Bibron, 1840: Pl. 13, figs. 5–7; 1841:406. Type locality: Not stated. Type: Guibé, 1950 "1948":30 indicating that MNHN 4490 was the holotype. de Sá, Dubois, and Ohler, 2007b:177 designated MNHN 4490 from Montevideo, Uruguay, as the Neotype of *C. gracilis* Duméril and Bibron, 1840.
Leptodactylus gracilis: Jiménez de la Espada, 1875:44.
Leptodactylus gracilis delattini Müller, 1968:48. Type locality: Brazil, Santa Catarina, Ilha Campeche. Holotype: MZUSP 56589, formerly SMF 4080.

Etymology. From the Latin *gracilis,* slender, thin.

Adult morphology. Small-moderate size, female SVL 37.2–55.3 mm ($\overline{X}$ = 44.0 mm), male SVL 31.0–52.7 mm ($\overline{X}$ = 42.9 mm); adult male snout calloused, not spatulate; males lack thumb spines and chest spines; light upper lip stripe almost always distinct (95% of specimens); distinct pair of dorsal folds; distinct pair of dorsolateral folds; lateral folds interrupted or complete; light posterior thigh stripe usually distinct (72% of specimens); upper shank barred with a narrow, longitudinal light stripe; belly usually uniform light, sometimes small spots encroaching on belly; toes without lateral fringes (Heyer, 1978:53–56).

Similar species. *Leptodactylus gracilis* occurs in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. *Leptodactylus fuscus* and *L. notoaktites* also occur within the range of *L. gracilis* and these taxa do not have a narrow light longitudinal stripe on the upper shank. While *Leptodactylus plaumanni* is within the geographical range of *L. gracilis,* there are no consistent morphological features that differentiate the two. *Leptodactylus gracilis* occurs in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. *Leptodactylus jolyi, L. marambaiae, L. plaumanni,* and *L. sertanejo* also occur within the range of *L. gracilis* and all of these taxa have narrow light longitudinal stripes (on narrow longitudinal folds) on the upper shanks (some individuals of *L. jolyi* have a series of light dots on the longitudinal shank folds). *Leptodactylus marambaiae* only occurs on the island of Marambaia in the State of Rio de Janeiro; *L. gracilis* does not occur on Marambaia. There are no consistent morphological features that differentiate *L. gracilis* from *L. jolyi, L. plaumanni,* and *L. sertanejo.* The advertisement call rate of *L. gracilis* is 3–4 calls per second; that of *L. jolyi* is 0.1–0.3 calls per second; that of *L. plaumanni* is 13–25 calls per second; that of *L. sertanejo* is 0.02–0.3 calls per second.

Larval morphology. Maximum total length (ca. Gosner 38) 36.7 mm; oral disk anteroventral; tooth row formula 2(1)/3(1); tail mottled (Langone and de Sá, 2005:50–54).

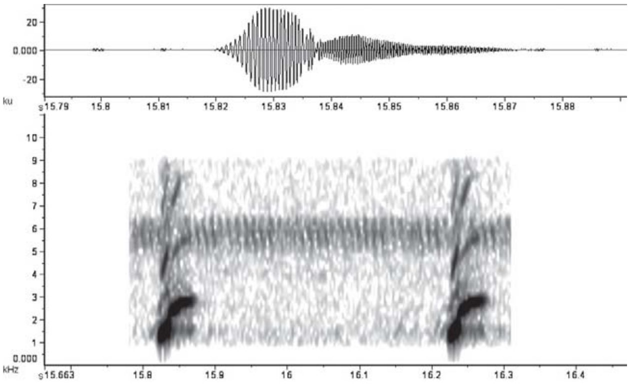

Figure 29. Advertisement call of *Leptodactylus gracilis* (recording USNM 11).

Figure 30. Distribution map of *Leptodactylus gracilis.*

Advertisement call. Dominant (= fundamental) frequency 500–2,400 Hz; call = partially pulsed note duration 0.04–0.05 s; call pulsed or partially pulsed; rising frequency modulations throughout call; note rate about 4/s; harmonic structure present or absent (Heyer, 1978:54–56) (Fig. 29).

Distribution. Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Fig. 30).

Comment. De Sá et al. (2007c:175–178) observed that *Cystignathus gracilis* Duméril and Bibron, 1840 was based on three figures showing a single specimen and bearing the name. However, no particular individual was identified as the source of the figures and no locality data was provided with the original illustration. Duméril and Bibron (1841:406–407) briefly described this species and stated that the description was based on several specimens (number not given) collected by d'Orbigny in Montevideo; however, no specimen was identified as the illustrated holotype. De Sá et al. (2007c) noted that Guibé designated the holotype without justification although several specimens comprise the type series and no extant specimen can be undoubtedly identified as the holotype. Consequently, de Sá et al. (2007c) designated and described adult male MNHN 4490 from Montevideo, Uruguay, as the neotype of *C. gracilis* Duméril and Bibron 1840.

The subspecies *Leptodactylus gracilis delattini* was rejected by Heyer (1978:36) and García-Pérez and Heyer (1993:51); and subsequently resurrected by Silva et al., (2004:185–196), stating "… differences in the vocalization are subtle, but they are distinguished by some morphological traits and reproductive patterns. *Leptodactylus gracilis delattini* is geographically isolated; it is confined to a coastal island in the State of Santa Catarina, and has a specific identity, distinct from that of *L. gracilis gracilis* that has a wider distribution. Analysis based on cytochrome b sequence indicated that *L. gracilis gracilis* and *L. gracilis delattini* do not have any divergence, so that they should remain as valid subspecies."

Leptodactylus jolyi Sazima and Bokermann, 1978 (Plate 3A)

Leptodactylus jolyi Sazima and Bokermann, 1978:902. Type locality: Brazil, São Paulo, Paranapiacaba, Campo Grande, 900 m. Holotype: MZUSP 73726 (formerly WCAB 47969), adult male.

Etymology. Named for Professor Aylthon B. Joly, who enthusiastically dedicated the last years of his life to botanical and zoological exploration in the Serra do Cipó.

Adult morphology. Data lacking for females. Moderate size, male SVL 43.3–48.6 mm ($\overline{X}$ = 46.3 mm); adult male snout weakly spatulate; males lacking thumb spines and chest spines; light upper lip stripe usually faint; dorsal, dorsolateral, and lateral folds well developed; posterior thigh with a light stripe or a series of light spots; upper shank barred with a thin longitudinal light stripe or a series of light dots; belly uniform light; toes without lateral fringes (Sazima and Bokermann, 1978:902–904; Giaretta and Costa, 2007:1–10).

Similar species. *Leptodactylus jolyi* was restricted to the vicinity of Paranapiacaba, State of São Paulo, Brazil (fide Giaretta and Costa, 2007); however, it has a more extensive distribution. In the Paranapiacaba region, only *L. gracilis* shares with *L. jolyi* thin and light longitudinal stripes on the upper shanks. A dark supratympanic stripe extends only above the tympanum in *L. jolyi;* in *L. gracilis* the supratympanic stripe extends from above the tympanum and continues posterolaterally behind the tympanum. The vomerine teeth of *L. jolyi* were reported to

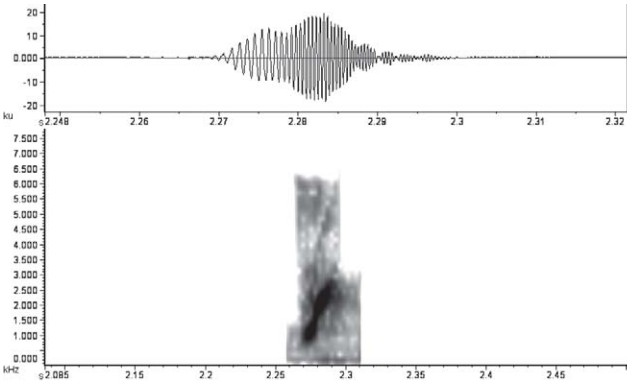

Figure 31. Advertisement call of *Leptodactylus jolyi* (recording USNM 238).

Figure 32. Distribution map of *Leptodactylus jolyi.*

be in two straight series, whereas those of *L. gracilis* are distinctly arched (Giaretta and Costa, 2007). The call rate of *L. jolyi* is 0.1–0.3/s, and that of *L. gracilis* is 2.5–4.0/s (Sazima and Bokermann, 1978:902–904; Giaretta and Costa, 2007:1–10).

Larval morphology. Maximum total length (Gosner state 38) 45.0 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Sazima and Bokermann, 1978:903, 909).

Advertisement call. Dominant (= fundamental) frequency 900–2,600 Hz (Sazima and Bokermann, 1978), 1,500–2,500 Hz (Giaretta and Costa, 2007); call duration 0.03–0.04 s; 1–3 pulses/call; rising frequency modulation throughout call; call rate 24/min; with or without harmonic structure (Sazima and Bokermann, 1978:903–904; Giaretta and Costa, 2007:3, 6) (Fig. 31).

Distribution. Paranapiacaba region, State of São Paulo, Brazil and in open areas of the Atlantic forest and in the Cerrados of eastern Brazil (Fig. 32).

Leptodactylus labrosus Jiménez de la Espada, 1875 (Plate 3B)

Leptodactylus labrosus Jiménez de la Espada, 1875:36. Type locality: Orillas del Río Daule, Pimocha, [Guayas], Ecuador. Lectotype: MNCN 3524, female.

Leptodactylus curtus Barbour and Noble, 1920:405. Type locality: Bellavista, Cajamarca, Peru. Holotype: MCZ 5281, juvenile female.

Etymology. The Latin *labrosus* translates as thick-lipped.

Adult morphology. Moderate size, female SVL 50.1–71.2 mm ($\overline{X}$ = 59.2 mm), male SVL 47.6–67.4 mm ($\overline{X}$ = 56.5 mm); males and females with spatulate snouts; males lack thumb spines and chest spines; light upper lip stripe indistinct or absent; dorsal folds absent; dorsolateral folds indistinct or absent; lateral folds interrupted or absent; posterior thigh light stripe almost always absent (94% of specimens) or indistinct (6% of specimens); upper shank barred; belly uniform light to small melanophore blotches scattered across the anterior belly and extending centrally; toes without lateral fringes, may have vestigial basal ridges and basal web between toes 1, 2, 3 (Heyer, 1978:56–57).

Similar species. *Leptodactylus labrosus* occurs west of the Andes from the Ecuadorian Province of Manabi south to the Peruvian Departments of Cajamarca, Libertad, and Ancash. University of Kansas specimens identified as *L. labrosus* from the Department of Cuzco, Peru, were probably misidentified; unfortunately, the specimens were destroyed. *Leptodactylus ventrimaculatus* is the only other species that occurs together with *L. labrosus* in Ecuador. The sole of the foot is usually (91% of specimens) smooth, without tubercles, in *L. labrosus;* the sole of the foot in *L. ventrimaculatus* has distinct, scattered or very few, white tubercles.

Figure 33. Distribution map of *Leptodactylus labrosus.*

Larval morphology. Chondrocranial morphology was described by Larson and de Sá (1998) based on USNM 520294–95; the external morphology has not been reported.

Advertisement call. The call consists of a single note with slight frequency modulation; call duration is 64–133 ms; 118–135 calls/minute; the dominant (= fundamental) frequency is 358–726 Hz (de Carvalho and Ron, 2011).

Distribution. Lowlands west of the Andes in Ecuador and Peru (Fig. 33).

Leptodactylus laticeps Boulenger, 1918 (Plate 3C)

Leptodactylus laticeps Boulenger, 1918:431. Type locality: "Santa Fé, Argentina." Holotype: BMNH 98.11.24.7, female.

Leptodactylus (*Pachypus*) *laticeps:* Vellard, 1947:464.

Etymology. The Latin roots *latus* (*lata, latum*) and *ceps* refer to a broad head.

Adult morphology. Large size, female SVL 88.0–117.0 mm ($\overline{X}$ = 105.1 mm), male SVL 94.2–109.7 mm ($\overline{X}$ = 101.3 mm); adult male snout not spatulate; adult males with two black spines on each thumb; adult males with a pair of black chest spines; light upper lip stripe absent; no dorsal, dorsolateral, or lateral folds; posterior thigh lacking a light longitudinal stripe; upper shank with broad dark bands; belly light to having small spots on anterior and lateral portions of belly; toes without lateral fringes (Cei, 1980:355–357).

Similar species. *Leptodactylus laticeps* is among the most distinctive and colorful species in the genus *Leptodactylus*. The species has dorsal body and limb patterns of black squares and rectangles enclosing red markings on an overall yellow background. In preservative, the black squares and rectangles have white areas within and are separated by white areas. Most *Leptodactylus syphax* have a more glandular dorsum with muted tile-like dorsal pattern of darker and lighter browns, but no *L. syphax* have white (in preservative) marks separating the dorsal "tiles."

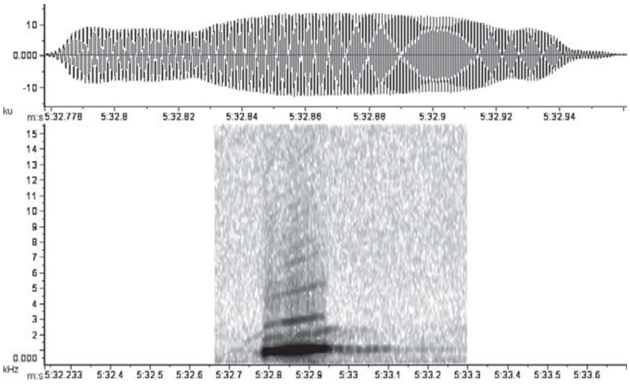

Figure 34. Advertisement call of *Leptodactylus laticeps* (recording USNM 327).

Figure 35. Distribution map of *Leptodactylus laticeps*.

Larval morphology. Unknown.

Advertisement call. Dominant (= fundamental) frequency 844–1,033 Hz; call = note duration 0.18–0.21 s; calls pulsatile; rising frequency modulations throughout call; call rate 45–48 calls/min; at least a second harmonic (Heyer and Scott, 2006:190–191) (Fig. 34).

Distribution. Gran Chaco of Argentina, Bolivia, and Paraguay (Fig. 35).

Leptodactylus latinasus Jiménez de la Espada, 1875 (Plate 3D)

Leptodactylus latinasus Jiménez de la Espada, 1875:40. Type locality: Montevideo, Uruguay. Holotype: MNCN 1695, adult female.

Leptodactylus prognathus Boulenger, 1888:187. Type locality: Rio Grande do Sul, Brazil; restricted to "Rio Grande do Sul, provávelmente São Lourenção do Sul" by Bokermann, 1966:74; restricted to "Camaquã, Estado de Rio Grande do Sul, Brasil" by Klappenbach and Langone, 1992:189. Holotype: BMNH 1947.2.17.52, juvenile male. Synonymy by Heyer, 1969c:3.

Leptodactylus anceps Gallardo, 1964c:100. (Type locality –: "Argentina, prov. de Tucumán, Tucumán." Holotype –: MACN 531, adult male.) Synonymy by Barrio, 1965:408 (as *Leptodactylus prognathus*). Synonymy by Heyer, 1978:34.

Leptodactylus latinasus latinasus: Cei, 1980:325.

Leptodactylus latinasus anceps: Cei, 1980:325. Subspecies rejected by Ponssa and Lavilla, 1998:57–63.

Etymology. The Latin adjective *latus* (*lata, latum*), meaning wide, broad, and the noun *nasus* (*nasi*) meaning snout or nose, indicate that the species has a broad snout.

Adult morphology. Small size, female SVL 29.1–36.7 mm ($\overline{X}$ = 33.2 mm), male SVL 27.0–37.9 mm ($\overline{X}$ = 30.9 mm); adult male snout spatulate; males lacking thumb spines and chest spines; light upper lip strip indistinct; dorsal folds absent; dorsolateral folds indistinct to absent; lateral folds interrupted to absent; posterior thigh with a light stripe; upper shank barred; belly usually uniform light (90% of specimens), rarely lightly mottled laterally (10%); toes without lateral fringes (Heyer, 1978:57–59; Heyer and Juncá, 2003).

Similar species. *Leptodactylus latinasus* is morphologically very similar to *L. fragilis,* but their distributions are distinct with *L. latinasus* occurring in Argentina, Brazil, Paraguay, and Uruguay, and *L. fragilis* occurring from southernmost Texas, USA through Mexico to Panamá and Caribbean drainages of Colombia and Venezuela. In South America, *L. latinasus* occurs in sympatry with a single species that lacks toe fringes and has distinct white tubercles on the posterior surfaces of the shank and sole of foot—*L. elenae.* The dorsolateral folds in *L. elenae* are distinct; those of *L. latinasus* are indistinct or absent. *Leptodactylus latinasus* has a mid-dorsal irregular mark, usually reddish or copper in color (in life); this marking is absent in *L. elenae. Leptodactylus latinasus* and *L. caatingae* have considerable morphological and color pattern overlap. However, *L. latinasus* and *L. caatingae* have allopatric distributions and the advertisement calls of *L. latinasus* are not pulsed and have higher dominant frequencies (3,000–3,780 Hz) than the calls of *L. caatingae* that are pulsed and have lower dominant frequencies (940–1,620 Hz).

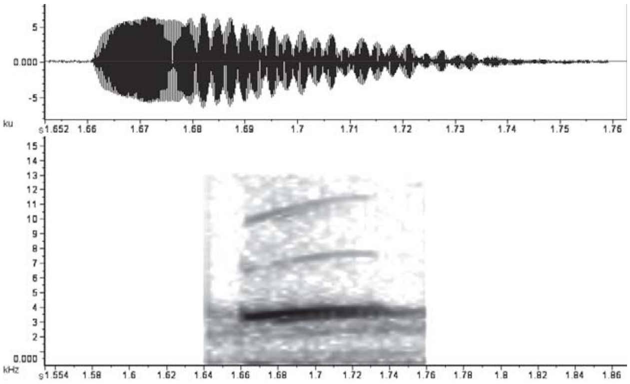

Figure 36. Advertisement call of *Leptodactylus latinasus* (recording USNM 19).

Figure 37. Distribution map of *Leptodactylus latinasus.*

Larval morphology. Maximum total length (Gosner 36) 26.4 mm; oral disk anteroventral; tooth row formula 2(2)/3(1), P1 gap very narrow; tail mottled (Cei, 1980:326, 329; Borteiro and Kolenc, 2007:3–6).

Advertisement call. Dominant (= fundamental) frequency 3,100–4,000 Hz; call duration 0.11–0.20 s; each call a single pulse; rising frequency modulations throughout call; call rate 2.3/s; no harmonic structure (Heyer, 1978:58–59) (Fig. 36).

Distribution. Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Fig. 37).

***Leptodactylus longirostris* Boulenger, 1882 (Plate 3E)**

Leptodactylus longirostris Boulenger, 1882:240. Type locality: "Santarem," Pará, Brazil; see Crombie and Heyer, 1983:291–296, for discussion of type locality. Lectotype: BMNH 76.5.26.4, female, designated by Heyer, 1978:32.

Etymology. From Latin *longus* (long) and *rostrum* (snout).

Adult morphology. Small to moderate size, female SVL 33.3–45.6 mm ($\overline{X}$ = 40.0 mm), male SVL 33.1–44.2 mm ($\overline{X}$ = 38.0 mm); adult male snout spatulate; males lack thumb spines and chest spines; light upper lip stripe either indistinct (60% of specimens) or distinct (40%); dorsal folds present or absent; dorsolateral folds present; lateral folds interrupted or absent; posterior thigh with distinct light stripe (80%) or indistinct (20%); upper shank barred; belly uniform light to weakly speckled in area next to arm insertion; toes without lateral fringes (Heyer, 1978:61–64; Crombie and Heyer, 1983:293–294).

Similar species. *Leptodactylus longirostris* occurs in the Guiana shield region and the Brazilian states of Amazonas, Pará, and Roraima. Similar species within the distribution of *L. longirostris* are *L. fuscus, L. mystaceus,* and *L. poecilochilus*. Only individuals of *L. longirostris* with light mid-dorsal stripes have dorsal folds; all *L. fuscus* have a pair of dorsal folds (individual *L. longirostris* with light mid-dorsal stripes are morphologically difficult to distinguish from *L. fuscus*). The duration of the advertisement call of *L. fuscus* ranges from 0.16–0/17 s; the call duration of *L. longirostris* ranges from 0.01–0.04 s. *Leptodactylus longirostris* lack white tubercles on the sole of the foot; *L. mystaceus* have white tubercles on the sole of the foot. *Leptodactylus longirostris* have indistinct (60% of specimens) to distinct (40%) light upper lip stripes; *L. poecilochilus* lack distinct light lip stripes but often (67%) have a dark suborbital bar not found in *L. longirostris*.

Larval morphology. Maximum total length (Gosner 41) 37.0 mm; oral disk anteroventral; tooth row formula 2(2)/3(0,1); tail mottled (Duellman, 1997:24, fig. 20; Crombie and Heyer, 1983:295–296

Advertisement call. Dominant (= fundamental) frequency 940–2,500 or 1,150–3,000 or 1,500–3,600 Hz; call duration 0.04–0.08 s; calls typically of a single pulse; rising frequency modulations throughout call; call rate 1.4–2.0/s; harmonic structure apparently present or absent (Crombie and Heyer, 1983:294–295; Lescure and Marty, 2000:372) (Fig. 38).

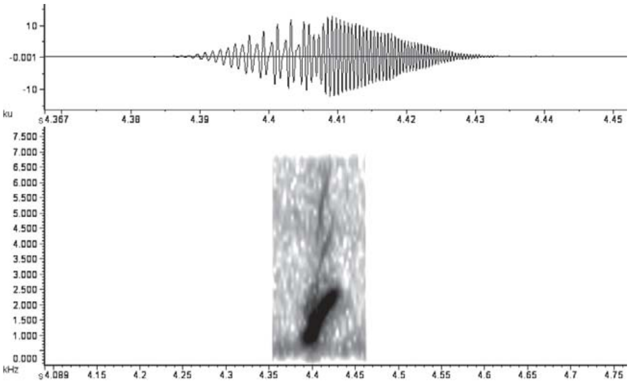

Figure 38. Advertisement of *Leptodactylus longirostris* (recording USNM 53).

Figure 39. Distribution map of *Leptodactylus longirostris*.

Distribution. Guiana Shield region and adjacent Brazil (Fig. 39).

***Leptodactylus marambaiae* Izecksohn, 1976 (Plate 3F)**

Leptodactylus marambaiae Izecksohn, 1976:528. Type locality: "Restinga da Marambaia, Estado do Rio de Janeiro, vivendo nas proximidades do mar [aproximadamente 23°03'S, 43°38~]," Brazil. Holotype: EI 4123, male.

Etymology. Named for the island, Restinga da Marambaia, the only known locality for the species.

Adult morphology. Small–moderate size, female SVL 40.0–41.3 mm ($\overline{X}$ = 40.6 mm), male SVL 35.8–39.3 mm ($\overline{X}$ = 37.0 mm); males lack thumb spines and chest spines; light upper lip stripe distinct; a pair of well-defined dorsal folds; a pair of well-defined dorsolateral folds; a pair of lateral folds; light stripe on posterior thigh usually distinct; upper shank with light longitudinal pin stripes; belly speckled; toes without lateral fringes (Izecksohn, 1976:528; Heyer, 1978:64).

Similar species. *Leptodactylus marambaiae* occurs only on the island of Restinga da Marambaia; there are no other similar species occurring on the island. There is only one similar species in the State of Rio de Janeiro, *Leptodactylus fuscus*. *Leptodactylus marambaiae* has light, narrow longitudinal stripes on the upper shank; *L. fuscus* lacks such light upper shank stripes.

Larval morphology. Unknown.

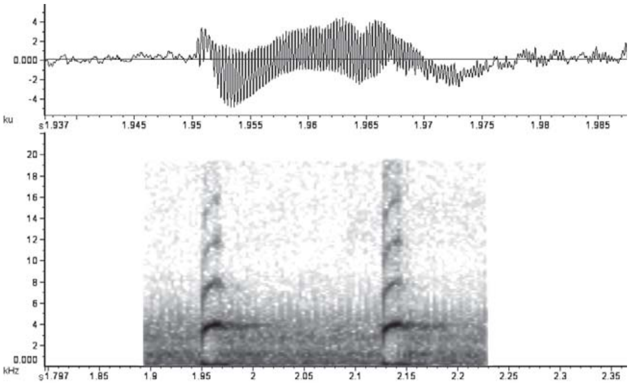

Figure 40. Advertisement of *Leptodactylus marambaiae* (recording USNM 329).

Figure 41. Distribution map of *Leptodactylus marambaiae.*

Advertisement call. Dominant (= fundamental) frequency 3,000–3,700 Hz; call duration about 2 s; about 17 notes per call; note duration about 0.02 s; rising frequency modulations throughout call; no harmonic structure (Heyer, 1978:64–65) (Fig. 40).

Distribution. Restinga da Marambaia, State of Rio de Janeiro (Fig. 41).

Leptodactylus mystaceus **(Spix, 1824) (Plate 4A)**

Rana mystacea Spix, 1824:27. Type locality: "ad Bahiam [now Salvador, Bahia] in aqua fluviatili; differt ab illa prope flumen Solimoens," Brazil; restricted to Solimões (Brazil) by lectotype designation of Méhely, 1904:219; restricted in error to "Salvador, Bahia", Brazil, by Bokermann, 1966:90. Syntypes: Not specifically stated, but including animals figured on pl. 3, figs. 1 and 3 in the original publication, ZSM 2504/0 and 2505/0 (lost after 1955 according to Hoogmoed and Gruber, 1983:357); specimen figured in pl. 3, fig. 1 designated lectotype by implication of Peters, 1872a:196–227; Méhelÿ, 1904:219 designated ZSM 2504/0 as lectotype.

Leptodactylus mystaceus: Fitzinger, 1826:64; Méhelÿ, 1904:219.

Cystignathus mystaceus: Wagler, 1830:203; Hensel, 1867:125.

Leptodactylus (Cavicola) *mystaceus:* Lutz, 1930:22.

Leptodactylus amazonicus Heyer, 1978:38. Type locality: "Ecuador; Napo Province, Limoncocha, 00°24'S, 76°37'W, elevation 260 m." Holotype: LACM 92111, by original designation.). Synonymy by Heyer, 1983:270.

Etymology. From the Greek *mystax, mystakos,* upper lip, mustache, referring to the obvious light facial stripe.

Adult morphology. Moderate size, female SVL 44.5–56.1 mm ($\bar{X}$ = 50.1 mm), male SVL 42.4–52.2 mm ($\bar{X}$ = 47.4 mm); adult male snout spatulate; males lacking thumb spines and chest spines; light upper lip stripe distinct (56% of specimens) or indistinct (44%); dorsal folds absent; dorsolateral folds distinct, complete; lateral folds absent; posterior thighs with light, transverse stripe (93%); upper shank barred; belly uniform light to small melanophore blotches scattered across anterior belly and extending centrally; toes without lateral fringes (Heyer, 1978:38–44, as *L. amazonicus*).

Similar species. *Leptodactylus mystaceus* has a broad distribution in the Amazon basin and extending as far as the interior portions of the Brazilian states of Minas Gerais and São Paulo, as well as the northern Atlantic Forests of Brazil. Similar species lacking toe fringing that occur with *L. mystaceus* are *L. didymus, L. fuscus, L. gracilis,* and *L. longirostris. Leptodactylus didymus* and *L. mystaceus* are morphologically indistinguishable. The advertisement

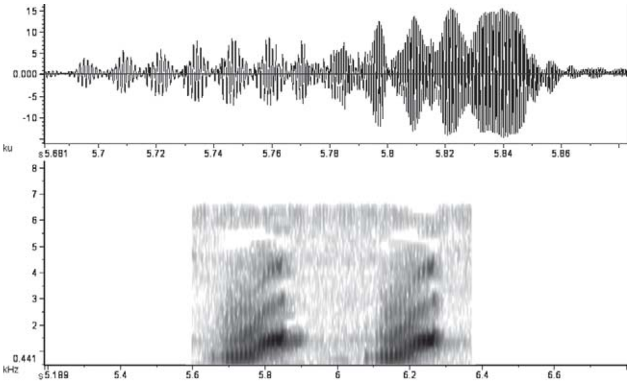

Figure 42. Advertisement of *Leptodactylus mystaceus* (recording USNM 22).

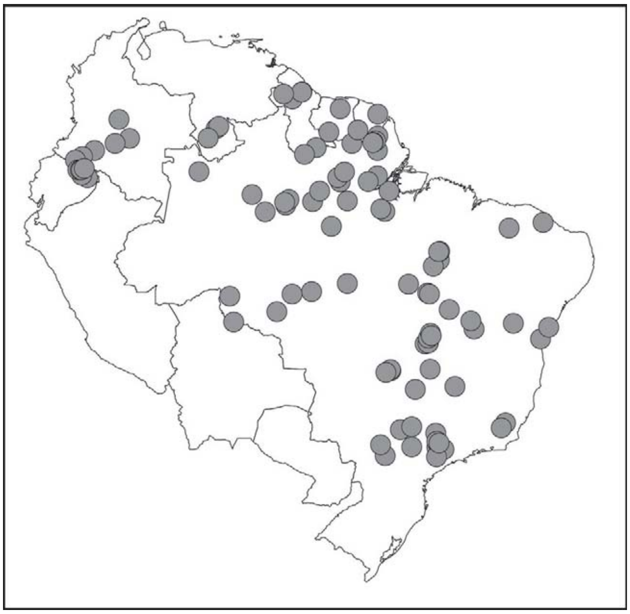

Figure 43. Distribution map of *Leptodactylus mystaceus.*

call of *L. mystaceus* is pulsed; the call of *L. didymus* is unpulsed. *Leptodactylus fuscus* and *L. gracilis* have a pair of dorsal folds; *L. mystaceus* lacks dorsal folds. *Leptodactylus mystaceus* has light tubercles on the sole of the foot; *L. longirostris* lacks tubercles on the sole of the foot.

Larval morphology. Maximum total length (Gosner 40) 36.2 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Heyer, 1978:41–42).

Advertisement call. Dominant (= fundamental) frequency 700–1,400 Hz; note duration 0.2 s; notes pulsed; rising frequency modulations throughout call; call = note rate 1.8/s; no harmonic structure (Heyer, 1978:41, 43; Heyer et al., 1996a:7–31) (Fig. 42).

Distribution. Amazonia, extending into interior portions of the Brazilian states of Minas Gerais and São Paulo and in mesic enclaves in northeastern Brazil as well as northern portions of the Atlantic Forests of Brazil (Fig. 43).

Leptodactylus mystacinus (Burmeister, 1861) (Plate 4B)

Cystignathus mystacinus Burmeister, 1861:532. Type locality: "Rozario," Argentina. Holotype: MLU unnumbered male according to Heyer, 1978:68.

Cystignathus labialis Cope, 1877:90. Type locality: "The precise habitat of this species is at present uncertain. It is probably a part of Sumichrast's Mexican collection." Other specimens Cope described in the same paper had the following statement: "Habitat unknown, but supposed to be the Argentine Confederation" (page 92). It is likely that the specimens Cope described as *C. labialis* were from Argentina. Type locality restricted in error by Smith and Taylor, 1950:350, to "Potrero Viejo," Veracruz; rendered as "probably Tehuantepec, Oaxaca, Mexico" by Cochran, 1961:40. Previous statements and restrictions of type locality are in error according to Heyer, 2002:321, who made the synonymy, following Heyer, 1978:84. Types: Kellogg, 1932:84 considered USNM 31300–31305 to be syntypes of *C. labialis*. Cochran, 1961:40, however, considered USNM 31302 to be the holotype and the other specimens paratypes, thus a lectotype designation by implication.

Leptodactylus labialis: Brocchi, 1881–1883:20.

Leptodactylus mystacinus: Boulenger, 1882:244.

Leptodactylus (*Cavicola*) *mystacinus:* Lutz, 1930:22.

Etymology. From the Greek *mystax,* upper lip, in allusion to the striking light upper lip stripe.

Adult morphology. Moderate size, female SVL 53.5–67.1 mm ($\overline{X}$ = 57.4 mm), male SVL 43.6–65.0 mm ($\overline{X}$ = 54.1 mm); adult male snout spatulate; males lacking thumb spines and chest spines; light upper lip stripe usually distinct (86% of specimens); dorsal folds absent; usually a pair of distinct dorsolateral folds; dorsum between the dorsolateral folds without markings or pattern; lateral folds interrupted or absent; light posterior thigh stripe usually absent (94% of specimens), rarely indistinct (6%); upper shank barred; belly lightly mottled; toes without lateral fringes (Heyer, 1978:65–68; Heyer et al., 2003:1; Sazima 1975:7–11).

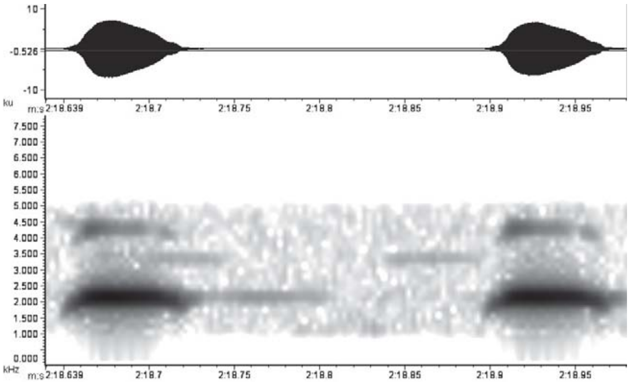

Figure 44. Advertisement of *Leptodactylus mystacinus* (recording USNM 16).

Figure 45. Distribution map of *Leptodactylus mystacinus.*

Similar species. *Leptodactylus mystacinus* occurs in Bolivia, Argentina, central, eastern, and southern Brazil, Paraguay, and Uruguay. The only similar species that occurs with *L. mystacinus* (with no light thigh stripe and distinct white tubercles on the posterior surface of the tarsus) is *L. bufonius. Leptodactylus mystacinus* has distinct dorsolateral folds; dorsolateral folds in *L. bufonius* are indistinct or absent.

Larval morphology. Maximum total length (Gosner 38) 45.0 mm; oral disk anteroventral; tooth row formula 2(1)/3(1); tail mottled (Heyer et al., 2003:1–2; Sazima, 1975:32–34; note that Cei's, 1980, illustration on page 332 is likely not of *L. mystacinus*). Langone and de Sá (2005) reviewed available descriptions for the species.

Advertisement call. Dominant (= fundamental) frequency between 2,050–2,500 Hz; call duration 0.04–0.06 s; call a single note; call lacking or with negligible amplitude modulation; call rate 250–400/min; harmonic structure present or absent (Heyer et al., 2003:2–3) (Fig. 44).

Distribution. Argentina, Bolivia, central- eastern- and southern Brazil, Paraguay, and Uruguay (Fig. 45).

Leptodactylus notoaktites **Heyer, 1978 (Plate 4C)**

Leptodactylus notoaktites Heyer, 1978:68. Type locality: "Brasil: São Paulo, Iporanga." Holotype: MZUSP 25428, female.

Etymology. From the Greek *notos,* south, and *aktites,* coast dweller, in reference to the distribution of the species.

Adult morphology. Moderate size, female SVL 43.4–55.8 mm ($\bar{X}$ = 48.0 mm), male SVL 42.5–54.2 mm ($\bar{X}$ = 47.5 mm); male snout weakly spatulate; males lacking thumb spines; males lacking chest spines; light upper lip stripe from tip of snout to jaw commissure; a pair of dorsal folds only in individuals with a light mid-dorsal stripe; dorsolateral folds distinct; lateral folds interrupted; posterior thigh with light stripe; upper shank barred; belly uniform light to having small spots on lateral and anterior portions of belly (Heyer, 1978:68–69).

Similar species. *Leptodactylus notoaktites* occurs in the Atlantic Forest Morphoclimatic Domain in the Brazilian states of Paraná, Santa Catarina, and São Paulo. The only other similar species that occurs in the more interior regions of the State of São Paulo is *L. mystaceus.* Only individual *L. notoaktites* with a light mid-dorsal stripe also have a pair of dorsal folds; no *L. mystaceus* have a pair of dorsal folds or a light mid-dorsal stripe. Some *L. notoaktites* have a smooth sole of the foot; all *L. mystaceus* have white tubercles on the sole of the foot.

Larval morphology. Maximum total length (Gosner 33) 22.3 mm; oral disk anteroventral; tooth row formula 2(2)/3; tail finely speckled with dark melanophores (de Sá et al., 2007b:70).

Advertisement call. Dominant (= fundamental) frequency modulated between 567–631 Hz at beginning of call, rising to 1,700–1,788 Hz at end of call; call duration 0.086–0.096 s; each call a single partially pulsed note; rising frequencies throughout most of call with short plateaus at beginning and end of call; call rate 0.7 calls/s; calls with pronounced harmonic structure (Fig. 46).

Distribution. Atlantic forests in the Brazilian states of Paraná, Santa Catarina, and São Paulo (Fig. 47).

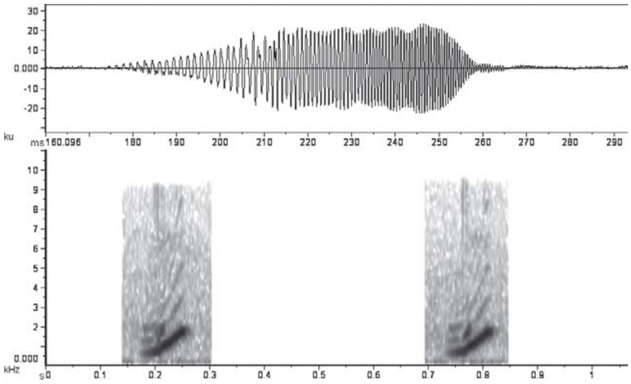

Figure 46. Advertisement of *Leptodactylus notoaktites* (recording USNM 10).

Figure 47. Distribution map of *Leptodactylus notoaktites.*

Leptodactylus oreomantis **Carvalho, Fortes, Pezzuti, 2013**

Leptodactylus oreomantis Carvalho, Fortes, Pezzuti, 2013:350. Type locality: Brazil, Bahia, Municipality of Rio de Contas, Serra das Almas, Vale do Queiroz. Holotype: UFMG 3825, adult male.

Etymology. From the Greek *oreos,* mountain + *mantis* prophet, but also used to refer to frogs as weather forecasters.

Adult morphology. Small, female SVL 33.2–38.3 mm ($\overline{X}$ = 36.1 mm), male SVL 28.1–33.8 mm ($\overline{X}$ = 31.2 mm); snout pointed, weakly spatulate; body slender; males without thumb and chest spines; irregular brown upper lip stripe overlaid with a white band; dorsal folds present; continuous, sinuous dorsolateral folds; lateral folds present; light stripe on posterior surface of thigh present; upper surfaces of thigh and shank uniformly barred; belly uniform light; toes lacking expanded tips, fringing, or webbing.

Similar species. *Leptodactylus oreomantis* occurs in Campo Rupestre areas from Chapada Diamantina. Morphological similar species are *L. furnarius* and *L. tapiti* that have peep-like advertisement calls whereas *L. oreomantis* has a trill-like call.

Larval morphology. Unknown.

Advertisement call. Dominant (= fundamental) frequency between 2,700–3,100 Hz; call = note duration 0.74–5.09 s; non-pulsed notes; rising frequency modulations throughout call; call rate 7–13/min; harmonic structure present (Carvalho et al. 2013).

Distribution. Known only from the type locality in the State of Bahia, Brazil.

Leptodactylus plaumanni **Ahl, 1936 (Plate 4D)**

Leptodactylus plaumanni Ahl, 1936:389. Type locality: "Nova Teutonia, [Santa Catarina State], Brasilien," 22°17'S, 52°20'W. Holotype: Originally in Deutsch Kolonial and Uebersee Museum, Bremen, now SMF 22469, male.

Leptodactylus geminus Barrio, 1973:199. Type locality: "Bernardo de Irigoyen, Misiones, Argentina." Holotype: CHINM 5860, by original designation, now in MACN as MACN 5860, sex uncertain (the jar label indicates the specimen is a male, but WRH could not detect vocal slits and he considers the specimen to be a female). Synonymy by Kwet et al., 2001:56.

Etymology. Ernst Ahl named *Leptodactylus plaumanni* for Fritz Plaumann, who lived and collected around Nova Teutonia (now Seara), Santa Catarina, Brazil. Plaumann collected insects primarily but also sent frogs to Dr. Ahl for incorporation in the German collection curated by Dr. Ahl.

Adult morphology. Moderate size, female SVL 40–46 mm, male SVL 35–42 mm (data from Kwet and Di-Bernardo, 1999:66); male snout calloused, not spatulate; males lacking thumb spines and chest spines; light upper lip stripe distinct; a pair of distinct dorsal folds; a pair of distinct dorsolateral folds; a pair of distinct lateral folds;

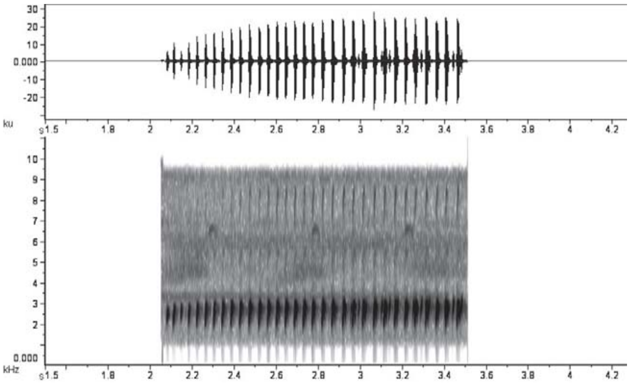

Figure 48. Advertisement of *Leptodactylus plaumanni* (recording USNM 226).

Figure 49. Distribution map of *Leptodactylus plaumanni*.

posterior thigh with light stripe; upper shank with narrow longitudinal light stripes; belly uniform light; toes without lateral fringes (Barrio, 1973:199–206 [as *L. geminus*], Kwet and Di-Bernardo, 1999:66–67).

Similar species. *Leptodactylus plaumanni* occurs in the Province of Misiones, Argentina and the states of Rio Grande do Sul and Santa Catarina, Brazil. The only other species that occurs in this region that has narrow light longitudinal stripes on the upper shanks is *L. gracilis*. There are no morphological features that differentiate *L. plaumanni* from *L. gracilis*. The advertisement call rate of *L. plaumanni* is 13–23 calls/s; that of *L. gracilis* is 3–4 calls/s.

Larval morphology. The larva has not been described. A recent examination of larvae at the Herpetological collection of the Museu de Ciencias e Tecnologia, PUCRS, discovered a single tadpole with catalog number MCP3913 from Potreiro Vivo, Sao Francisco de Paula, Rio Grande do Sul, Brazil. Email communication (November 11, 2013) with Dr. Mirco Solé informed that this specimen is from a clutch laid by adults of *L. plaumanni* within one of his experimental enclosures (1 m^2). The larva has a maximum total length (Gosner 26) 32 mm; oral disk anteroventral; with ventrolateral folds on each side; tooth row formula 2(2)/3(2); tail light-brown without markings; fins transparent.

Advertisement call. Dominant (= fundamental) frequency 2,700–3,100 Hz; note duration 0.02–0.03 s; notes of 1–3 pulses; rising frequency modulation throughout call; no harmonic structure (Barrio, 1973:199–206; Cardoso, 1985:87–90) (Fig. 48).

Distribution. Argentina (Misiones) and southern Brazil (Rio Grande do Sul, Paraná, and Santa Catarina) (Fig. 49).

***Leptodactylus poecilochilus* (Cope, 1862) (Plate 4E)**

Cystignathus poecilochilus Cope, 1862:156. Type locality: “Near Turbo, [Antioquia,] New Granada [= Colombia].” Syntype: “Mus. Smithsonian [USNM], [No. 4347] Acad., Philadelphia,” male. Cope apparently had two specimens in hand that he considered as types. One of the types was clearly designated as belonging in the USNM; the other specimen was presumably deposited in the ANSP but seemingly has since been lost. Cochran, 1961:40, reported USNM “4347a” to be the holotype, but the specimen tag on the USNM type does not bear an “a.”

Leptodactylus poecilochilus: Boulenger, 1882:343.

Leptodactylus quadrivittatus Cope, 1894 “1893”:339. Type locality: “Buenos Ayres” [= Buenos Aires], Cantón de Buenas Aires, Provincia de Puntarenas, Costa Rica (for comments on the type locality see Savage, 1974:82). Holotype: Originally No. 365 in Museo Nacional de Costa Rica; now lost according to Dunn, 1940:106. Synonymy by Dunn, 1940:106; Heyer, 1970b “1968”:182; Heyer, 1978:33.

Leptodactylus maculilabris Boulenger, 1896:404–405. Type locality: “Bebedero, [Cantón de Cañas, Province of Guanacaste,] Costa Rica” (for comments on the type locality see Savage, 1974:78). Holotype: BMNH 94.11.15.27. Synonymy by Dunn, 1940:106; Heyer, 1970b “1968”:182; Heyer, 1978:33.

Leptodactylus diptychus Boulenger, 1918:431. Type locality: “Andes of Venezuela.” Holotype: BMNH 94.8.31.11, female.) Synonymy by Heyer, 1978:34.

Leptodactylus poecilochilus poecilochilus: Rivero, 1961:43.

Leptodactylus poecilochilus dyptichus: Rivero, 1961:42. Incorrect subsequent spelling for *diptychus*.

Etymology. From the Greek *poikilos,* variegated, and *cheilos,* lip.

Adult morphology. Moderate size, female SVL 39.0–54.1 mm ($\overline{X}$ = 46.2 mm), male SVL 39.0–48.7 mm ($\overline{X}$ = 44.6 mm); adult male snout spatulate; males lacking thumb spines and chest spines; light upper lip stripe indistinct; a pair of dorsal folds only in individuals with a light mid-dorsal stripe; distinct pair of dorsolateral folds; lateral folds complete; posterior thigh light stripe usually distinct (77% of specimens), sometimes indistinct (21%), rarely absent (2%); upper shank barred; belly usually light or with light speckling; toes without lateral fringes (Heyer, 1970b “1968”:182–184, 1978:69–71).

Similar species. Species that lack toe fringes and co-occur with *Leptodactylus poecilochilus* are *L. fragilis* and *L. fuscus*. *Leptodactylus poecilochilus* have a pair of distinct dorsolateral folds; *L. fragilis* have indistinct dorsolateral folds. Only specimens of *L. poecilochilus* that have a broad mid-dorsal light stripe also have a pair of dorsal folds, most lack scattered dorsal blotches, and most (67% of specimens) have a dark sub-orbital bar; all *L. fuscus* have a pair of dorsal folds, scattered dorsal blotches, and no suborbital bar.

Larval morphology. Maximum total length (Gosner 41) 37 mm; oral disk anteroventral; tooth row formula 2(2)/3[1]; tail mottled (Heyer, 1970b “1968”:183–184, 195–199).

Advertisement call. Dominant (= fundamental) frequency 350–550 Hz (Panamá) or 700–1,300 Hz (Costa Rica); call/note duration 0.055–0.080 s; call not pulsed; rising frequency modulations throughout call; call rate 1.7/s; harmonic structure present or absent (Fouquette, 1960:205, 207–209 [as *L. quadrivittatus*], Heyer, 1978:69) (Fig. 50).

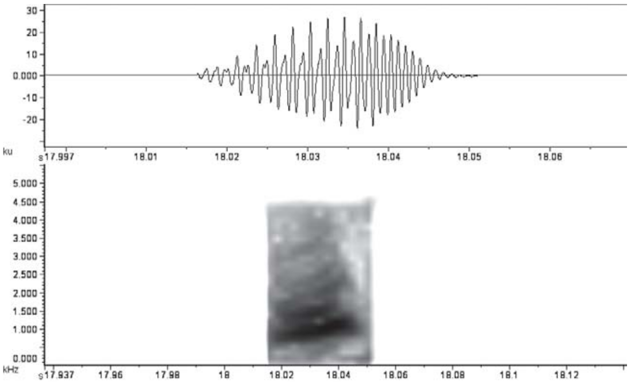

Figure 50. Advertisement of *Leptodactylus poecilochilus.*

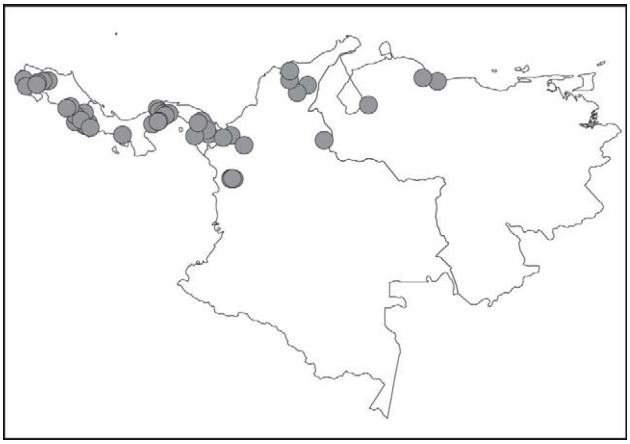

Figure 51. Distribution map of *Leptodactylus poecilochilus.*

Distribution. Lowlands of Costa Rica to north coastal South America as far as Venezuela (Fig. 51).

Leptodactylus sertanejo Giaretta and Costa, 2007 (Plate 4F)

Leptodactylus sertanejo Giaretta and Costa, 2007:3. Type locality: “Clube de Caça e Pesca Itororó de Uberlândia (around 19°00’00”S, 48°18’53”W, 850 m asl), municipality of Uberlândia, State of Minas Gerais, Brazil.” Holotype: ZUEC 13657, adult male.

Etymology. “The specific name ‘*sertanejo*’ is a Portuguese word to those people who live in the wilderness, far from civilization. It also can refer to the Brazilian country music, generally performed by duets. We use it as a noun in apposition to make reference to our preferred way of life which includes a lot of outdoor activities, including field works, sometimes listening to traditional Brazilian music.” (Giaretta and Costa, 2007:9).

Adult morphology. Moderate size, female SVL $\overline{X}$ = 54.3 mm (1.4 SD), male SVL $\overline{X}$ = 51.0 mm (1.7 SD); adult male snout not spatulate (based on illustration in Giaretta and Costa, 2007:7, fig. 4); males lack thumb spines and chest spines; distinct light upper lip stripe; distinct pair of dorsal folds; distinct pair of dorsolateral folds; distinct pair of lateral folds; posterior thigh with light stripe (based on similarity with *L. jolyi*); upper shank with a light longitudinal pin stripe; belly and throat cream; toes without lateral fringes (Giaretta and Costa, 2007:1–10).

Similar species. *Leptodactylus sertanejo* is very similar to *L. jolyi*. At present, the only verified locality for *L. sertanejo* is the Municipality of Uberlândia, Minas Gerais, Brazil, in the Cerrado Morphoclimatic Domain of Brazil. Giaretta and Costa (2007) indicated that the type locality of *L. jolyi* was degraded Atlantic Forest Morphoclimatic Domain; Giaretta and Costa (2007) predicted that frogs currently identified as *L. jolyi* from Cerrado habitats will prove to be *L. sertanejo*. *Leptodactylus jolyi* and *L. sertanejo* cannot be reliably differentiated from each other morphologically. The advertisement call rate of *L. jolyi* is 0.1–0.3/s; that of *L. sertanejo* is 0.02–0.3/s; the call of *L. jolyi* is longer (mode = 0.04 ms) than that of *L. sertanejo* (mode = 0.02 ms).

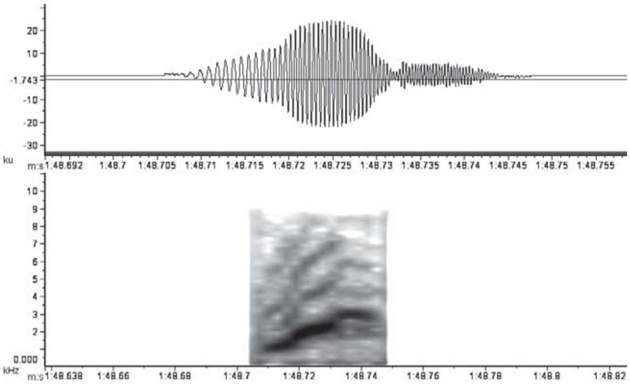

Figure 52. Advertisement of *Leptodactylus sertanejo.*

Figure 53. Distribution map of *Leptodactylus sertanejo.*

Larval morphology. Unknown.

Advertisement call. Dominant frequency 2,000–2,400 Hz; call duration 0.02–0.03 s; call (= note) single or double-pulsed; rising frequency modulations throughout call; call rate 1–18/min.; no harmonic structure (Giaretta and Costa 2007:1–10) (Fig. 52).

Distribution. Currently known from the Municipality of Uberlândia, Minas Gerais; predicted to occur more broadly in the Cerrado Morphoclimatic Domain (Fig. 53).

Leptodactylus spixi Heyer, 1983 (Plate 5A)

Leptodactylus spixi Heyer, 1983:270. Type locality: "Brazil: Rio de Janeiro; Saco de São Francisco, Niteroi." Holotype: USNM 96409, adult male.

Etymology. Named for Johann Baptist von Spix, one of the earliest naturalists to collect and report on Brazilian amphibians and reptiles.

Adult morphology. Moderate size, female SVL 38.7–48.6 mm ($\overline{X}$ = 43.8 mm), male SVL 38.8–47.1 mm ($\overline{X}$ = 42.6 mm); adult male snout variable, spatulate in some males, rounded in others; males lack thumb spines and chest spines; light upper lip stripe usually distinct (79% of specimens); dorsal folds present only in individuals with a light mid-dorsal stripe; distinct pair of dorsolateral folds; lateral folds interrupted or absent; posterior thigh with light stripe; upper shank barred; belly without pattern or with small spots on lateral and anterior belly; toes without lateral fringes (Heyer, 1978:64–65 [as *L. mystaceus*]; Heyer, 1983:270–272).

Similar species. *Leptodactylus spixi* occurs in the Atlantic Forests of the Brazilian states of Bahia, Espírito Santo, and Rio de Janeiro. It is unclear whether there is distributional overlap of *L. spixi* with *L. mystaceus* in Bahia or more northern coastal Brazilian states (Alagoas, Pernambuco, Rio Grande do Sul, Sergipe). In addition to *L. mystaceus,* other similar species are *L. fuscus* and *L. marambaiae;* all of these species lack toe fringes and have light transverse stripes on the posterior thighs. Only individuals of *L. spixi* that have a median light dorsal stripe have a pair of dorsal folds and all *L. spixi* have white tubercles on the dorsal shank surface; all specimens of *L. fuscus* have a pair of dorsal folds and lack white tubercles on the dorsal shank surface. *Leptodactylus spixi* lacks a narrow, light longitudinal stripe on the upper surface of the shank; *L. marambaiae* has a light longitudinal stripe on the upper shank. *Leptodactylus spixi* has white tubercles on the upper shank surface; *L. mystaceus* has no white tubercles on the upper shank surface.

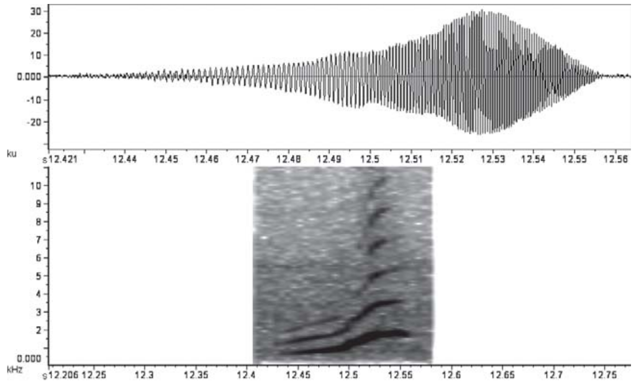

Figure 54. Advertisement of *Leptodactylus spixi.*

Figure 55. Distribution map of *Leptodactylus spixi.*

Larval morphology. Maximum total length (Gosner 35) 25.6 mm; oral disk anteroventral; tooth row formula 2(2)/3; tail mottled (Bilate et al., 2007 "2006":238–240).

Advertisement call. Dominant (= fundamental) frequency 1,500–1,722 and 1,981–2,067 Hz; call duration 120 ± 10 ms; call consisting of a single unpulsed note; rising frequency modulations through most of call; call rate 80–97/min; call with pronounced harmonic structure (Bilate et al., 2007 "2006":237–238) (Fig. 54).

Distribution. Atlantic forests in the Brazilian states of Bahia, Espírito Santo, and Rio de Janeiro (Fig. 55).

Leptodactylus syphax Bokermann, 1969 (Plate 5B)

Leptodactylus syphax Bokermann, 1969:13. Type locality: "São Vicente [Gustavo Dutra], Cuiabá, 600 m, Mato Grosso, Brasil." Holotype: MZUSP 73851, originally WCAB 16141, adult male.

Etymology. From the Greek *syphax* (sweet new wine) in allusion to the bright red color in life of the groin, belly, and ventral surfaces of the thighs and shanks occurring in some, but not all, specimens.

Adult morphology. Moderate size, female SVL 70.5–89.8 mm ($\overline{X}$ = 78.8 mm), male SVL 57.5–83.4 mm ($\overline{X}$ = 72.7 mm); adult male snout not spatulate; adult males with a pair of large, black, sharp thumb spines and a pair of black sharp chest spines; light upper lip stripe absent; dorsal folds absent; dorsolateral folds absent; lateral folds absent or largely interrupted; posterior thigh without a light stripe; upper shank barred; belly lightly to moderately mottled with light gray or brown markings; lateral surfaces of toes smooth or weakly ridged (not fringed) (Heyer et al., 2010a:1).

Similar species. *Leptodactylus syphax* occurs in open habitats, characteristically rocky outcrops, in Bolivia (Department of Santa Cruz), Brazil (States of Ceará, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraiba, Piauí, São Paulo, Tocantins, and Distrito Federal), and Paraguay (Departments of Concepción, La Cordillera). Other species that occur with *L. syphax* that lack dorsolateral folds and toe fringes are *L. bufonius, L. labyrinthicus, L. laticeps,* and *L. troglodytes*. *Leptodactylus syphax* is larger than *L. bufonius* (male SVL 45–49 mm, female SVL 49–62 mm SVL) and male *L. syphax* have thumb and chest spines; male *L. bufonius* lack thumb and chest spines. *Leptodactylus syphax* is smaller (maximum 90 mm SVL) than *L. labyrinthicus* (minimum 117 mm SVL) and *L. syphax* has no dorsolateral folds; most *L. labyrinthicus* have a distinct short pair of dorsolateral folds extending varying distances from behind the eye to the sacrum. The dorsal pattern of *L. syphax* is muted; the dorsal pattern of *L. laticeps* is visually arresting with an aposematic, contrasting dark and light tile-like pattern that is bright yellow, red, and black in life. *Leptodactylus syphax* is larger than *L. troglodytes* (male SVL 45–53 mm, female SVL 45–53 mm SVL) and male *L. syphax* have thumb and chest spines; *L. troglodytes* males have neither thumb nor chest spines. *Leptodactylus syphax* lacks a pseudo-odontoid on lower jaw; *L. troglodytes* has a pseudo-odonotid on lower jaw.

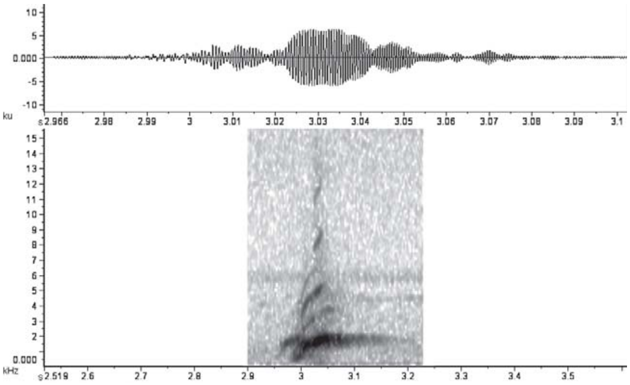

Figure 56. Advertisement of *Leptodactylus syphax* (recording USNM 319).

Figure 57. Distribution map of *Leptodactylus syphax.*

Larval morphology. Maximum total length (Gosner 41) 43.9 mm; oral disk anteroventral, tooth row formula 2(2)/3(1); tail mottled (Heyer et al., 2010a:1–2).

Advertisement call. Dominant (= fundamental) frequency 1,310–1,330, 1,640–1,680, or 1,800–1,850 Hz; call duration 53–64 ms; calls with 2–3 pulses; rising frequency modulations throughout call; call rate 48–90/min; harmonic structure present (Heyer et al., 2010a:2) (Fig. 56).

Distribution. *Leptodactylus syphax* occurs in open habitats, usually rocky outcrops, in Bolivia, Brazil, and Paraguay (Fig. 57).

Leptodactylus tapiti Sazima and Bokermann, 1978 (Plate 5C)

Leptodactylus tapiti Sazima and Bokermann, 1978:910. Type locality: "Chapada dos Veadeiros, [1800 m], Alto Paraíso de Goiás, Goiás, Brasil." Holotype: MZUSP 73680, originally WCAB 47622, adult male.

Etymology. Sazima and Bokermann (1978) did not provide an etymology for their new species *Leptodactylus tapiti*. "*Tapiti*" is an indigenous name for rabbit, presumably named as for their other new species *L. cunicularius,* which excavates the incubating chamber in a manner similar to rabbits.

Adult morphology. Small, female SVL 35.8–41.4 mm ($\overline{X}$ = 38.3 mm), male SVL 29.8–33.4 mm ($\overline{X}$ = 31.6 mm);

adult male snout spatulate; males lacking thumb spines and chest spines; uniform or irregular light upper lip stripe; dorsal folds present; continuous, sinuous dorsolateral folds; lateral folds present; posterior thigh with a light stripe or a line of small light spots; upper shank with interrupted, narrow, longitudinal folds highlighted by small, light dots and lines; belly uniform light; toes without lateral fringes (Sazima and Bokermann, 1978:910).

Similar species. Other species without fringed toes and complete, interrupted, or no light stripes on the posterior thigh in some or possibly all specimens occurring with *L. tapiti* are *L. fuscus, L. mystaceus,* and *L. mystacinus. Leptodactylus tapiti* have interrupted narrow longitudinal folds on the upper shanks; *L. fuscus, L. mystaceus,* and *L. mystacinus* lack any folds or interrupted fold-like structures on the upper shank.

Larval morphology. Maximum total length (Gosner 38) 41.0 mm; oral disk anteroventral; tooth row formula 2(2)/3(1); tail mottled (Sazima and Bokermann, 1978:909, 911).

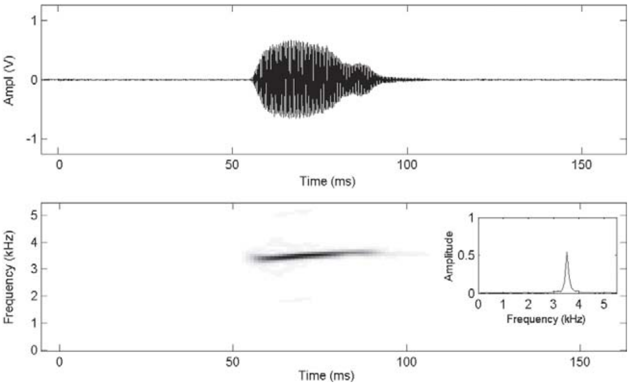

Figure 58. Advertisement of *Leptodactylus tapiti.*

Figure 59. Distribution map of *Leptodactylus tapiti.*

Advertisement call. Dominant (= fundamental) frequency 3,273–3,617 Hz; call duration 31.5–43.9 ms; calls with 2–3 pulses;; call rate 3.0 ± 1.5 notes per second; call without harmonics and an ascendant modulation frequency (Brandão et al., 2013) (Fig. 58).

Distribution. Chapada dos Veadeiros (1800 m), Alto Paraíso, Goiás, Brazil (Sazima and Bokermann, 1978:910) (Fig. 59).

***Leptodactylus troglodytes* Lutz, 1926a (Plate 5D)**

Leptodactylus troglodytes Lutz, 1926a:149. Type locality: “Pernambuco,” Brazil. Holotype: AL-MN 816, adult female.
Leptodactylus (*Cavicola*) *troglodytes:* Lutz, 1930:2, 22.

Etymology. From the Greek *trōglē* (hole made by gnawing) and *dytēs* (burrower), one who creeps into holes.

Adult morphology. Small–moderate size, female SVL 44.9–52.7 mm ($\overline{X}$ = 50.0 mm), male SVL 45.5–52.8 mm ($\overline{X}$ = 48.3 mm); adult male snout spatulate; males lack thumb spines and chest spines; light upper lip stripe absent; dorsal folds absent; dorsolateral folds indistinct, usually absent; lateral folds interrupted or absent; posterior thigh without light stripe; upper shank barred; belly uniform light; toes without lateral fringes (Heyer, 1978:71–73).

Similar species. *Leptodactylus troglodytes* occurs from the state of Minas Gerais in southeast to northeast Brazil (States of Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia). Within the distribution of *L. troglodytes* the only other species that lacks toe fringes, lacks a light thigh stripe, and has distinct white tubercles on the posterior surface of the tarsus is *L. mystacinus. Leptodactylus troglodytes* has either indistinct or (usually) no dorsolateral folds; *L. mystacinus* has distinct, continuous dorsolateral folds. *Leptodactylus troglodytes* is unique in the genus in having a pseudo-odontoid on the lower jaw.

Larval morphology. Maximum total length (Gosner 36) 43.0 mm; oral disk anteroventral; tooth row formula 2(2)/2–3[1]; tail mottled (Cascon and Peixoto, 1985:361–364).

Advertisement call. Dominant (= fundamental) frequency 3,144 Hz with a frequency modulation range of 517–603 Hz; call duration 364–576 ms; call of a single unpulsed note; rising frequency modulations throughout call = note; call rate 56–80/min; no harmonic structure (Kokubum et al., 2009:120–123) (Fig. 60).

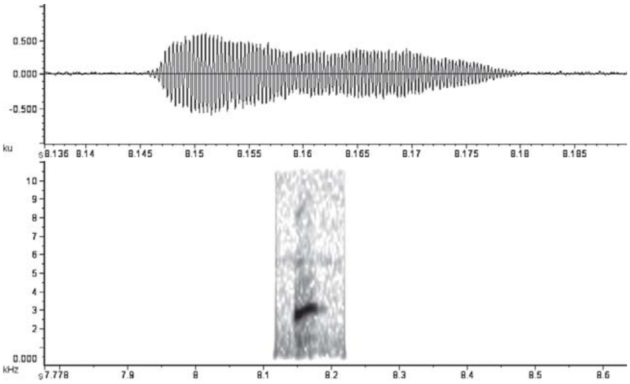

Figure 60. Advertisement of *Leptodactylus troglodytes* (recording USNM 318).

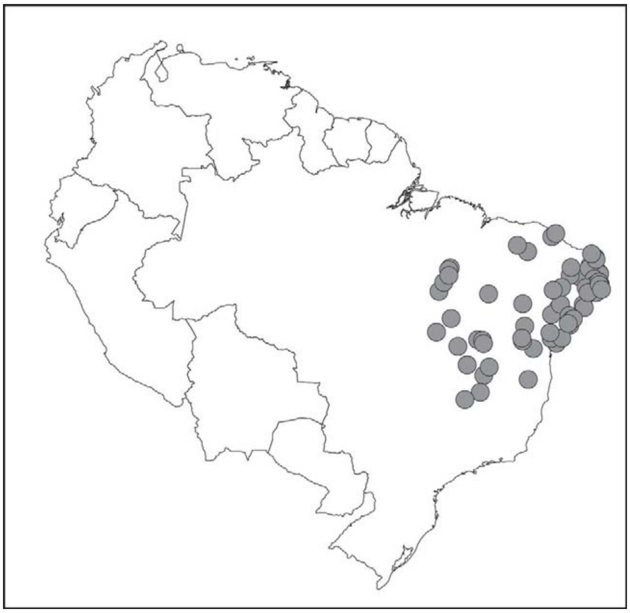

Figure 61. Distribution map of *Leptodactylus troglodytes.*

Distribution. Minas Gerais State in southeast to Northeast Brazil (Fig. 61).

Leptodactylus ventrimaculatus Boulenger, 1902 (Plate 5E)

Leptodactylus ventrimaculatus Boulenger, 1902:53. Type locality: "Bulún [Pulún], 160 feet," Esmeraldas Province, Ecuador. Syntypes: BMNH 1947.2.17.78–80 [3 specimens], BMNH 1947.2.17.78 designated lectotype by Heyer and Peters, 1971:166, adult female.

Etymology. From the Latin *venter* (belly) and *maculatus* (spotted, variegated, full of spots).

Adult morphology. Moderate size, female SVL 46.8–63.2 mm ($\bar{X}$ = 53.2 mm), male SVL 43.5–60.3 mm ($\bar{X}$ = 51.4 mm); adult male snout not spatulate; males lacking thumb spines and chest spines; light upper lip stripe absent; dorsal folds absent; dorsolateral folds usually present; lateral folds absent; light stripe on posterior thigh almost always absent (97% of specimens), rarely indistinct (3%); upper shank barred; belly slightly to heavily mottled; toes without lateral fringes (Heyer, 1978:73–74).

Figure 62. Distribution map of *Leptodactylus ventrimaculatus.*

Similar species. *Leptodactylus ventrimaculatus* occurs in the Chocó of Colombia and adjacent coastal rainforests in Ecuador. The only species that lack a distinct light posterior thigh stripe and lack toe fringes that co-occur with *L. ventrimaculatus* are *L. labrosus* and *L. rhodomerus. Leptodactylus ventrimaculatus* has distinct, scattered, or very few, white tubercles on the sole of the foot; *L. labrosus* usually (91% of specimens) lack white tubercles on the sole of the foot. *Leptodactylus ventrimaculatus* commonly lack flank folds and, if present, are of moderate size; *L. rhodomerus* usually have continuous to interrupted flank folds and are of large size.

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Chocó of Colombia and adjacent Ecuador (Fig. 62).

Leptodactylus pentadactylus species group

Leptodactylus fallax Müller, 1926 (Plate 5F)

Leptodactylus dominicensis Müller, 1923:42. Type locality: "Dominica," Lesser Antilles. Holotype: ZSM 258/1909, female). Junior homonym of *Leptodactylus dominicensis* Cochran, 1923.

Leptodactylus fallax Müller, 1926:200. Replacement name for *Leptodactylus dominicensis* Müller, 1923.

Etymology. The Latin word *fallax* means deceptive.

Adult morphology. Large, female SVL 129.2–167.2 mm ($\overline{X}$ = 148.6 mm), male SVL 121.0–158.7 mm ($\overline{X}$ = 141.6 mm); adult male snout not spatulate; males with one keratinized thumb spine; males lacking chest spines; light upper lip stripe absent; dorsal folds absent; dorsolateral folds usually complete; lateral folds complete, interrupted, or absent; upper shank barred; belly uniformly light or with small melanophore blotches scattered across anterior belly; weak to noticeable lateral ridges on toes (Kaiser, 1994).

Similar species. *Leptodactylus fallax* currently occurs on the islands of Dominica and Monteserrat and is the only species of *Leptodactylus* on these islands.

Larval morphology. Maximum total length (Gosner 42) 110.5 mm; oral disk anteriorly positioned; tooth row formula 1/0; tail patternless (no melanophores) (Lescure and Letellier, 1983:63).

Advertisement call. Dominant (= fundamental) frequency 500–1,500 Hz; call duration 0.18–0.20 s; calls pulsed; rising frequency modulations through most of call with terminal falling frequency; call rate up to 42/min; no harmonic structure (Kaiser 1994:1) (Fig. 63).

Distribution. Kaiser (1994:1–2) indicates that only three Lesser Antillean islands are well documented for natural occurrence of *L. fallax:* Dominica, Montserrat, and Martinique (*L. fallax* is now extinct on Martinique). Doubtful island occurrences on Antigua, Guadaloupe, and St. Lucia are not supported by voucher specimens. Attempts to introduce *L. fallax* on Grenada, Martinique, and Puerto Rico have failed (Kaiser, 1994:2) (Fig. 64).

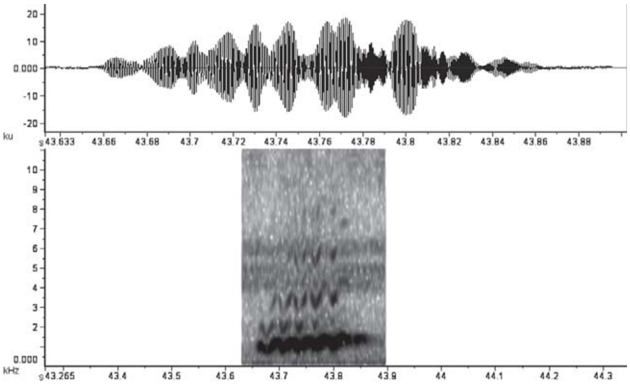

Figure 63. Advertisement call of *Leptodactylus fallax* (recording USNM 96).

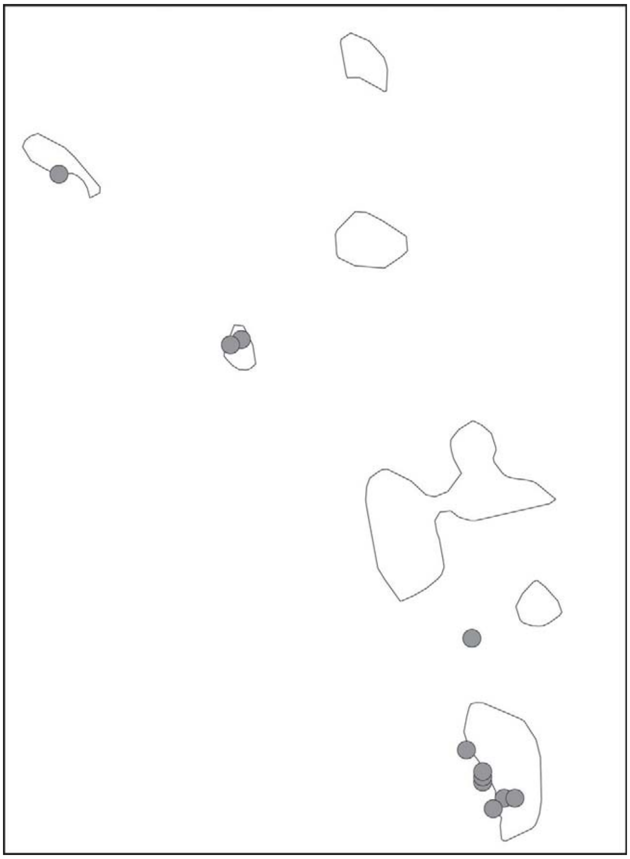

Figure 64. Distribution map of *Leptodactylus fallax.*

Leptodactylus flavopictus **Lutz, 1926a (Plate 6A)**

Leptodactylus flavopictus Lutz, 1926a:144. Type locality: "Mont Serrat na base do Itatiaia," Rio de Janeiro, Brazil. Holotype: AL-MN 870, female.

Leptodactylus pachyderma Miranda-Ribeiro, 1926:150. Type locality: "Ilha Victoria, S[ão] Paulo," Brazil. Holotype: MZUSP 351, adult female.

Leptodactylus pentadactylus flavopictus: Cochran, 1955 "1954":320.

Leptodactylus flavopictus: Heyer, 1979:18.

Etymology. From the Latin *flavus,* yellow, and *pictus,* painted. The color illustration of the venter of *L. flavopictus* in Lutz 1926a plate 31 displays small yellow spots on the throat and large yellow blotches on the chest, belly, and ventral thigh surfaces.

Adult morphology. Large, female SVL 130.0–145.0 mm ($\overline{X}$ = 135.8 mm), male SVL 110.0–135.0 mm ($\overline{X}$ = 124.6 mm); adult male snout not spatulate; males with two keratinized spines on each thumb; adult males with chest spines; narrow to broad light upper lip stripes; dorsal folds absent; weak dorsolateral folds; lateral folds absent; posterior thigh lacking distinct light stripe; upper shank banded; belly mottled; toes with weak ridges (Heyer, 1979:18–20).

Similar species. *Leptodactylus flavopictus* ranges from the Brazilian states of Espírito Santo to Santa Catarina. *Leptodactylus labyrinthicus* is the only similar species found in the general distribution of *L. flavopictus*. *Leptodactylus flavopictus* has a light stripe on the upper lip; *L. labyrinthicus* lacks a light upper lip stripe.

Larval morphology. Unknown.

Advertisement call. Dominant (= fundamental) frequency ca. 650 Hz; call duration 0.06–0.09 s; call of single note/pulse; call without noticeable rising or falling frequency; call rate about 1 call/s; call apparently lacking harmonic structure (Fig. 65).

Distribution. Atlantic forests from the Brazilian states of Espírito Santo to Santa Catarina (Fig. 66).

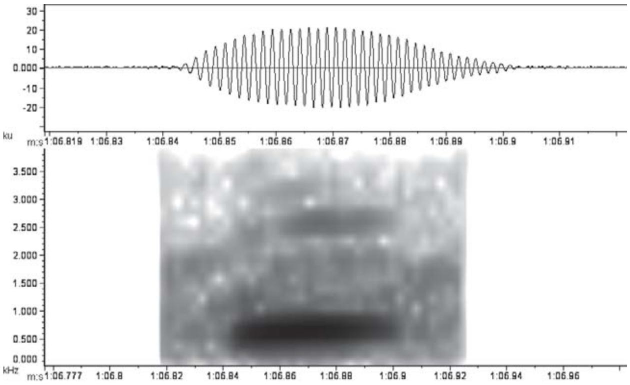

Figure 65. Advertisement call of *Leptodactylus flavopictus*.

Figure 66. Distribution map of *Leptodactylus flavopictus*.

Leptodactylus knudseni **Heyer, 1972 (Plate 6B)**

Leptodactylus knudseni Heyer, 1972:3. Type locality: Ecuador, Napo, Limoncocha. Holotype: LACM 72117, juvenile female.

Etymology. Named for Dr. Jens W. Knudsen whose mentoring influenced W.R. Heyer's pursuit of biology as a profession.

Adult morphology. Large, female SVL 102.7–154.0 mm ($\overline{X}$ = 132.0 mm), male SVL 94.0–170.0 mm ($\overline{X}$ = 131.4 mm); adult snout not spatulate; adult males with a black spine on each thumb; adult males with a pair of large black chest spines; upper lip lacking a distinct light stripe; dorsal folds absent; a pair of dorsolateral folds, usually complete, sometimes interrupted, originating behind eye; lateral folds interrupted or absent; posterior thigh lacking a light stripe, usually dark with small to large light vermiculations or spots; upper shank barred; belly uniform light, uniform dark, mottled, or dark with small light spots or vermiculations; toes with or without weak lateral ridges (Heyer and Heyer, 2006a:1).

Similar species. *Leptodactylus knudseni* has a broad Amazonian distribution, occurring in the same general areas as *L. labyrinthicus, L. myersi, L. paraensis, L. pentadactylus,* and *L. stenodema*. Juvenile *L. knudseni* often have green dorsal coloration in life and solid black posterior thighs; juvenile *L. labyrinthicus, L. myersi, L. paraensis,* and *L. pentadactylus* are not green in life nor do they have solid black posterior thigh patterns. The advertisement calls of *L. knudseni* are pulsed, the advertisement calls of *L. labyrinthicus* are not pulsed. The dorsolateral folds of *L. knudseni* are usually complete, the dorsolateral folds in *L. paraensis* are interrupted and are often interrupted in *L. labyrinthicus*. Sexually active male *L. knudseni* have a pair of chest spines; chest spines are lacking in *L. myersi* and *L. pentadactylus*. The dorsolateral folds of *L. knudseni* originate behind the eye; the dorsolateral folds of *L. stenodema* originate above the posterior edge of the tympanum.

Larval morphology. Maximum total length (Gosner state 40) 69 mm; oral disk almost terminal; tooth row formula 2(2)/2–3(1); tail mottled (Heyer, 2005:316, Heyer and Heyer, 2006a:1–2).

Advertisement call. Dominant (= fundamental) frequency 340–690 Hz; call duration 0.16–0.43 s; 6–14 pulses/call; rising frequency modulations throughout call; call rate 16–66 calls/min; harmonic structure well-developed (Heyer, 2005:316; Heyer and Heyer, 2006a:1–2) (Fig. 67).

Distribution. Gran Sabana of Venezuela and adjacent Lavrado in northern Brazil; mesic, tropical habitats of

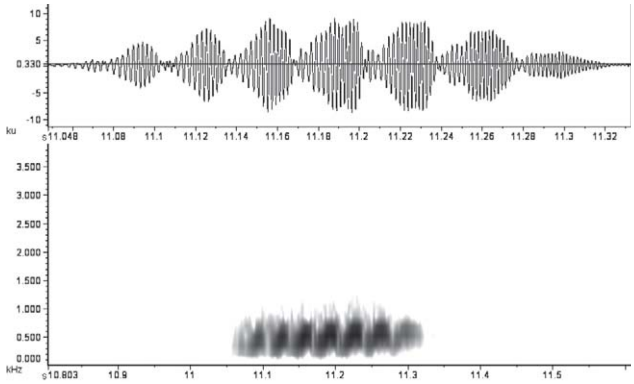

Figure 67. Advertisement call of *Leptodactylus knudseni* (recording USNM 267).

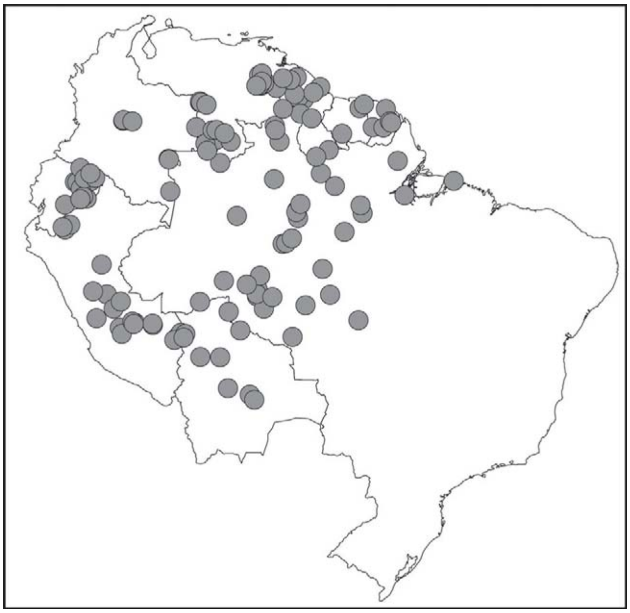

Figure 68. Distribution map of *Leptodactylus knudseni.*

southern Venezuela south to Bolivia and Brazil extending eastward from Ecuador, Colombia, Perú, through Guyana, Suriname, and French Guiana to Trinidad (Fig. 68).

Leptodactylus labyrinthicus (Spix, 1824) (Plate 6C-D)

Rana labyrinthica Spix, 1824:31. Type locality: "Provincia Rio de Janeiro," Brazil. Bokermann, 1966:89 considered the type locality to be in error and suggested that it was "Paraiba, já próximo da divisa com São Paulo." Holotype: ZSM 2501/0, now lost according to Hoogmoed and Gruber, 1983:360.

Cystignathus labyrinthicus: Wagler, 1830:203.

Leptodactylus labyrinthicus: Girard, 1853:420.

Pleurodema labyrinthicus: Günther, 1859b "1858":31.

Gnathophysa labyrinthica: Cope, 1865:112.

Leptodactylus wuchereri Jiménez de la Espada, 1875:68. Type locality: Imprecise; a rough translation (p. 72) is that the specimen was collected by Jiménez de la Espada's deceased companion, Sr. Amor, somewhere between Montevideo and Santiago de Chile and that Jiménez de la Espada did not know in which country (or countries) the frog was collected, nor anything about its habits. Holotype: MNCN 1694, female.

Leptodactylus bufo Andersson, 1911:1. Type locality: Ponta Grosso, Paraná, Brazil. Holotype: NRM 1495.

Leptodactylus pentadactylus labyrinthicus: Müller, 1927:276.

Leptodactylus pentadactylus mattogrossensis Schmidt and Inger, 1951:444. Type locality: "manganese mine, Urucum de Corumba, Matto Grosso," Brazil [locality is now in Mato Grosso do Sul]. Holotype: FMNH 9240, adult female.

Leptodactylus pentadactylus matogrossensis: Bokermann, 1966:74.

Etymology. A dictionary definition of labyrinth is "any intricate or involved enclosure; a maze of paths in a park or garden; also a representation of such a maze, as in a print, or as inlaid in a pavement." Presumably the holotype of *Rana labyrinthica* had a maze-like pattern on the posterior thighs and/or belly.

Adult morphology. Large, female SVL 124.0–166.0 mm ($\overline{X}$ = 145.0 mm), male SVL 110.6–188.0 mm ($\overline{X}$ = 149.4 mm); adult male snout not spatulate; adult males with a single black thumb spine; adult males with a pair of black chest spines; light upper lip stripe absent; dorsal folds absent; a pair of dorsolateral folds usually interrupted from at least midway to full distance from eye to sacrum, rarely absent; lateral folds absent; posterior thigh without light longitudinal stripe, usually dark with a variety of light marks; upper shank barred; belly pattern usually labyrinthine to immaculate; toes with or without lateral ridges (not flexible), vestigial basal web between toes II–III–IV (Heyer, 2005:316–318).

Similar species. *Leptodactylus labyrinthicus* occurs in open formation habitats, including Cerado enclaves in Amazonia. The species most likely to be confused with *L. labyrinthicus* are *L. knudseni, L. paraensis,* and *L. vastus*. Most adult *L. labyrinthicus* have a distinctive labyrinthine belly pattern; adult *L. knudseni* lack this pattern. The advertisement call of *L. labyrinthicus* is unpulsed; the advertisement call of *L. knudseni* is pulsed. *Leptodactylus paraensis* is documented only from closed canopy rain forest in the states of Mato Grosso and Pará, Brazil. There is no consistent morphological feature that completely distinguishes *L. labyrinthicus* from *L. paraensis*. *Leptodactylus labyrinthicus* is slightly larger (male SVL 117–188 mm, female SVL 124–166 mm) than *L. paraensis* (male SVL 94–170 mm, female SVL 102–154 mm). Heyer et al. (2005) indicated specimens from Pará previously identified as

L. labyrinthicus or *L. knudseni* represented a new species based on genetic data.

Larval morphology. Maximum total length (Gosner 40) 80 mm; oral disk almost terminal; tooth row formula 1/2(1); tail mottled (Vizotto, 1967:80–94).

Advertisement call. Dominant (= fundamental) frequency ca. 430 Hz; call duration 0.14–0.21 s; calls unpulsed; slowly rising frequency modulations throughout call; call rate 35–50/min; harmonic structure present (Heyer, 2005:297, 318) (Fig. 69).

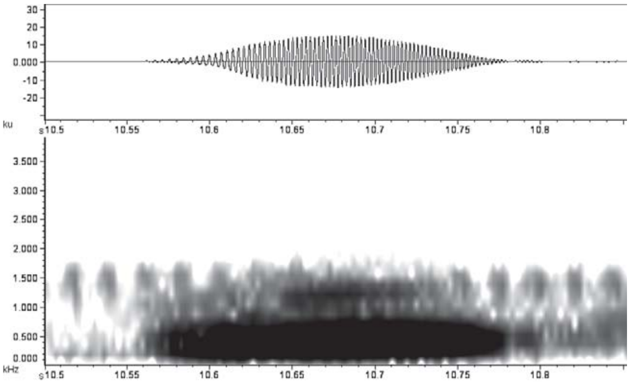

Figure 69. Advertisement call of *Leptodactylus labyrinthicus* (recording USNM 229).

Figure 70. Distribution map of *Leptodactylus labyrinthicus.*

Distribution. *Leptodactylus labyrinthicus* occurs in open formation habitats in Argentina (Provinces of Misiones and Corrientes), Brazil (including Cerrado enclaves in Amazonia), and Paraguay (Fig. 70).

Leptodactylus lithonaetes Heyer, 1995

Leptodactylus lithonaetes Heyer, 1995:708. Type locality: "Venezuela: Amazonas, SW sector Cerro Yapacana, 600 m, 03°57'N, 67°00'W." Holotype: AMNH 100656, adult male.

Etymology. From the Greek *lithos* (stone, rock) and *naetes* (inhabitant), in reference to the species association with rocky outcrops.

Adult morphology. Moderate size, female SVL 52.5–78.4 mm ($\overline{X}$ = 62.8 mm), male SVL 45.3–71.4 mm ($\overline{X}$ = 57.0 mm); adult male snout not spatulate; males with one keratinized thumb spine; males lacking chest spines; light lip stripe absent; dorsal folds absent; dorsolateral folds sometimes absent or usually with a series of short ridges or elongate warts in the shoulder region to series of ridges from eye to sacrum; lateral folds absent; posterior thigh without light stripe; upper shank with irregular bars to irregular spots/blotches; belly uniformly dark to dark with distinct light spots/flecks; toes without lateral fringes (Heyer, 1995:708–711; Heyer and Heyer, 2001:1–3).

Similar species. *Leptodactylus lithonaetes* occurs in Colombia and Venezuela. The only similar species within the general distribution of *L. lithonaetes* having toes not fringed and indistinct dorsolateral folds is *L. rugosus. Leptodactylus lithonaetes* and *L. rugosus* differ only in male secondary sexual characters. *Leptodactylus lithonaetes* males have a single black spine on each thumb and a patch of brown/black tubercles on the chin/throat; some *L. rugosus* have a single thumb spine and others have two spines on each thumb; however, all male *L. rugosus* lack chin tubercles.

Larval morphology. Maximum total length (Gosner 38) 36.1 mm; oral disk ventral; tooth row formulae 2(2)/3 or 2(2)/3(1); tail mottled (Heyer 1995:709,711).

Advertisement call. Initial dominant (= fundamental) frequency ca. 600–780 Hz, long portion of call dominant frequency 2,750–3,200 Hz; call duration 0.62–0.80 s; call of single pulsed notes; pronounced rising frequencies at beginning of call, followed by relatively stable frequencies; calls sporadic (separated by 2 to 20 s; initial portion of call with pronounced harmonics, most of call apparently

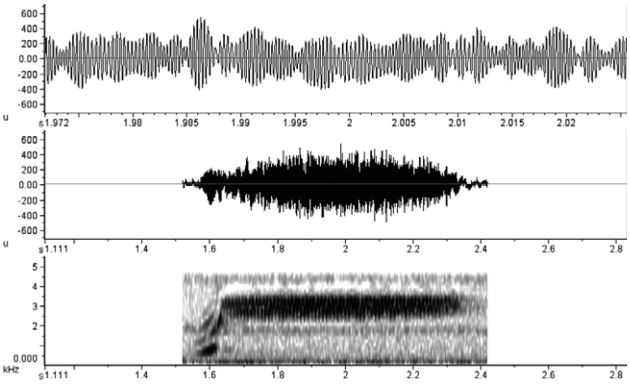

Figure 71. Advertisement call of *Leptodactylus lithonaetes*.

Figure 72. Distribution map of f *Leptodactylus lithonaetes*.

lacking harmonic structure (Heyer and Barrio-Amorós, 2009:282–288) (Fig. 71).

Distribution. Rocky outcrops in Colombian Departments of Amazonas, Guainía, Vaupés, Vichada and Venezuelan States of Amazonas, Apure, and Bolívar (Fig. 72).

Leptodactylus myersi **Heyer, 1995 (Plate 6E)**

Leptodactylus myersi Heyer, 1995:712. Type locality: "Brazil: Roraima; Mucajaí, 02°25'N, 60°55'W". Holotype: MZUSP 66089, adult male.

Etymology. Named for Dr. Charles W. Myers for his contributions to Neotropical herpetology in general and for bringing this new species to W.R. Heyer's attention in particular.

Adult morphology. Moderate–large size, female SVL 78.9–112.9 mm ($\overline{X}$ = 103.2 mm), male SVL 74.2–123.4 mm ($\overline{X}$ = 100.5 mm); adult males with one large (rarely small) keratinized thumb spine; males lack chest spines; upper lips rarely with a broad light stripe; dorsal folds absent; dorsolateral folds often absent or interrupted from at least ¼ to full distance from eye to sacrum; lateral folds absent; posterior thigh dark with various kinds of light marks; upper shank barred; belly ranging from dark, with various kinds of light marks, to almost uniformly light with very few melanophores; toes without lateral fringes (Heyer, 1995:710, 712–713; 2005:318–320).

Similar species. *Leptodactylus myersi* occurs in French Guiana, Suriname, and adjacent Brazil. The moderate to large species that co-occur with *L. myersi* are *L. knudseni* and *L. pentadactylus*. *Leptodactylus myersi* usually lacks distinct, complete lateral folds; *L. pentadactylus* has distinct, complete lateral folds. *Leptodactylus myersi* is typically limited to rocky outcrops in French Guiana, Suriname, and northeastern Brazil; *L. knudseni* is widely distributed throughout the Amazon basin and does not occupy rocky

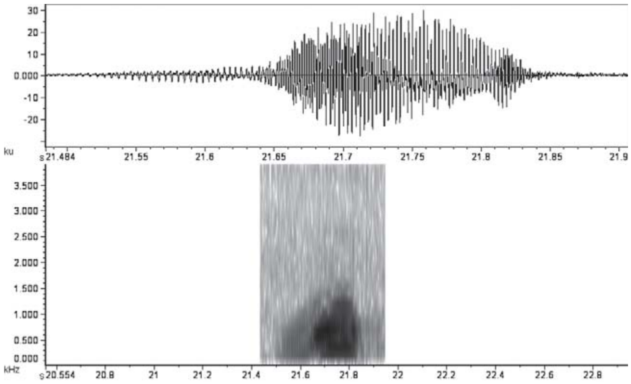

Figure 73. Advertisement call of *Leptodactylus myersi*.

7Figure 74. Distribution map of *Leptodactylus myersi*.

outcrops. Reproductively active males of *L. myersi* lack chest spines; adult males of *L. knudseni* have chest spines. Juvenile *L. myersi* are bright red on their venters and posterior thighs; juvenile *L. knudseni* lack red coloration and often have obvious dorsal green coloration.

Larval morphology. Unknown.

Advertisement call. Dominant (= fundamental) frequency 600–690 Hz; call duration 0.33–0.36 s; each call with 2–3 pulses; rising frequency modulations throughout call, from about 330–920 Hz; call rate 36 calls/min; harmonic structure not apparent (Lescure and Marty, 2000:348, 372) (Fig. 73).

Distribution. Rocky outcrops in French Guiana, Suriname, and adjacent Brazil (Fig. 74).

Leptodactylus paraensis **Heyer, 2005 (Plate 6F)**

Leptodactylus paraensis Heyer, 2005:320. Type locality: "Brazil: Pará, Serra de Kukoinhokren, 07°46'S, 51°57'W." Holotype: MZUSP 69321, adult male.

Etymology. The species is named after the Brazilian State of Pará. At the time of description, all specimens were known only from the State of Pará.

Adult morphology. Large, female SVL 110.8–139.8 mm ($\overline{X}$ = 127.0 mm), male SVL 99.1–128.7 mm ($\overline{X}$ = 117.3 mm); adult male snout not spatulate; male thumb usually with 1 large black spine, rarely with 1 small to tiny spine; breeding males with a pair of chest spines; upper lip without a light stripe; dorsal folds absent; dorsolateral folds usually interrupted, extending from eye to ½ distance to sacrum; lateral folds absent; posterior thigh dark with various sized light markings; upper shank barred; belly pattern variable, from uniformly dark to various sized light markings on a dark background; toes with weak lateral ridges, not with moveable lateral fringes (Heyer, 2005:320–322).

Figure 75. Distribution map of *Leptodactylus paraensis.*

Similar species. *Leptodactylus paraensis* has an eastern Amazonian distribution (states of Mato Grosso and Pará) occurring in the same general area with *L. knudseni, L. myersi,* and *L. pentadactylus. Leptodactylus paraensis* is smaller (male SVL 99–129 mm, female SVL 110–140 mm) than *L. knudseni* (male SVL 94–170 mm, female SVL 102–154 mm). The dorsolateral folds in *L. paraensis* are interrupted; most *L. knudseni* have continuous dorsolateral folds. Juvenile *L. paraensis* lack green coloration in life; juvenile *L. knudseni* are often green on the dorsum in life. Sexually active males of *L. paraensis* have a pair of black chest spines; sexually active *L. myersi* males lack chest spines. *Leptodactylus myersi* typically occurs on rocky outcrops; *L. paraensis* does not occur on rocky outcrops; the species have allopatric distributions. *Leptodactylus paraensis* dorsolateral folds are interrupted and extend no further from the eye to the sacrum; the dorsolateral folds of *L. pentadactylus* are either continuous or, if interrupted, extend beyond the sacrum.

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Rainforest habitats in eastern Amazonia in the Brazilian states of Mato Grosso and Pará (Fig. 75).

Leptodactylus pentadactylus **(Laurenti, 1768) (Plate 7A)**

Rana pentadactyla Laurenti, 1768:32. Type locality: "Indiis;" corrected to Surinam by Müller, 1927:276. Type(s): By indication including frog illustrated by Seba, 1734: pl. 75, fig. 1 and Laurenti's "Var. β) specimen[s] in "Museo Illustrissini Comitis Turriani" [current location unknown and presumed lost]. Neotype locality: "Suriname, Marowijne, Lelygebergte, Suralcokamp." Neotype: RMNH 29559, adult male, designated by Heyer, 2005:310).

Rana gigas Spix, 1824:25. Type locality: "*in locis paludosis fluminis Amazonum,*" Brazil. Types: Not specifically stated but including animal figured on plate 1 of the original publication; ZSM 89/1921 (now lost) according to Hoogmoed and Gruber, 1983:355 and Glaw and Franzen, 2006:175. Synonymy by Peters, 1872:198, 225; Boulenger, 1882:241; Heyer, 1979:26. Preoccupied by *Rana gigas* Wallbaum, 1784 (= *Bufo marinus*); see Smith et al., 1977.

Rana coriacea Spix, 1824:29. Type locality: "*aquis lacustribus fluvii Amazonum*" = Amazon River, Brazil. Holotype: Not specifically designated, but including animal figured on plate 5, figure 2 of the original publication; ZSM 2502/0 [now lost] according to Hoogmoed and Gruber, 1983:355 and Glaw and Franzen, 2006:175. Synonymy by Peters, 1872:205, 225; Heyer, 1979:26.

Rana pachypus bilineata Mayer, 1835:24. Type locality: Not stated. Type(s): Deposition not stated, presumed lost. Named as a synonym of *Rana gigas* Spix, 1824. Not addressed by Heyer, 2005:320, 322.

Doryphoros gigas: Mayer, 1835:28, plate III, fig. 8.

Gnathophysa gigas: Cope, 1866:73.

Cystignathus pentadactylus: Peters, 1872:198.

Leptodactylus pentadactylus: Boulenger, 1882:241.

Leptodactylus goliath Jiménez de la Espada, 1875:57. Type localities: "Archidona [Oriente del Ecuador] … and Chinitambo, Sierra de Guacamayos [Or. Del Ecaudor]; locality of lectotype given in error as "Quijos, Ecuador" by Heyer and Peters, 1971:167 according to González-Fernández, García-Díez, and San Segundo, 2009:273, who noted that the lectotype is from "Archidona [Oriente de Ecuador]." Syntypes: MNCN (3 specimens); MNCN 328 designated lectotype by Heyer and Peters, 1971:167. Synonymy by Boulenger, 1882:242; Heyer and Peters, 1971:167; Heyer, 1979:26.

Leptodactylus pentadactylus – Nieden, 1923:472.

Leptodactylus macroblepharus Miranda-Ribeiro, 1926:144. Type locality: "Manáos–Amazonas", Brazil. Lectotype: MZUSP 377, adult male. Synonymy by Heyer, 1974b:43.

Leptodactylus pentadactylus pentadactylus: Müller, 1927:276.

Leptodactylus (*Pachypus*) *pentadactylus:* Lutz, 1930:1,21.

Leptodactylus pentadactylus dengleri Melin, 1941:51. Type locality: "Roque, [San Martín,] Perú," noted by Heyer, 2005:322 to be at 06°24'S, 76°48'W. Type: GNM 497 designated lectotype by Heyer, 2005:322. Synonymy by Heyer, 1979:26.

Leptodactylus pentadactylus rubidoides Andersson, 1946 "1945":51. Type locality: "Rio Pastaza," eastern Ecuador. Holotype: NRM 1928, juvenile female. Synonymy by Heyer and Peters, 1971:168; Heyer, 1979:26.

Etymology. From the Greek *penta* (five) and *dactylos* (finger, toe). Seba's illustrator for *Rana pentadactyla* obviously took liberties with the specimen being illustrated. The illustration (Seba, 1734: plate 75, figure 1) unambiguously shows five fingers. No known frogs have five fingers.

Adult morphology. Large, female SVL 133.9–174.2 mm ($\overline{X}$ = 153.2 mm), male SVL 100.2–195.0 mm ($\overline{X}$ = 140.3 mm); adult male snout not spatulate; male thumb usually with one tiny to small spine, male thumb often lacking spines, male thumb rarely with one moderate spine; males lacking chest spines; light upper lip stripe absent; dorsal folds absent; dorsolateral folds usually complete from eye to groin, complete from eye to sacrum, or interrupted between sacrum and groin; lateral folds absent; posterior thigh lacking a light stripe; upper shank barred; belly usually dark with small light vermiculations, or often with large light vermiculations, or rarely mottled or uniform dark; toes lacking flexible lateral fringes, toes may have non-flexible ridges (Heyer, 2005:322–324).

Similar species. *Leptodactylus pentadactylus* has an Amazonian distribution that overlaps with *L. knudseni, L. labyrinthicus, L. myersi, L. paraensis* and *L. stenodema. Leptodactylus pentadactylus* occurs in the tropical wet forests; *L. labyrinthicus* occurs in open formations (the forest canopy is not closed) within Amazonia, *L. myersi* is limited to rocky outcrops, *L. knudseni* occurs in primary rain forest, secondary forest, and open habitats, the few data for *L. paraensis* indicate that it is also limited to primary rain forest habitat. Most *L. pentadactylus* have a pair of well-developed and continuous dorsolateral folds from the eye to at least the sacrum; most *L. labyrinthicus* and *L. paraensis* have less developed and usually incomplete folds. Sexually active male *L. pentadactylus* usually lack a large black spine on each thumb; sexually active male *L. knudseni, L. labyrinthicus, L. myersi,* and *L. paraensis* have a large black spine on each thumb. Sexually active male *L. pentadactylus* lack chest spines; sexually active *L. knudseni, L. labyrinthicus,* and *L. paraensis* have a pair of black chest spines. The dorsolateral fold originates from the posterior eye in *L. pentadactylus;* the dorsolateral fold originates from above the posterior edge of the tympanum in *L. stenodema.*

Larval morphology. Maximum total length (Gosner 40) 92 mm; oral disk terminal; tooth row formula 1/2(1); dorsal part of caudal musculature light brown, fins pale cream (Menin et al., 2010). Hero (1990) illustrated and briefly described larvae at stage 39; description and illustration of larvae at stage 30 and their oophagous habit was recently reported (Heyer et al., 2011).

Advertisement call. Mean dominant (= fundamental) frequency among individual ca. 680–1,030 Hz; call duration 0.18–0.40 s; calls pulsed, 12–18 pulses/call; call frequency modulated, a rising whoop at least in first half of call; call = note rate 4–37 calls/min; no clear harmonic structure (Heyer, 2005:324) (Fig. 76).

Distribution. *Leptodactylus pentadactylus* occurs in closed canopied rain forest habitat throughout the Amazonian Morphoclimatic Domain as defined by Ab'Sáber (1977) (Fig. 77).

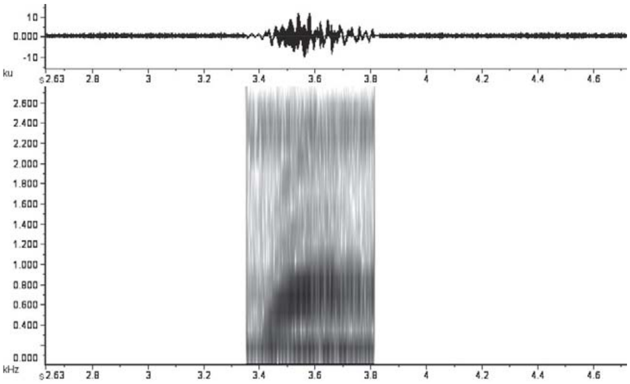

Figure 76. Advertisement call of *Leptodactylus pentadactylus* (recording USNM 251).

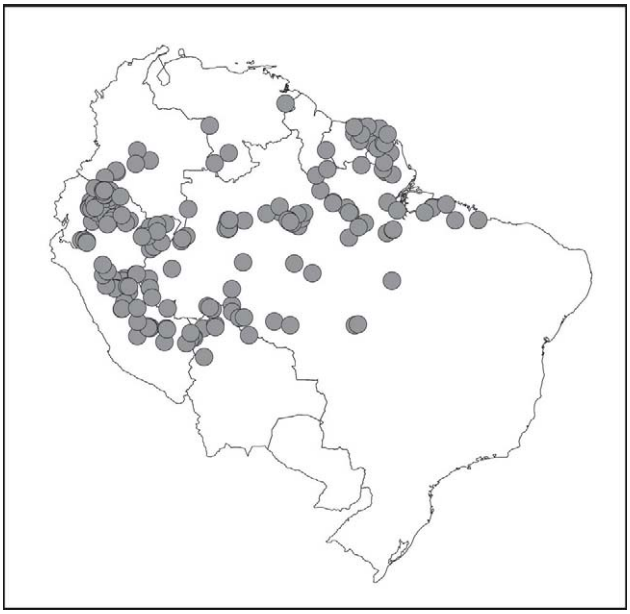

Figure 77. Distribution map of *Leptodactylus pentadactylus.*

Leptodactylus peritoaktites Heyer, 2005 (Plate 7B)

Leptodactylus peritoaktites Heyer, 2005:325. Type locality: "Hacienda Equinox, 38 km NNW of Santo Domingo de los Colorados, Esmeraldas, Ecuador, 1000', 00°03'S, 79°20'W." Holotype: USNM 196739, adult male.

Etymology. From the Greek *peritos* (west) and *aktites* (coast dweller), in allusion to the geographic distribution of the species.

Adult morphology. Large, female SVL 115.3–133.1 mm (*n* = 5), male SVL 124.0–146.3 mm (*n* = 3); adult male snout not spatulate; males usually with a moderate to large thumb spine; males lacking chest spines; upper light lip stripe absent (upper lip usually with dark triangular marks); dorsal folds absent; dorsolateral folds usually complete from at least ¼ to full distance from eye to sacrum or complete to at least between sacrum and some distance to groin; lateral folds interrupted or absent; belly usually dark with large light discrete spots or often mottled, uniformly dark, or dark with small light vermiculations; sides of toes weakly ridged (not fringed) (Heyer, 2005:325–327).

Similar species. In comparing *L. peritoaktites* with other species, it is important to note that in the original description (Heyer, 2005) the male secondary characteristics section on pages 284–285 includes errors in the text with respect to specimens from geographic areas F and G (p. 283, figure 7). The text on p. 326 for *L. peritoaktites* is correct for adult males: male thumb usually with one moderate to large spine; male thumb often lacking spines; males without chest spines. The text on p. 329 for *L. rhodomerus* is correct for adult males: male thumb with one tiny to small spine; males without chest spines.

Leptodactylus peritoaktites occurs on the coastal lowlands of Ecuador. The only other species of *Leptodactylus* that occur in the coastal lowlands of Ecuador that lack toe fringes are *L. labrosus, L. rhodomerus,* and *L. ventrimaculatus.* In life, juvenile *L. peritoaktites* have bright red coloration on the posterior thighs and groin (adult life coloration not known); juvenile (and adult) *L. labrosus* and *L. ventrimaculatus* lack red coloration on their posterior thighs. Sexually active male *L. peritoaktites* have a single moderate to large black spine on each thumb and never exhibit the vermiculated belly pattern of *L. rhodomerus;* sexually active *L. rhodomerus* males have one tiny to small white or black spine on the thumb and a dark belly with large light vermiculations. The outer tarsal surface of *L. peritoaktites* is smooth; the outer tarsal surfaces of *L. rhodomerus* and *L. ventrimaculatus* have white tubercles; the outer tarsal surfaces of *L. labrosus* usually have scattered white tubercles (78% of specimens). Adult *Leptodactylus peritoaktites* are larger (female SVL 115–133 mm, male SVL 124–146 mm) than *L. labrosus* (female SVL 50–71 mm, male SVL 48–67 mm).

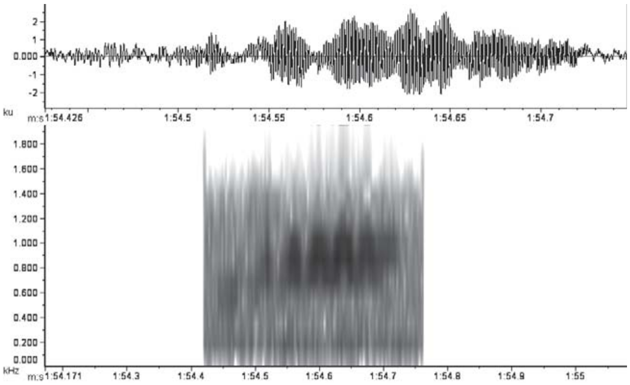

Figure 78. Advertisement call of *Leptodactylus peritoaktites* (recording USNM 98).

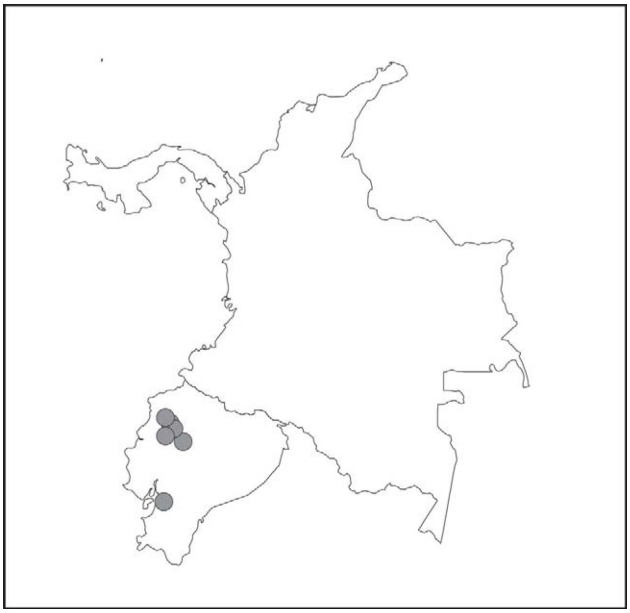

Figure 79. Distribution map of *Leptodactylus peritoaktites.*

Larval morphology. Unknown.

Advertisement call. Dominant frequency ca. 860 Hz (recording too poor to determine accurately); call duration 0.2–0.3 s; each call with 5–8 pulses; rising frequency modulations throughout call; call rate 34–37/min; no clear harmonic structure (Heyer, 2005:327) (Fig. 78).

Distribution. Coastal Ecuador (Fig. 79).

Leptodactylus rhodomerus Heyer, 2005 (Plate 7C)

Leptodactylus rhodomerus Heyer, 2005:327. Type locality: "campamento Chancos, Vereda Campo Alegre, Municipio de Restrepo, Valle de Cauca, Colombia, 460 m, 03°58'N, 76°44'W." Holotype: ICNMHN 13322, adult male.

Etymology. From the Greek *rhodon,* rose, and *meros,* thigh, in reference to the red coloration on the posterior thighs in life.

Adult morphology. Large, female SVL 133.5–157.8 mm, male SVL 112.2–143.8 mm; adult male snout not spatulate; male thumb with one tiny to small black spine; males without chest spines; light upper lip stripe absent; dorsal folds absent; dorsolateral folds usually complete from eye to groin; lateral folds interrupted or absent; posterior thigh without a light stripe; upper shank barred; belly usually dark with light vermiculations or spots; toes ridged (not fringed) (Heyer, 2005:327–330).

Similar species. *Leptodactylus rhodomerus* is most similar morphologically to *L. pentadactylus* and *L. peritoaktites,* which have allopatric or parapatric distributions with *L. rhodomerus*. *Leptodactylus rhodomerus* occurs in the wet tropical forest regions of western Colombia and adjacent Ecuador; *L. pentadactylus* occurs in the Amazonian wet tropical forests. *Leptodactylus rhodomerus* has bright red markings on the posterior thigh surfaces in life; *L. pentadactylus* does not have red on the thighs in life. *Leptodactylus rhodomerus* has a parapatric distribution with *L. savagei* to the north and *L. peritoaktites* to the south along Pacific coastal South America. Sexually active male *L. rhodomerus* have single tiny white to small white or black thumb spines and lack chest spines; sexually active male *L. savagei* have a single large black spine on each thumb and have a pair of black chest spines. *Leptodactylus rhodomerus* specimens often have extensive distinct light areas (bright red in life) on the posterior thigh surfaces; *L. savagei* individuals rarely have this pattern. Sexually active *L. rhodomerus* males have one tiny to small spine on the thumb and a dark belly with large light vermiculations; sexually active male *L. peritoaktites* have a single moderate to large thumb spine and never exhibit the vermiculated belly pattern of *L. rhodomerus*. *Leptodactylus rhodomerus* commonly have continuous to interrupted large flank folds.

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Chocó region of Pacific coastal Colombia and northern coastal Ecuador (Fig. 80).

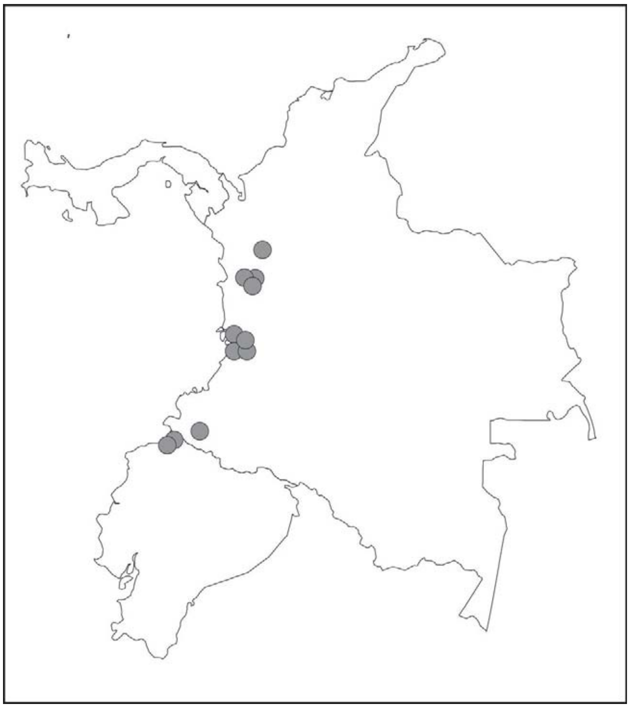

Figure 80 Distribution map of *Leptodactylus rhodomerus.*

Leptodactylus rhodomystax **Boulenger, 1884 "1883" (Plate 7D-E)**

Leptodactylus rhodomystax Boulenger, 1884 "1883":637. Type locality: "Yurimaguas, Huallaga River, [Loreto,] Northern Perú." Syntypes: BMNH (2 specimens); BMNH 1947.12.17.81 designated lectotype by Heyer, 1979:30, juvenile.

Leptodactylus stictigularis Noble, 1923:293. Type locality: "Kartabo, British Guiana." Holotype: AMNH 10398, adult male. Synonymy by Parker, 1935:508; Heyer 1979:30.

Etymology. From the Greek *rhodon,* rose and *mystax,* upper lip.

Adult morphology. Moderate size, female SVL 58.5–91.4 mm ($\overline{X}$ = 78.6 mm), male SVL 59.0–89.6 mm ($\overline{X}$ = 72.6 mm); adult male snout not spatulate; adult males with one black thumb spine and a pair of black chest spines; upper lip with a distinct light stripe; dorsal folds absent; a pair of distinct, complete dorsolateral folds; lateral folds interrupted or absent; posterior thigh with distinct light spots on a dark background, no light thigh stripe; upper shank barred or uniform brown or gray; belly gray with large irregular spots at least anteriorly; toes with weak lateral ridges or smooth (Heyer, 1979:30–31).

Similar species. *Leptodactylus rhodomystax* occurs in amazonian Bolivia, Brazil, Colombia, Ecuador, French Guiana, Perú, and Suriname. Other species that occur with *L. rhodomystax* that share lack of toe fringes and have complete dorsolateral folds in some or all individuals are *L. didymus, L. elenae, L. fuscus, L. knudseni, L. mystaceus, L. paraensis, L. pentadactylus, L. rhodonotus,* and *L. stenodema.* All these species lack the characteristic posterior thigh pattern of distinct light spots on a dark background of *L. rhodomystax. Leptodactylus rhodomystax* lacks a light longitudinal stripe on the posterior thigh; *L. didymus, L. elenae, L. fuscus,* and *L. mystaceus* have light posterior thigh stripes. *Leptodactylus rhodomystax* has a distinct light upper lip stripe (brilliant white or reddish in life); *L. knudseni, L. paraensis, L. pentadactylus,* and *L. stenodema* lack light upper lip stripes.

Larval morphology. Maximum total length (Gosner 37) 46.7 mm; oral disk anteroventral; tooth row formula 2(2)/3; tail black or dark brown (Rodrigues et al., 2007).

Advertisement call. Dominant frequency (= fundamental frequency 3,700–5,400 Hz; call duration 0.12–0.23 s; call a single pulse; rising frequency modulations for most of call; call rate 0.23/s; calls with harmonic structure (Zimmerman and Bogart 1988:104–105) (Fig. 81).

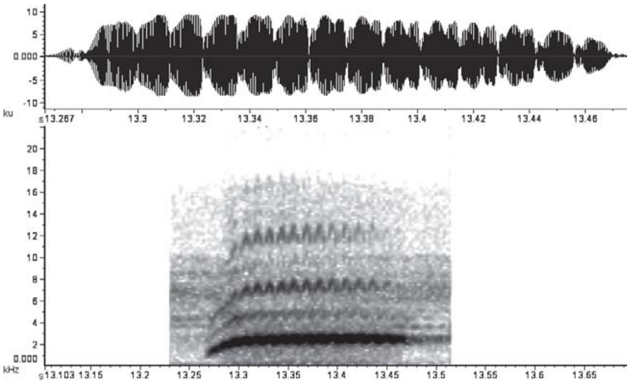

Figure 81. Advertisement of *Leptodactylus rhodomystax* (recording USNM 255).

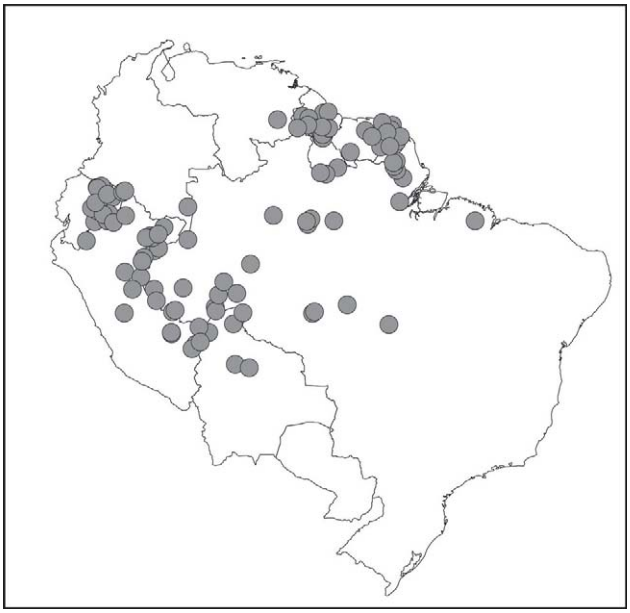

Figure 82. Distribution map of *Leptodactylus rhodomystax.*

Distribution. Amazonian Basin and Guyana Shield (Fig. 82).

Leptodactylus rhodonotus **(Günther, 1869) (Plate 7F)**

Cystignathus rhodonotus Günther, 1869 "1868":481. Type locality: "Chyavetes [= Chayavitas], Eastern Perú." Holotype: BMNH 1947.2.17.39, sex unknown, presumably juvenile.

Gnathophysa rubido Cope, 1874:128. Type locality: "Moyabamba, [San Martín,] Perú." Syntypes: Total of 3 specimens, ANSP 11392 (female), ANSP 11394 (male) and MCZ 4780 (ANSP 11393, male, exchanged to ANSP; Barbour and Loveridge, 1929:293); MCZ 4780 designated lectotype by Heyer, 1969c:3. Synonymy by Heyer, 1969c:3.

Leptodactylus rubido: Boulenger, 1882:243.

Leptodactylus rhodonotus: Boulenger, 1882:239.

Pleurodema (*Gnathophysa*) *rubida:* Knauer, 1883:106. Error for *rubido*. *Leptodactylus rubidus* – Boulenger, 1884 “1883”:637. Error for *rubido*.

Etymology. From the Greek *rhodon,* rose, red and *nōtos,* back.

Adult morphology. Moderate size, female SVL 55.8–89.7 mm ($\overline{X}$ = 74.2 mm), male SVL 54.4–79.4 mm ($\overline{X}$ = 66.9 mm); male snout not spatulate; males with a pair of black spines on thumb; all males larger than 65 mm SVL with a pair of black chest spines; light upper lip stripe rare, most individuals with uniform or dark triangles on upper lip; dorsal folds absent; a pair of dorsolateral folds extending from eye to sacrum or groin; lateral folds interrupted or absent; posterior thigh without a light longitudinal stripe; upper shank with transverse bars or uniform; belly dark with various kinds of light marks; juveniles with pronounced lateral ridges on toes (not fringed), adults lacking lateral toe ridges and fringes (Duellman, 2005:289; Heyer, 1979:30–32).

Similar species. *Leptodactylus rhodonotus* occurs on the western slopes of the Andes in Bolivia and Perú. Other species that occur with *L. rhodonotus* and have a pair of dorsolateral folds extending from eye to sacrum or groin and lacking a light stripe on the posterior thigh in at least some specimens that occur with *L. rhodonotus* are: *L. knudseni, L. leptodactyloides, L. pentadactylus, L. petersii, L. podicipinus, L. rhodomystax, L. stenodema,* and *L. wagneri*. The toes of adult *L. rhodonotus* are neither fringed nor ridged whereas toes of juveniles have pronounced lateral ridges; toes are fringed in juvenile and adult *L. leptodactyloides, L. petersii, L. podicipinus,* and *L. wagneri*. *Leptodactylus rhodonotus* is a moderate size species (adults 54–90 mm SVL) with two spines per thumb in adult males; *L. knudseni* and *L. pentadactylus* are large species (adult SVL 94–195 mm) and adult males have a single spine on each thumb. The posterior thigh of *L. rhodonotus* is variably mottled; *L. rhodomystax* has a thigh pattern of distinct light spots on a dark background. The dorsolateral folds of *L. rhodonotus* originate at the eye; the dorsolateral folds in *L. stenodema* originate at the level of the posterior tympanum.

Larval morphology. Maximum total length (Gosner 40) 59.0 mm; oral disk anteroventral; tooth row formula 2(2)/3[1]; tail mottled (Duellman, 2005:290; Heyer 1969c:3–4).

Advertisement call. Dominant (= fundamental) frequency 1,680–2,530 Hz; call duration 0.045–0.066 s; call pulsatile; rising frequency modulation most notable in first half of call; call rate 106–214/min; harmonic structure present (Duellman, 2005:290; Köhler and Lötters, 1999:217–218) (Fig. 83).

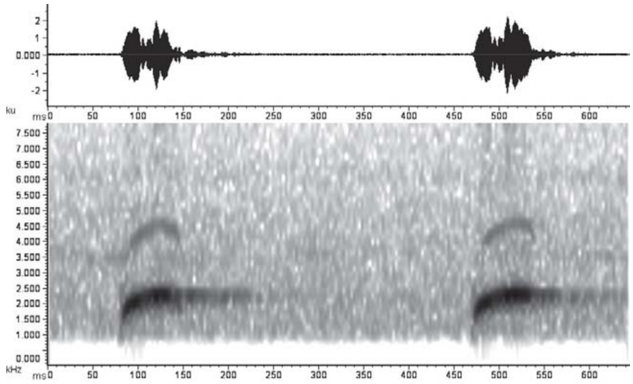

Figure 83. Advertisement of *Leptodactylus rhodonotus* (recording USNM 305).

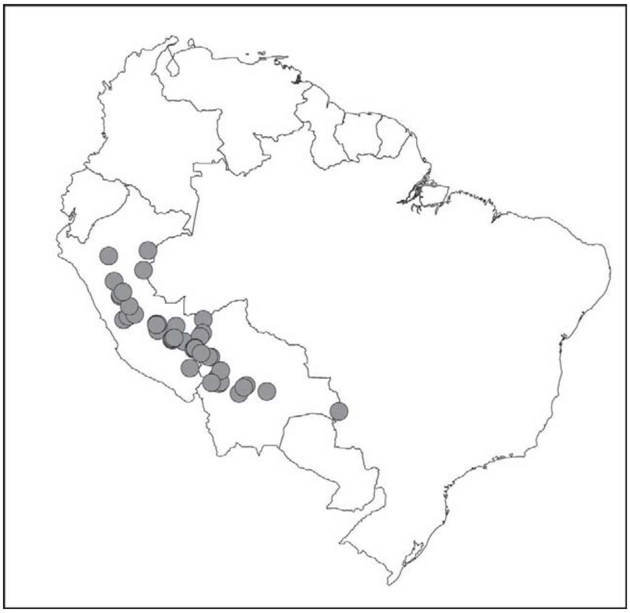

Figure 84. Distribution map of *Leptodactylus rhodonotus.*

Distribution. Western slopes and adjacent lowlands of Bolivia and Peru (Fig. 84).

Leptodactylus rugosus **Noble, 1923 (Plate 8A)**

Leptodactylus rugosus Noble, 1923:297. Type locality: “near Kaieteur Falls, British Guiana [= Guyana].” Holotype: AMNH 1169, adult male.

Etymology. From the Latin *rugosus,* wrinkled.

Adult morphology. Moderate size, female SVL 53.6–73.5 mm ($\overline{X}$ = 61.0 mm), male SVL 50.9–71.6 mm ($\overline{X}$ = 58.9 mm); adult male snout not spatulate; adult males with one or two black thumb spines; adult males with a pair of black chest spines; chin/throat tubercles absent; upper lip without a light stripe; dorsal folds absent; dorsolateral folds short or absent; lateral folds absent; posterior thigh without light stripe; upper shank barred, spotted, or blotched; belly dark with various kinds of light marks to almost uniformly light with very few melanophores; toes ridged or smooth, not fringed (Duellman, 1997:25–26; Heyer, 1979:32–35; Heyer and Thompson, 2000:1–5).

Similar species. *Leptodactylus rugosus* occurs on rocky habitats in Venezuela and Guyana. The only other similar species occurring on rocky outcrop habitats is *L. lithonaetes,* which occurs only in Colombia and Venezuela (apparently the two species have allopatric distributions). The sole morphological features that differentiate *L. lithonaetes* from *L. rugosus* are secondary male characters. *Leptodactylus rugosus* males have one or two thumb spines and all adult male *L. rugosus* lack chin tubercles; *L. lithonaetes* adult males have a single thumb spine and have a patch of brown/black tubercles on the chin/throat.

Larval morphology. Maximum total length (Gosner 38) 36.1 mm; oral disk ventral; tooth row formula 2(2)3[1]; tail mottled (Heyer, 1995:709, 711).

Advertisement call. Dominant (= fundamental) frequency 600–2,700 Hz (Heyer 1979:34) or 1,670–2,540 Hz (Duellman, 1997:26); call duration 0.52–0.67 s; calls with numerous pulses; rising frequency modulations much more pronounced in first half of call; call rate ca. 3/min; harmonic structure present or absent (Duellman, 1997:26; Heyer, 1979:34–35; Heyer and Barrio-Amorós, 2009:285–287) (Fig. 85).

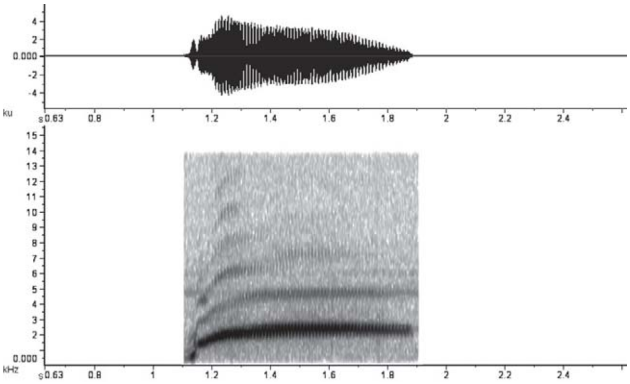

Figure 85. Advertisement of *Leptodactylus rugosus* (recording USNM 113).

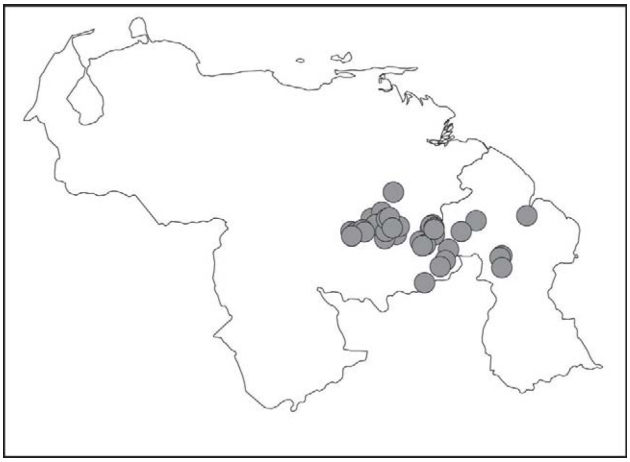

Figure 86. Distribution map of *Leptodactylus rugosus.*

Distribution. Rocky outcrops in Venezuela and Guyana (Fig. 86).

Leptodactylus savagei Heyer, 2005 (Plate 8B)

Leptodactylus savagei Heyer, 2005:330. Type locality: "Rincon de Osa, Puntarenas, Costa Rica, 08°42'N, 83°29'W." Holotype: USNM 227652, adult male.

Etymology. "The species is named in honor of Jay M. Savage for his substantial contributions to furthering biological research in the Neotropics in general and those of the Middle American herpetofauna in particular."

Adult morphology. Large, female SVL 110.2–164.1 mm ($\overline{X}$ = 137.1 mm), male SVL 106.0–156.3 mm ($\overline{X}$ = 133.2 mm); adult male snout not spatulate; adult males with a single tiny to large black thumb spine; breeding males with a pair of chest spines; light upper lip stripe absent; dorsal folds absent; dorsolateral folds may be continuous from eye to ¼ distance to sacrum, continuous from eye to groin, or intermediate lengths in between; lateral folds interrupted or absent; posterior thigh usually dark with varying light marks, rarely distinctly light with few irregular dark marks; upper shank barred; belly dark with various kinds of light marks; toes ridged or smooth, not fringed (Heyer, 2005:330–333; Heyer et al., 2010b:1–19).

Similar species. *Leptodactylus savagei* occurs from Honduras to north coastal Colombia. Within this distribution, *L. savagei* differs from *L. insularum, L. melanonotus,* and *L. silvanimbus* by lacking toe fringes and from *L. fragilis, L. fuscus,* and *L. poecilochilus* by lacking a longitudinal light stripe on the posterior thigh. *Leptodactylus savagei* and *L. rhodomerus* apparently have a parapatric distribution pattern, with *L. savagei* occurring in north coastal Colombia and *L. rhodomerus* occurring in the Colombian Choco and adjacent Pacific coastal rainforests in neighboring Ecuador. Sexually active *L. savagei* males have a single large black thumb spine and a pair of black chest spines, and the posterior thigh patterns of *L. savagei* specimens are usually dark with varying light marks, rarely distinctly light with few irregular dark marks; sexually active male *L. rhodomerus* have a tiny white to small white or black spine on each thumb and no chest spines, while the posterior thigh pattern of *L. rhodomerus* individuals is often distinct with extensively light areas (bright red in life) with a few irregular dark markings.

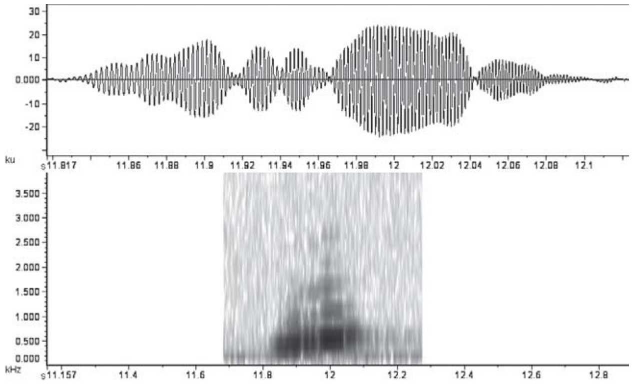

Figure 87. Advertisement of *Leptodactylus savagei.*

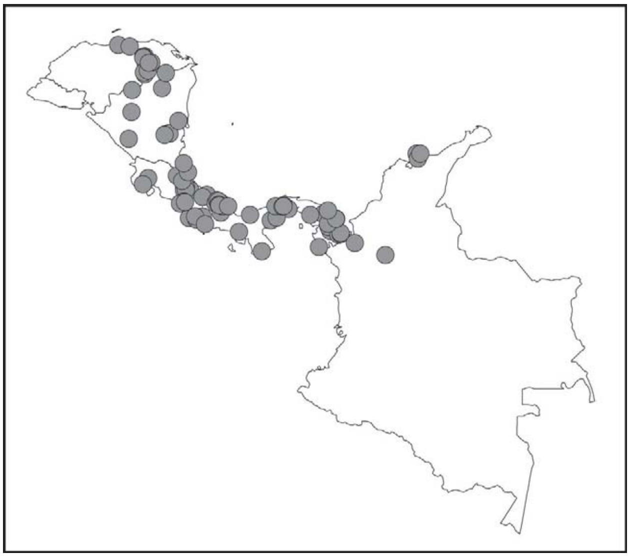

Figure 88. Distribution map of *Leptodactylus savagei.*

Larval morphology. Maximum total length (Gosner 40) 83 mm; oral disk terminal; tooth row formula 2(2)/3(1); tail mottled (Heyer, 1970b "1968":181, 195, fig. 9, 197, fig. 14, 199, fig. 19).

Advertisement call. Dominant (= fundamental) frequency 300–520 Hz; call duration 0.24–0.42 s; calls (= notes) with 5–13 pulses/call; rising frequency modulations throughout call; call rate 40–49 calls (= notes)/s; calls with harmonic structure (Heyer et al., 2010b:2) (Fig. 87).

Distribution. Honduras through Panamá and north coastal Colombia (Fig. 88).

Leptodactylus stenodema Jiménez de la Espada, 1875 (Plate 8C)

Leptodactylus stenodema Jiménez de la Espada, 1875:64. Type locality: "San José de Moti [Canton de Quíjos]." Napo, Ecuador. (Confirmed by González-Fernández et al., 2009:273). Syntype: MNCN (2 specimens); MNCN 190 designated lectotype by Heyer and Peters, 1971:168, adult female, now numbered MNCN 1687 according to González-Fernández et al., 2009:273.

Leptodactylus vilarsi Melin, 1941:52. Type locality: "Taracuá, Rio Uaupés, [Amazonas,] Brazil". Holotype: GNM 498, adult female. Synonymy by Heyer, 1979:14.

Etymology. From the Greek *stenos* (narrow) and *demas* (body).

Adult morphology. Moderate–large size, female SVL 66.0–105.0 mm ($\overline{X}$ = 90.2 mm) mm, male SVL 75.6–99.7 mm ($\overline{X}$ = 86.0 mm); adult male snout not spatulate; males without thumb spines or chest spines; light upper lip stripe absent; dorsal folds absent; distinct dorsolateral folds; lateral folds absent; no light stripe on posterior thigh; upper shank with wide or narrow bars; belly dark with various kinds of light marks; lateral surface of toes smooth or weakly ridged (not fringed) (Heyer, 1979:34–36).

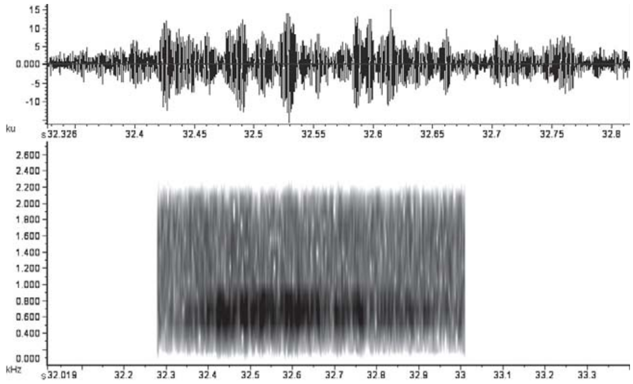

Figure 89. Advertisement of *Leptodactylus stenodema.*

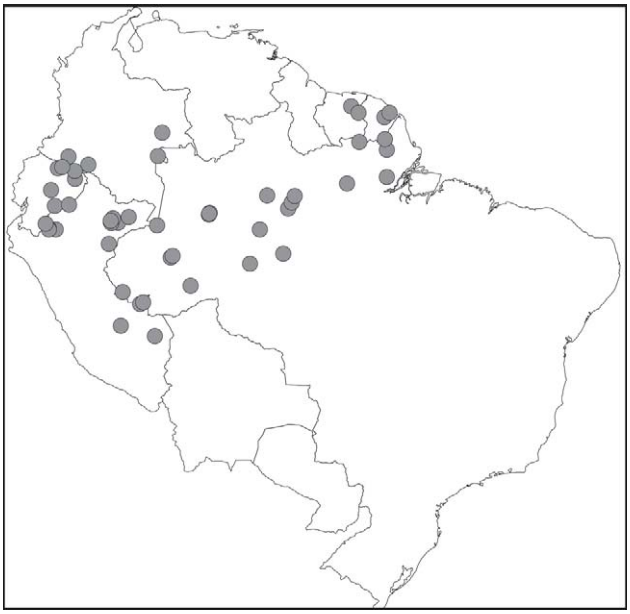

Figure 90. Distribution map of *Leptodactylus stenodema.*

Similar species. *Leptodactylus stenodema* is the only species in the genus in which the dorsolateral fold originates just posterior to the tympanum rather than the eye (other species with dorsolateral folds with posterior eye and dorsolateral fold abutting).

Larval morphology. Unknown.

Advertisement call. Dominant (= fundamental) frequency 120–680 to 760–900 Hz; call duration 0.26–0.36 s; call a single multi-pulsed note; modest rising frequency modulations throughout call; call rate 30/min; no harmonic structure (Heyer, 1979:36; Lescure and Marty, 2000:348, 374) (Fig. 89).

Distribution. Lowland Amazonian rainforests (excluding Bolivia) of Brazil, Colombia, Ecuador, Peru, French Guiana, and Surinam (Fig. 90).

Leptodactylus turimiquensis Heyer, 2005 (Plate 8D)

Leptodactylus turimiquensis Heyer, 2005:333. Type locality: "Caripito, Monagas, Venezuela, ~ 100 m, 10°08'N, 63°06'W." Holotype: AMNH 70667, adult male.

Etymology. Jaime E. Péfaur, at W.R. Heyer's request, kindly suggested naming this species *L. turimiquensis* after the Serranía de Turimiquire, which encompasses the known distribution of the species. Spanish and English authors have transliterated the indigenous name for the mountain range involved as Turimiquire and Turumiquire.

Adult morphology. Large, female SVL 122.4–128.0 mm, male SVL 127.2–160.0 ($\bar{X}$ = 144.0 mm); adult male snout not spatulate; adult males with a single black thumb spine and often with a prepollical bump; breeding males with a pair of black chest spines; light upper lip stripe absent; dorsal folds absent; dorsolateral folds often absent, rarely continuous from eye to groin; lateral fold interrupted; posterior thigh without a light stripe; upper shank barred; belly dark with various light marks (Heyer, 2005:317, 333–335).

Similar species. *Leptodactylus turimiquensis* is the only large species of *Leptodactylus* without fringed toes that occurs in the Serranía de Turimiquire, Venezuela.

Larval morphology. Unknown.

Advertisement call. Dominant frequency about 400 Hz; call duration 0.33 s; call of a single note of about 9 pulses; call weakly frequency modulated; (call rate not given); well defined harmonics (Rivero and Eloy Esteves, 1969:3 published an audiospectrogram but provided not descriptive data; herein data are interpreted from their audiospectrogram).

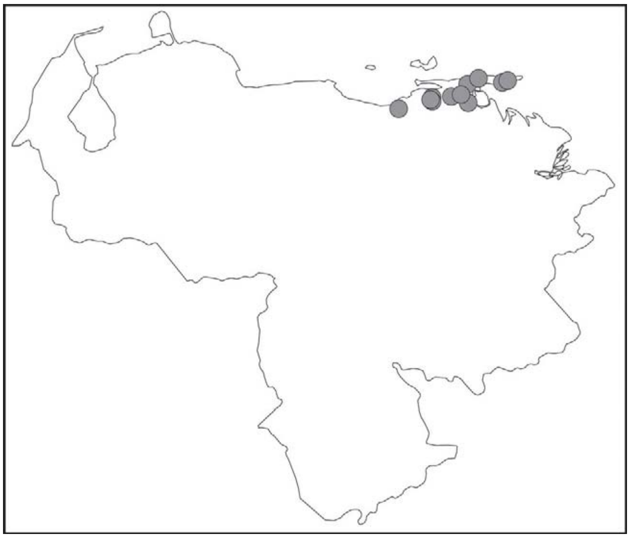

Figure 91. Distribution map of *Leptodactylus turimiquensis.*

Distribution. Serranía de Turimiquire, Venezuela (Fig. 91).

Leptodactylus vastus Lutz, 1930 (Plate 8E-F)

Leptodactylus vastus Lutz, 1930:32. Type locality: "Independencia [Parayba]," Brazil, now Guarabira, Paraíba, at 06°51'S, 35°29'W. Lectotype: AL-MN 70, adult male. See Comments, below.

Etymology. From the Latin *vastus* (enormous), characterizing the large size of the species.

Adult morphology. Large, female SVL 120.4–167.0 mm ($\bar{X}$ = 150.7 mm), male SVL 135.0–180.3 mm ($\bar{X}$ = 158.2 mm); adult male snout not spatulate; adult males usually with one large thumb spine, rarely with a tiny or small spine; breeding males with a pair of chest spines; no light stripe on upper lip; dorsal folds absent; dorsolateral folds usually interrupted from ½ to full distance from eye to sacrum, rarely continuous from at least ¼ to full distance from eye to sacrum, rarely interrupted to at least between sacrum and some distance to groin; lateral fold interrupted or absent; posterior thigh without a light stripe; upper shank barred; belly usually labyrinthine patterned, often mottled or uniform dark, or light with dark vermiculations, or dark with light vermiculations; lateral surfaces of toes ridged (not fringed) (Heyer, 2005:297, 335–337, 347–348).

Similar species. *Leptodactylus vastus* occurs in open formations in the Brazilian states of Alagoas, Ceará, Goiás, Maranhão, Pernambuco, Rio Grande do Norte, and Sergipe. The only similar species of large size, toes not fringed, and no light posterior thigh stripe is *L. labyrinthicus*. The available distributional data are inadequate to ascertain whether *L. labyrinthicus* has a parapatric distribution with *L. vastus* or whether there is some geographic overlap of the two species. There are no definitive morphological features that consistently separate *L. vastus* from *L. labyrinthicus*. Adolfo Lutz (1926a) published two color plates (30, 31) containing dorsal and ventral figures of the species he subsequently named as *L. vastus*. Plate 30, figures 3 and 4 have yellow mottling on the venter and posterior thigh surfaces. Plate 31, figures 1 and 2 have white mottling on the venter and posterior thighs; presumably the specimen illustrated was faded at the time it was illustrated. Lutz (1926a:143) considered *L. labyrinthicus* a synonym of *L. pentadactylus*. His color plate 30, figures 1–2, shows bold red mottling on the posterior thighs and a labyrinthine ventral surface of brown and yellow. Further fieldwork is needed to verify if the color differences between Lutz's figures are diagnostic for *L. labyrinthicus* and *L. vastus*. The two species differ in their advertisement calls. *Leptodactylus vastus* has a pulsed advertisement call; *L. labyrinthicus* has an unpulsed advertisement call Heyer et al. (2005) provided genetic data that supported *L. labyrinthicus, L. paraensis,* and *L. vastus* as valid species.

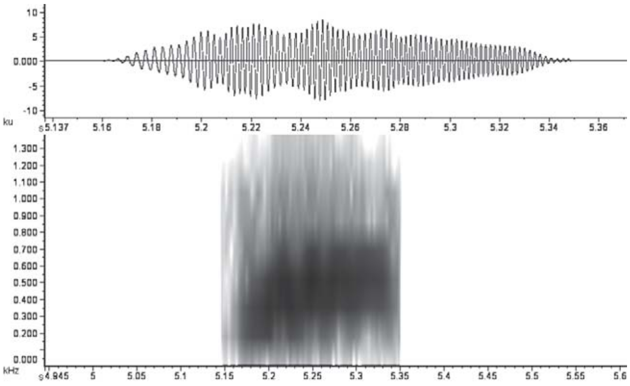

Figure 92. Advertisement call of *Leptodactylus vastus* (recording USNM 233).

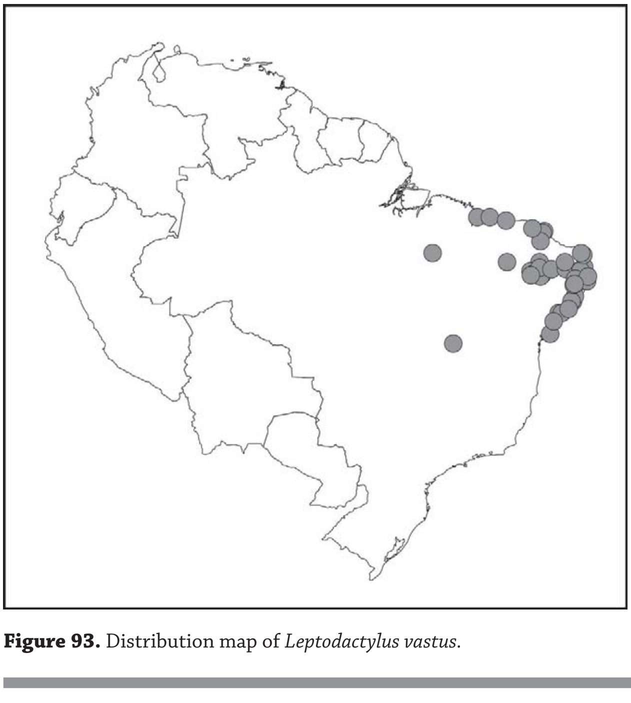

Figure 93. Distribution map of *Leptodactylus vastus.*

Larval morphology. Maximum total length (Gosner 38–40) 52 mm; oral disk anterior; tooth row formulae 1/2-3(1); tail mottled (Vieira et al., 2007:62–63).

Advertisement call. Dominant (= fundamental) frequency ca. 430 Hz; call duration 0.14–0.19 s; call of single pulsed note; rising frequency modulations throughout call; call rate 54–61/min; call with harmonic structure (Heyer, 2005:296–297, 336) (Fig. 92).

Distribution. Open habitats in northeast Brazil (Fig. 93).

Comments. Adolpho Lutz proposed the name *Leptodactylus vastus* for three specimens that he had previously reported and figured as *L. ? gigas*. When the Lutz collection was transferred from the Instituto Oswaldo Cruz to MNRJ, there was but a single specimen labeled as the type of *L. vastus,* AL-MN 70 (Ulisses Caramaschi, pers. comm.). Bokermann (1966:75) listed in his type locality publication "*Leptodactylus vastus* A. Lutz, 1930:4" with the comment "Nome nôvo para *Leptodactylus gigas* A. Lutz, 1926[a]:144." Lutz's English text (1930:29) states: "The remarks made by Peters and Lorenz Mueller on the type of Spix do not permit to refer to it the frog from Independencia (Parahyba) mentionned [sic] in my first paper as ? *gigas*. I have not been able to obtain more specimens in the same region … I shall now call this species *Leptodactylus vastus* n. sp." Bokermann's characterization of Lutz applying a new name for *Leptodactylus gigas* is misleading. Lutz (1926a) may have thought that the three specimens involved were the same species as *Leptodactylus gigas* Spix, from the Amazon river. By 1930, Lutz was convinced that the specimens he had from the Brazilian state of Paraíba were not conspecific with Spix's *L. gigas* from the Amazon river. Thus, Lutz 1930:29 named the new species *L. vastus* for the three specimens (from Paraíba) he originally thought might be conspecific with the Amazonian *L. gigas*.

Leptodactylus latrans species group

Leptodactylus bolivianus Boulenger, 1898 (Plate 9A)

Leptodactylus bolivianus Boulenger, 1898:131. Type locality: Bolivia, Río Madidi, Barraca. Lectotype: MSNG 28875A, male.
Leptodactylus romani Melin, 1941:54. Type locality: Brazil, Rio Uaupés, Taracuá. Lectotype: GNM 499, juvenile.

Etymology. The species is named for the country of Bolivia from which the specimens were collected.

Adult morphology. Moderate–large size, female SVL 61.2–107.7 mm ($\overline{X}$ = 85.3 mm), male SVL 79.0–121.5 mm ($\overline{X}$ = 104.6 mm); adult male snout not spatulate; sexually active males with single large, markedly chisel-shaped thumb spine, chin tubercles present, but no chest spines; light upper lip stripe usually present (70% of specimens); dorsal folds absent; dorsolateral folds well developed; lateral folds present, interrupted or complete; posterior thigh lacking light stripe; upper shank barred; belly uniform light, rarely mottled anteriorly; toes fringed (Heyer and de Sá, 2011).

Similar species. The species that co-occur with *Leptodactylus bolivianus* in the Amazonian portions of Bolivia, Brazil, Colombia, Peru, and Venezuela that have distinct dorsolateral folds and toe fringes are *L. latrans* complex species, *L. petersii,* and *L. riveroi*. *Leptodactylus bolivianus* lacks dorsal folds; *L. latrans* complex species has dorsal folds. The belly is uniform light or rarely mottled in *L. bolivianus;* the entire bellies of *L. petersii* and *L. riveroi* are moderately to boldly mottled.

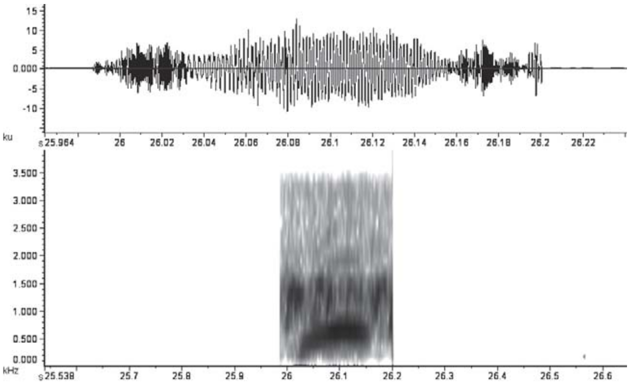

Figure 94. Advertisement call of *Leptodactylus bolivianus.*

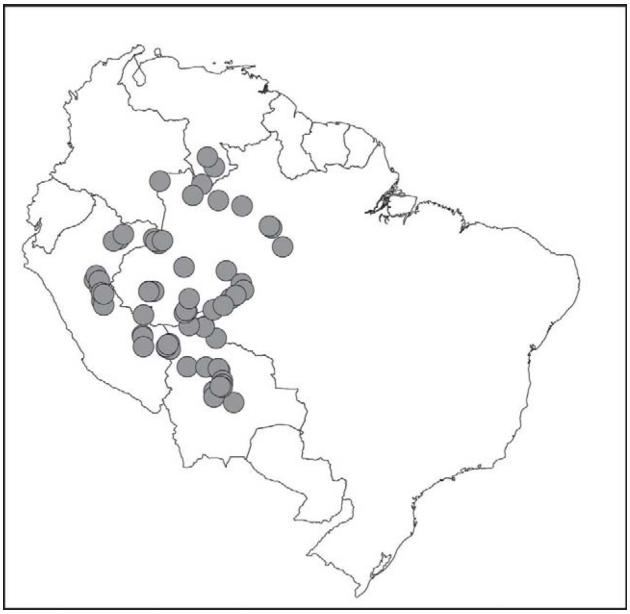

Figure 95. Distribution map of *Leptodactylus bolivianus.*

Larval morphology. Unknown. Available descriptions purported to be *Leptodactylus bolivianus* correspond to *L. insularum* (Heyer and de Sá, 2011).

Advertisement call. Dominant (= fundamental) frequency 600–690 Hz; call duration 0.12–0.16 s; 1–2 notes/call; rising frequencies most pronounced in first 1/3–1/2 of call; call rate 0.5/s; no apparent harmonic structure (Heyer and de Sá, 2011) (Fig. 94).

Distribution. Central and western portions of the Amazon basin in Bolivia, Brazil, Colombia, Peru, and Venezuela (Fig. 95).

Leptodactylus chaquensis Cei, 1950 (Plate 9B)

Leptodactylus ocellatus var. *typica* Cei, 1948:308 Type locality: Not explicitly stated, presumably Tucumán, Argentina. Anonymous, 2003:173 (Opinion 2044) suppressed this name for purposes of synonymy.

Leptodactylus chaquensis Cei, 1950:417. Type locality: Multiple localities in Argentina cited; Lavilla, 1994 “1992”:85 gave Simoca, Tucumán as the type locality. Holotype: FML 979, adult male, specimen lost according to Lavilla, 1994 “1992”:85.

Etymology. The name *chaquensis* refers to the geographical region of the Gran Chaco of Argentina.

Adult morphology. Moderate–large size, female SVL 68.1–97.6 mm ($\overline{X}$ = 76.8 mm), male SVL 65.4–94.3 mm ($\overline{X}$ = 79.5 mm); adult male snout not spatulate; sexually active males with a pair of keratinized thumb spines; males without chest spines; light upper lip stripe absent; mid-dorsal fold interrupted (Fig. 2, fold 1); a pair of complete dorsal folds (Fig. 2, fold 2), a pair of complete or interrupted auxiliary dorsal folds extending from eye to the sacral region (Fig. 2, fold 3), dorsolateral folds (Fig. 2, fold 4) complete from eye to groin; auxiliary lateral fold (Fig. 2, fold 5) extending from mid-body to groin; lateral fold (Fig. 2, fold 6) complete or interrupted; posterior thigh almost uniform, slightly mottled, greenish in life; upper shank barred; belly uniform light; toes with lateral fringes (Cei, 1980:348, 350).

Similar species. *Leptodactylus chaquensis* from Argentina, Bolivia, Brazil, Paraguay, and Uruguay have fringed toes and a pair of dorsal folds. The other species sharing the same characteristics (with potentially overlapping distributions) are the *L. latrans* species complex and *L. viridis*. *Leptodactylus chaquensis* almost always have complete or interrupted auxiliary dorsal folds (Fig. 2, fold 3); no

L. latrans complex specimens have this fold. The post-tympanic dark stripe that extends to the forelimb may differentiate southern populations (Argentina and Uruguay) of *L. chaquensis* and *L. latrans* complex – triangular-shaped in specimens of the *L. latrans* complex, not triangular in *L. chaquensis*. *Leptodactylus chaquensis* has well-developed dorsal folds and adult males have a pair of black spines on each thumb; *L. viridis* has weak dorsal folds and adult males have a single black spine on each thumb. Live specimens of *L. viridis* are easily distinguished from *L. chaquensis* and *L. latrans* complex specimens by their characteristic overall green body coloration.

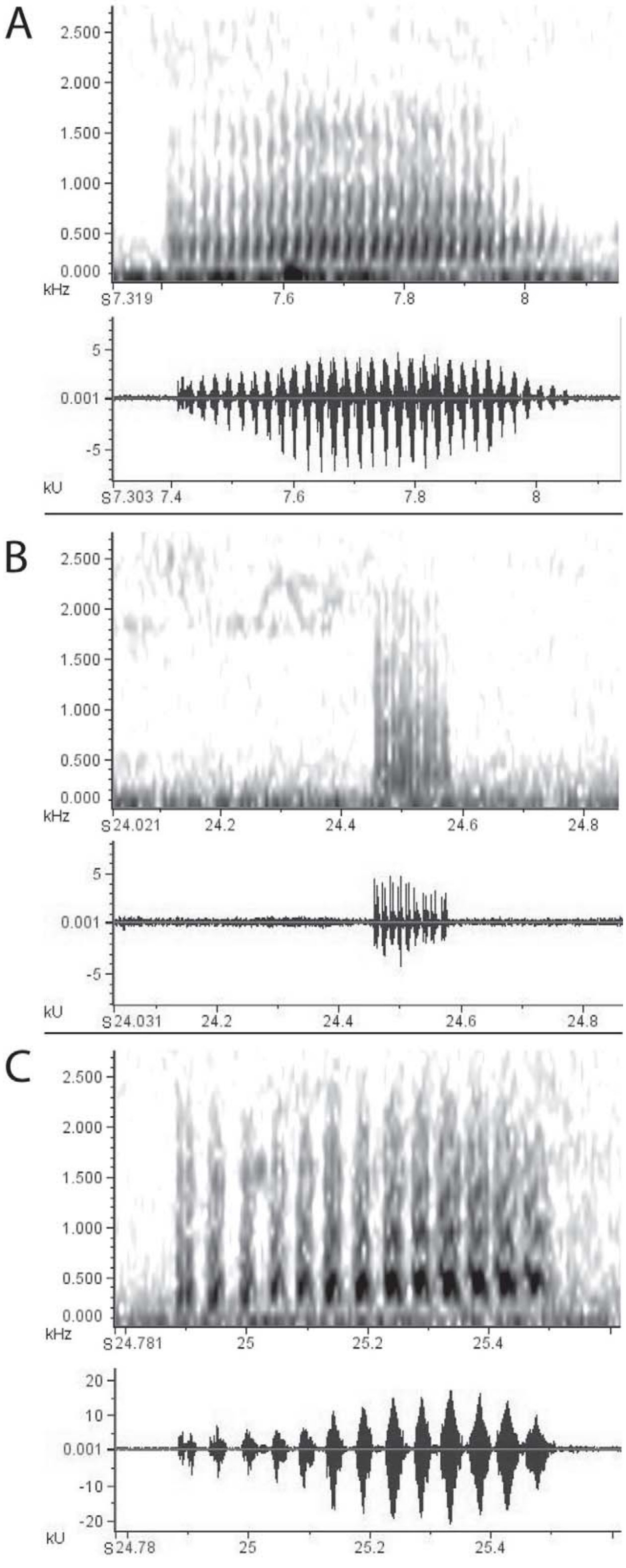

Figure 96. Advertisement calls of *Leptodactylus chaquensis.* **(A)** Growl. **(B)** Grunt. **(C)** Trill.

Larval morphology. Total length (Gosner 36) 42 mm; oral disk anteroventral; tooth row formula 2/3 or 2/3[1], P1 interruption very short when present; tail musculature uniform brown/black (data from Cei, 1980:351–352; Heyer and Giaretta, 2009:301).

Advertisement call. Three distinctive advertisement calls known: growls (most frequent), grunts, and trills. Growls (Fig. 96A): dominant (= fundamental) frequency 343–515 Hz; call duration 0.41–0.66 s; call composed of 16–30 notes, notes single or double pulsed throughout call; weak frequency modulation throughout call; call rate 46–49/s. Grunts (Fig. 96B): dominant (= fundamental) frequency 263–343 Hz; call duration 0.10–0.12 s; call composed of 8–10 notes/pulses per call; frequency modulation not apparent; call rate 71–100/s. Trills (Fig. 96A):

Figure 97. Distribution map of *Leptodactylus chaquensis*.

dominant (= fundamental) frequency 424–520 Hz; call duration 0.48–0.81 s; call composed of 11–16 notes per call; frequency modulation not apparent over entire call. All three call types with at least one harmonic (Heyer and Giaretta, 2009:295–300) (Fig. 96).

Distribution. Arid ecosystems in northern Argentina and adjacent Bolivia, Brazil, Paraguay, and northern Uruguay; northern extent of distribution unknown in Brazil (Fig. 97; for new records in southern Brazil see Oda et al., 2014).

Leptodactylus guianensis **Heyer and de Sá, 2011 (Plate 9C)**

Leptodactylus guianensis Heyer and de Sá, 2011:35. Type locality: "Guyana; Rupununi, Iwokrama Forest Reserve, Sipuruni River, Pakatau Camp, 04°45'17"N, 59°01'28"W. 85 m." Holotype: USNM 531509, adult male.

Etymology. Named for the species distribution that coincides in large part with the Guiana Shield.

Adult morphology. Moderate–large size, female SVL 66.0–109.2 mm ($\overline{X}$ = 88.2 mm), male SVL 79.5–109.5 mm ($\overline{X}$ = 94.2 mm); adult snout not spatulate; adult males with a modestly chisel-shaped black thumb spine; light upper lip stripe present or absent; dorsal folds absent; dorsolateral folds complete, distinct; lateral folds interrupted; posterior thigh lacking a light stripe; upper shank barred; belly variously mottled to no pattern (no melanophores); toes with lateral fringes (Heyer and de Sá, 2011:35–37).

Similar species. *Leptodactylus guianensis* occurs in the State of Roraima in Brazil, Guyana, Suriname, and the State of Bolívar in Venezuela. Other species occurring in this area with complete dorsolateral folds and toe fringes in at least some individuals are *L. latrans* complex species and *L. leptodactyloides*. *Leptodactylus latrans* complex species have dorsal folds; *L. guianensis* lacks dorsal folds. The dorsolateral folds of *L. leptodactyloides* are interrupted and usually do not extend to the groin; the dorsolateral folds of *L. guianensis* are complete, extending to the groin.

Figure 98. Distribution map of *Leptodactylus guianensis.*

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Lowland portions of Guiana Shield regions of Guyana, Suriname, Venezuela, and adjacent Brazil (Fig. 98).

Leptodactylus insularum **Barbour, 1906 (Plate 9D)**

Leptodactylus insularum Barbour, 1906:228. Type locality: Saboga Island in the Gulf of Panamá. Syntypes: originally a lot of 12 specimens with the single MCZ number 2424. The type description is not based on a single specimen but is a composite description including male and female data. Eleven of the 12 original syntypes were exchanged or had new MCZ catalogue numbers assigned to them. A single specimen was retained MCZ 2424. MCZ 2424 (adult female) was designated the lectotype of *L. insularum* Barbour 1906 by Heyer and de Sá (2011:28).

Leptodactylus insularum: Heyer and de Sá, 2011:38–40. Recognition of *L. insularum* as a distinct species.

Etymology. Name indicates original belief that the species was restricted to islands in the Gulf of Panamá.

Adult morphology. Moderate–large size, female SVL 60.4–99.1 mm ($\overline{X}$ = 81.4 mm), male SVL 66.0–104.6 mm ($\overline{X}$ = 86.6 mm); adult male snout not spatulate; adult males with 2 round black thumb spines; light upper lip stripe indistinct or absent; dorsal folds absent; dorsolateral folds well developed, complete; lateral folds distinct and complete to slightly interrupted; posterior thigh without a light stripe; upper shank barred; belly lightly to heavily mottled; toes with lateral fringes (Heyer and de Sá, 2011:40).

Similar species. *Leptodactylus insularum* occurs from Costa Rica through Panamá and along Caribbean drainages of Colombia, Venezuela, and Trinidad as well as islands in the Gulf of Panamá and the Colombian islands of Providencia and San Andrés. Within its distribution, *L. insularum* is the only *Leptodactylus* species with complete dorsolateral folds and toe fringing.

Larval morphology. Maximum total length (Gosner 37) 35.2 mm; oral disk anteroventral; tooth row formula 2/3;

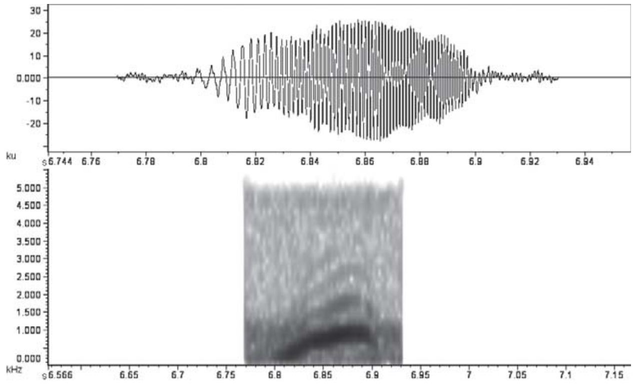

Figure 99. Advertisement of *Leptodactylus insularum.*

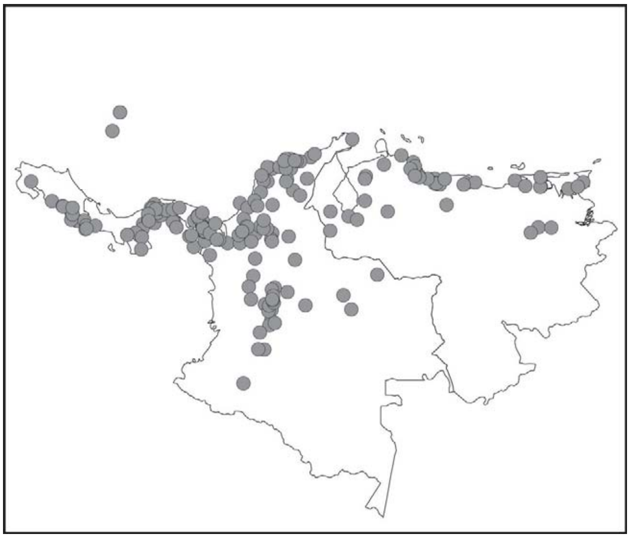

Figure 100. Distribution map of *Leptodactylus insularum.*

tail musculature uniformly moderate to dark brown, tail fins ranging from same pattern as tail musculature to ventral tail fin with a gradient of no melanophores next to the body to uniform brown around mid-fin (Heyer and de Sá, 2011:24–25, 40).

Advertisement call. Dominant (= fundamental) frequency 110–120 to 890–1,200 Hz; call duration 0.08–0.12 s; call consisting of a single note; call frequency modulated with rising frequencies from beginning to about 1/3 call length; call rate 1.2–2.5/s; harmonic structure is present or absent (Heyer and de Sá, 2011:25–27, 41) (Fig. 99).

Distribution. Costa Rica through Panamá, along Caribbean drainages of Colombia, Venezuela, and Trinidad, on islands in the Gulf of Panamá, and on the Colombian islands of Providencia and San Andrés (Fig. 100).

Leptodactylus latrans (Steffen, 1815) (Plate 9E)

Rana latrans Steffen, 1815:13. Neotype locality: "Vale dos Agriões [22°25'S, 42°58'W, approx. 900 m above sea level], Municipality of Teresópolis, State of Rio de Janeiro, Brazil." Neotype: MNRJ 30733, adult male, described by Lavilla, Langone, Caramaschi, Heyer, and de Sá, 2010:8.

Rana gibbosa Raddi, 1823:67. Type locality: Rio de Janeiro [Brazil]. Holotype: Not stated, presumably originally MZUF. Synonymy by Bokermann, 1965:9–12.

Rana fusca Raddi, 1823:68. Type locality: "Rio-janeiro," Brazil. Holotype: MZUF ???. Junior homonym of *Rana fusca* Schneider. Synonymy by Bokermann, 1966:88.

Rana pygmaea Spix, 1824:30. Type locality: "Provincia Bahiae," Brazil. Type(s): Not specifically designated, although including animal figured on plate 6, figure 2 of the original publication. Holotype lost from ZSM according to Heyer, 1973:26 and Hoogmoed and Gruber, 1983:356 (who implied that type material may never have been deposited in the ZSM and noted that RMNH 2041 might be a syntype). Synonymy by Günther, 1859b "1858":27; Peters, 1872:225; Boulenger, 1882:247; Hoogmoed and Gruber, 1983:355.

Rana pachypus Spix, 1824:26. Type localities: "Habitat in locis humidis Provinciae Rio de Janeiro," [var. 1] "locis humidis Bahiae," and [var. 2] "locis aquosis Parae," Brazil. See comments on types of varieties by Glaw and Franzen, 2006:176. Syntypes: ZSM (10 specimens, presumed lost), ZMB, and presumably ZMH; ZSM 122/0.1 designated lectotype by Hoogmoed and Gruber, 1983:356 (who implied that type material may never have been deposited in the ZSM and noted that RMNH 2041 might be a syntype). Synonymy by Tschudi, 1838:78; Duméril and Bibron, 1841:396; Peters, 1872:225. Variety 2 shown to be a junior synonym of *Rana fusca* Schneider by Peters, 1872:199 and Hoogmoed and Gruber, 1983:356.

Rana pachybrachion Wied-Neuwied, 1824:671. Type locality: "Brasiliens." Types: Not designated. Possibly an incorrect subsequent spelling or emendation of *Rana pachypus* Spix, 1824. Synonymy by W.R. Heyer (pers. comm. to D. Frost, Amphibian Species of the World website accessed 27 April 2011).

Rana macrocephala Wied-Neuwied, 1825:544. Type locality: "Urwälden an der Lagoa d'Arara unweit des Flusses Mucuri," Brazil (regarded as being somewhere in southern Bahia, Brazil by Bokermann, 1966:89). Type(s): not designated, not found at AMNH. Tentative synonymy with *Leptodactylus ocellatus* by Bokermann, 1966:89.

Cystignathus pachypus: Wagler, 1829:9; Wagler 1830:203.

Rana pachypus pachypus: Mayer, 1835:24.

Rana pachypus octolineatus Mayer, 1835:24. Type locality: not stated. Type(s): Deposition not stated, now presumed lost.

Leptodactylus serialis Girard, 1853:421. Type locality: "Rio de Janeiro," Rio de Janeiro, Brazil. Syntypes: Not designated; USNM 7389 (2 specimens) according to Cochran, 1961:64. Synonymy with *Leptodactylus pachypus* by Jiménez de la Espada, 1875:48. Synonymy by Girard, 1858:29; Boulenger, 1882:247.

Leptodactylus caliginosus Girard, 1853:422. Type locality: "Rio de Janeiro, [Rio de Janeiro,] Brazil." Syntypes: not designated, USNM 7352 (2 specimens) according to Cochran, 1961:64. Synonymy by Nieden, 1923:490; Lutz, 1930:22.

Leptodactylus ocellatus: Girard, 1853:420.

Cystignathus pachypus: Günther, 1859b "1858":27.

Cystignathus caliginosus: Günther, 1859b "1858":28.

Leptodactylus pachypus: Jiménez de la Espada, 1875:48.

Rana luctator Hudson, 1892:78. Type locality: presumably vicinity of "Buenos Ayres," Argentina. Holotype: lost according to original publication. Synonymy by Gallardo, 1964b:373–384; Lavilla, 1994 "1992":87.

Rana octoplicata Werner, 1893:83. Type locality: "Nordamerika." Type: Not designated. Synonymy by Werner, 1894:125; Nieden, 1923:491.

Cystignathus oxycephalus Philippi, 1902:105. Type locality: "ad Montevideo, Arrechavaleta," Uruguay. Syntypes: MNHNC (2 specimens) according to original publication. Synonymy by Klappenbach, 1968:150.

Cystignathus oxicephalus: Philippi, 1902:124. Incorrect subsequent spelling.

Leptodactylus pygmaeus: Miranda-Ribeiro, 1927:15.

Leptodactylus ocellatus var. *reticulata* Cei, 1948:308. Type locality: "Arroyo, Isla Apipé, Ituzaingó [Corrientes]" and "Puerto Bemberg [Misiones]," Argentina. Syntypes: not designated, presumably at FML.

Leptodactylus ocellatus var. *bonaerensis* Cei, 1949a:127. Syntypes: Not designated, but in MACN and FML (total of 59 examples, source of information unclear). Type locality: "Río Colorado y Bahía Blanca," Argentina. Restricted to Bahia Blanca, Argentina by Gorham, 1966:133.

Leptodactylus latrans: Lavilla, Langone, Caramaschi, Heyer, and de Sá, 2010:8.

Etymology. From the Latin word *latrans* (barker).

Adult morphology. Large, male neotype 107.0 mm SVL; adult male snout not spatulate; male with two black keratinized spines on each thumb; male lacking chest spines; light upper lip stripe absent; a pair of dorsal folds from the posterior interocular region to the end of the body; a pair of complete dorsolateral folds from the posterior corner of the eye to groin; complete auxiliary lateral fold from the shoulder region to the groin; complete lateral fold from the posterior corner of the eye to groin; posterior thigh lacking light stripe; upper shank with faint bars; belly white with scattered irregular gray spots; toes with lateral fringes (Lavilla et al., 2010:4–5).

Similar species. The neotype of *Leptodactylus latrans* can be distinguished from *L. chaquensis* by the presence of an additional pair of lesser developed but discernible dorsal folds situated between the medial dorsal folds and the dorsolateral folds extending from the post-tympanic region to the sacral region in most *L. chaquensis.*

Larval morphology. Larvae from the type locality are unknown. Several purported descriptions corresponding to this species complex are available; however, until the systematics and species composition of this complex are determined (see below), the species allocation of those larval descriptions should be considered with caution.

Advertisement call. Unknown.

Distribution. Range beyond the type locality unknown.

Comment. *Leptodactylus latrans* is currently considered a species complex. In Argentina, Paraguay, and Uruguay there are two species of the *L. latrans* complex that are readily distinguishable from each other. One of them is *L. chaquensis,* while the other species is a member of the *L. latrans* species complex. Outside of Argentina, Paraguay, and Uruguay the distribution of *L. chaquensis* is uncertain and the taxonomic status of *L. macrosternum* is unclear as to whether it is distinct from *L. chaquensis.* The only solid taxonomic statement that can be made currently is that *L. chaquensis* from Argentina is a valid species and *L. latrans* from the type locality in the State of Rio de Janeiro, Brazil, is a valid species. The distribution of *L. latrans*-like specimens outside of the type locality of *L. latrans* is notoriously clouded. An analysis of color patterns and size variation in the *L. latrans* concluded that the data were not sufficient to determine species limits within this complex (Heyer, 2014). For present purposes, information provided herein for *L. latrans* is solely based on the type specimen from the State of Rio de Janeiro, Brazil.

Leptodactylus macrosternum Miranda-Ribeiro, 1926 (Plate 9F)

Leptodactylus ocellatus macrosternum Miranda-Ribeiro, 1926:147. Type locality: "Bahia", Brazil; Bokermann, 1966:73, considered the type locality to be "provàvelmente Salvador," Bahia, Brazil. Holotype: MZUSP 448, juvenile.

Leptodactylus ocellatus macrosternus: Miranda-Ribeiro, 1927:125. Incorrect subsequent spelling.

Leptodactylus macrosternum: Gallardo, 1964b:379. First usage of *macrosternum* at the species level.

Morphology. Juvenile holotype 65 mm SVL; no information on upper lip stripe; five longitudinal folds on each side of body; no information on extent of folds on each side of body or whether folds continuous or interrupted; no information on posterior thigh pattern, upper shank pattern, or belly pattern; toes fringed.

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Limited to type locality.

Comment. The juvenile holotype of *Leptodactylus ocellatus macrosternum,* MZUSP 448, is in very poor condition. Based on the holotype, it is difficult to discern what other specimens are conspecific with it. The taxonomic status of the holotype cannot be made until the relationships of the *L. latrans* group have been clarified.

Leptodactylus silvanimbus **McCranie, Wilson, and Porras, 1980 (Plate 10A)**

Leptodactylus silvanimbus McCranie, Wilson, and Porras, 1980:361. Type locality: "Belén Gualcho, Cordillera de Celaque, Depto. Ocotepeque, Honduras, elevation 1700–1900 m [14°29'N, 88°47'W]." Holotype: USNM 212046, adult male.

Etymology. "The scientific name *silvanimbus* is formed from the Latin words *silva* (forest) and *nimbus* (raincloud). The name refers to this species occurring in cloud forests, although not restricted to that habitat."

Adult morphology. Moderate size, female SVL 35.9–48.0 mm ($\overline{X}$ = 45.2 mm), male SVL 35.8–55.0 mm ($\overline{X}$ = 47.8 mm); adult male snout not spatulate; adult males with a pair of black thumb spines; males lack chest spines; light stripe from posterior corner of eye to tympanum or arm insertion present or absent; dorsal folds absent; dorsolateral folds absent; lateral folds interrupted or absent; no posterior thigh light stripe; upper shanks barred to uniform; belly mottled; toes with lateral ridges or fringes (Heyer et al., 2002).

Similar species. The only other species in Honduras with lateral toe fringing is *Leptodactylus melanonotus*. *Leptodactylus melanonotus* and *L. silvanimbus* are very similar morphologically. *Leptodactylus silvanimbus* reach larger sizes (female SVL 35.9–48.0 mm, male SVL 35.8–55.0 mm) than *L. melanonotus* (female SVL 34.3–45.1 mm, male SVL 32.2–43.4 mm). Adult male *L. silvanimbus* have greater arm hypertrophy than male *L. melanonotus*. All *L. melanonotus* have toe fringes; *L. silvanimbus* have lateral toe ridges or fringes. *Leptodactylus silvanimbus* occurs at 1700–1900 m; *L. melanonotus* occurs below 1500 m.

Larval morphology. Maximum total length (Gosner 36) 46.5 mm; oral disk anteroventral; tooth row formula 2(2)/3; tail fins translucent, heavily marked with dark brown especially posteriorly, stages 30+ are considerably darker than earlier stages (McCranie and Wilson, 2002:456–457).

Advertisement call. Dominant frequency varies from fundamental frequencies of 420–620 Hz or first harmonic of 1,310–1,400 Hz or third harmonic of 1,640–1,820 Hz, or fourth harmonic of 1,380–1,920 Hz; average call duration 152 ms; call of about 160 partial pulses per call; fundamental frequency is typically initiated at 440 Hz, quickly rising to 510 Hz, then slowly falls to 440 Hz by end of call; call rate 22/min; harmonic structure present (Heyer et al., 2002:743.2 (Fig. 101).

Distribution. Moderate and intermediate elevations along the Continental Divide in the Department of Ocotepeque in southwestern Honduras (Fig. 102).

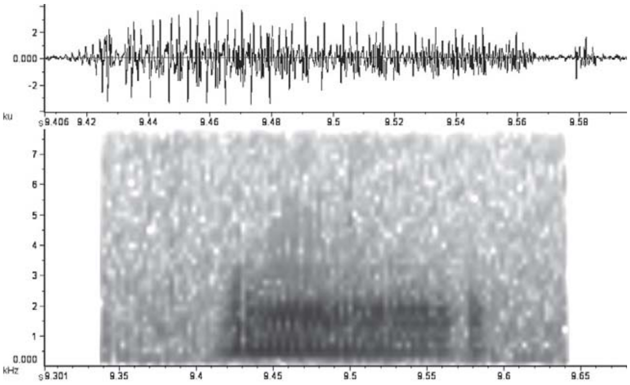

Figure 101. Advertisement call of *Leptodactylus silvanimbus* (recording USNM 113).

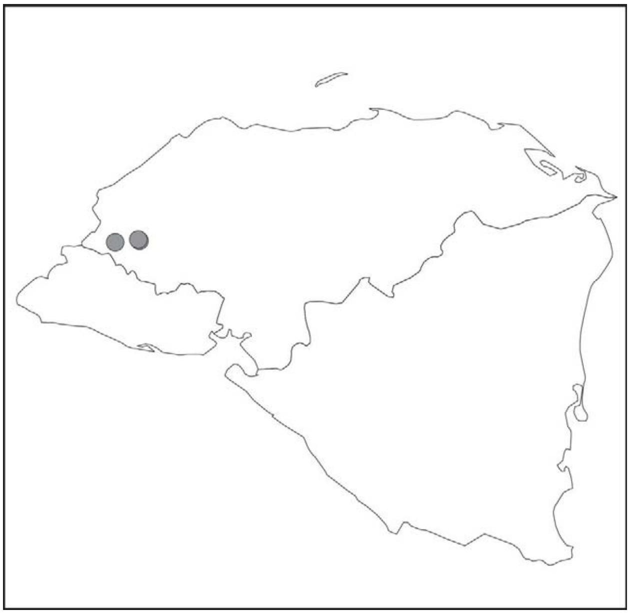

Figure 102. Distribution map of *Leptodactylus silvanimbus.*

Leptodactylus viridis Jim and Spirandeli-Cruz, 1973 (Plate 10B)

Leptodactylus viridis Jim and Spirandeli-Cruz, 1973:13. Type locality: "Fazenda Pedra Branca, Município de Itajibá, Estado da Bahia," Brazil. Holotype: MZUSP 50175, adult male).

Etymology. From the Latin *viridis* (green), for the overall body coloration in life.

Adult morphology. Moderate size, female SVL 55.8–72.2 mm, male SVL 63.0–70.9 mm; male snout not spatulate; males with a single black thumb spine; males without chest spines; light lip stripe absent; very weak dorsal folds; distinct continuous dorsolateral folds; lateral folds interrupted or continuous; posterior thigh without light stripe; upper shank barred; belly lightly speckled; toes with lateral fringes (Jim and Spirandeli-Cruz, 1979:707–710).

Similar species. The only other species that co-occurs with *L. viridis* that has dorsal folds and toe fringing is the *Leptodactylus latrans* complex species. The dorsal folds of *L. viridis* are weak but discernible; the dorsal folds of the *L. latrans* complex species are distinct.

Larval morphology. Unknown.

Advertisement call. Unreported. The species was heard calling on December 09–10, 2010, close to the type locality (RdS pers. obs.), the area did not have rain for at least 3 days. Males were calling on muddy grounds around a pond (not in the water) and under relatively thick vegetation. A single note call could be heard and a second longer, but barely audible, call also was heard.

Figure 103. Distribution map of *Leptodactylus viridis.*

Distribution. Known from four localities in the states of Bahia (3) and Minas Gerais (1), Brazil (Fig. 103).

Comment. The original description reports the authors' names as "Jim, J. e Spirandelli, E.F." Spirandeli is the correct spelling of the second author's last name. Subsequently, a more complete description was published by the authors in 1979, with Elieth Floret Spirandeli Cruz as the second author. Presumably the second author married and added her husband's name (Cruz). A subsequent citation (Freitas et al., 2001) uses the last name combination of Spirandeli-Cruz.

Leptodactylus melanonotus species group

Leptodactylus colombiensis Heyer, 1994 (Plate 10C)

Leptodactylus colombiensis Heyer, 1994:82. Type locality: Colombia; Santander; Charalá, Virolín [= Inspección Policía Cañaverales], confluencia del Río Cañaverales con el Río Guillermo, vertiente occidental, 1600–1700 m, 06°13'N, 73°05'W. Holotype: ICNMHN 7409, adult male.

Etymology. The name *colombiensis* refers to the geographic area of Colombia; at the time of description, *Leptodactylus colombiensis* was known only to occur in Colombia.

Adult morphology. Moderate size, female SVL 39.9–62.5 mm ($\overline{X}$ = 53.3 mm), male SVL 36.0–55.9 mm ($\overline{X}$ = 44.4 mm); adult male snout not spatulate; adult males with 2 black medium to large spines on each thumb; males lack chest spines; distinct to indiscernible light lip stripes from just past mid-eye or usually from posterior corner of eye to jaw commissure; dorsolateral folds absent to complete; lateral folds absent or interrupted; light posterior thigh stripe very distinct to indiscernible; upper shank barred; belly lightly to extensively mottled; toes with lateral fringes (Heyer, 1994:82–84).

Similar species. Species occurring in the Caribbean drainages of Colombia (and possibly adjacent State of Táchira in Venezuela) with fringed toes are *Leptodactylus colombiensis* and *L. insularum.* Dorsolateral folds, if present in *L. colombiensis,* are not bordered by dark stripes; all well-preserved *L. insularum* have well developed dorsolateral folds that are bordered by a dark stripe. *Leptodactylus colombiensis* adults are smaller (female SVL less than 62 mm, male SVL less than 56 mm) than adult *L. insularum* (female SVL greater than 59 mm, male SVL greater than 66 mm).

Sexually active males of *L. colombiensis* lack chest spines, *L. insularum* have a central patch of chest spines.

Larval morphology. Total length data not reported. Oral disk anteroventral; tooth row formula 2/3; tail fins uniformly dark (data from illustration in Lynch, 2006:453).

Advertisement call. Dominant (= fundamental) frequency of initial pulse of 620–740 Hz, remainder composed of 5–8 partial pulses modulating between 1,470–1,980 Hz; call duration 0.031–0.034 s; call rate 0.6 calls/s; no harmonic structure (Fig. 104).

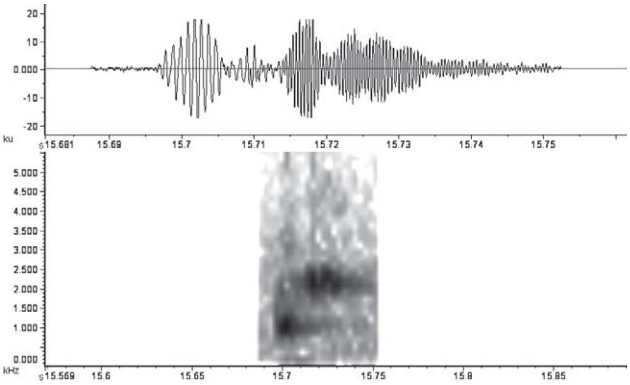

Figure 104. Advertisement call of *Leptodactylus colombiensis.*

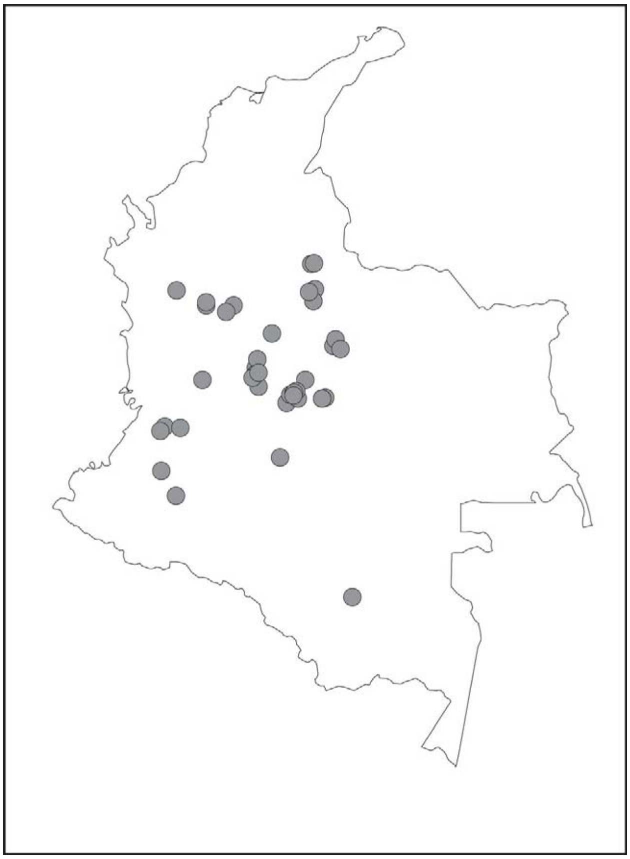

Figure 105. Distribution map of *Leptodactylus colombiensis.*

Distribution. Caribbean drainages in Colombia. The locality in the State of Táchira, Venezuela (Barrio-Amarós and Chacón-Ortiz, 2001:55) should be verified (Fig. 105).

Leptodactylus diedrus Heyer, 1994 (Plate 10D)

Leptodactylus diedrus Heyer, 1994:86. Type locality: Colombia; Vaupés, ½ mile NE Timbó, ~ 01°06'N, 70°01'W. Holotype: UTA 3726, adult male.

Etymology. From the Greek *diedrus,* sitting apart, separated, in allusion to the distinctiveness of this species within the *Leptodactylus podicipinus-wagneri* species complex.

Adult morphology. Small–moderate size, female SVL 34.4–47.9 mm ($\bar{X}$ = 41.1 mm), male SVL 29.7–40.4 mm ($\bar{X}$ = 36.2 mm); adult male snout not spatulate; males with two keratinized spines on each thumb, males lack chest spines; indistinct to indiscernible light upper lip stripe; dorsal folds absent; dorsolateral folds absent; lateral folds absent; most (95%) individuals lack light stripes on the posterior thighs (5% of individuals with indistinct light stripes); upper shank barred; belly usually (80%) lacking melanophores or other pattern, belly sometimes (20%) lightly mottled; toes with lateral fringes (Heyer, 1994:86–87).

Similar species. *Leptodactylus diedrus* inhabits areas of the Amazon basin and might be expected to occur with the following *Leptodactylus* species with toe fringes: *L. bolivianus, L. colombiensis, L. latrans* complex species, *L. leptodactyloides, L. petersii, L. podicipinus, L. riveroi, L. validus,* and *L. wagneri. Leptodactylus diedrus* lack dorsolateral folds, the bellies usually lack melanophores, the mottled ventral thigh patterns usually are in sharp contrast to the patternless bellies, and the toe tips usually are expanded into small discs. *Leptodactylus bolivianus, L. latrans* complex species, *L. riveroi,* and *L. wagneri* have distinct dorsolateral folds. The belly and thigh patterns blend and the bellies usually have distinct patterns in *L. colombiensis, L. petersii, L. podicipinus,* and *L. validus.*

Larval morphology. Unknown.

Advertisement call. Heyer (1998) described the call with the following characteristics: dominant (= fundamental) frequency 490–1,170 Hz; call duration 0.18–0.30 s; call rate 0.7 calls/s; call composed of 2–6 pulses per note; call frequency modulated, rising throughout the call; definite harmonic structure, well developed second harmonic.

Distribution. Western Amazonia (Brazil, Colombia, Peru, and Venezuela) (Fig. 106).

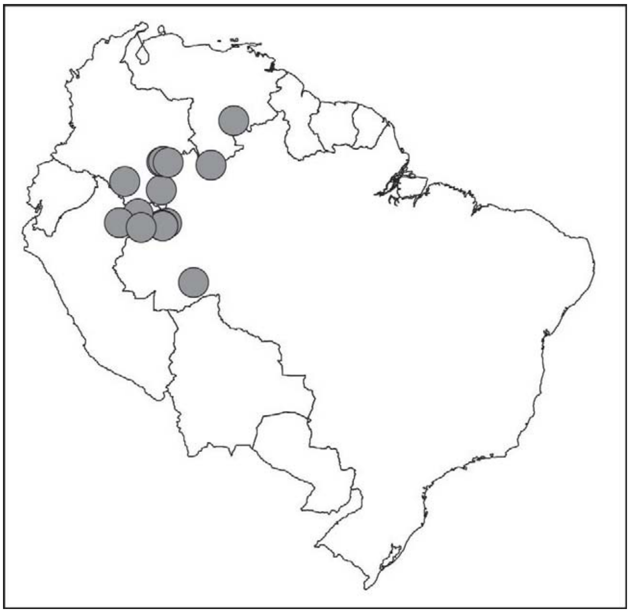

Figure 106. Distribution map of *Leptodactylus diedrus.*

Leptodactylus discodactylus **Boulenger, 1884 "1883" (Plate 10E)**

Leptodactylus discodactylus Boulenger, 1884 "1883":637. Type locality: Yurimaguas, Huallaga River [Loreto] Northern Perú. Holotype: BMNH 84.2.18.44, re-registered as BMNH 1947.2.17.40, female.

Leptodactylus nigrescens Andersson, 1946 "1945":57. Type locality: Rio Napo, Watershed, 400 m, Ecuador. Lectotype: NRM 1930, not an adult male, either juvenile or female.

Vanzolinius discodactylus: Heyer, 1974b:88. New genus allocation for the taxon.

Leptodactylus discodactylus: de Sá, Heyer, and Camargo, 2005:87–97 and Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green, and Wheeler, 2006:362 synonymized the genus *Vanzolinius* Heyer, 1974 with the genus *Leptodactylus* Fitzinger, 1826.

Etymology. From the Greek *diskos,* disk, and *daktylos,* finger/toe, characterizing the species as having disk-shaped toe tips.

Adult morphology. Small, female SVL 27.9–39.9 mm ($\overline{X}$ = 34.5 mm), male SVL 22.3–34.2 mm ($\overline{X}$ = 28.1 mm); male snout not spatulate; males without thumb and chest spines; light upper lip stripe absent; no dorsal, dorsolateral, or lateral folds; posterior thigh usually mottled, some specimens with dark and/or light stripes; upper shank barred; belly mottled; toes fringed (Heyer, 1970a, 1974a).

Similar species. *Leptodactylus discodactylus* occurs in Amazonian Brazil (Acre, Amazonas), Colombia, Ecuador, and Peru. Similar species within the distribution of *L. discodactylus* are *L. bolivianus, L. diedrus, L. griseigularis, L. leptodactyloides, L. pascoensis, L. petersii, L. podicipinus,* and juveniles of *L. wagneri.* The dorsal toe disks of *L. discodactylus* have between 1–5 longitudinal grooves (visible under magnification); all listed similar species lack dorsal longitudinal grooves (on the dorsal toe tips) except *L. diedrus. Leptodactylus diedrus* have a single longitudinal dorsal groove on the largest toe disks; furthermore, the ventral and posterior thigh patterns abut in *L. diedrus,* whereas the ventral and posterior thigh patterns blend together in *L. discodactylus.*

Larval morphology. Duellman's (1978) description and Heyer's (1998) illustration may or may not correspond to *L. discodactylus.* Maximum total length (Gosner 30) 25 mm; oral disk anteroventral; tooth row formula 2/3; tail uniform dark (Duellman, 1978:106; Heyer, 1998:5–6).

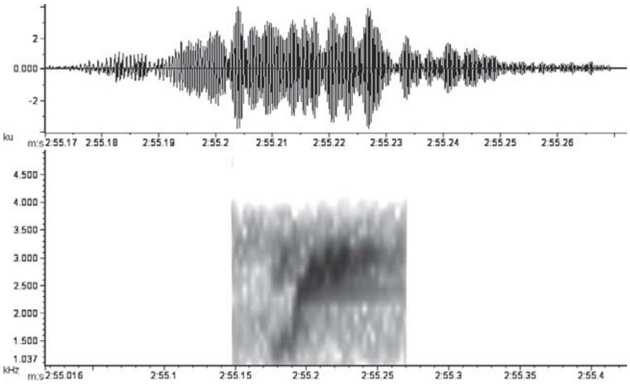

Figure 107. Advertisement call of *Leptodactylus discodactylus* (recording USNM 18).

Figure 108. Distribution map of *Leptodactylus discodactylus.*

Advertisement call. Dominant (= fundamental) frequency 1,160–3,190 Hz; call mean duration 0.12–0.14 s; calls pulsed or partially pulsed (ca. 14–19 pulses/call); rising frequency throughout call, most abrupt at beginning of call; call = note rate 1.1/s; harmonic structure weak or absent (Heyer, 1997) (Fig. 107).

Distribution. Amazonian Brazil (Acre, Amazonas), Colombia, Ecuador, and Peru (Fig. 108).

Leptodactylus griseigularis **(Henle, 1981) (Plate 10F)**

Adenomera griseigularis Henle, 1981:139. Type locality: Perú, Huanuco, Potanischer Garten in Tingo Maria, 641 m. Holotype: ZFMK 31800, juvenile.

Leptodactylus griseigularis: Heyer, 1985 "1984":97–100. First association of *griseigularis* with the genus *Leptodactylus; L. griseigularis* considered a synonym of *L. wagneri.*

Leptodactylus griseigularis: Heyer, 1994:87.

Etymology. From Latin *griseus* (gray) and *gula* (throat).

Adult morphology. Moderate size, female SVL 35.1–59.3 mm ($\overline{X}$ = 47.8) mm, male SVL 34.1–52.9 ($\overline{X}$ = 43.5) mm; adult male snout not spatulate; adult males with a pair of black keratinized spines on each thumb; males lack chest spines; light posterior upper lip stripe usually indistinct or absent; dorsal folds absent; dorsolateral folds of moderate length to absent; lateral folds interrupted or absent; posterior thigh light stripes usually indiscernible (86%); upper shank uniform to barred; belly mottled; toes with lateral fringes (Heyer, 1994:87–88).

Similar species. *Leptodactylus griseigularis* occurs in the Bolivian Department of La Paz and the Peruvian Departments of Ayacucho, Huanuco, Junin, Pasco, San Martín, and Ucayali between 100–1800 m. Other similar species with toe fringes overlapping in distribution with *L. griseigularis* are: *L. bolivianus, L. chaquensis, L. leptodactyloides, L. pascoensis, L. petersii,* and *L. podicipinus. Leptodactylus chaquensis* has a pair of dorsal folds; *L. griseigularis* lacks dorsal folds. *Leptodactylus griseigularis* is a moderate-size species (females 39–58 mm SVL, males 35–51 mm SVL) in which most individuals have interrupted dorsolateral folds; *L. bolivianus* is a large species (females to 88 mm SVL, males to 94 mm SVL) in which the dorsolateral folds are complete. *Leptodactylus griseigularis* is most likely to be confused with *L. leptodactyloides;* the commonest posterior thigh pattern in *L. griseigularis* is mottled, without any indication of light stripes; the commonest posterior thigh pattern in *L. leptodactyloides* is with distinct light stripes; almost all male *L. griseigularis* have large black thumb spines; almost all male *L. leptodactyloides* have medium black thumb spines. *Leptodactylus griseigularis* is smaller than *L. pascoensis* (*L. pascoensis* females 52–67 mm SVL, males 60–61 mm SVL). *Leptodactylus griseigularis* is larger than *L. petersii* (*L. petersii* females 31–51 mm SVL, males 27–41 mm SVL); the commonest belly pattern is a light mottle in *L. griseigularis,* whereas the commonest belly pattern in *L. petersii* is an extensive mottle in an anastomotic pattern. *Leptodactylus griseigularis* is larger than *L. podicipinus* (*L. podicipinus* females 30–54 mm SVL, males 24–43 mm SVL) and the bellies of *L. podicipinus* often are dark with distinct small light spots whereas the bellies of *L. griseigularis* are mottled.

Larval morphology. Unknown.

Advertisement call. Dominant (= fundamental) frequency 1,380–3,060 Hz; call duration 0.08–0.14 s; each call a single pulse; calls frequency modulated, rising through the call; call rate 1.8/s; harmonic structure equivocal (Heyer and Morales, 1995:91–92) (Fig. 109).

Distribution. Bolivia and Perú (Fig. 110).

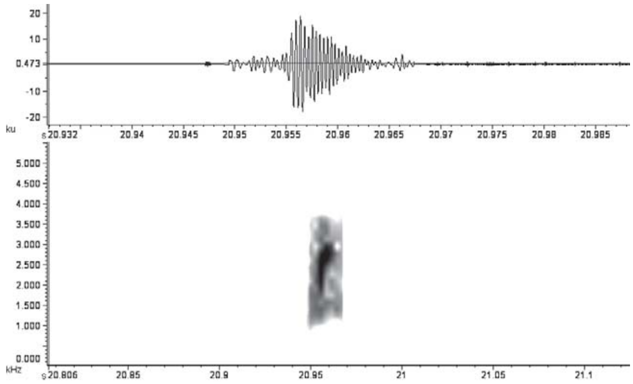

Figure 109. Advertisement call of *Leptodactylus griseigularis.*

Figure 110. Distribution map of *Leptodactylus griseigularis* (recording USNM 274).

Leptodactylus leptodactyloides **(Andersson, 1945) (Plate 11A)**

Eleutherodactylus leptodactyloides Andersson, 1946 "1945":43. Type locality: "Rio Pastaza," eastern Ecuador. Holotype: NRM 1945, adult male.
Leptodactylus leptodactyloides: Heyer, 1994:88.

Etymology. Andersson considered the type specimen to be a new species in the genus *Eleutherodactylus* that resembled frogs of the genus *Leptodactylus.*

Adult morphology. Moderate size, female SVL 34.8–56.2 mm ($\overline{X}$ = 46.3 mm), male SVL 28.3–47.9 mm ($\overline{X}$ = 40.1 mm); adult male snout not spatulate; adult males with a pair of medium-sized black keratinized thumb spines; males lacking chest spines; light upper lip stripe absent between tip of snout to under eye, light stripe from under eye to jaw commissure very distinct to indiscernible; dorsal folds absent; dorsolateral folds absent or extending partially or totally from eye to groin; lateral folds absent or interrupted; upper shank barred to rarely uniform; belly mottled; toes with lateral fringes (Heyer, 1994:88–89).

Similar species. *Leptodactylus leptodactyloides* occurs sympatrically with or in the same general region as the following *Leptodactylus* species with toe fringes: *L. bolivianus, L. colombiensis, L. diedrus, L. griseigularis, L. latrans* complex species, *L. pascoensis, L. petersii, L. podicipinus, L. riveroi, L. sabanensis, L. validus,* and *L. wagneri* (among these, *L. leptodactyloides* most closely resembles *L. colombiensis, L. griseigularis,* and *L. sabanensis*). *Leptodactylus leptodactyloides* rarely (5% of specimens) have long dorsolateral folds but when present they are interrupted, not smooth; the dorsolateral folds in *L. bolivianus* and *L. riveroi* are always long and complete. *Leptodactylus leptodactyloides* is smaller than *L. colombiensis* (*L. leptodactyloides* females 35–56 mm SVL, males 28–48 SVL; *L. colombiensis* females 40–62 mm SVL, males 36–56 mm SVL) and fewer *L. leptodactyloides* (10% of specimens) have light-spotted chins/throats than do *L. colombiensis* (44%). *Leptodactylus leptodactyloides* almost always has some indication of short to long, interrupted or continuous dorsolateral folds; *L. diedrus* lacks dorsolateral folds. Almost all *L. leptodactyloides* have melanophores on the belly; most *L. diedrus* usually lack belly melanophores (81% of specimens). Posterior and ventral thigh patterns blend into each other in *L. leptodactyloides;* the patterns abut in *L. diedrus.* The commonest posterior thigh pattern in *L. leptodactyloides* is with distinct light stripes whereas in *L. griseigularis* the commonest pattern is mottled, with no indication of light stripes; almost all reproductively active male *L. leptodactyloides* have a pair of medium-size black thumb spines, almost all male *L. griseigularis* have a pair of large thumb spines. Members of the *L. latrans* complex have a pair of dorsal folds; *L. leptodactyloides* lacks dorsal folds. *Leptodactylus leptodactyloides* is smaller than *L. pascoensis* (*L. leptodactyloides* females 35–56 mm SVL, males 28–50 mm SVL; *L. pascoensis* females 52–67 mm SVL, males 60–61 mm SVL); *L. leptodactyloides* individuals usually have some indication of light stripes on the posterior thigh, whereas most *L. pascoensis* specimens have mottled thighs and lack light stripes. *Leptodactylus leptodactyloides* have more intense belly patterns anteriorly and most individuals are moderately mottled; *L. petersii* specimens have more uniformly patterned bellies, often in an anastomotic pattern, and most individuals have extensively mottled bellies. *Leptodactylus leptodactyloides* never has distinct light belly spots; *L. podicipinus* often has distinct light belly spots. Most *L. leptodactyloides* have distinct light stripes on the posterior thighs; the thighs of most *L. podicipinus* are entirely mottled with no indication of light stripes. Most *L. leptodactyloides* have at least indications of light posterior upper lip stripes; *L. sabanensis* lacks upper lip stripes. *Leptodactylus leptodactyloides* differs from *L. sabanensis* in advertisement call. In *L. leptodactyloides* the call duration is 0.01–0.04 s with a dominant frequency range of 650–1,600 Hz and with maximum energy between 1,100–1,300 Hz; in *L. sabanensis* the call duration is 0.04–0.06 s with a dominant frequency range of 900–2,300 Hz and with maximum energy between 1,400–1,800 Hz. *Leptodactylus validus* occurs on the Lesser Antilles, Trinidad and Tobago, while *L. leptodactyloides* does not. *Leptodactylus leptodactyloides* is larger than mainland *L. validus* (*L. leptodactyloides* females 35–56 mm SVL, males 28–48 mm SVL; mainland *L. validus* females 30–43 mm SVL, males 28–37 mm SVL). The commonest upper lip stripe condition in *L. leptodactyloides* is indistinct stripes with all posterior lip stripes extending from the posterior corner of the eye; in mainland *L. validus* the commonest condition is distinct stripes that often extend from under the middle of the eye. Few *L. leptodactyloides* have light spotted chin/throat patterns; many mainland *L. validus* have light chin/throat spots. *Leptodactylus leptodactyloides* is smaller than *L. wagneri* (*L. leptodactyloides* females 35–56 mm SVL, males 28–48 mm SVL; *L. wagneri* females 52–82 mm SVL, males 39–61 mm SVL). Very few *L. leptodactyloides* specimens have long dorsolateral folds; most *L. wagneri* have long dorsolateral folds. The bellies of *L. leptodactyloides* characteristically are finely mottled; many *L. wagneri* have boldly mottled bellies.

Larval morphology. Maximum total length (Gosner 40) 28.3 mm; oral disk anteroventral; tooth row formula stages 25–27 2[2]/3, stages 28–40 2/3; tail almost uniform brown, heaviest over musculature (Heyer, 1994:89).

Advertisement call. Dominant (= fundamental) frequency 650–1,600 Hz; call duration 0.01–0.04 s; calls unpulsed

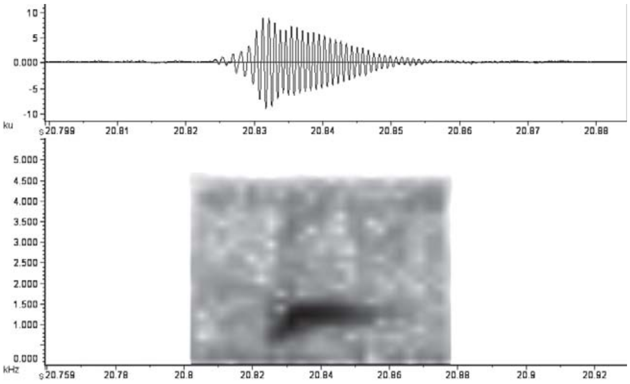

Figure 111. Advertisement call of *Leptodactylus leptodactyloides.*

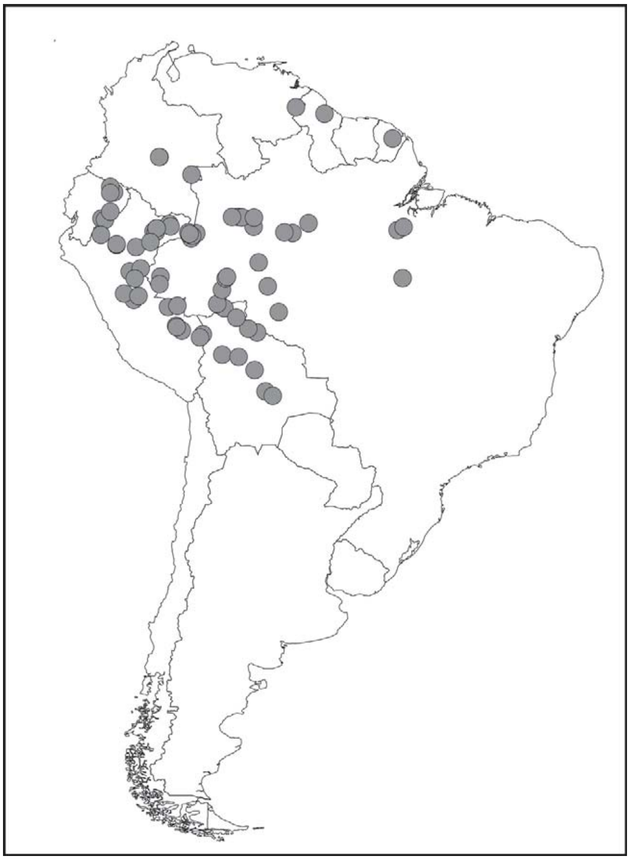

Figure 112. Distribution map of *Leptodactylus leptodactyloides* (recording USNM 207).

or with 3–5 partial pulses; rising frequency modulation throughout call; call rate 0.3–3.3 calls/s; harmonic structure present or absent (Heyer 1994:16, 17, 37, 38, 89) (Fig. 111).

Distribution. Throughout the greater Amazon basin and the Guianas from known elevations of 15–400 m (Fig. 112).

Leptodactylus magistris Mijares-Urrutia, 1997

Leptodactylus magistris Mijares-Urrutia, 1997:114. Type locality: "Cerro Socopó, cerca de 30 km [por carretera] al SO de Guajiro, Municipio Mauroa, Estado Falcón, Venezuela, cerca de 1250 m." Holotype: EBRG 3284, adult male.

Etymology. According to Mijares-Urrutia, the Latin *magistris* honors three of his professors: Pascual Soriano, Enrique La Marca, and Alexis Arends.

Adult morphology. Small/moderate size, female SVL 27.9–45.1 mm ($\overline{X}$ = 38.6 mm), male SVL 39.0–30.1 mm; adult male snout not spatulate; males with a pair of keratinized spines on each thumb; males lacking chest spines; upper lip pattern uniform, without stripe; dorsal folds absent; dorsolateral folds absent; lateral folds absent; thigh with or without a light stripe; upper shank with distinct to incomplete bars; belly with mottling anteriorly, lacking pigment posteriorly; toes with lateral fringes (Mijares-Urrutia, 1997:113–120).

Similar species. *Leptodactylus magistris* is known only from the Cerro Socopó region in Venezuela. There are no other described species having toe fringes and lacking dorsolateral folds in the area where the Venezuelan states of Falcón, Lara, and Zulia converge. Heyer (1994:113–114) noted that several populations in Colombia and Venezuela (i.e., Lake Maracaibo, Maracaibo Drainage, and Venezuelan Andes) could not be assigned to diagnosable species. Further work is needed to clarify their taxonomic status and the geographic distribution of *L. magistris.*

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Cerro Socopó region in Venezuela (Fig. 113).

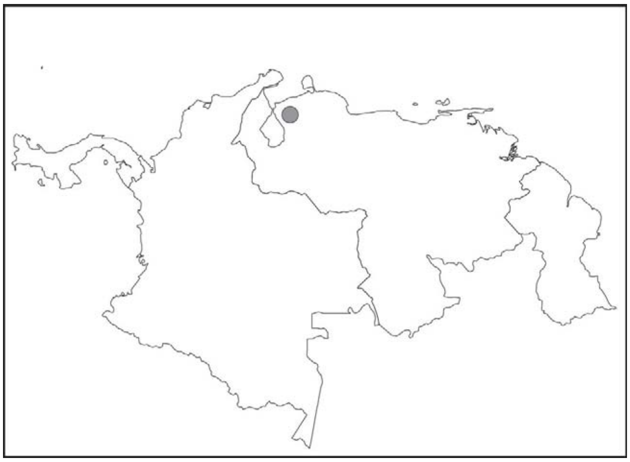

Figure 113. Distribution map of *Leptodactylus magistris.*

Leptodactylus melanonotus **(Hallowell, 1861 “1860”) (Plate 11B)**

Cystignathus melanonotus Hallowell, 1861 “1860”:485. Type locality: “Nicaragua” restricted to “Recero, Nicaragua,” by Smith and Taylor, 1950:320; restriction disputed by Dunn and Stuart, 1951:58. Holotype: USNM 6264 according to Kellogg, 1932:88, apparently lost, according to Heyer, 1970a:9; KU 84848 designated Neotype by Heyer, 1970a:11, Neotype from “Nicaragua, Zelaya, Bonanza.”

Cystignathus echinatus Brocchi, 1877:181. Type locality: “Rio Madre Nieja [Vieja?] [Guatemala occidental].” Syntypes: MNHN 6322–23 according to Guibé, 1950 “1948”:30. Synonymy by Heyer, 1970a:9.

Cystignathus microtis Cope, 1879:265. Type locality: “Guanajuato,” Mexico (presumed to be in error by Heyer, 1970a:12). Restricted to “Apatzingán (de la Constitución),” Michoacán, Mexico, by Smith and Taylor, 1950:35. Syntypes: USNM 9906, 9908, and 9909, according to Heyer, 1970a:9 (in error). Kellogg, 1932:88 considered USNM 9906 the “type” and Cochran, 1961:40 considered USNM 9906 to be the “holotype,” a lectotype designation by implication. Synonymy by Cochran, 1961:40 and Heyer, 1970a:9.

Cystignathus perlaevis Cope, 1879:269. Type locality: “near a well near Japana,” Oaxaca, Mexico = Tapanatepec according to Smith and Taylor, 1948:57 = Tapana, Tehuantepec, Oaxaca, Mexico, according to Cochran, 1961:40. Holotype: USNM 10041, female, by original designation and according to Kellogg, 1932:89. Synonymy by Kellogg, 1932:89; Cochran, 1961:40; Heyer, 1970a:12.

Leptodactylus echinatus: Brocchi, 1881–1883:20.

Leptodactylus melanonotus: Brocchi, 1881–1883:20.

Leptodactylus microtis: Boulenger, 1882:244.

Leptodactylus perlaevis: Boulenger, 1882:215.

Leptodactylus occidentalis Taylor, 1937 “1936”:349. Type locality: “Tepic, Nayarit, Mexico.” Holotype: EHT 3322 by original designation; now FMNH 100015 according to Marx, 1976:57, adult female. Synonymy by Heyer, 1970a:9.

Etymology. From Greek *mela, melan* (black) and *notos* (back).

Adult morphology. Small/moderate size, female SVL 34.3–48.1 mm ($\bar{X}$ = 40.6 mm), male SVL 32.2–43.4 mm ($\bar{X}$ = 37.7 mm); adult male snout not spatulate; males with a pair of keratinized thumb spines; males lacking chest spines; light upper lip stripe absent or light stripe from eye to tympanum or arm; dorsal folds absent; dorsolateral folds weak or absent; lateral folds interrupted; posterior thigh mottled; upper shank barred; belly uniform light to mottled; toes fringed (McCranie and Wilson, 2002:446–448).

Similar species. *Leptodactylus melanonotus* occurs from Mexico through Panamá, extending west of the Andes in mesic habitats of Colombia and Ecuador. The only similar species that occur with *L. melanonotus* that have toe fringes are *L. insularum* and *L. silvanimbus*. *Leptodactylus melanonotus* have weak or absent dorsolateral folds and adult males have a pair of keratinized thumb spines; *L. insularum* have well defined dorsolateral folds extending from eye to groin and adult males have a single black spine on each thumb. *Leptodactylus silvanimbus* reach larger sizes (female SVL 35.9–48.0 mm, male SVL 35.8–55.0 mm) than *L. melanonotus* (female SVL 34.3–45.1 mm, male SVL 32.2–43.4 mm). Adult male *L. silvanimbus* have either lateral toe ridges or fringes; all *L. melanonotus* have toe fringes. *Leptodactylus melanonotus* occurs below 1500 m, *L. silvanimbus* occurs at 1700–1900 m.

Larval morphology. Maximum total length (Gosner 37) 41.6 mm; oral disk anteroventral; tooth row formula 2[2]/3; tail almost uniform dark (Heyer, 1970b “1968”:178–179, figs. 8, 13, 18; McCranie and Wilson, 2002:448–449, Orton, 1951:62–66, Savage, 2002:215–217).

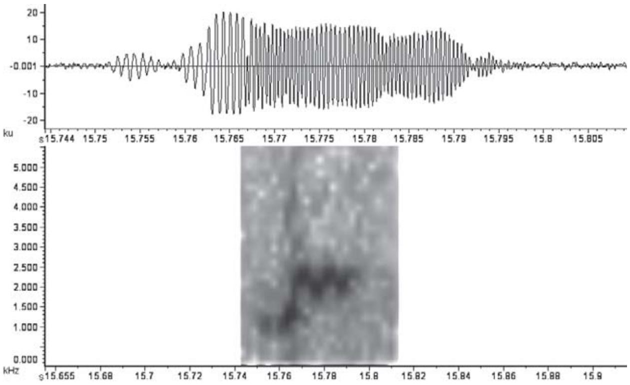

Figure 114. Advertisement call of *Leptodactylus melanonotus* (recording USNM 83).

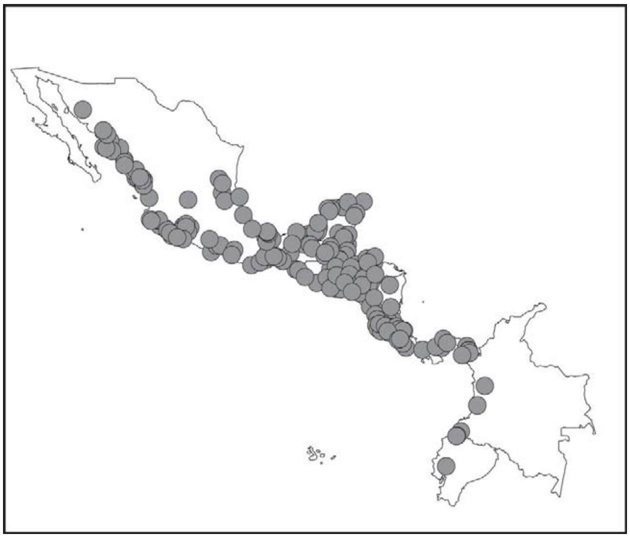

Figure 115. Distribution map of *Leptodactylus melanonotus.*

Advertisement call. Dominant frequency (either fundamental frequency or first harmonic) 1,000–1,500 Hz or 2,000–3,000 Hz; note duration 0.02–0.09 s; weak falling frequency modulations; each call consisting of one or two pulsed notes; call rate 150–160/min; harmonic structure usually present (Heyer, 1970a:31–32; Straughan and Heyer, 1976:227) (Fig. 114).

Distribution. Lowland Atlantic and Pacific coasts of Mexico through Panamá and wet Pacific lowlands of Colombia and Ecuador (Fig. 115).

Leptodactylus natalensis Lutz, 1930 (Plate 11C)

Leptodactylus natalensis Lutz, 1930:7. Type locality: "Natal, Rio Grande do Norte. Rio Baldo e outros lugares," Brazil [Portuguese text]; "Rio Bahú and other places near Natal [Rio Grande do Norte]" [English text]. Heyer and Heyer, 2006b:3, suggested that the type locality is "Rio Baldum, 06°09'S, 35°08'W." Syntypes: Including USNM 81130 according to Cochran, 1961:64; USNM 81130 designated lectotype by Heyer, 1970a:22.

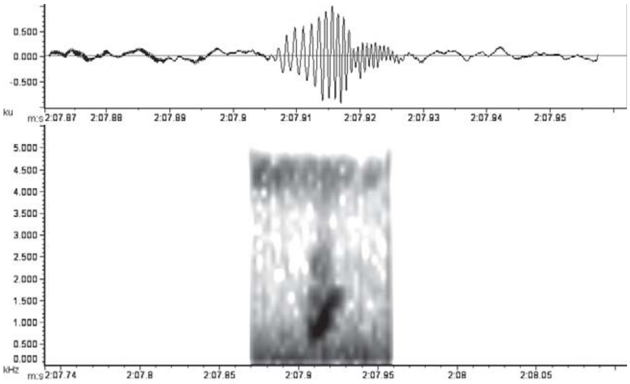

Figure 116. Advertisement call of *Leptodactylus natalensis* (recording USNM 323).

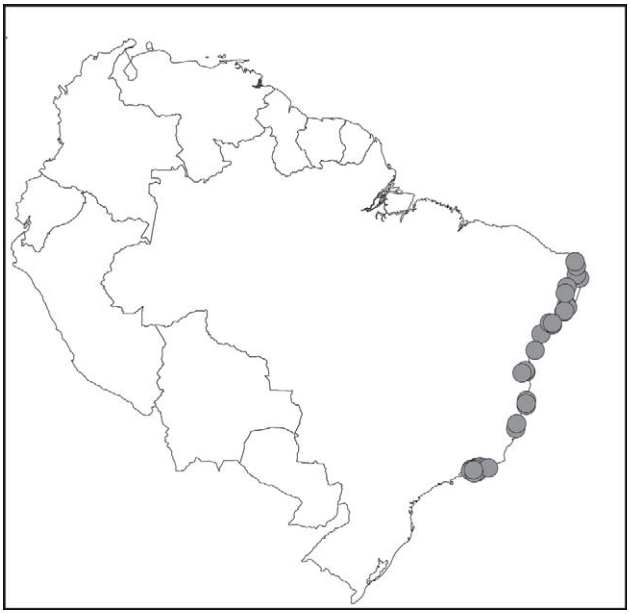

Figure 117. Distribution map of *Leptodactylus natalensis.*

Etymology. The name alludes to the general locality (Natal, Brazil) where the species was initially collected.

Adult morphology. Small–moderate size, female SVL 33.1–48.9 mm ($\bar{X}$ = 40.0 mm), male SVL 28.7–42.1 mm ($\bar{X}$ = 34.4 mm); adult male snout not spatulate; adult males with 2 keratinized spines on each thumb; males lacking chest spines; a light stripe extending from under eye to below the tympanum, sometimes interrupted or continuous with a light commissural gland stripe; no dorsal folds; dorsolateral folds absent (2%), short (46%), or moderate length (53%); lateral folds absent; posterior thigh rarely with distinct light stripes (5%), otherwise (95%) stripes indistinct, usually(79%) light stripes indiscernible; upper shank barred; belly rarely lacking melanophores (1%), usually lightly mottled (43%), moderately mottled (47%), or rarely extensively mottled (9%); toes with lateral fringes (Heyer 1994:89–91; Heyer and Heyer 2006b:1).

Similar species. The only other *Leptodactylus* species with toe fringing that occur with *L. natalensis* are *L. latrans* complex species and *L. podicipinus. Leptodactylus natalensis* lacks dorsal folds; the members of the *L. latrans* complex have dorsal folds. *Leptodactylus natalensis* lack distinct light belly spots; *L. podicipinus* often (42% of specimens) have a spotted belly. Just over half of *L. natalensis* specimens have toe tips larger than narrow or just-swollen categories; all *L. podicipinus* have either narrow or just-swollen toe tips.

Larval morphology. Maximum total length (Gosner 39/40) 28 mm; oral disk anteroventral; tooth row formula 2/3; tail uniformly dark (Heyer and Heyer, 2006b:1–2).

Advertisement call. Beginning call/note dominant (= fundamental) frequency ranging from 550–1,040 Hz to final frequencies of 1,370–1,830 Hz; note duration 0.06–0.07 s; notes pulsed, from 2–7 (modally 7) pulses or partial pulses per note; rapidly rising frequency modulations throughout call; call rate 3.0–4.1/s; harmonics present or indiscernible (Amorim et al., 2009:1–7; Heyer and Carvalho, 2000:284–289; Heyer and Heyer, 2006b:2; Prado et al., 2007:97–103) (Fig. 116).

Distribution. *Leptodactylus natalensis* occurs in the Brazilian State of Maranhão (Leite Jr. et al., 2008:153–156), northern and central portions of the Brazilian Atlantic Forest Morphoclimatic Domain (Ab'Sáber, 1977) from its most northern extent in the State of Rio Grande do Norte to and including the State of Rio de Janeiro (Fig. 117).

Leptodactylus nesiotus **Heyer, 1994 (Plate 11D)**

Leptodactylus nesiotus Heyer, 1994:91. Type locality: "Trinidad; St. Patrick; Icacos Peninsula, Icacos." Holotype: USNM 306179, adult male.

Etymology. From the Greek *nesiotes,* islander, in reference to its only known occurrence on the Island of Trinidad.

Adult morphology. Small, male SVL 31.7–33.0 mm (n = 3); adult male snout not spatulate; distinct broad light upper lip stripe present; males with two small black spines on thumb; males lack chest spines; no dorsal folds; weakly developed dorsolateral folds from posterior eye to sacrum; lateral folds absent; posterior thighs with or without light stripes; upper shank barred; belly speckled; toes with lateral fringes (Heyer, 1994:91). Osteology was described by Ponssa et al. (2010).

Similar species. *Leptodactylus nesiotus* is known only from Trinidad, where *L. insularum* and *L. validus* are the only other *Leptodactylus* with toe fringes. *Leptodactylus nesiotus* is a small species (males 32–33 mm SVL) with moderate-length, interrupted dorsolateral folds; *L. insularum* is a moderate/large species (males to 88 mm SVL, males to 94 mm SVL) with long, complete dorsolateral folds. *Leptodactylus nesiotus* has a broad light stripe on the entire upper lip or at least to under the eye; in individuals of *L. validus* with discernible light lip stripes, the stripes extend from the posterior corner of the eye posteriorly.

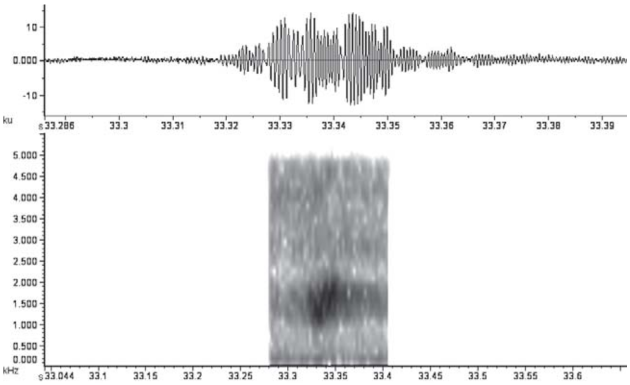

Figure 118. Advertisement call of *Leptodactylus nesiotus.*

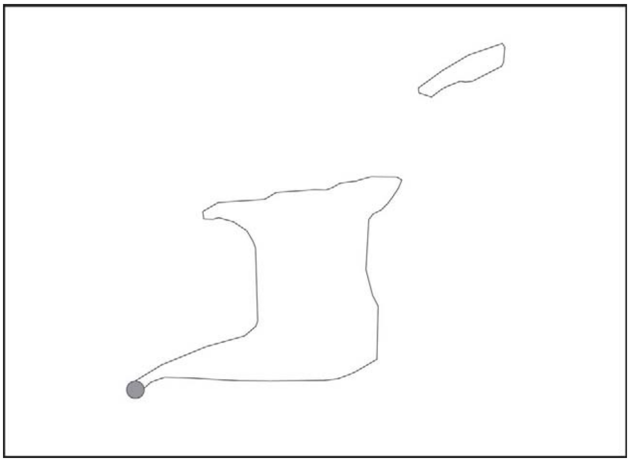

Figure 119. Distribution map of *Leptodactylus nesiotus.*

Larval morphology. Unknown.

Advertisement call. Dominant (= fundamental) frequency 1,500–2,000 Hz; call duration 0.03 s; calls with 4–5 partial pulses; calls frequency modulated with fast rise times; call rate ca. 3.8 calls per second; harmonic structure ambiguous (Heyer, 1994:94) (Fig. 118).

Distribution. Icacos Peninsula, Trinidad (Fig. 119).

Leptodactylus pascoensis **Heyer, 1994**

Leptodactylus pascoensis Heyer, 1994:94. Type locality: "Perú; Pasco; Iscozazin Valley, Contilla, 780 m, ≈ 10°17'S, 75°13'W." Holotype: LACM 40665, adult male.

Etymology. Named for the Peruvian department of Pasco where most of the known specimens have been collected.

Adult morphology. Moderate size, female SVL 52.4–66.6 mm ($\overline{X}$ = 59.3 mm), male SVL 60.3–61.4 mm ($\overline{X}$ = 60.7 mm); male snout not spatulate; adult males with a pair of large black thumb spines; males lacking chest spines; somewhat distinct light stripe from posterior corner of eye passing under tympanum through jaw commissure or indiscernible light upper lip stripe; dorsal folds absent; dorsolateral folds absent, short, or medium length; lateral folds absent; posterior thigh light stripe indistinct or usually indiscernible; upper shank weakly cross-banded; belly lightly to moderately mottled; toes with lateral fringes (Heyer, 1994:94–96).

Similar species. *Leptodactylus pascoensis* occurs in a restricted region along the Amazonian flanks of the Andes in central Perú, Departments of Huanuco and Pasco. Other *Leptodactylus* with toe fringes that may occur with *L. pascoensis* are *L. bolivianus, L. diedrus, L. griseigularis, L. latrans* complex species, *L. leptodactyloides, L. petersii,* and *L. wagneri.* Both *Leptodactylus bolivianus* and *L. latrans* complex species have distinct, complete dorsolateral folds; *L. pascoensis* does not have complete distinct dorsolateral folds. *Leptodactylus pascoensis* is larger than *L. diedrus* (*L. pascoensis* females 52–67 mm SVL, males 60–61 mm SVL; *L. diedrus* females 34–48 mm SVL, males 30–40 mm SVL); the ventral and posterior thigh patterns merge in *L. pascoensis* whereas they abut in *L. diedrus. Leptodactylus pascoensis* is larger than *L. griseigularis* (female

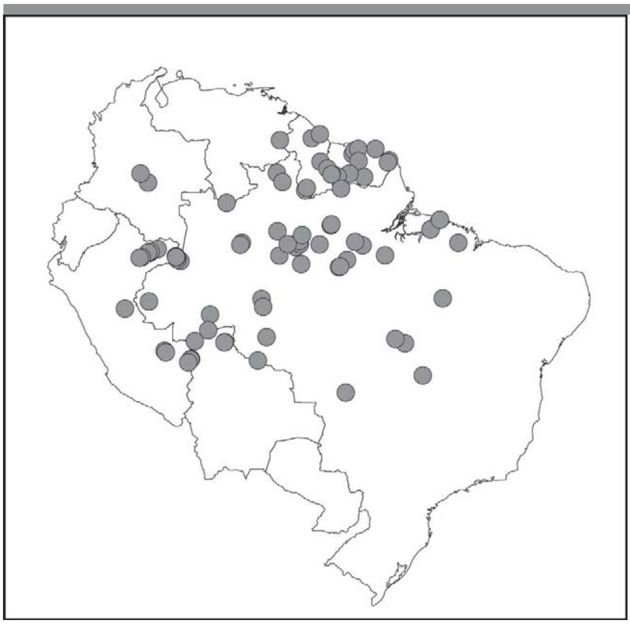

Figure 120. Distribution map of *Leptodactylus pascoensis.*

L. griseigularis 35–59 mm SVL, males 34–53 mm SVL. *Leptodactylus latrans* complex species have distinct, complete dorsolateral folds; *L. pascoensis* dorsolateral folds are not distinct and complete; *Leptodactylus pascoensis* is larger than *L. leptodactyloides* (female *L. leptodactyloides* 35–56 mm SVL, males 28–48 mm SVL); most *L. pascoensis* individuals have mottled posterior thigh surfaces with no indication of light stripes, whereas *L. leptodactyloides* individuals usually have at least some indication of light posterior thigh stripes. *Leptodactylus pascoensis* is larger than *L. petersii* (*L. petersii* females 31–51 mm SVL, males 27–41 mm SVL) and the belly is never extensively mottled in an anastomotic pattern whereas most *L. petersii* have extensively patterned bellies and often with an anastomotic pattern. *Leptodactylus pascoensis* lack dorsolateral folds extending from posterior to the eye to the sacrum; *L. wagneri* most commonly have dorsolateral folds extending from the eye to the sacrum. The bellies of *L. pascoensis* are lightly to moderately mottled, but never boldly mottled; the bellies of most *L. wagneri* are moderately mottled and some are extensively mottled with a bold pattern, approaching an anastomotic configuration.

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Central Peru east of the Andes between 780–2500 m (Fig. 120).

Leptodactylus petersii (Steindachner, 1864) (Plate 11E)

Platymantis petersii Steindachner, 1864:254. Type locality: “Marabitanas” Amazonas, Brazil. Holotype: NMW lost according to Heyer, 1970a:17. Neotype designation of AMNH 23182 by Heyer, 1970a:21 considered invalid by Heyer, 1994:79.

Leptodactylus brevipes Cope, 1887:51. Type locality: “at or near … Chupada [= Chapada dos Guimarães], thirty miles north-east of Cuyabá, and near the headwaters of the Xingu, an important tributary of the Amazon,” Mato Grosso, Brazil. Holotype: ANSP 11270, female.

Leptodactylus intermedius Lutz, 1930:8, 27. Syntypes: AL-MN 1438–1441. Type locality: “Manacapuri [= Manacapurú] perto do Manaos,” Amazonas, Brazil [Portuguese text]; “Manacapuri near Manaos” Brazil [English text]).

Leptodactylus (*Platymantis*) *petersii:* Lutz, 1930:1, 21.

Leptodactylus caliginosus petersi [sic]: Parker, 1935:507.

Leptodactylus podicipinus petersii: Gans, 1960:305.

Leptodactylus petersii: Rivero, 1961:48.

Etymology. Dr. Franz Steindachner described *Platymantis petersii* in honor of Dr. Wilhelm Carl Hartwig Peters, a prolific herpetologist, who was the Director of the Zoologisches Museum in Berlin for over 25 years.

Adult morphology. Small to moderate size, female SVL 31.2–51.3 mm ($\bar{X}$ = 39.2 mm), male SVL 26.6–41.1 mm ($\bar{X}$ = 32.9 mm); adult snout not spatulate; males with a pair of black spines on each thumb; males lacking chest spines; light upper lip stripes extending from posterior corner of eye distinct to not discernible; dorsal folds absent; dorsolateral folds absent, short, or of moderate length, interrupted; lateral folds absent; posterior thigh light stripes usually absent (90% of specimens); upper shank barred, belly usually extensively mottled (66%); toes with lateral fringes (Heyer, 1994:96–97).

Similar species. *Leptodactylus petersii* occurs in greater Amazonia and the Guiana shield region. The other *Leptodactylus* species with toe fringes that occur with *L. petersii* are *L. bolivianus, L. diedrus, L. griseigularis, L. guianensis, L. leptodactyloides, L. pascoensis, L. podicipinus, L. riveroi, L. sabanensis, L. validus,* and *L. wagneri. Leptodactylus petersii* is smaller than *L. bolivianus, L. guianensis,* and *L. riveroi* (*L. petersii* females 31–51 mm SVL, males 27–41 mm SVL; *L. bolivianus* females 61–108 mm SVL, males 79–122 mm SVL; *L. guianensis* females 66–109 mm SVL, males 80–110 mm SVL; *L. riveroi* females 57–89 mm SVL, males 42–64 mm SVL), and *L. petersii* individuals have at most a pair of medium-length, distinct dorsolateral folds whereas all *L. bolivianus, L. guianensis,* and *L. riveroi* have a pair of distinct dorsolateral folds extending from eye to groin. The belly of *L. petersii* usually is extensively mottled (66%), whereas the belly of *L. diedrus* usually lacks melanophores. In addition, the ventral and posterior thigh patterns merge in *L. petersii,* whereas they abut in *L. diedrus. Leptodactylus petersii* is smaller than

L. griseigularis (*L. griseigularis* females 39–58 mm SVL, males 35–51 mm SVL). The commonest belly pattern in *L. petersii* is an extensive mottle in an anastomatic pattern, whereas in *L. griseigularis* it is a light mottle without an anastomatic pattern. *Leptodactylus petersii* individuals have relatively uniformly and extensively patterned bellies, often in an anastomotic pattern; *L. leptodactyloides* belly patterns are more developed anteriorly, and most individuals have moderate mottling but not in an anastomotic pattern. Most (90%) *L. petersii* lack distinct light posterior thigh stripes; most *L. leptodactyloides* have distinct light posterior thigh stripes. *Leptodactylus petersii* is smaller than *L. pascoensis* (*L. pascoensis* females 52–67 mm SVL, males 60–61 mm SVL), and the belly is usually darker in *L. petersii* than in *L. pascoensis* (*L. pascoensis* bellies are never extensively mottled nor in an anastomotic pattern). *Leptodactylus petersii* lack distinct light spots on the belly, whereas the belly of *L. podicipinus* is commonly and densely spotted. The commonest toe-tip state in *L. petersii* is just swollen, and some individuals have swollen and just-expanded toe tips; the commonest toe tip state in *L. podicipinus* is narrow, and *L. podicipinus* lack swollen or just expanded toe tips. *Leptodactylus petersii* is smaller than *L. sabanensis* (*L. sabanensis* females 42–57 mm SVL, males 35–46 mm SVL). Usually, *L. petersii* (56%) have light chin/throat spots; few *L. sabanensis* (15%) have light chin/throat spots, and no *L. sabanensis* have anastomotic or speckled belly patterns. *Leptodactylus petersii* bellies usually are extensively mottled; *Leptodactylus validus* usually have lightly mottled bellies with a pattern ranging from a fine mottle to distinct, rather dark blotches, with the pattern usually more intensely developed anteriorly. *Leptodactylus petersii* is smaller than *L. wagneri* (*L. wagneri* females 52–82 mm SVL, males 39–61 mm SVL) and *L. petersii* lack dorsolateral folds extending from eye to groin, whereas most *L. wagneri* have them.

Larval morphology. Maximum total length (Gosner 36) 20.8 mm; oral disk anteroventral; tooth row formula 2(2)/3; tail almost uniformly brown or musculature moderately mottled brown (Duellman, 2005:288; Heyer, 1994:96–97).

Advertisement calls. Call type 1 (Fig. 121A): Dominant (= fundamental) frequency 700–1,200 Hz; call duration 0.04–0.05 s; calls of 3–4 partially pulsed notes; calls not noticeably frequency modulated; call rate 2.9–4.2 notes/s; harmonics weakly to strongly developed. Call type 2 (Fig. 121B): Calls of two juxtaposed notes. Dominant frequency of first note 800–1,600 Hz, of second note 1,800–2,800 Hz; call duration 0.03–0.05 s; first note of 2–4 partial pulses, second note not noticeably pulsed; first note frequency modulated upward with a fast rise time, second note often frequency modulated downward; call rate 0.6–1.3 s; first note with harmonic structure, second note apparently without harmonic structure (Heyer, 1994:97).

Distribution. Guianas, Amazon basin, and isolated gallery forests in Cerrado open formations in central Brazil (Fig. 122).

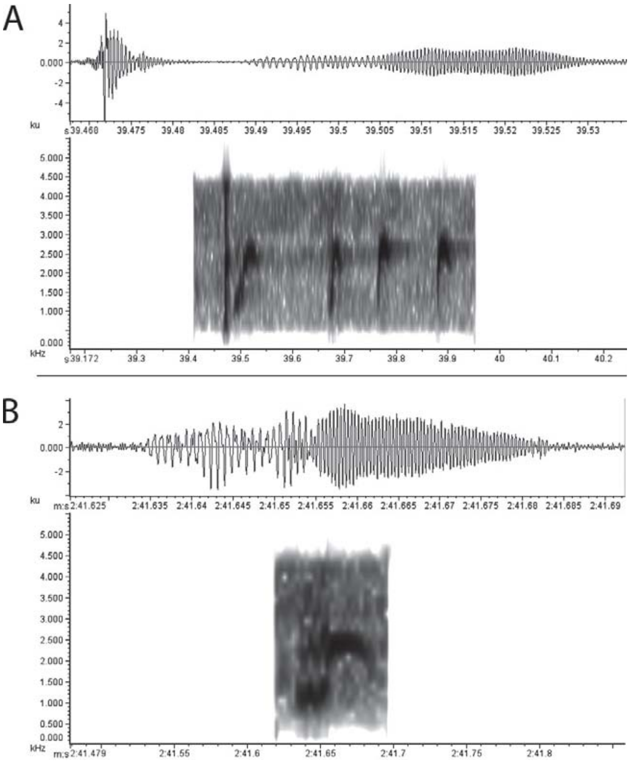

Figure 121. Advertisement call of *Leptodactylus petersii.* **(A)** Call type 1. **(B)** Call type 2.

Figure 122. Distribution map of *Leptodactylus petersii* (recording USNM 207).

Leptodactylus podicipinus **(Cope, 1862) (Plate 11F)**

Cystignathus podicipinus Cope, 1862:156. Type locality: "Paraguay." Type: ANSP 14539, female. USNM 5831 marked in ledger as "Type." Remark in USNM ledger states: "Type now in ANS[P], 14539. See Dunn's list."
Leptodactylus podicipinus: Boulenger, 1882:248.
Leptodactylus nattereri Lutz, 1926b:1011. Type locality: "la station de Ilha Sêca (Chemin de fer Noroeste do Brazil. Etat de S[ão]. Paulo" and "Cachoeira do Maribondo, … Etat de S[ão]. Paulo," Brazil. Syntypes: AL-MN 1314–15 (plus unnumbered specimen in same jar). Synonymy by Cochran, 1955 "1954":326.
Leptodactylus podicipinus podicipinus – Gans, 1960:305.

Etymology. From the Greek *podicus* (belonging to a foot) and *pinos* (dirt).

Adult morphology. Small–moderate size, female SVL 29.3–54.0 mm ($\bar{X}$ = 38.8 mm), male SVL 24.5–43.3 mm ($\bar{X}$ = 34.0 mm); adult snout not spatulate; males with a pair of keratinized spines on thumb; males lack chest spines; light upper lip stripe distinct (22% of specimens), indistinct (43%) or absent (35%); dorsal folds absent; dorsolateral folds absent (9%), short (44%), moderate (46%), or extending from eye to groin (1%); lateral folds absent; posterior thighs usually completely mottled with no indication of light stripes (79%), stripes sometimes indistinct (17%), or stripes rarely distinct (4%); upper shank barred; distinct light spots on belly (42%), otherwise light to dark profusion of melanophores; toes with lateral fringes (Heyer, 1994:97–99).

Similar species. Other species with toe fringes that occur sympatrically with *L. podicipinus* are *L. bolivianus, L. diedrus, L. griseigularis, L. latrans* complex species, *L. leptodactyloides, L. natalensis, L. petersii, L. pustulatus,* and *L. riveroi. Leptodactylus podicipinus* is smaller than *L. bolivianus* and *L. riveroi* (*L. podicipinus* females 30–54 mm SVL, males 24–43 mm SVL; *L. bolivianus* females to 88 mm SVL, males to 94 mm SVL; *L. riveroi* females to 81 mm SVL, males to 63 mm SVL); dorsolateral folds are poorly developed and rarely long in *L. podicipinus,* whereas dorsolateral folds in all *L. bolivianus* and *L. riveroi* extend from eye to groin and are well-developed. The bellies of *L. podicipinus* usually are extensively mottled and the ventral and posterior thigh patterns merge; the bellies of *L. diedrus* usually lack melanophores and the ventral and posterior thigh patterns abut. *Leptodactylus podicipinus* is smaller than *L. griseigularis* (*L. griseigularis* females 39–58 mm SVL, males 35–51 mm SVL) and the bellies of *L. podicipinus* are usually darker than those of *L. griseigularis; L. griseigularis* bellies are usually lightly mottled and no individuals have light belly spots. *Leptodactylus podicipinus* lacks dorsal folds; *L. latrans* complex specimens have a pair of dorsal folds. The posterior thighs of most *L. podicipinus* are mottled with no indication of light stripes and *L. podicipinus* usually have distinct light belly spots; the commonest posterior thigh state in *L. leptodactyloides* is a distinct stripe and *L. leptodactyloides* lacks distinct light belly spots. All *L. podicipinus* have either narrow or just-swollen toe tips and often have distinct light belly spots; just over 50% of all *L. natalensis* have toe tips larger than just swollen toe tips, and no *L. natalensis* have distinct light belly spots. All *L. podicipinus* have narrow or just-swollen toe tips and often have distinct

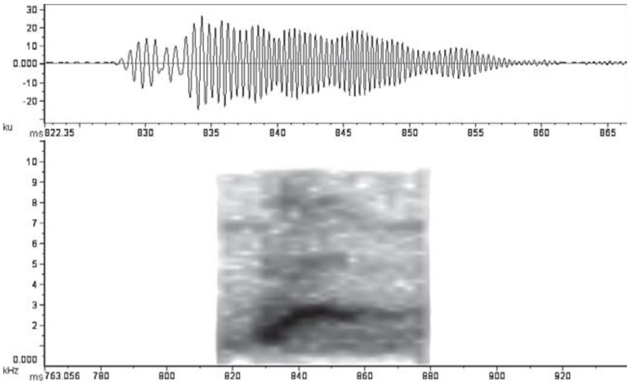

Figure 123. Advertisement call of *Leptodactylus podicipinus.*

Figure 124. Distribution map of *Leptodactylus podicipinus.*

light belly spots; the commonest toe tip state in *L. petersii* is just swollen and some individuals have swollen and just-expanded toe tips and no *L. petersii* have distinct light belly spots. No *L. podicipinus* have discrete, distinct light spots on the posterior face of the thigh; all *L. pustulatus* do.

Larval morphology. Maximum total length (Gosner 38) 28.1 mm; oral disk anteroventral; tooth row formula 2(2)/3; tail uniform brown or brown with few small light specks (Rossa-Feres and Nomura, 2006: unnumbered pages 8, 20; Vizotto, 1967:109–112).

Advertisement call. Dominant (= fundamental) frequency 1,000–3,500 Hz; call duration 0.02–0.04 s; calls with 3–7 pulses/partial pulses; rising frequency modulations; call rate 0.5–8.4/s; harmonics weakly to moderately developed (Guimarães et al., 2001:9; Heyer, 1994:99; Silva et al., 2008:123–134) (Fig. 123).

Distribution. Open formations of Paraguay, adjacent Argentina, Bolivia, northwestern Uruguay, and central Brazil, extending along the Rio Madeira and Rio Amazonas within the Amazon Basin (Fig. 124).

Leptodactylus pustulatus **(Peters, 1870) (Plate 12A)**

Entomoglossus pustulatus Peters, 1870:647. Type locality: "Ceara [Nördl. Brasilien]," northeastern Brazil. Holotype: ZMB 6951 according to Bauer et al., 1995:45. Heyer, 1970a:16, incorrectly reported the type as lost and designated MCZ 373 as neotype).

Leptodactylus pustulatus: Boulenger, 1882:239.

Etymology. From the Latin *pustulatus,* blistered, referring to the rough texture of the dorsum.

Adult morphology. Moderate size, female SVL 36.5–61.0 mm ($\overline{X}$ = 50.4 mm), male SVL 33.1–47.7 mm ($\overline{X}$ = 39.8 mm); adult male snout not spatulate; males lacking thumb and chest spines; light upper lip stripe absent (area behind eye may be light); dorsal folds absent; dorsolateral folds interrupted or absent; lateral folds interrupted or absent; posterior thigh almost always with large, light spots, no light stripe; upper shank almost uniform dark; belly dark with large, discrete light spots; toes with lateral fringes (Heyer, 1970a:16–17).

Similar species. *Leptodactylus pustulatus* occurs in the Brazilian states of Ceará, Goiás, Mato Grosso, Pará, and Tocantins. The other species most similar to *L. pustulatus* that have fringed toes and dorsolateral folds that are interrupted or absent and co-occur with *L. pustulatus* are *L. leptodactyloides, L. petersii,* and *L. podicipinus.* *Leptodactylus pustulatus* has large discrete light spots on the belly and posterior thigh; *Leptodactylus leptodactyloides* and *L. petersii* lack light spots on the belly; *L. podicipinus* often has small light belly spots and no distinct light spots on the posterior thighs.

Larval morphology. Total length (Gosner 39) 30.2 mm; oral disk anteroventral; tooth row formula 2(2)/3; tail dark gray (de Sá et al., 2007a:49–58).

Advertisement call. Dominant (= fundamental) frequency 775–861 Hz; call duration 0.081–0.088 s; call of two notes, each pulsed; rising and falling frequency modulations throughout call; call rate 26/min; harmonic structure variable throughout call (Brandão and Heyer, 2005:566–570) (Fig. 125).

Distribution. Arid and semi-arid habitats in central and northeastern Brazil (Fig. 126).

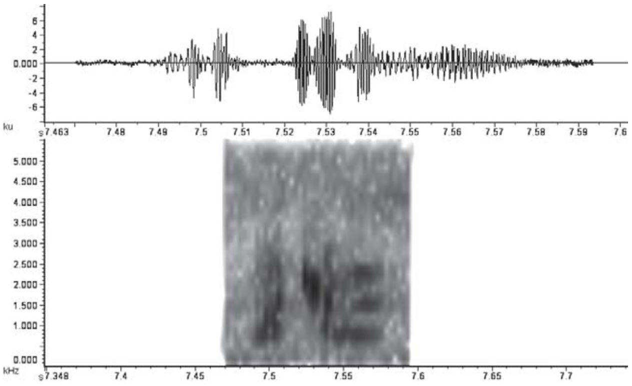

Figure 125. Advertisement call of *Leptodactylus pustulatus* (recording USNM 330).

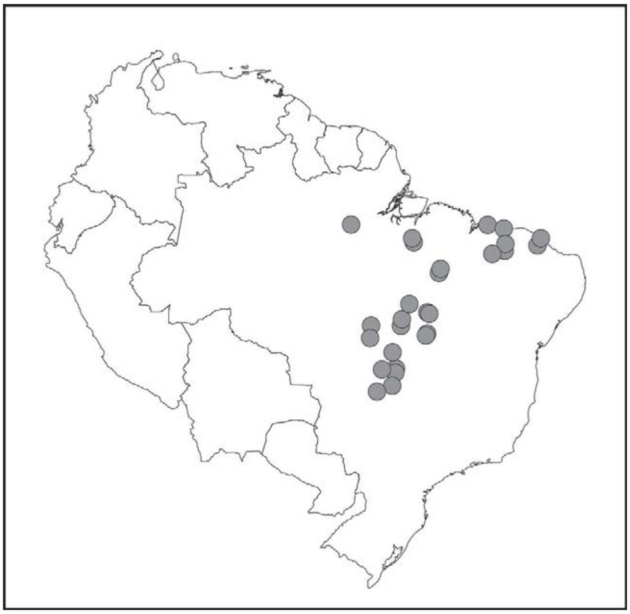

Figure 126. Distribution map of *Leptodactylus pustulatus.*

Leptodactylus riveroi **Heyer and Pyburn, 1983 (Plate 12B)**

Leptodactylus riveroi Heyer and Pyburn, 1983:560. Type locality: "Colombia; Vaupés, Timbó, 01°06'S, 70°01'W, elevation 170 m." Holotype: USNM 232400, male.

Etymology. Named for Dr. Juan A. Rivero "in recognition of Dr. Rivero's [numerous frog systematic and distribution] contributions."

Adult morphology. Moderate size, female SVL 56.8–89.0 mm ($\overline{X}$ = 72.5 mm), male SVL 42.1–63.5 mm ($\overline{X}$ = 52.3 mm); adult male snout not spatulate; males with a pair of black thumb spines; males lacking chest spines; distinct light stripe from under eye to tympanum; dorsal folds absent; distinct pair of dorsolateral folds; lateral folds absent; posterior thigh lacking light stripe; upper shank variegated or with transverse bars; belly boldly mottled; toes with lateral fringes (Heyer and Pyburn, 1983:560–566).

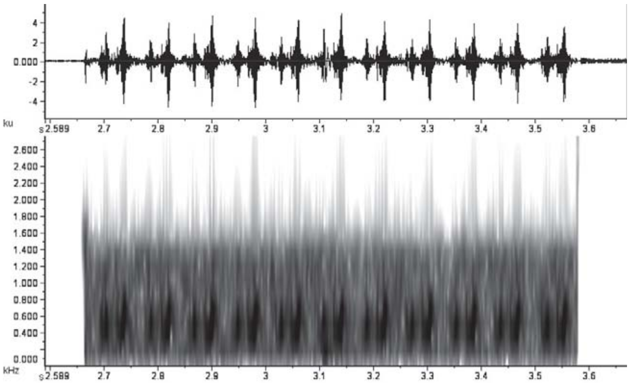

Figure 127. Advertisement call of *Leptodactylus riveroi* (recording USNM 128).

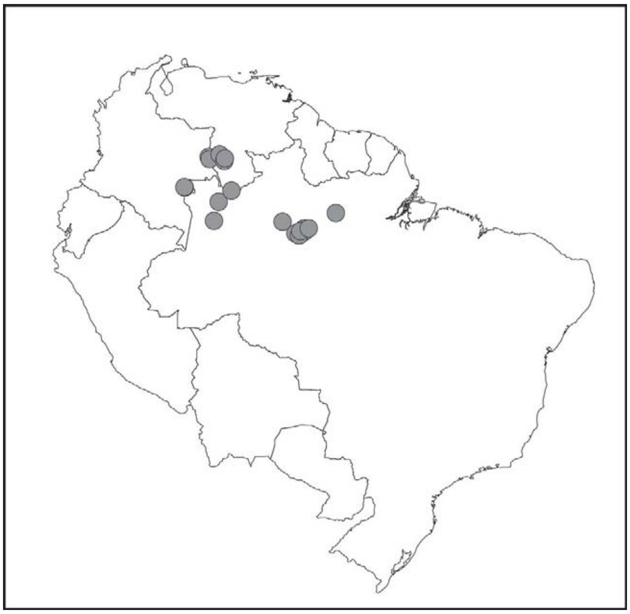

Figure 128. Distribution map of *Leptodactylus riveroi.*

Similar species. *Leptodactylus riveroi* occurs in Amazonian drainages of Colombia and Venezuela and the states of Amazonas and Pará in Brazil. Similar species with well defined complete dorsolateral folds and toe fringes that occur with *L. riveroi* are *L. bolivianus, L. guianensis, L. latrans* complex, and *L. leptodactyloides. Leptodactylus riveroi* have complete black-bordered dorsolateral folds and adult males lack chest tubercles; *L. bolivianus* and *L. guianensis* have interrupted dark borders next to the dorsolateral folds and sexually active adult male *L. bolivianus* and *L. guianensis* have patches of chest tubercles. *Leptodactylus riveroi* lacks dorsal folds; *L. latrans* complex species have dorsal folds. *Leptodactylus riveroi* has complete dorsolateral folds; *L. leptodactyloides* dorsolateral folds are interrupted, short to long.

Larval morphology. Maximum total length (Gosner 40) 44.7 mm; oral disk anteroventral; tooth row formula 2(2)/3; up to stage 37, tails transparent brown, beyond stage 37, tails black (Lima, 1992:91–93).

Advertisement call. Dominant frequencies range from 360–830 Hz; call duration 0.7–2.3 s; each call of 9–28 double-pulsed notes; falling and rising frequency modulations within notes; call rate about 2 per s; no harmonic structure (Heyer and Pyburn, 1983:563–564) (Fig. 127).

Distribution. Amazonian drainages in Colombia and Venezuela and the states of Amazonas and Pará in Brazil (Fig. 128).

Leptodactylus sabanensis **Heyer, 1994 (Plate 12C)**

Leptodactylus sabanensis Heyer, 1994:99. Type locality: "Venezuela; Bolívar; km 127, El Dorado–Santa Elena de Uairen [= Vairen] road, 1250 m, ≈ 06°00'N, 61°30'W." Holotype: KU 166559, adult male.

Etymology. "Named to indicate this species is geographically centered on the Gran Sabana of Venezuela."

Adult morphology. Moderate size, female SVL 42.1–56.9 mm ($\overline{X}$ = 51.0 mm), male SVL 35.0–46.4 mm ($\overline{X}$ = 43.3 mm); adult male snout not spatulate; adult males with a pair of medium to large black thumb spines; males without chest spines; light upper lip stripe usually absent, if present extending from posterior corner of eye to jaw commissure (15% of specimens); dorsal folds absent; dorsolateral folds extending from eye to sacral area or absent; lateral folds indistinct; posterior thigh light stripe distinct (23% of specimens) to indistinct or not discernible (77%); upper shank uniform to faintly barred; belly lightly (15% of specimens), moderately (61% of specimens) or extensively (24% of specimens) mottled; toes with lateral fringes (Duellman, 1997:26–27; Heyer, 1994:99–103).

Similar species. *Leptodactylus sabanensis* is known from the Gran Sabana of Venezuela (State of Bolívar) and the adjacent lavrado of the State of Roraima, Brazil. Similar species having toe fringes in the distribution of *L. sabanensis* are *L. guianensis, L. latrans* complex species, *L. petersii,* and *L. validus.* Most *L. sabanensis* lack long complete dorsolateral folds, if present, they are indistinct or interrupted; *L. guianensis* has smooth, complete dorsolateral folds. *Leptodactylus sabanensis* lacks dorsal folds; *L. latrans* complex species has dorsal folds. *Leptodactylus sabanensis* is larger than *L. petersii* (*L. petersii* females 31–51 mm SVL, males 27–41 mm SVL), few *L. sabanensis* (15%) have light chin/throat spots, and *L. sabanensis* have a lightly to extensively mottled belly pattern; most (56%) *L. petersii* specimens have light chin and throat spots and an anastomotic or speckled belly pattern; *L. sabanensis* do not have anastomotic or speckled belly patterns that characteristically occur in *L. petersii. Leptodactylus sabanensis* is larger than *L. validus* (female *L. validus* 29.5–51.5 mm SVL, males 27.8–42.9 mm SVL); the most common upper lip stripe condition in *L. sabanensis* is indiscernible (when discernible, the light stripes extend from the posterior corner of the eye); the commonest upper lip stripe condition in mainland *L. validus* is distinct light stripes that often extend posteriorly from under the middle of the eye.

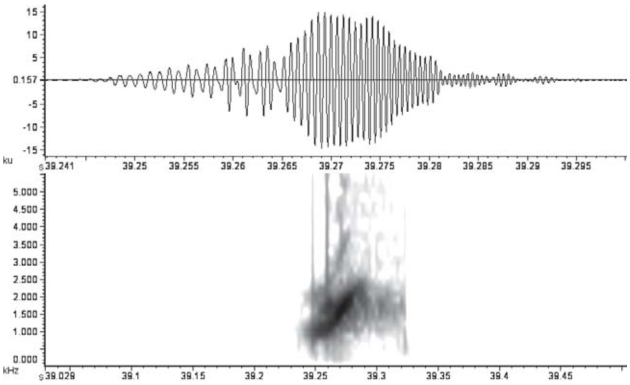

Figure 129. Advertisement call of *Leptodactylus sabanensis* (recording USNM 225).

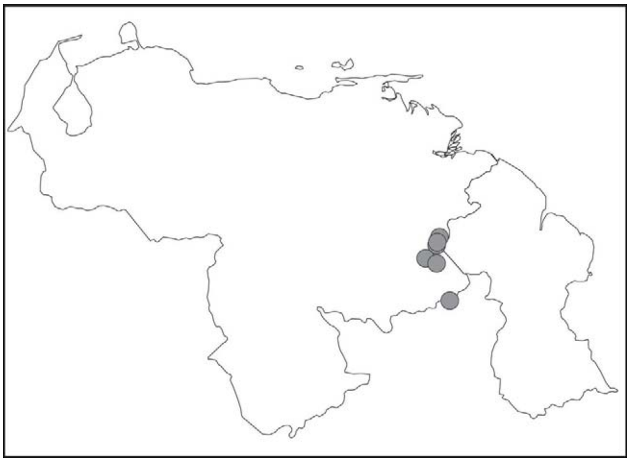

Figure 130. Distribution map of *Leptodactylus sabanensis.*

Larval morphology. Maximum total length (Gosner 37) 35.0 mm; oral disk anteroventral; tooth row formula 2(1)/3[1]; tail brown with white flecks (Duellman, 1997:27).

Advertisement call. Dominant (= fundamental) frequency 1,400–1,800 Hz; call duration 0.04–0.06 s; call slightly pulsed; rising frequency modulations throughout call; call rate 1.2/s; weak harmonic structure (Heyer, 1994:54, 102) (Fig. 129).

Distribution. Gran Sabana of Venezuela and adjacent Lavrado in Roraima, Brazil (Fig. 130).

***Leptodactylus validus* Garman, 1888 (Plate 12D)**

Leptodactylus validus Garman, 1888 "1887":14. Type locality: "Kingston, St. Vincent," Lesser Antilles. Syntypes: MCZ 2185 (42 specimens, according to Barbour and Loveridge, 1929:294), ANSP 19425 and 26108 (according to Malnate, 1971:353), and UMMZ 55761 (3 specimens, according to Peters, 1952:19); MCZ 71920 designated lectotype by Heyer, 1970a:21; see Comments, below.

Leptodactylus pallidirostris Lutz, 1930:1–20. Type locality: "Kartarbo [= Kartabo]," Guyana. Syntypes: AL-MN 1829 adult male designated lectotype by Heyer, 1994:93. Synonymy by Yanek, Heyer, and de Sá, 2006:192.

Adult morphology. Small–moderate size, female SVL 29.5–51.5 mm ($\overline{X}$ = 38.4 mm), male SVL 27.8–42.9 mm ($\overline{X}$ = 35.2 mm); adult male snout not spatulate; adult males with a pair of black thumb spines; males lacking chest spines; distinct light upper lip stripes originating from the posterior corner of the eye and extending posteriorly or indiscernible; dorsal folds absent; dorsolateral folds usually short, rarely absent or rarely ½ distance from posterior eye to groin; lateral folds absent; posterior thigh with distinct to indiscernible light stripe; upper shank lightly barred or uniform; belly mottled; toes with lateral fringes (Heyer, 1994:93–94, 102–104).

Similar species. *Leptodactylus validus* is the only *Leptodactylus* species with lateral toe fringes that occurs in the Lesser Antilles. On the islands of Trinidad and Tobago, *L. validus* occurs with fringe-toed *L. insularum* and

L. nesiotus. *eptodactylus validus* does not have complete dorsolateral folds, *L. insularum* does. In individuals of *L. validus* with light upper lip stripes, the light lip stripes extend posteriorly from the posterior corner of the eye. *Leptodactylus nesiotus* has a broad light stripe on the entire upper lip or at least to under the eye. Mainland South American *Leptodactylus validus* occur in the Guiana shield region. Other species of *Leptodactylus* that occur in the same area with toe fringes are *L. diedrus, L. guianensis, L. latrans* complex species, *L. leptodactyloides, L. petersii,* and *L. sabanensis.* Some individuals of *L. validus* lack dorsolateral folds and the ventral and posterior thigh patterns merge; all *L. diedrus* lack dorsolateral folds and the ventral and posterior thigh patterns abut. Mainland *L. validus* have short to medium dorsolateral folds; *L. guianensis* have dorsolateral folds that extend from behind the eye posteriorly to the groin. *Leptodactylus validus* lacks dorsal folds; *L. latrans* complex species have complete dorsal folds. Mainland *L. validus* are smaller than *L. leptodactyloides* (*L. leptodactyloides* females 35–56 mm SVL, males 28–48 mm SVL) and are commonly characterized by an upper lip stripe that extends extends posteriorly from the middle of the eye and light chin/throat spots; *L. leptodactyloides* usually have indistinct upper lip stripes that extend from the posterior corner of the eye and few *L. leptodactyloides* have light chin/throat spots. Many *L. validus* individuals have light chin/throat spots; few *L. leptodactyloides* do. The belly of *L. validus* usually is lightly mottled with patterns ranging from a fine mottle to distinct, rather dark blotches and the commonest toe-tip condition in *L. validus* is swollen with some individuals having expanded tips or small disks; the belly of *L. petersii* usually is extensively mottled, often in an anastomotic pattern, and the commonest toe-tip condition in *L. petersii* is just swollen and no individuals have expanded toe tips or small toe disks. *Leptodactylus validus* is smaller than *L. sabanensis* (*L. sabanensis* females 42–57 mm SVL, males 35–46 mm SVL), the upper lip stripe of *L. validus* is distinct and extends posteriorly from under the middle of the eye and its advertisement call broadcast frequency ranges from 1,500–3,500 Hz with a maximum energy of 2,500–3,500 Hz; the most common upper lip stripe condition in *L. sabanensis* is indiscernible, and, when lip stripes are discernible, they extend from the posterior corner of the eye; the broadcast frequency range of the advertisement call of *L. sabanensis* is 900–2,300 Hz with maximum energy of 1,400–1,800 Hz.

Larval morphology. Based on St. Vincent larvae. Maximum total length (Gosner 36) 25.8 mm; oral disk anteroventral; tooth row formula at Gosner stage 25, 2(2)/3, Gosner stages 29–38, 2/3; tail gray with heavy profusion of melanophores on entire tail except for a large very distinct to indistinct light spot over anterior tail musculature (Heyer, 1994:104).

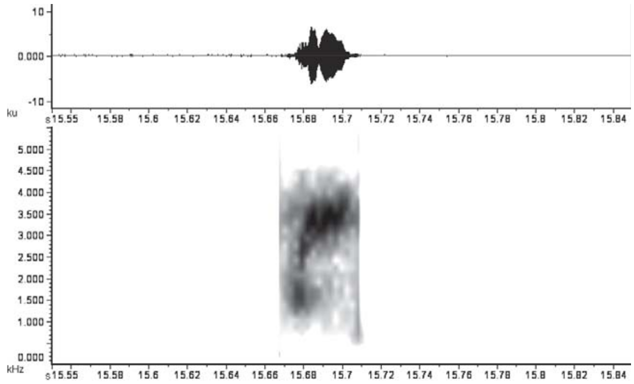

Figure 131. Advertisement call of *Leptodactylus validus*.

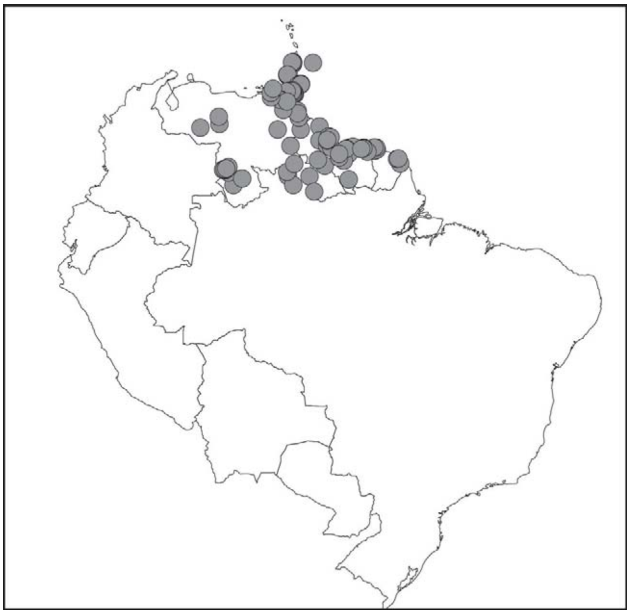

Figure 132. Distribution map of *Leptodactylus validus*.

Advertisement call. Call data from mainland and island populations are very similar (Yanek et al., 2006), both consisting of two notes. The first note consists of a single pulse and calls have fast rising frequency modulations throughout. Call differences were reported between mainland and island populations (Heyer, 1994, figs. 27–29, 31–33). The differences are in mainland populations having (1) dominant broadcast frequency range 1,500–3,500 Hz (2,300–3,500 Hz for island populations), (2) call duration 0.03–0.05 s (0.03–0.06 for island populations), (3) second note with 2–5 pulses (2–6 pulses for island populations), (4) and call rate 0.8–2.7/s (call rate 1.1–1.9/s for island populations) (Fig. 131).

Distribution. Guiana shield region, Trinidad, Tobago, and Lesser Antilles (Fig. 132).

Comments. Designation of a lectotype for *Leptodactylus validus* has a tortuous history. Garman's (1888 "1887") original description did not specify how many specimens were syntypes. He did not designate any of the specimens as types nor did he provide any museum numbers for the frogs. The only information relating to the frogs of the new species is: "A male measures in length of body one and five–eighths inches and in leg two and three–eighths; a female is one and three-fourths in body and two and a half inches in length of leg."

Barbour and Loveridge (1929:294) stated that the type specimens of *Leptodactylus validus* comprised a lot of 42 specimens (all assigned the same MCZ catalogue number 2185). Two syntypes were deposited in the Academy of Natural Sciences at Philadelphia (ANSP 19425, 26108).

Heyer (1970a:21) designated the first lectotype: "I hereby designate MCZ 71920, an adult male, from Kingston, St. Vincent, as the lectotype of *Leptodactylus validus* Garman." Subsequently, Schwartz and Thomas (1975:44) stated: "Heyer (op. cit. [1970a]:21) designated MCZ 71920 as lectotype of *L. validus,* but since this specimen is not part of the syntypic series the designation is invalid."

Heyer (1994:80) seemingly ignored some of the preceding history when he wrote: "Garman described *L. validus* on the basis of three specimens, ANSP 19425, 26108, and MCZ 2185 from Kingston, St. Vincent. Schwartz and Thomas (1975:44) pointed out that my previous designation of MCZ 71920 as the lectotype (Heyer, 1970a:21) was invalid, as MCZ 71920 was not part of the syntypic series. In my folder of data and photographs of *Leptodactylus* types, I have written on the back of the photograph of the frog, '*L. validus* Garman Lectotype MCZ 2185,' Why I have the correct number in my type file but cited an incorrect number in the publication is a mystery at this point. MCZ 2185 is an adult male in good condition, and as the Garman article refers to specimens in the Museum of Comparative Zoology, it is appropriate to designate MCZ 2185 as the lectotype of *Leptodactylus validus* Garman."

E-mail correspondence with Jose Rosado, MCZ (22 July 2010) clarifies the situation: "Your 'error' [Heyer 1970a:102{sic, correct page is 21}] as such may not be a mistake after all because MCZ A-71920 is part of the syntypic series. … Schwartz and Thomas may never have checked the actual situation. The original catalogue entry indicated that we had 57 specimens listed under MCZ A-2185, B and L [Barbour and Loveridge, 1929] listed 42 remaining in the collection in 1929, at present there are 40. You are correct in that the 'duplicates' were recatalogued and the original number MCZ A-2185 was arbitrarily assigned to the adult male. The remaining specimens were retagged and given the numbers MCZ A-71920–71958, so your designation is correct. Schwartz and Thomas were just not informed."

Consequently, herein it is considered that the first designation for the lectotype of *Leptodactylus validus,* MCZ A-71920 by Heyer (1970a:21) takes priority over Heyer's (1994:80) subsequent lectotype designation of MCZ A-2185.

Leptodactylus wagneri **(Peters, 1862) (Plate 12E)**

Plectromantis wagneri Peters, 1862:232. Type locality: Published originally "an den Westseite der Anden in Ecuador" but data associated with the lost type specimen was "Pastassathal" [= Pastaza Valley], Ecuador; by neotype designation of Heyer, 1970a:39, the type locality became Pastaza, Ecuador, on the east side of the Andes. Neotype designation rejected by Heyer (1994); consequently the type locality reverts to the original statement by Peters. Type[s]: ZSM 1080/0, lost according to Heyer, 1970a:19 and Glaw and Franzen, 2006:174; neotype designated by Heyer, 1970a:19, as NRM 1945 [holotype of *Eleutherodactylus leptodactyloides*]). This neotype designation considered invalid by Heyer, 1994:78, who determined that *Eleutherodactylus leptodactyloides* and *Plectromantis wagneri* represented different species.

Leptodactylus wagneri: Nieden, 1923:479.

Leptodactylus (*Plectromantis*) *wagneri:* Lutz, 1930:1, 21.

Etymology. Named for the collector, Dr. Moritz Wagner.

Adult morphology. Moderate size, female SVL 52.3–81.7 mm ($\overline{X}$ = 65.7 mm), male SVL 39.1–60.7 mm ($\overline{X}$ = 51.6 mm); adult male snout not spatulate; adult males with a pair of black thumb spines; males without chest spines; light upper lip stripe distinct to not discernible; dorsal folds absent; dorsolateral folds usually extending from eye to groin; lateral folds absent; posterior thigh light stripe distinct to not discernible; upper shank uniform to barred; belly moderately mottled, sometimes boldly mottled; toes with lateral fringes (Heyer, 1994:103–105).

Similar species. *Leptodactylus wagneri* occurs along the Amazonian flanks of the Andes and is known to occur with or in the same general region as the following *Leptodactylus* species with toe fringes: *L. bolivianus, L. colombiensis, L. diedrus, L. discodactylus, L. griseigularis, L. latrans* complex species, *L. leptodactyloides, L. pascoensis,* and *L. petersii. Leptodactylus wagneri* (female SVL 52–82 mm, male SVL 39–61 mm) does not reach the same size as *L. bolivianus* (female SVL 61–108 mm, male SVL 79–122 mm; few *L. wagneri* have distinct posterior lip stripes that extend from the posterior corner of the eye; many (70%) *L. bolivianus* have light stripes on the upper lip including under the eye. *Leptodactylus wagneri* is larger than *L. colombiensis* (*L. colombiensis* females 40–62 mm SVL, males 36–56 mm SVL), and most (96%) *L. wagneri* have dorsolateral folds extending from eye to groin; only some *L. colombiensis* have dorsolateral folds extending from eye to groin. *Leptodactylus wagneri* is larger than *L. diedrus* (*L. diedrus* females 34–48 mm SVL, males 30–40 mm SVL), and the ventral and posterior thigh patterns merge in *L. wagneri;* the ventral and posterior thigh patterns abut in *L. diedrus.*

Leptodactylus wagneri does not have expanded toe tips with dorsal grooves; *L. discodactylus* has expanded toe tips with dorsal grooves. *Leptodactylus wagneri* is larger than *L. griseigularis* (*L. griseigularis* females 35–59 mm SVL, males 34–53 SVL) and the dorsolateral folds of *L. wagneri* commonly extend from behind the eye to the groin, whereas the most common fold condition in *L. griseigularis* is moderate (fold not reaching groin); the most common belly pattern is lightly mottled in *L. griseigularis* and the most common belly pattern is moderately to boldly mottled in *L. wagneri*. *Leptodactylus wagneri* lacks dorsal folds; *L. latrans* complex species have dorsal folds. *Leptodactylus wagneri* is larger than *L. leptodactyloides* (*L. leptodactyloides* females 35–56 mm SVL, males 28–48 mm SVL); most *L. wagneri* have dorsolateral folds extending from eye to groin; few *L. leptodactyloides* have folds extending from eye to groin. Many *L. wagneri* have moderately to boldly mottled bellies, whereas the bellies of *L. leptodactyloides* characteristically are finely mottled. *Leptodactylus wagneri* have boldly mottled and moderately mottled bellies; the bellies of *L. pascoensis* are lightly to moderately, but never boldly mottled. *Leptodactylus wagneri* is larger than *L. petersii* (females 31–51 mm SVL, males 27–41 mm SVL); the dorsolateral folds of *L. wagneri* commonly extend from behind the eye to the groin, no *L. petersii* have dorsolateral folds extending from eye to groin.

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Amazonian slopes of the Andes in southern Colombia, Ecuador, northern Perú, with a few records from lowland Amazonia (Brazil, Colombia, Ecuador, Peru) and a single specimen from the Pacific slopes in Colombia (Fig. 133).

Leptodactylus species not assigned to a species group

Leptodactylus hylodes (Reinhardt and Lütken, 1862)

Cystignathus hylodes Reinhardt and Lütken, 1862 “1861”:168. Type locality: Cotinguiba [now Nossa Senhora do Socorro], Sergipe, Brazil; see Heyer, 2000 for clarification of type locality. Lectotype: ZMUC R 11105, sex unclear, probably a juvenile.

Leptodactylus hylodes: Heyer, 2000:150–153.

Etymology. From the Greek *hylodes,* woody, bushy.

Morphology. Small, 25.3 mm (lectotype); snout not spatulate; males without thumb or chest spines; upper lip faintly barred; no visible dorsal, dorsolateral, or lateral folds; light stripe on posterior thigh; upper shank barred; belly uniform light; toes with well developed lateral fringes (Heyer, 2000).

Similar species. *Leptodactylus hylodes* is known only from the type locality. One other species that occurs in the same area is *L. natalensis*. *Leptodactylus hylodes* has heterogeneous fingertips with fingers II and III with rounded, non-expanded tips and fingers IV and V with small, ungrooved disks, unique within *Leptodactylus*.

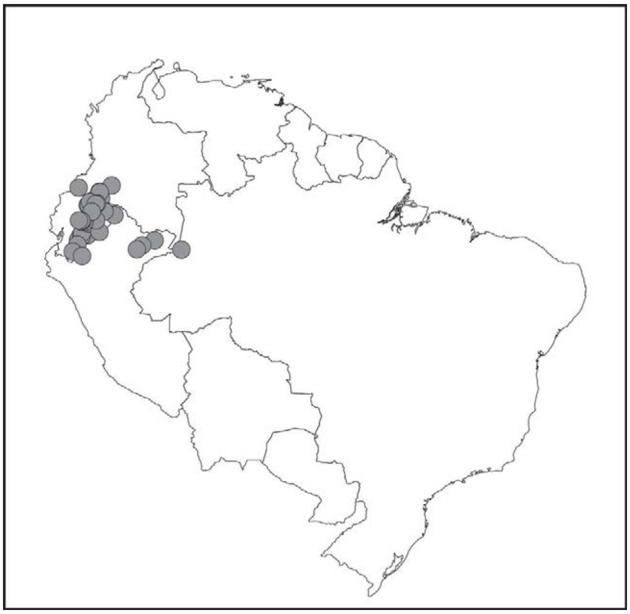

Figure 133. Distribution map of *Leptodactylus wagneri*.

Figure 134. Distribution map of *Leptodactylus hylodes*.

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Known only from the type locality (Fig. 134).

Leptodactylus lauramiriamae Heyer and Crombie, 2005 (Plate 12F)

Leptodactylus lauramiriamae Heyer and Crombie, 2005:590. Type locality: “Brazil, Rondônia, north end of the town of Vilhena, km 16, 12°43’S, 60°07’W [coordinates for Vilhena]”. Holotype: MZUSP 132772, adult female.

Etymology. Named for a daughter of M.H. and W.R. Heyer.

Adult morphology. Small, female SVL 29.5–31.2 mm ($\overline{X}$ = 30.6 mm), male 32.3 mm; adult male snout spatulate; male lacking thumb spines and chest spines; light upper lip stripe absent; dorsal, dorsolateral, and lateral folds absent; posterior thigh without light stripe; upper shank barred; belly uniform light; toes without lateral fringes (Heyer and Crombie, 2005:590–595).

Figure 135. Distribution map of *Leptodactylus lauramiriamae.*

Similar species. *Leptodactylus lauramiriamae* is unique in the genus *Leptodactylus* in having an areolate belly.

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. This rare species is known only from the type material, an additional topotype (CHUNB 11921, field label GRCOLLI 04689), and six uncataloged specimens at MZUSP (LTT 39, 95, 101, 103, 105, and T 01) from Tangará da Serra, Mato Gross, Brazil (14°37’10”S, 57°29’09”W) (Fig. 135).

Leptodactylus ochraceus Lutz, 1930

Leptodactylus ochraceus Lutz, 1930:28. Type locality: State of Pernambuco (? Tapera), Brazil; see Caramaschi, 2008, for discussion of type locality. Holotype: AL-MN 1445, female.

Etymology. From the Greek *ochre,* earthy oxide of iron.

Adult Morphology. Medium size, 41.7 mm SVL (Holotype), see below.

Larval morphology. Unknown.

Advertisement call. Unknown.

Distribution. Known only from the type locality.

Comments. The species was described based on a single specimen by Lutz (1930); no other specimens have been collected. Recently, Caramaschi (2008) examined the holotype and provided measurements and a description of the current state of preservation (“poor condition, very damaged”) and confirmed that the specimen is a female by the presence of eggs; in addition, he reviewed historical data on the type locality. Caramaschi (2008) also described and discussed the species morphology and coloration based on the illustration through examination of the original plate. The holotype is a leptodactylid but cannot be assigned to any of the 10 species of *Leptodactylus* inhabiting the “Caatingas” domain of northeastern Brazil (Caramaschi, 2008). The species has never been associated with any of the *Leptodactylus* species group.

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REFERENCES

Ab'Sáber A.N. 1977. Os domínios morfoclimáticos na América do Sul: Primeira aproximação. *Geomorfologia* 52:1–22.

Abrunhosa P.A., Wogel H., Pombal Jr. J.P. 2001. Vocalização de quatro espécies de anuros do Estado do Rio de Janeiro, sudeste do Brasil (Amphibia, Hylidae, Leptodactylidae). *Boletim do Museu Nacional, Zoologia, Nova Série* 472:1–12.

Aichinger M. 1985. Niederschlagsbedingte Aktivitätsmuster von Anuren des tropischen Regenwaldes. Eine quantitative Studie durchgeführt im Forschungsgebiet von Panguana (Peru). Ph.D. Dissertation. University of Vienna, Austria.

Agostinho C.A. 1994. Characterization of *Leptodactylus labyrinthicus* (Spix, 1824) population, and evaluation of its performance in captivity. Ph.D. Dissertation, Universidade Federal de São Carlos, Brasil.

Ahl E. 1936. Zwei neue Froscharten der Gattung *Leptodactylus* aus Südamerika. Veröffentlichungen aus dem Deutschen Kolonial und Uebersee-Museum, Bremen 1:389–392.

Allmon W.D. 1991. A plot study of forest floor litter frogs, Central Amazon, Brazil. *Journal of Tropical Ecology* 7:503–22. doi:10.1017/S0266467400005885

Almeida de Padua A., Angulo A. 2002. Natural history notes: *Adenomera* aff. *marmorata* (NCN) reproduction. *Herpetological Review* 33:197–198.

Altig R. 1970. A key to the tadpoles of the continental United States and Canada. *Herpetologica* 26:180–207.

Altig R., McDiarmid R.W. 1999. Body plan: development and morphology. Pp. 24–51, in: McDiarmid, R.W., Altig, R. (Eds.), Tadpoles: The Biology of Anuran Larvae. University of Chicago Press, Chicago.

Amaro-Ghilardi R.C., Skuk G., de Sá R.O., Rodrigues M.T., Yonenaga-Yassuda Y. 2006. Karyotypes of eight species of *Leptodactylus* (Anura, Leptodactylidae) with a description of a new karyotype for the genus. *Phyllomedusa* 5:119–133.

Amorim F.O., Schmaltz-Peixoto K.E., Araújo L.C.S.S., Santos E.M. 2009. Temporada e turno de vocalização de *Leptodactylus natalensis* Lutz, 1930 (Amphibia, Anura) na mata atlântica de Pernambuco, Brasil. *Papéis Avulsos de Zoologia* 49:1–7.

Andersson L.G. 1946 "1945". Batrachians from East Ecuador collected 1937, 1938 by Wm. Clarke-Macintyre and Rolf Blomberg. Arkiv för Zoologi 37A:1–88.

Angulo A., Icochea J. 2010. Cryptic species complexes, widespread species and conservations: lessons from Amazonian frogs of the *Leptodactylus marmoratus* group (Anura: Leptodactylidae). *Systematics and Biodiversity* 8:357–370. doi:10.1080/14772000.2010.507264

Anonymous. 2003. *Leptodactylus chaquensis* Cei, 1950 (Amphibia, Anura): Specific name conserved. *The Bulletin of Zoological Nomenclature* 60:173.

Arzabe C., Prado C. 2006. Distinct architectures of subterranean nests in the genus *Leptodactylus* of the *fuscus* group (Anura, Leptodactylidae). *Herpetological Review* 37:23–26

Barbour T. 1906. Vertebrata from the savanna of Panamá. Reptilia and Amphibia. *Bulletin of the Museum of Comparative Zoology at Harvard College* 46:224–229.

Barbour T., Loveridge A. 1929. Typical reptiles and amphibians. *Bulletin of the Museum of Comparative Zoology at Harvard College* 69:205–360.

Barbour T., Noble G.K. 1920. Some amphibians from northwestern Peru, with a revision of the genera *Phyllobates* and *Telmatobius*. *Bulletin of the Museum of Comparative Zoology at Harvard College* 63:395–427 + 3 plates.

Barlow L.A. 1998. The biology of amphibian taste. Pp. 743–782, in Heatwole H.F. Dawley E.M. (Eds.), Amphibian Biology. Vol. 3. Sensory Perception. Surrey Beatty and Sons, Chipping Norton.

Barrio A. 1965. Afinidades del canto nupcial de las especies cavícolas del genero *Leptodactylus* (Anura, Leptodactylidae). *Physis* 25:401–410.

Barrio A. 1973. *Leptodactylus geminus* una nueva especie del grupo *fuscus* (Anura, Leptodactylidae). *Physis* 32:199–206.

Barrio-Amorós C.L., Chacon-Ortiz A. 2001. Geographic distribution. *Leptodactylus colombiensis*. *Herpetological Review* 32:55.

Bauer A.M., Günther R., Klipfel M. 1995. The herpetological contributions of Wilhelm C.H. Peters (1815–1883). Facsimile Reprints in Herpetology, Dexter, Michigan.

Bilate M., Wogel H., Weber, L.N., Abrunhosa P.A. 2007 "2006". Vocalizações e girino de *Leptodactylus spixi* Heyer, 1983 (Amphibia, Anura, Leptodactylidae). *Arquivos do Museu Nacional, Rio de Janeiro* 64:235–245.

Bioacoustics Research Program. 2011. Raven Pro: Interactive sound analysis software, version 1.4. Accessible at www.birds.cornell.edu/raven

Böhme W., Bischoff W. 1984. Die Wirbeltiersammlungen des Museums Alexander Koenig. III. Amphibien und Reptilien. *Bonner Zoologische Monographien* 19:151–213 + one unnumbered page.

Bokermann W.C.A. 1965. Nota sobre los anfibios Brasileños citados y descriptos por Raddi. *Neotropica* 11:9–12.

Bokermann W.C.A. 1966. Lista Anotada das Localidades Tipo de Anfíbios Brasileiros. Serviço de Documentação - RUSP, São Paulo.

Bokermann W.C.A. 1969. Uma nova espécie de *Leptodactylus* de Mato Grosso (Anura, Leptodactylidae). *Revista Brasileira de Biologia* 29:13–16.

Borteiro C., Kolenc F. 2007. Redescription of the tadpoles of three species of frogs from Uruguay (Amphibia: Anura: Leiuperidae and Leptodactylidae), with notes on natural history. *Zootaxa* 1638:1–20.

Boulenger G.A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. Second Edition, Trustees of the British Museum, London.

Boulenger G.A. 1884 "1883". Notes on batrachians. *Annals and Magazine of Natural History* series 5, XIV:387–391.

Boulenger G.A. 1888. Descriptions of new Brazilian batrachians. *Annals and Magazine of Natural History* series 6 I:187–189.

Boulenger G.A. 1894. List of reptiles and batrachians collected by Dr. J. Bohls near Asuncion, Paraguay. *Annals and Magazine of Natural History* series 6, XIII:342–348.

Boulenger G.A. 1896. Descriptions of new batrachians in the British Museum. *Annals and Magazine of Natural History* series 6, XVII:401–406 + plate XVII.

Boulenger G.A. 1898. A list of the reptiles and batrachians collected by the late Prof. L. Balzan in Bolivia. *Annali del Museo Civico di Storia Naturale di Genova* series 2, XIX:128–133.

Boulenger G.A. 1902. Descriptions of new batrachians and reptiles from north-western Ecuador. *Annals and Magazine of Natural History* series 7, IX:51–57.

Boulenger G.A. 1918. Descriptions of new South-American batrachians. *Annals and Magazine of Natural History* series 9, II:427–433.

Brandão R.A., Álvares G.F.R., de Sá R.O. 2013. The advertisement call of the poorly known *Leptodactylus tapiti* (Anura, Leptodactylidae). *Zootaxa* 3616:284–286. doi:10.11646/zootaxa.3616.3.6

Brandão R.A., Heyer W.R. 2005. The complex calls of *Leptodacytlus pustulatus* (Amphibia, Anura, Leptodactylidae). *Amphibia-Reptilia* 26:566–570. doi:10.1163/156853805774806278

Bremer K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42:795–803. doi:10.2307/2408870

Brocchi P. 1877. Sur quelques batraciens raniformes et bufoniformes de l'Amérique Centrale. *Bulletin de la Société Philomathique de Paris* series 7, I:175–197.

Brocchi P. 1881–1883. Étude des Batraciens de l'Amérique Centrale. Imprimerie Nationale, Paris.

Brooks G.R. 1968. Natural history of a West Indian frog, *Leptodactylus fallax. Virginia Journal of Science* 19:176.

Burmeister H. 1861. Reise durch die La Plata-Staaten, mit besonderer Rücksicht auf die physische Beschaffenbeit und den Culturzustand der Argentinischen Republik. Ausgeführt in den Jahren 1857, 1858, 1859 und 1860. Zweiter Band. Die nordwestlichen Provinzen und die Cordilleren zwischen Catamarca und Copiapó umsassend. Nebst einer systematischen Uebersichst der beobachteten Rüdgratthiere. Druck und Verlag von H.W. Schmidt, Halle.

Caldwell J.P. 1992. Variation in tadpole schooling behavior and female attendance among species in the *Leptodactylus ocellatus* group [Abstract]. P. 79, in Joint Meeting of the American Society of Ichthyologists and Herpetologists, The Herpetologists' League and the American Elasmobranch Society. Program and Abstracts. Urbana-Champaign, Illinois. Illinois Natural History Survey, University of Illinois at Urbana-Champaign.

Caldwell J.P., Lopez P.T. 1989. Foam-generating behavior in tadpoles of *Leptodactylus mystaceus*. *Copeia* 1989:498–502. doi:10.2307/1445453

Camargo A., de Sá R.O., Heyer W.R. 2006. Phylogenetic analyses of mtDNA sequences reveal three cryptic lineages in the widespread neotropical frog *Leptodactylus fuscus* (Schneider, 1799) (Anura, Leptodactylidae). *Biological Journal of the Linnean Society* 87:325–341. doi:10.1111/j.1095-8312.2006.00581.x

Caramaschi U. 2008. Taxonomic status of *Leptodactylus ochraceus,* a forgotten species (Anura: Leptodactylidae). *Revista Brasileira de Zoologia* 25:523–528. doi:10.1590/S0101-81752008000300020

Caramaschi U., Feio R.N., São-Pedro V.A. 2008. A new species of *Leptodactylus* Fitzinger (Anura, Leptodactylidae) from Serra do Brigadeiro, State of Minas Gerais, southeastern Brazil. *Zootaxa* 1861:44–54.

Cardoso A.J. 1985. Revalidation of *Leptodactylus plaumanni* (Amphibia: Leptodactylidae). *Papéis Avulsos de Zoologia* 36:87–90.

Cardoso A.J., Heyer W.R. 1995. Advertisement, aggressive, and possible seismic signals of the frog *Leptodactylus syphax* (Amphibia, Leptodactylidae). *Alytes* 13:67–76.

Cardoso A.J., Sazima I. 1977. Batracophagy in the adult and larval phase of *Leptodactylus labyrinthicus* (Spix, 1824)—Anura, Leptodactylidae. *Ciência e Cultura* 29:1130–1132.

Carvalho T.R., Leite F.S.F., Pezzuti T.L. 2013. A new species of *Leptodactylus*_Fitzinger (Anura, Leptodactylidae, Leptodactylinae) from montane rock fields of the Chapada Diamantina, northeastern Brazil. *Zootaxa* 3701:349–364. doi:10.11646/zootaxa.3701.3.5

Cascon P., Peixoto O.L. 1985. Observações sobre a larva de *Leptodactylus troglodytes* A. Lutz, 1926 (Amphibia, Anura, Leptodactylidae). *Revista Brasileira de Biologia* 45:361–364.

Cassini C.S., Orrico V.G.D, Dias I.R, Solé M., Haddad C.F.B. 2013. Phenotypic variation of *Leptodactylus cupreus* Caramaschi, São Pedro and Feio, 2008 (Anura, Lepodactylidae). *Zootaxa* 3616:73–84. doi:10.11646/zootaxa.3616.1.6

Cei J.M. 1948. El ritmo estacional en los fenómenos cíclicos endocrino-sexuales de la rana criolloa (*Leptodactylus ocellatus* (L.) del norte Argentino. *Acta Zoológica Lilloana* 6:283–331 + 16 plates.

Cei J.M. 1949a. Costumbres nupciales y reproducción de un batracio característico chaqueño (*Leptodactylus bufonius* Boul.). *Acta Zoológica Lilloana* 8:105–110.

Cei J.M. 1949b. Factores genético-raciales que diferencian la regulación hormonal del ciclo sexual en *Leptodactylus ocellatus* (L.) de la Argentina: "Razas de temperatura" y sus relaciones con algunas características climáticas regionales. *Acta Zoológica Lilloana* 7:113–134 + 5 plates.

Cei J.M. 1950. *Leptodactylus chaquensis* n. sp. y el valor sistemático real de la especie linneana *Leptodactylus ocellatus* en la Argentina. *Acta Zoológica Lilloana* 9:395–423 + 3 plates.

Cei J.M. 1956. Nueva lista sistemática de los batracios de Argentina y breves notas sobre su biología y ecología. *Investigaciones Zoológicas Chilenas* 3:35–68 + 9 plates.

Cei J.M. 1962. Mapa preliminar de la distribución continental de las "sibling species" del grupo ocellatus (género Leptodactylus). *Revista de las Sociedad Argentina de Biología* 38:258–265

Cei J.M. 1980. Amphibians of Argentina. *Monitore Zoologico Italiano (N.S.), Monografia* (2): xii + 1–609.

Cei J.M., Erspamer V., Roseghini M. 1967. Taxonomic and evolutionary significance of biogenic amines and polypeptides occurring in amphibian skin. I. Neotropical leptodactylid frogs. *Systematic Zoology* 16:328–342. doi:10.2307/2412152

Chippindale P.T., Bonett R.M., Baldwin A.S., Wiens J.J. 2004. Phylogenetic evidence for a major reversal of life-history evolution in plethodontid salamanders. *Evolution* 58:2809–2822. doi:10.1554/04-185R

Chippindale P.T., Wiens J.J. 2005. Re-evolution of the larval stage in the plethodontid salamander genus *Desmognathus. Herpetological Review* 36:113–117.

Cochran D.M. 1923. A new frog of the genus *Leptodactylus. Journal of the Washington Academy of Sciences* 13:184–185.

Cochran D.M. 1955 "1954". Frogs of Southeastern Brazil. *Bulletin of the United States National Museum* 206: xvi + 1–423 + 34 plates. doi:10.5479/si.03629236.206.1

Cochran D.M. 1961. Type specimens of reptiles and amphibians in the U.S. National Museum. *Bulletin of the United States National Museum* 220: xv + 1–291. doi:10.5479/si.03629236.220

Cochran D.M., Goin C.J. 1959. A new frog of the genus *Limnomedusa* from Colombia. *Copeia* 1959:208–210.

Conlon J.M., Abdel-Wahab Y.H.A., Flatt P.R., Leprince J., Vaudry H., Jouenne T., Condamine E. 2009. A glycine-leucine-rich peptide structurally related to the plasticins from skin secretions of the frog *Leptodactylus laticeps* (Leptodactylidae). *Peptides* 30, 888–92. doi:10.1016/j.peptides.2009.01.008

Conte C.E., Machado R.A. 2005. Riqueza de espécies e distribuição espacial e temporal em comunidade de anuros (Amphibia, Anura) em uma localidade de Tijucas do Sul, Paraná, Brasil. *Revista Brasileira de Zoologia* 22:940–948.

Cook C.L., Ferguson J.W.H., Telford S.R. 2001. Adaptive male parental care in the giant bullfrog *Pyxicephalus adsperus. Journal of Herpetology* 35:310–315.

Cope E.D. 1862. On some new and little known American Anura. *Proceedings of the Academy of Natural Sciences of Philadelphia* 14:151–159.

Cope E.D. 1865. Sketch of the primary groups of Batrachia Salientia. *The Natural History Review* 5:97–120.

Cope E.D. 1866. On the structures and distribution of the genera of the arciferous Anura. *Journal of the Academy of Natural Sciences, Philadelphia* 6, Second Series: 67–112 + plate 25.

Cope E.D. 1874. On some Batrachia and Nematognathi brought from the upper Amazon by Prof. Orton. *Proceedings of the Academy of Natural Sciences of Philadelphia* 26:120–137.

Cope E.D. 1877. Tenth contribution to the herpetology of tropical America. *Proceedings of the American Philosophical Society* 17:85–98.

Cope E.D. 1879. Eleventh contribution to the herpetology of tropical America. *Proceedings of the American Philosophical Society* 18:261–277.

Cope E.D. 1887. Synopsis of the Batrachia and Reptilia obtained by H.H. Smith, in the Province of Mato Grosso, Brazil. *Proceedings of the American Philosophical Society* 24:44–60.

Cope E.D. 1894 "1893". Second addition to the knowledge of the Batrachia and Reptilia of Costa Rica. *Proceedings of the American Philosophical Society* 31:333–347.

Costello M.J., May R.M., Stork N.E. 2013. Can we name earth's species before they go extinct? *Science* 339:413–416. doi:10.1126/science.1230318

Crombie R.I., Heyer W.R. 1983. *Leptodactylus longirostris* (Anura: Leptodactylidae): Advertisement call, tadpole, ecological and distributional notes. *Revista Brasileira de Biologia* 43:291–296.

Crump M.L. 1995. Parental care. Pp. 518–67, in H. Heatwole, B.K. Sullivan (Eds.). Amphibian Biology, Vol. 2: Social Behaviour. Surrey Beatty and Sons, New South Wales.

da Silva W.R., Giaretta A.A. 2008. Further notes on the natural history of the South American pepper frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura, Leptodactylidae). *Brazilian Journal of Biology* 68:403–407.

da Silva W.R., Giaretta A.A. 2009. On the natural history of *Leptodactylus syphax* with comments on the evolution of reproductive features in the *L. pentadactylus* species group (Anura, Leptodactylidae). *Journal of Natural History* 43:191–203. doi:10.1080/00222930802484618

da Silva W.R., Giaretta A.A., Facure K.G. 2005. On the natural history of South American pepper frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura: Leptodactylidae). *Journal of Natural History* 39:555–566. doi:10.1080/00222930410001671273

Daudin F.M. an XI (1802–1803). Histoire Naturelle des Rainettes, des Grenouilles et des Crapauds. Chez Levrault, Paris.

Davis S.L., Davis R.B., James A., Talin B.C.P. 2000. Reproductive behavior and larval development of *Leptodactylus fallax* in Dominica, West Indies. *Herpetological Review* 31:217–220.

de Carvalho R.R. Jr. 2005. *Leptodactylus mystacinus* (mustached frog). Deimatic behavior. *Herpetological Review* 36:161.

de Carvalho T., Ron S. 2011. Advertisement call of *Leptodactylus labrosus* Jiménez de la Espada, 1875 (Anura, Leptodactylidae): an unusual advertisement call within the *L. fuscus* group. *Herpetology Notes* 4:325–326.

De La Riva I. 1995. A new reproductive mode for the genus *Adenomera* (Amphibia: Anura: Leptodactylidae): taxonomic implications for certain Bolivian and Paraguayan populations. *Studies on Neotropical Fauna and Environment* 30:15–29.

De la Riva I. 1996. The specific name of *Adenomera* (Anura: Leptodactylidae) in the Paraguay River Basin. *Journal of Herpetology* 30:556–558.

De la Riva I., Köhler J., Lötters S., Reichle S. 2000. Ten years of research on Bolivian amphibians: updated checklist, distribution, taxonomic problems, literature and iconography. *Revista Española Herpetologica* 14:19–164.

de Sá R.O., Heyer W.R., Camargo, A. 2005a. A phylogenetic analysis of *Vanzolinius* Heyer, 1974 (Amphibia, Anura, Leptodactylidae): Taxonomic and life history implications. *Arquivos do Museu Nacional, Rio de Janeiro* 63:707–726.

de Sá R.O., Camargo, A., Heyer, W.R. 2005b. Are *Leptodactylus didymus* and *L. mystaceus* phylogenetically sibling species (Amphibia, Anura, Leptodactylidae)? Pp. 90–92, in Ananjeva A., Tsinenko O. (Eds.), *Herpetologia Petropolitana,* Proceeding of the 12th Ordinary General Meeting of the Societas Europaea Herpetologica, St. Peterbursg, Russia.

de Sá R.O., Brandão R.A., Guimarães L.D.A. 2007a. Description of the tadpole of *Leptodactylus pustulatus* Peters, 1870 (Anura: Leptodactylidae). *Zootaxa* 1523:49–58.

de Sá R.O., Langone J.A., Segalla M.V. 2007b. The tadpole of *Leptodactylus notoaktites* Heyer, 1978 (Anura, Leptodactylidae). *South American Journal of Herpetology* 2:69–75. doi:10.2994/1808-9798(2007)2[69:TTOLNH]2.0.CO;2

de Sá R.O., Dubois A., Ohler A. 2007c. Designation of a neotype for *Leptodactylus gracilis* (Duméril and Bibron, 1840) (Amphibia: Leptodactylidae). *South American Journal of Herpetology* 2:175–178. doi:10.2994/1808-9798(2007)2[175:DOANFL]2.0.CO;2

de Sá R.O., Streicher J.W., Sekonyela R., Forlani M.C., Loader S.P., Greenbaum E., …, Haddad, C.F.B. 2012. Molecular phylogeny of microhylid frogs (Anura: Microhylidae) with emphasis on relationships among New World genera. *BMC Evolutionary Biology* 12:241. doi:10.1186/1471-2148-12-241

Dourado F.S., Leite J.R.S.A., Silva L.P., Melo J.A.T., Bloch C. Jr., Schwartz E.N.F. 2007. Antimicrobial peptide from the skin secretion of the frog *Leptodactylus syphax. Toxicon* 50:572–580. doi:10.1016/j.toxicon.2007.04.027

Downie J.R. 1984. How *Leptodactylus fuscus* tadpoles make foam, and why. *Copeia* 1984:778–780. doi:10.2307/1445168

Downie J.R. 1989. Observations on foam-making by *Leptodactylus fuscus* tadpoles. *Herpetological Journal* 1:351–355.

Downie J.R. 1990. Temporal changes in the behavior of foam-making *Leptodactylus fuscus* tadpoles. *Herpetological Journal* 1:498–500.

Downie J.R. 1994. Developmental arrest in *Leptodactylus fuscus* tadpoles (Anura: Leptodactylidae). I: descriptive analysis. *Herpetological Journal* 4:29–38.

Downie J.R. 1996. A new example of female parental behaviour in *Leptodactylus validus,* a frog of the leptodactylid "*melanonotus*" species group. *Herpetological Journal* 6:32–36.

Downie J.R., Smith J. 2003. Survival of larval *Leptodactylus fuscus* (Anura: Leptodactylidae) out of water: developmental differences and interspecific comparisons. *Journal of Herpetology* 17:107–115. doi:10.1670/0022-1511(2003)037[0107:SOLLFA]2.0.CO;2

Duellman W.E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *University of Kansas Museum of Natural History, Miscellaneous Publication* 65:1–352 + 4 plates.

Duellman W.E. 1985. Reproductive modes in anuran amphibians: Phylogenetic significance of adaptive strategies. *South African Journal of Science* 81:174–178.

Duellman W.E. 1997. Amphibians of La Escalera region, southeastern Venezuela: Taxonomy, ecology, and biogeography. *Scientific Papers, Natural History Museum, The University of Kansas* 2:1–52.

Duellman W.E. 2005. Cusco Amazónico. The Lives of Amphibians and Reptiles in an Amazonian Rainforest. Comstock Publishing Associates, Cornell University Press, Ithaca and London.

Duellman W.E., Trueb L. 1986. Biology of Amphibians. McGraw Hill Book Company, New York.

Duméril A.M.C., Bibron G. 1840. Plate 13, in A. d'Orbigny, G. Bibron (Eds.), Preprint of plate from "Voyage dans l'Amérique Méridionale (Le Brésil, La République Oriental de l'Uruguay, La République Argentine, La Patagonie, La République du Chili, La République de Bolivia, La République du Pérou) exécuté pendant las annees 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833. Volume 5, part 1". M. le Ministre de l'Instruction Publique, Paris and Strasbourg.

Duméril A.M.C., Bibron G. 1841. Erpétologie Générale ou Histoire Naturelle Complète des Reptiles. Tome Huitième. Librairie Encyclopédique de Roret, Paris.

Dunn E.R. 1940. New and noteworthy herpetological material from Panamá. *Proceedings of the Academy of Natural Sciences of Philadelphia* 92:105–122 + 1 plate.

Dunn E.R., Stuart L.C. 1951. Comments on some recent restrictions of type localities of certain South and Central American amphibians and reptiles. *Copeia* 1951:55–61. doi:10.2307/1438054

Duré M.I. 1999. *Leptodactylus chaquensis* (NCN). Diet. *Herpetological Review* 30:92

Emerson S.B. 1976. Burrowing in frogs. *Journal of Morphology* 149:437–458. doi:10.1002/jmor.1051490402

Emerson S.B., Boyd S.K. 1999. Mating vocalizations of female frogs: control and evolution mechanisms. *Brain, Behavior and Evolution* 53:187–197. doi:10.1002/jmor.1051490402

Eterovick P.C., Sazima I. 2000. Description of the tadpole of *Leptodactylus syphax,* with a comparison of morphological and ecological characters of tadpoles and adults of the species in the *L. pentadactylus* group (Leptodactylidae, Anura). *Amphibia-Reptilia* 21:341–350.

Fabrezi M. 2001. A survey of prepollex and prehallux variation in anuran limbs. *Zoological Journal of the Linnean Society* 131:227–248. doi:10.1111/j.1096-3642.2001.tb01316.x

Fabrezi M., Emerson S. 2003. Parallelism and convergence in anuran fangs. *Journal of Zoology* 260:41–51. doi:10.1017/S0952836903003479

Faivovich J. 2002. A cladistic analysis of *Scinax* (Anura: Hylidae). *Cladistics* 18:367–393. doi:10.1111/j.1096-0031.2002.tb00157.x

Faivovich J., Haddad C.F.B., Garcia P.C.A., Frost D.R., Campbell J.A., Wheeler W.C. 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History* 1–240. doi:10.1206/0003-0090(2005)294[0001:SROTFF]2.0.CO;2

Faivovich J., Ferraro D.P., Basso N.G., Haddad C.F.B., Rodrigues M.T., Wheeler W.C., Lavilla E.O. 2012. A phylogenetic analysis of *Pleurodema* (Anura: Leptodactylidae: Leiuperinae) based on mitochondrial and nuclear gene sequences, with comments on the evolution. *Cladistics* 28:460–482. doi:10.1111/j.1096-0031.2012.00406.x

Feng A.S., Narins P.M. 1991. Unusual mating behavior of Malaysian treefrogs, *Polypedates leucomystax. Naturwissenschaften* 78:362–365. doi:10.1007/BF01131610

Fenolio D., Silva H.L.R., Da Silva N.J. Jr. 2006. *Leptodactylus pustulatus* Peters, 1870 (Amphibia: Leptodactylidae): Notes on habitat, ecology, and color in life. *Herpetological Review* 37:140.

Fernández K., Fernández M. 1921. Sobre la biología y reproducción de algunos batracios argentinos. *Anales de la Sociedad Científica Argentina* 97:111–114.

Fernández M., Cole D., Heyer W.R., Reichle S., de Sá R.O. 2009. Predicting *Leptodactylus* (Amphibia, Anura, Leptodactylidae) distributions: Broad-ranging versus patchily distributed species using a presence-only environmental niche modeling technique. *South American Journal of Herpetology* 4:103–116. doi:10.2994/057.004.0202

Ferrão M., Fraga R., Simões P.I., Lima A.P. 2014. On the poorly sampled Amazonian frogs genus *Hydrolaetare* (Anura: Leptodactylidae): geographic ranges and species identification. *Salamandra* 50:77–84.

Fitzinger L.J. 1826. Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschafts - Tafel und einem Verzeichnisse der Reptilien - Sammlung des K.K. Zoologischen Museum's zu Wien. J.G. Heubner, Wien.

Fitzinger L.J. 1843. Systema Reptilium. Fasciculus Primus. Braumüller et Seidel, Wien.

Fouquet A., Gilles A., Vences M., Marty C., Blanc M., Gemmell N.J. 2007. Underestimation of species richness in neotropical frogs revealed by mtDNA analyses. *PLoS One* 2:10, e1109. doi:10.1371/journal.pone.0001109

Fouquet A., Blotto B.L., Maronna M.M., Verdade V.K., Junca F.A., de Sá R.O., Rodrigues M.T. 2013 Unexpected phylogenetic positions of the genera *Rupirana* and *Crossodactylodes* reveal insights into the biogeography and reproductive evolution of leptodactylid frogs. *Molecular Phylogenetics and Evolution* 67:445–457. doi:10.1016/j.bbr.2011.03.031

Fouquette M.J. Jr. 1960. Call structure in frogs of the Family Leptodactylidae. *The Texas Journal of Science* 12:201–215.

França L., Facure K., Giaretta A. 2004. Trophic and spatial niches of two large-sized species of *Leptodactylus* (Anura) in southeastern Brazil. *Studies on Neotropical Fauna and Environment* 39:243–248. doi:10.1080/01650520400007330

Freitas E.F.L., Spirandeli-Cruz E.F., Jim J. 2001. Comportamento reprodutivo de *Leptodactylus fuscus* (Schneider, 1799) (Anura: Leptodactylidae). *Comunicações do Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul, Série Zoológica* 14:121–132.

Frost D.R., Grant T., Faivovich J., Bain R.H., Haas A., Haddad C.F.B., …, Wheeler W.C. 2006. The amphibian tree of life. *Bulletin of the American Museum of NaturalHistory* 297:1–291. doi:10.1206/0003-0090(2006)297[0001:TATOL]2.0.CO;2

Fukuyama K. 1991. Spawning behaviour and male mating tactics of a foam-nesting treefrog, *Rhacophorus schlegelii. Animal Behaviour* 42:193–199. doi:10.1016/S0003-3472(05)80550-0

Gallardo J.M. 1958. Observaciones biológicas sobre *Leptodactylus prognathus* Boulenger. *Ciencia e Investigación* 14:460–465.

Gallardo J.M. 1963. *Hydrolaetare,* nuevo genero de Leptodactylidae (Amphibia) neotropical. *Neotropica* 9:42–48.

Gallardo J.M. 1964a. *Leptodactylus gracilis* (D. et B.) y especies aliadas (Amphibia, Leptodactylidae). *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Zoológicas* 9:37–57 + 2 plates.

Gallardo J.M. 1964b. Consideraciones sobre *Leptodactylus ocellatus* (L.) (Amphibia, Anura) y especies aliadas. *Physis* 24:373–384.

Gallardo J.M. 1964c. *Leptodactylus prognathus* Boul. y *L. mystacinus* (Burm.) con sus respectivas especies aliadas ("Amphibia, Leptodactylidae" del grupo "Cavícola"). *Revista del Museo de Ciencias Naturales "Bernardino Rivadavia." Ciencias Zoológicas* 9:91–121.

Gallardo J.M. 1970. Estudio ecológico sobre los anfibios y reptiles del sudoeste de la provincia de Buenos Aires, Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Zoología* 10:27–63

Gallardo J.M. 1979. Composición, distribución y origen de la herpetofauna chaqueña. *Museum of Natural History, University of Kansas, Monograph* 7:299–307.

Gans C. 1960. Notes on a herpetological collecting trip through the southeastern lowlands of Bolivia. *Annals of the Carnegie Museum* 35:283–314.

García Pérez L., Heyer W.R. 1993. Description of the advertisement call and resolution of the systematic status of *Leptodactylus gracilis delattini* Müller, 1968 (Amphibia: Leptodactylidae). *Proceedings of the Biological Society of Washington* 106:51–56.

Garman S.W. 1888 "1887". West Indian Batrachia in the Museum of Comparative Zoology. *Bulletin of the Essex Institute* 19:13–16.

Gascon C. 1991. Breeding of *Leptodactylus knudseni:* responses to rainfall variation. *Copeia* 1991:248–252. doi:10.2307/1446275

Gazoni T., Gruber S.L., Silva A.P.Z., Araújo O.G.S., Narimatsu H., Strüssmann C., …, Kashara, S. 2012. Cytogenetic analyses of eight species in the genus *Leptodactylus* Fitzinger, 1843 (Amphibia, Anura, Leptodactylidae) including a new diploid number and a karyotype with multiple translocations. *BMC Genetics* 13:109. doi:10.1186/1471-2156-13-109

Giaretta A.A., Costa H.C.M. 2007. A redescription of *Leptodactylus jolyi* Sazima and Bokermann (Anura, Leptodactylidae) and the recognition of a new closely related species. *Zootaxa* 1608:1–10.

Giaretta A.A., Facure K.G. 2009. Habitat, egg-laying behaviour, eggs and tadpoles of four sympatric species of *Pseudopaludicola* (Anura, Leiuperidae). *Journal of Natural History* 43:995–1009. doi:10.1080/00222930802702456

Giaretta A.A., Kokubum M.N.C. 2004. Reproductive ecology of *Leptodactylus furnarius* Sazima and Bokermann, 1978, a frog that lays eggs in underground chambers. *Herpetozoa* 16:115–126.

Giaretta A.A., De Freitas F.G., Antoniazzi M.M., Jared C. 2011. Tadpole buccal secretory glands as new support for a Neotropical clade of frogs. *Zootaxa* 3011:38–44.

Gibson R. 2001. Mountain Chicken, *Leptodactylus fallax. Species Management Guidelines* [unnumbered]:1–3.

Gibson R.C., Buley K.R. 2004. Maternal care and obligatory oophagy in *Leptodactylus fallax:* A new reproductive mode in frogs. *Copeia* 2004:128–135. doi:10.1643/CE-02-091R2

Girard C.F. 1853. Descriptions of new species of reptiles, collected by the U.S. Exploring Expedition, under the command of Capt. Charles Wilkes, U.S.N. *Proceedings of the Academy of Natural Sciences of Philadelphia* 6:420–424.

Girard C.F. 1858. United States Exploring Expedition. During the Years 1838, 1839, 1840, 1841, 1842. Under the Command of Charles Wilkes, U.S.N. Vol. XX. Herpetology. Prepared under the Superintendence of S.F. Baird. C. Sherman and Son, Philadelphia, 492 pp.

Glaw F., Franzen M. 2006. Type catalogue of amphibians in the Zoologische Staatssammlung München. *Spixiana* 29:153–192.

Goloboff P.A. 1996. Methods for faster parsimony analysis. *Cladistics* 12:199–220. doi:10.1111/j.1096-0031.1996.tb00009.x

Goloboff P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics* 15:415–428. doi:10.1111/j.1096-0031.1999.tb00278.x

Goloboff P.A. 2008. Calculating SPR distances between trees. *Cladistics* 24:591–597. doi:10.1111/j.1096-0031.2007.00189.x

Goloboff P.A., Farris J.S., Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786. doi:10.1111/j.1096-0031.2008.00217.x

Gómez R.O., Pérez Ben C.M., Stefanini M.I. 2013. Oldest record of *Leptodactylus* Fitzinger, 1826 (Anura, Leptodactylidae), from the early Pliocene of the South American Pampas. *Journal of Vertebrate Paleontology* 33:1321–1327. doi:10.1080/02724634.2013.771779

González-Fernández J.E., García-Díez T., San Segundo L. 2009. The amphibian type specimens preserved in the Museo Nacional de Ciencias Naturales (CSIC) of Madrid, Spain. *Spixiana* 32:265–283.

Goodman M., Olson C.B., Beeber, J.E., Czelusniak, J. 1982. New perspectives in the molecular biological analysis of mammalian phylogeny. *Acta Zoologica Fennica* 169:19–35.

Gorham S.W. 1966. Liste der rezenten Amphibien und Reptilien: Ascaphidae, Leiopelmatidea [sic], Pipidae, Discoglossidae, Pelobatidae, Leptodactylidae, Rhinophrynidae. *Das Tierreich* 85: xvi + 1–222.

Gosner K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190. Grant T., Kluge A.G. 2003. Data exploration in phylogenetic inference: Scientific, heuristic, or neither. *Cladistics* 19:379–418. doi:10.1111/j.1096-0031.2003.tb00311.x

Grant T., Kluge A.G. 2004. Transformation series as an ideographic character concept. *Cladistics* 20:23–31. doi:10.1111/j.1096-0031.2004.00003.x

Grant T., Kluge A.G. 2007. Ratio of explanatory power (REP): a new measure of group support. *Molecular Phylogenetics and Evolution* 44:483–487. doi:10.1016/j.ympev.2006.11.027

Grant T., Kluge A.G. 2008a. Clade support measures and their adequacy. *Cladistics* 24:1051–1064. doi:10.1111/j.1096-0031.2008.00231.x

Grant T., Kluge A.G. 2008b. Credit where credit is due: The Goodman-Bremer support metric. *Molecular Phylogenetics and Evolution* 49:405–406. doi:10.1016/j.ympev.2008.04.023

Grant T., Kluge A.G. 2009. Parsimony, explanatory power, and dynamic homology testing. *Systematics and Biodiversity* 7:357–363. doi:10.1017/S147720000999017X

Grant T., Kluge A.G. 2010. REP provides meaningful measurement of support across datasets. *Molecular Phylogenetics and Evolution* 55:340–342. 10.1016/j.ympev.2009.10.028

Grant T., Frost, D.R., Caldwell J.P., Gagliardo R., Haddad C.F.B., Kok P.J.R., …, Wheeler W.C. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Anura: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History* 299:1–262.doi:10.1206/0003-0090(2006)299[1:PSODFA]2.0.CO;2

Gross M.R., Sargent R.C. 1985. The evolution of male and female parental care in fishes. *American Zoologist* 25:807–822.

Gross M.R., Shine R. 1981. Parental care and mode of fertilization in ectothermic vertebrates. *Evolution* 35:775–793. doi:10.2307/2408247

Guayasamin J.M., Castroviejo-Fisher S., Trueb L., Ayarzagüena J., Rada M., Vilà C. 2009. Phylogenetic systematics of Glassfrogs (Amphibia: Centrolenidae) and their sister taxon *Allophryne ruthveni*. *Zootaxa* 2100:1–97.

Guibé J. 1950 "1948". Catalogue des types d'amphibiens du Musém National d'Histoire Naturelle. Muséum National d'Histoire Naturelle, Paris.

Guimarães L.D.A., Lima L.P., Juliano R.F., Bastos R.P. 2001. Vocalizações de espécies de anuros (Amphibia) no Brasil central. *Boletim do Museu Nacional, Nova Série, Zoologia* 474:1–14.

Günther A.C.L.G. 1859a. On the reptiles from St. Croix, West Indies, collected by Messrs. A. and E. Newton. *Annals and Magazine of Natural History 4,* Third Series:209–217.

Günther A.C.L.G. 1859b "1858". Catalogue of the Batrachia Salientia in the Collection of the British Museum. Trustees of the British Museum, London.

Günther A.C.L.G. 1869 "1868". First account of species of tailless batrachians added to the collection of the British Museum. *Proceedings of the Zoological Society of London* 1868:478–490 + plates XXXVII–XL.

Haas A. 2003. Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura). *Cladistics* 19:23–89. doi:10.1016/S0748-3007(03)00006-9

Habermehl G.G. 1981. Venomous Animals and their Toxins. Springer-Verlag, Berlin, Heidelberg, New York (Translation of the 2nd German edition, 1977).

Haddad C.F.B., Prado C.P.A. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. *Bioscience* 55:207–217. doi:10.1641/0006-3568(2005)055[0207:RMIFAT]2.0.CO;2

Hallowell E. 1861 "1860". Report upon the Reptilia of the North Pacific Exploring Expedition, under command of Capt. John Rogers, U.S.N. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1860:480–510.

Heatwole H., Solano H., Heatwole A. 1965. Notes on amphibians from the Venezuelan Guayanas with description of two new forms. *Acta Biológica Venezuelica* 4:349–364.

Henle K. 1981. *Adenomera griseigularis,* eine neue Leptodactyliden-Art aus Peru (Amphibia: Salientia: Leptodactylidae). *Amphibia-Reptilia* 2:139–142. doi:10.1163/156853881X00186

Hensel R. 1867. *Beiträge zur Kenntniss der Wirbelthiere Südbrasiliens. Archiv für Naturgeschichte* 33:120–162.

Hero J.-M. 1990. An illustrated key to tadpoles occurring in the Central Amazon rainforest, Manaus, Amazonas, Brasil. *Amazoniana* 11:201–262.

Hero J-M., Galatti U. 1990. Characteristics distinguishing *Leptodactylus pentadactylus* and *L. knudseni* in the Central Amazon Rainforest. *Journal of Herpetology* 24:227–228.

Heyer M.H., Heyer W.R., de Sá R.O. 2009a. Bibliography of frogs of the *Leptodactylus* clade (Amphibia, Anura, Leptodactylidae – *Adenomera, Hydrolaetare, Leptodactylus, Lithodytes*). I. Bibliography. *Smithsonian Herpetological Information Series Special Publication* 1:1–677.

Heyer M.H., Heyer W.R., de Sá R.O. 2009b. Bibliography of frogs of the *Leptodactylus* clade (Amphibia, Anura, Leptodactylidae – *Adenomera, Hydrolaetare, Leptodactylus, Lithodytes*). II. Indices. *Smithsonian Herpetological Information Series Special Publication* 2:1–167.

Heyer M.M., Heyer W.R., Spear S., de Sá R.O. 2003. *Leptodactylus mystacinus. Catalogue of American Amphibians and Reptiles* 767:1–11.

Heyer M.M., Heyer W.R., de Sá R.O. 2006. *Leptodactylus fragilis. Catalogue of American Amphibians and Reptiles* 830:1–26.

Heyer M.M., Heyer W.R., de Sá R.O. 2011. *Leptodactylus pentadactylus. Catalogue of American Amphibians and Reptiles* 887:1–48.

Heyer W.R. 1968. The proper name for the type-species of the genus *Leptodactylus*. *Copeia* 1968:160–162. doi:10.2307/1441563

Heyer W.R. 1969a. Studies on the genus *Leptodactylus* (Amphibia, Leptodactylidae). III. A redefinition of the genus *Leptodactylus* and a description of a new genus of leptodactylid frogs. *Contributions in Science, Los Angeles County Museum of Natural History* 155:1–14.

Heyer W.R. 1969b. The adaptive ecology of the species groups of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution* 23:421–428. doi:10.2307/2406697

Heyer W.R. 1969c. Studies on frogs of the genus *Leptodactylus* (Amphibia, Leptodactylidae). V. Taxonomic notes on *L. latinasus, rhodonotus, romani,* and *wuchereri*. *Herpetologica* 25:1–8.

Heyer W.R. 1970a. Studies on the frogs of the genus *Leptodactylus* (Amphibia: Leptodactylidae). VI. Biosystematics of the *melanonotus* group. *Natural History Museum of Los Angeles County, Contributions in Science* 191:1–48.

Heyer W.R. 1970b "1968". Studies on the genus *Leptodactylus* (Amphibia: Leptodactylidae). II. Diagnosis and distribution of the *Leptodactylus* of Costa Rica. *Revista de Biología Tropical* 16:171–205.

Heyer W.R. 1972. The status of *Leptodactylus pumilio* Boulenger (Amphibia, Leptodactylidae) and the description of a new species of *Leptodactylus* from Ecuador. *Natural History Museum of Los Angeles County, Contributions in Science* 231:1–8.

Heyer W.R. 1973. Systematics of the *marmoratus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Natural History Museum of Los Angeles County, Contributions in Science* 251:1–50.

Heyer W.R. 1974a. *Vanzolinius,* a new genus proposed for *Leptodactylus discodactylus* (Amphibia, Leptodactylidae). *Proceedings of the Biological Society of Washington* 87:81–90.

Heyer W.R. 1974b. Relationships of the *marmoratus* species group (Amphibia, Leptodactylidae) within the Subfamily Leptodactylinae. *Natural History Museum of Los Angeles County, Contributions in Science* 253:1–46.

Heyer W.R. 1978. Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Natural History Museum of Los Angeles County, Science Bulletin* 29:1–85.

Heyer W.R. 1979. Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology* 301: iii + 1–43. doi:10.5479/si.00810282.301

Heyer W.R. 1983. Clarification of the names *Rana mystacea* Spix, 1824, *Leptodactylus amazonicus* Heyer, 1978 and a description of a new species, *Leptodactylus spixi* (Amphibia: Leptodactylidae). *Proceedings of the Biological Society of Washington* 96:270–272.

Heyer W.R. 1985 "1984". The systematic status of *Adenomera griseigularis* Henle, with comments on systematic problems in the genus *Adenomera* (Amphibia: Leptodactylidae). *Amphibia-Reptilia* 5:97–100.

Heyer W.R. 1994. Variation within the *Leptodactylus podicipinus-wagneri* complex of frogs (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology* 546: iv + 1–124.

Heyer W.R. 1995. South American rocky habitat *Leptodactylus* (Amphibia: Anura: Leptodactylidae) with description of two new species. *Proceedings of the Biological Society of Washington* 108:695–716.

Heyer W.R. 1997. Geographic variation in the frog genus *Vanzolinius* (Anura: Leptodactylidae). *Proceedings of the Biological Society of Washington* 110:338–365.

Heyer W.R. 1998. The relationships of *Leptodactylus diedrus* (Anura, Leptodactylidae). *Alytes* 16:1–24.

Heyer W.R. 2000. The lectotype of *Cystignathus hylodes* Reinhardt and Lütken, 1862. *Journal of Herpetology* 34:150–153.

Heyer W.R. 2002. *Leptodactylus fragilis,* the valid name for the Middle American and northern South American white-lipped frog (Amphibia: Leptodactylidae). *Proceedings of the Biological Society of Washington* 115:321–322

Heyer W.R. 2005. Variation and taxonomic clarification of the large species of the *Leptodactylus pentadactylus* species group (Amphibia: Leptodactylidae) from Middle America, northern South America, and Amazonia. *Arquivos de Zoologia* 37:269–348.

Heyer W.R. 2014. Morphological analyses of frogs of the *Leptodactylus latrans* complex (Amphibia, Leptodactylidae) from selected localities in South America. *Proceedings of the Biological Society of Washington* 126:369–378. doi:10.2988/0006-324X-126.4.369

Heyer W.R., Barrio-Amorós C.L. 2009. The advertisement calls of two sympatric frogs, *Leptodactylus lithonaetes* (Amphibia: Anura: Leptodactylidae) and *Pristimantis vilarsi* (Amphibia: Anura: Strabomantidae). *Proceedings of the Biological Society of Washington* 122:282–291. doi:10.2988/09-02.1

Heyer W.R., Bellin M.S. 1973. Ecological Notes on Five Sympatric *Leptodactylus* (Amphibia, Leptodactylidae) from Ecuador. *Herpetologica* 29:66–72.

Heyer W.R., Carvalho C.M. 2000. Calls and calling behavior of the frog *Leptodactylus natalensis* (Amphibia: Anura: Leptodactylidae). *Proceedings of the Biological Society of Washington* 113:284–290.

Heyer W.R., Crombie R.I. 2005. *Leptodactylus lauramiriamae,* a distinctive new species of frog (Amphibia: Anura: Leptodactylidae) from Rondônia, Brazil. *Proceedings of the Biological Society of Washington* 118:590–595. doi:10.2988/0006-324X(2005)118[590:LLADNS]2.0.CO;2

Heyer W.R., de Sá R.O. 2011. Variation, systematics, and relationships of the *Leptodactylus bolivianus* complex (Amphibia: Anura: Leptodactylidae). *Smithsonian Contributions to Zoology* 635:1–58. doi:10.5479/si.00810282.635.1

Heyer W.R., Giaretta A.A. 2009. Advertisement calls, notes on natural history, and distribution of *Leptodactylus chaquensis* (Amphibia: Anura: Leptodactylidae) in Brasil. *Proceedings of the Biological Society of Washington* 122:292–305. doi:10.2988/08-42.1

Heyer W.R., Heyer M.M. 2001. *Leptodactylus lithonaetes. Catalogue of American Amphibians and Reptiles* 723:1–3.

Heyer W.R., Heyer M.M. 2002. *Leptodactylus elenae. Catalogue of American Amphibians and Reptiles* 742:1–5.

Heyer W.R., Heyer M.M. 2004. *Leptodactylus furnarius. Catalogue of American Amphibians and Reptiles* 785:1–5.

Heyer W.R., Heyer M.M. 2006a. *Leptodactylus knudseni. Catalogue of American Amphibians and Reptiles* 807:1–12.

Heyer W.R., Heyer M.M. 2006b. *Leptodactylus natalensis. Catalogue of American Amphibians and Reptiles* 808:1–5.

Heyer W.R., Juncá F.A. 2003. *Leptodactylus caatingae,* a new species of frog from eastern Brazil (Amphibia: Anura: Leptodactylidae). *Proceedings of the Biological Society of Washington* 116:317–329.

Heyer W.R., Maxson L.R. 1982. Distributions, relationships, and zoogeography of lowland frogs: The *Leptodactylus* complex in South America, with special reference to Amazonia. Pp. 375–388, in G.T. Prance (Ed.), Biological Diversification in the Tropics. Columbia University Press, New York.

Heyer W.R., Morales V.R. 1995. The advertisement call of the leptodactylid frog *Leptodactylus griseigularis*. *Amphibia-Reptilia* 16:91–92. doi:10.1163/156853895X00235

Heyer W.R., Peters J.A. 1971. The frog genus *Leptodactylus* in Ecuador. *Proceedings of the Biological Society of Washington* 84:163–170.

Heyer W.R., Pyburn W.F. 1983. *Leptodactylus riveroi,* a new frog species from Amazonia, South America (Anura: Leptodactylidae). *Proceedings of the Biological Society of Washington* 96:560–566.

Heyer R.W., Rand S. 1977. Foam nest construction in the *Leptodactylus* frogs *Leptodactylus pentadactylus* and *Physalaemus pustulosus*

(Amphibia, Anura, Leptodactylidae). *Journal of Herpetology* 11:225–228.

Heyer W.R., Scott Jr. N.J. 2006. The advertisement call of *Leptodactylus laticeps* (Amphibia, Anura, Leptodactylidae): Predatory aural luring? *Herpetological Natural History* 9:189–194.

Heyer W.R., Silverstone P.A. 1969. The larva of the frog *Leptodactylus hylaedactylus* (Leptodactylidae). *Fieldiana Zoology* 51:141–145.

Heyer W.R., Thompson A.S. 2000. *Leptodactylus rugosus. Catalogue of American Amphibians and Reptiles* 708:1–5.

Heyer W.R., McDiarmid R.W., Weigmann, D.L. 1975. Tadpoles, predation and pond habitats in the tropics. *Biotropica* 7:100–111. doi:10.2307/2989753

Heyer W.R., García-Lopez J.M., Cardoso A.J. 1996a. Advertisement call variation in the *Leptodactylus mystaceus* species complex (Amphibia: Leptodactylidae) with a description of a new sibling species. *Amphibia-Reptilia* 17:7–31. doi:10.1163/156853896X00252

Heyer W.R., de Sá R.O., McCranie J.R., Wilson L.D. 1996b. *Leptodactylus silvanimbus* (Amphibia: Anura: Leptodactylidae): Natural history notes, advertisement call, and relationships. *Herpetological Natural History* 4:169–174.

Heyer W.R., de Sá, R.O., Muller, S. 2002. *Leptodactylus silvanimbus. Catalogue of American Amphibians and Reptiles* 743:1–3.

Heyer W.R., de Sá R.O., Muller S. 2005a. The enigmatic distribution of the Honduran endemic *Leptodactylus silvanimbus* (Amphibia: Anura: Leptodactylidae). Pp. 81–101, in Donnelly M.A., Guyer C., Wake M.H. (Eds.), Ecology and Evolution in the Tropics: A Herpetological Perspective. University of Chicago Press, Chicago.

Heyer W.R., de Sá R.O., Rettig A. 2005b. Sibling species, advertisement calls, and reproductive isolation in frogs of the *Leptodactylus pentadactylus* species cluster (Amphibia, Leptodactylidae). *Russian Journal of Herpetology* 12 (supplement):90–92.

Heyer W.R., Heyer M.M., de Sá R.O. 2008. *Leptodactylus cunicularius. Catalogue of American Amphibians and Reptiles* 845:1–5.

Heyer W.R., Heyer M.M., de Sá, R.O. 2010a. *Leptodactylus syphax. Catalogue of American Amphibians and Reptiles* 868:1–9.

Heyer W.R., Heyer M.M., de Sá R.O. 2010b. *Leptodactylus savagei. Catalogue of American Amphibians and Reptiles* 867:1–19.

Hissa D.C., Vasconcelos I.M., Carvalho A.F.U., Nogueira V.L.R., Cascon P., Antunes A.S.L., ..., Melo V.M.M. 2008. Novel surfactant proteins are involved in the structure and stability of foam nests from the frog *Leptodactylus vastus. The Journal of Experimental Biology* 211:2707–11. doi:10.1242/jeb.019315

Hissa D.C., Bezerra G.A., Birner-Gruenberger R., Silva L.P., Usón I., Gruber K., Melo V.M.M. 2014. Unique crystal structure of a novel surfactant protein from the foam nest of the frog *Leptodactylus vastus. Chembiochem* 15:393–8. doi:10.1002/cbic.201300726

Hödl W., Gollmann G. 1986. Distress calls in Neotropical frogs. *Amphibia-Reptilia* 7:11–21. doi:10.1163/156853886X00226

Hoegg S., Vences M., Brinkmann H., Meyer A. 2004. Phylogeny and comparative substitution rates of frogs inferred from sequences of three nuclear genes. *Molecular Biology and Evolution* 21:1188–1200. doi:10.1093/molbev/msh081

Hoffmann H. 2006. Observations on behavior and parental care of *Leptodactylus melanonotus* (Hallowell) in Costa Rica. *Salamandra* 42:109–116

Hoogmoed M.S., Gruber U. 1983. Spix and Wagler type specimens of reptiles and amphibians in the Natural History Musea in Munich (Germany) and Leiden (The Netherlands). *Spixiana Supplement* 9:319–415.

Hudson W.H. 1892. The Naturalist in La Plata. Chapman and Hall, Ltd., London.

Izecksohn E. 1976. Um nova espécie de *Leptodactylus,* do Estado do Rio de Janeiro, Brasil (Amphibia, Anura, Leptodactylidae). *Revista Brasileira de Biologia* 36:527–530.

Jaeger E.C. 1955. A Source-book of Biological Names and Terms. Third Edition. Charles C. Thomas Publisher, Springfield.

Jansen M., Schulze A. 2012. Molecular, morphology and bioacoustic data suggest Bolivian distribution of a large species of the *Leptodactylus pentadactylus* group (Amphibia: Anura: Leptodactylidae). *Zootaxa* 3307:35–47.

Jansen M., Bloch R., Schulze A., Pfenninger M. 2011. Integrative inventory of Bolivia's lowland anurans reveals hidden diversity. *Zoologica Scripta* 40:567–583. doi:10.1111/j.1463-6409.2011.00498.x

Jennions M.D., Blackwell P.R.Y., Passmore N.I. 1992. Breeding behaviour of the African frog, *Chiromantis xerampelina:* multiple spawning and polyandry. *Animal Behaviour* 44:1091–1100. doi:10.1016/S0003-3472(05)80321-5

Jim J., Spirandeli-Cruz E.F. 1973. Uma nova espécie de *Leptodactylus* da Bahia, Brasil (Amphibia, Anura). [Abstract]. *Anais da Jornada Científica da Faculdade de Ciências Mêdicas e Biológicas de Botucatu* 3:13.

Jim J., Spirandeli-Cruz E.F. 1979. Uma nova espécie de *Leptodactylus* do Estado da Bahia, Brasil (Amphibia, Anura). *Revista Brasileira de Biologia* 39:707–710.

Jiménez de la Espada M. 1875. Vertebrados del Viaje al Pacífico Verificado de 1862 a 1865 por una Comisión de Naturalistas Enviada por el Gobierno Español. Batracios. Miguel Ginesta, Madrid.

Joglar R.L., Rentas V., Li F.C. 2005. Ranita de labio blanco (*Leptodactylus albilabris*). Pp. 74–88, 90–94, in R.L. Joglar (Ed.), Biodiversidad de Puerto Rico: Vertebrados Terrestres y Ecosistemas. Editorial de Insituto de Cultura Puertorriqueña, San Juan, Puerto Rico.

Joly C.A., Aidar M.P.M., Klink C.A, McGrath D.G, Moreira A.G., Moutinho P., ..., Sampaio E.V.S.B. 1999. Evolution of the Brazilian phytogeography classification systems: implications for biodiversity conservation. *Ciência e Cultura* 51:331–348.

Kaiser H. 1994. *Leptodactylus fallax. Catalogue of American Amphibians and Reptiles* 583:1–3.

Kaminsky S.K., Linsernmair K.E., Grafe T.U. 1999. Reproductive timing, nest construction and tadpole guidance in the African pig-nosed frog, *Hemisus marmoratus. Journal of Herpetology* 33:119–123.

Katoh K., Kuma K., Toh H., Miyata T. 2005. MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* 33:511–8. doi:10.1093/nar/gki198

Kellogg R. 1932. Mexican tailless amphibians in the United States National Museum. *United States National Museum Bulletin* 160:1 plate + iv + 1–224.

King J.D., Rollins-Smith L.A., Nielsen P.F., John A., Conlon J.M. 2005a. Characterization of a peptide from skin secretions of male specimens of the frog, *Leptodactylus fallax* that stimulates aggression in male frogs. *Peptides.* 26:597–601. doi:10.1016/j.peptides.2004.11.004

King J.D., Al-Ghafari N., Abraham B., Sonnevend A., Leprince J., Nielsen P.F., Conlon J.M. 2005b. Pentadactylin: an antimicrobial peptide from the skin secretions of the South American bullfrog *Leptodactylus pentadactylus. Comparative biochemistry and physiology. Toxicology & Pharmacology* 141:393–397. doi:10.1016/j.cbpc.2005.09.002

Klappenbach M.A. 1968. Notas herpetológicas, III. Identificación de las especies Uruguayas descriptas por Philippi en el "Suplemento a los batraquios chilenos". *Investigaciones Zoológicas Chilenas* 23:147–151.

Klappenbach M.A., Langone J.A. 1992. Lista sistemática y sinonímica de los anfibios del Uruguay. Con comentarios y notas sobre su distribución. *Anales del Museo Nacional de Historia Natural de Montevideo, Segunda Série* 8:163–222.

Kluge A.G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology* 38:7–25. doi:10.2307/2992432

Kluge A.G. 2004. On total evidence: for the record. *Cladistics* 20:205–207. doi:10.1111/j.1096-0031.2004.00020.x

Kluge A.G., Grant T. 2006. From conviction to anti-superfluity: old and new justifications of parsimony in phylogenetic inference. *Cladistics* 22:276–288. doi:10.1111/j.1096-0031.2006.00100.x

Knauer F.K. 1883. Naturgeschichte der Lurche. (Amphibiologie). Eine Umfassendere Darlegung unserer Kenntnisse von dem

Anatomischen Bau, der Entwicklung und Systematischen Eintheilung der Amphibien sowie eine Eingehende Schilderung des Lebens dieser Thiere. Zweite Ausgabe. 2 edition. A. Pichler's Witwe and Sohn, Wien und Leipzig.

Köhler J., Lötters S. 1999. Advertisement calls of two Bolivian *Leptodactylus* (Amphibia: Anura: Leptodactylidae). *Amphibia-Reptilia* 20:215–219. doi:10.1163/156853899X00222

Köhler J., Lötters S. 2002. *Leptodactylus didymus*. Pp. 32 and CD2, track 11, in R. Márquez R., De la Riva I.J., Bosch J., Matheu E. (Eds.), Guía Sonora de las Ranas y Sapos de Bolivia. Sounds of Frogs and Toads of Bolivia. Alosa, Museo Nacional de Ciencias Naturales, Fonoteca Zoológica, Madrid.

Kok A.D., Du Preez, H., Channing, A. 1989. Channel construction by the African bullfrog: another parental care strategy. *Journal of Herpetology* 223:435–437.

Kokubum M.N.C., Giaretta A.A. 2005. Reproductive ecology and behaviour of a species of *Adenomera* (Anura, Leptodactylinae) with endotrophic tadpoles: Systematic implications. *Journal of Natural History* 39:1745–1758. doi:10.1080/00222930400021515

Kokubum M.N.C., Maciel N.M., Matsushita R.H., Queiróz-Júnior A.T., Sebben A. 2009. Reproductive biology of the Brazilian sibilator frog *Leptodactylus troglodytes*. *Herpetological Journal* 19:119–126.

Krintler K. 1986. Dominica - herpetologisches Kleinod in der Karibik. *Herpetofauna* 45:26–30

Kwet A., Di-Bernardo M. 1999. Pró-Mata - Anfíbios. Amphibien. Amphibians. EDIPUCRS, Porto Alegre.

Kwet A., Di-Bernardo M., Garcia P.C.A. 2001. The taxonomic status of *Leptodactylus geminus* Barrio, 1973. *Journal of Herpetology* 35:56–62.

Kwet A., Steiner J., Zillikens A. 2009 A new species of *Adenomera* (Amphibia: Anura: Leptodactylidae) from the Atlantic rain forest in Santa Catarina, southern Brazil. *Studies on Neotropical Fauna and Environment* 44:93–107. doi:10.1080/01650520902901659

Lamar W.W., Wild E.R. 1995. Comments on the natural history of *Lithodytes lineatus* (Anura: Leptodactylidae), with description of the tadpole. *Herpetological Natural History* 3:135–142.

Langone J.A., de Sá R.O. 2005. Redescripción de la morfología larval externa de dos especies del grupo de *Leptodactylus fuscus* (Anura, Leptodactylidae). *Phyllomedusa* 4:49–59.

Larson P.M., de Sá R.O. 1998. Chondrocranial morphology of *Leptodactylus* larvae (Leptodactylidae: Leptodactylinae): Its utility in phylogenetic reconstruction. *Journal of Morphology* 238:287–305. doi:10.1002/(SICI)1097-4687(199812)238:3<287::AID-JMOR2>3.0.CO;2-8

Latreille P.A. an X (1801–1802). "des Tortues, des Lézards, des Grenouilles, des Crapauds, des Raines et des Serpens," p. 136–332. *In* Sonnini and Latreille. Histoire naturelle des reptiles. Volume 2:1–332, 20 plates. Déterville, Paris.

Laurenti J.N. 1768. Specimen Medicum, exhibens Synopsin Reptilium emendatam cum Experimentis circa Venena et Antidota Reptilium Austriacorum. Typ. Joan. Thom. Nob. De Trattnern, Viennae.

Lavilla E.O. 1994 "1992". Tipos portadores de nombre y localidades tipo de anfibios de Argentina. *Acta Zoológica Lilloana* 42:61–100 + 1 unnumbered.

Lavilla E.O., Langone J.A., Caramaschi U., Heyer W.R., de Sá R.O. 2010. The identification of *Rana ocellata* Linnaeus, 1758. Nomenclatural impact on the species currently known as *Leptodactylus ocellatus* (Leptodactylidae) and *Osteopilus brunneus* (Gosse, 1851) (Hylidae). *Zootaxa* 2346:1–16.

Leite J.M.A. Jr., Sampaio J.M.S., Silva-Leite R.R., Leite J.R.S.A. 2008. *Leptodactylus natalensis* (Lutz, 1930) (Amphibia, Anura, Leptodactylidae): First record from Maranhão state and new geographic distribution map. *Biotemas* 21:153–156.

Leite J.M.A. Jr., Silva L.P., Silva-Leite R.R., Ferrari A.S., Noronha S.E., da Silva H.R., …, Leite J.R.S.A. 2010. *Leptodactylus ocellatus* (Amphibia): mechanism of defense in the skin and molecular phylogenetic relationships. *Journal of Experimental Zoology Part A, Ecological Genetics and Physiology* 313A:1–8. doi:10.1002/jez.551

Lescure J. 1972. Contribution à l'étude des amphibiens de Guyane Française II. *Leptodactylus fuscus* (Schneider). Observations écologiques et éthologiques. *Annales Musém d'Histoire naturelle de Nice* 1:91–100.

Lescure J. 1979. Étude taxinomique et éco-éthologique d'un Amphibien des petites Antilles: *Leptodactylus fallax* Müller, 1926 (Leptodactylidae). *Bulletim Musém d'Histoire naturelle* 1:757–774.

Lescure J., Letellier F. 1983. Reproduction en captivité de *Leptodactylus fallax* Müller, 1926 (Amphibia, Leptodactylidae). *Revue Française d'Aquariologie* 10:61–64.

Lescure J., Marty C. 2000. Atlas des amphibiens de Guyane. *Patrimoines Naturels* 45:1–388.

Lewis E.R., Narins P.M. 1985. Do frogs communicate with seismic signals? *Science* 227:187–189. doi:10.1126/science.227.4683.187

Lewis E.R., Narins P.M., Cortopassi K.A., Yamada W.M., Poinar E.H., Moore S.W., Yu X.-L. 2001. Do male white-lipped frogs use seismic signals for intraspecific communication? *American Zoologist* 41:1185–1199. doi:10.1668/0003-1569(2001)041[1185:DMWLFU]2.0.CO;2

Lezcano M.J., Pardiñas U.F., Tonni E.P. 1993. Restos de vertebrados en el Holoceno del Nordeste de la provincia de Buenos Aires, Argentina. Sistemática y paleoambientes. *Ameghiniana* 30:332.

Libério M.D.S., Bastos I.M.D., Pires Júnior O.R., Fontes W., Santana J.M., Castro M.S. 2014. The crude skin secretion of the pepper frog *Leptodactylus labyrinthicus* is rich in metallo and serine peptidases. *PLoS One* 9:e96893. doi:10.1371/journal.pone.0096893

Lima A.P. 1992. The tadpole of *Leptodactylus riveroi* Heyer and Pyburn, 1983 (Anura: Leptodactylidae). *Journal of Herpetology* 26:91–93.

Limaverde P.T., Nascimento N.R.F., Evangelista J.S.A.M., Tomé A.R., Fonteles M.C., Santos C.F., …, Carvalho K.M. 2009. Isolation and pharmacological effects of leptoxin, a novel proteic toxin from *Leptodactylus pentadactylus* skin secretion. *Toxicon* 54:531–538. doi:10.1016/j.toxicon.2009.05.029

Lopez P.T., Narins P.M., Lewis E.R., Moore S.W. 1988. Acoustically induced call modification in the white-lipped frog, *Leptodactylus albilabris*. *Animal Behavior* 36:1295–1308. doi:10.1016/S0003-3472(88)80198-2

Lourenço L.B., Bacci-Júnior M., Martins V.G., Recco-Pimentel S.M., Haddad C.F.B. 2008. Molecular phylogeny and karyotype differentiation in *Paratelmatobius* and *Scythrophrys* (Anura, Leptodactylidae). *Genetica* 132:255–266. doi:10.1007/s10709-007-9169-y

Love A.C. 2003. Evolutionary morphology, innovation, and the synthesis of evolutionary and developmental biology. *Biology and Philosophy* 18:309–345. doi:10.1023/A:1023940220348

Lucas E.M., Brasileiro C.A., Oyamaguchi H.M., Martins M. 2008. The reproductive ecology of *Leptodactylus fuscus* (Anura, Leptodactylidae): new data from natural temporary ponds in the Brazilian Cerrado and a review throughout its distribution. *Journal of Natural History* 42:2305–2320. doi:10.1080/00222930802254698

Lutz A. 1926a. Observações sobre batrachios brasileiros. Parte I: O genero *Leptodactylus* Fitzinger. Observations on brazilian batrachians. Part I: The genus *Leptodactylus*. *Memórias do Instituto Oswaldo Cruz* 19:139–157 (Portuguese) + plates 30–37 + 159–174 (English).

Lutz A. 1926b. Sur deux espèces nouvelles de batraciens brésiliens. *Comptes Rendus des Séances de la Société de Biologie et de ses Filiales et Associées* 95:1011–1012.

Lutz A. 1930. Segunda memória sobre espécies brasileiras do género *Leptodactylus*, incluindo outras alliadas. Second paper on brasillian and some closely related species of the genus *Leptodactylus*. *Memórias do Instituto Oswaldo Cruz* 23:1–20 (Portuguese), 21–34 (English) + plates 1–5.

Lynch J.D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *University of Kansas Museum of Natural History, Miscellaneous Publication* 53:1–238.

Lynch J.D. 2006. The tadpoles of frogs and toads found in the lowlands of northern Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 30:443–457.

Magalhães F.M., Garda A.A., Amado T.F., de Sá, R.O. 2013. The tadpole of *Leptodactylus caatingae* Heyer & Juncá, 2003 (Anura: Leptodactylidae): External morphology, internal anatomy, and natural history. *South American Journal of Herpetology* 8:203–210. doi:10.2994/SAJH-D-13-00033.1

Maglia A.M., Pugener L., Mueller J.M. 2007. Skeletal morphology and postmetamorphic ontogeny of *Acris crepitans* (Anura: Hylidae): A Case of Miniaturization in Frogs. *Journal of Morphology* 268:194–223. doi:10.1002/jmor.10508

Magnusson W.E., Hero J.M. 1991. Predation and the evolution of complex oviposition behaviour in Amazon Rainforest Frogs. *Oecologia* 86:310–318. doi:10.1007/BF00317595

Malnate E.V. 1971. A catalog of primary types in the herpetological collections of the Academy of Natural Sciences, Philadelphia (ANSP). *Proceedings of the Academy of Natural Sciences of Philadelphia* 123:345–375.

Marquez R., De la Riva I., Bosch J. 1995. Advertisement calls of Bolivian Leptodactylidae (Amphibia, Anura). *Journal of Zoology, London* 237:313–336. doi:10.1111/j.1469-7998.1995.tb02765.x

Martin L., Morton M.N., Hilton G.M., Young R.P., Garcia G., Cunningham A.A., …, Mendes S. (Eds.). 2007. A Species Action Plan for the Montserrat mountain chicken *Leptodactylus fallax*. Department of Environment, Montserrat.

Martins I.A. 2001. Parental care behaviour in *Leptodactylus podicipinus* (Cope, 1862) (Anura, Leptodactylidae). *Herpetological Journal* 11:29–32.

Martins M. 1988. Biología reprodutiva de *Leptodactylus fuscus* em Boa Vista, Roraima (Amphinia: Anura). *Revista Brasileira de Biologia* 48:969–977.

Marx H. 1976. Supplementary catalogue of type specimens of reptiles and amphibians in Field Museum of Natural History. *Fieldiana, Zoology* 69:33–94.

Maxson L.R., Heyer, W.R. 1988. Molecular systematics of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Fieldiana: Zoology, New Series* 41:1–13.

Mayer A.F.J.C. 1835. Analecten für Vergleichende Anatomie. Eduard Weber, Bonn, 2 unnumbered + 93 pp. + 7 plates.

Mayr E. 1942. Systematics and the Origin of Species from the Viewpoint of a Zoologist, Dover Publication, Inc., reprint of Columbia Univ. Press. Cambridge.

McCranie J.R., Wilson L.D. 2002. The amphibians of Honduras. *Contributions to Herpetology* 19: x + 625 + 20 color plates.

McCranie J.R., Wilson L.D., Porras L. 1980. A new species of *Leptodactylus* from the cloud forests of Honduras. *Journal of Herpetology* 14:361–367.

McCranie J.R., Wilson L.D., Williams K.L. 1986. The tadpole of *Leptodactylus silvanimbus,* with comments on the relationships of the species. *Journal of Herpetology* 20:560–562

Méhelÿ L. 1904. Investigations on Paraguayan batrachians. *Annales Historico-Naturales Musei Nationalis Hungarici* 2:207–232 + plate 13.

Melin D. 1941. Contributions to the knowledge of the Amphibia of South America. *Göteborgs Kungliga Vetenskaps - och Vitterhets - Samhälles Handlingar Sjätte Följden, Series B* 1:1–71.

Menin M., Lima A.P., Rodrigues D.J. 2010. The tadpole of *Leptodactylus pentadactylus* (Anura: Leptodactylidae) from central Amazonia. *Zootaxa* 2508:65–68.

Merrem B. 1820. Versuch eines Systems der Amphibien. Johann Christian Krieger, Marburg.

Mijares-Urrutia A. 1997. Un nuevo *Leptodactylus* (Anura, Leptodactylidae) de un bosque nublado del oeste de Venezuela. *Alytes* 15:113–120.

Miranda N.E.O., Maciel N.M., Tepedino K.P., Sebben A. 2014. Internal larval characters in anuran systematic studies: a phylogenetic hypothesis for Leptodactylus (Anura, Leptodactylidae). *Journal of Zoological Systematics and Evolutionary Research.* doi:10.1111/jzs.12073

Miranda-Ribeiro A. 1926. Notas para servirem ao estudo dos Gymnobatrachios (Anura) Brasileiros. Tomo primeiro. *Archivos do Museu Nacional* 27:1–227 + 22 plates.

Miranda-Ribeiro A. 1927. Os Leptodactylidae do Museu Paulista. *Revista do Museu Paulista* 15:113–134 + 3 plates.

Mones A. 1975. Notas paleontológicas uruguayas, III. Vertebrados fósiles nuevos o poco conocidos (Chondrichthyes, Osteichthyes, Amphibia, Mammalia). *Ameghiniana* 12:343–349.

Motta A.P., Silva E.T., Feio R.N., Dergam J.A. 2010. The tadpole of *Leptodactylus cupreus* Caramaschi, Feio and São Pedro, 2008 (Anura, Leptodactylidae). *Zootaxa* 2640:65–68.

Muedeking M.H., Heyer, W.R. 1976. Descriptions of eggs and reproductive patterns of *Leptodactylus pentadactylus* (Amphibia: Leptodactylidae). *Herpetologica* 32:137–139.

Müller L. 1923. Neue oder seltene Reptilien und Batrachier der Zoologischen Sammlung des bayr. Staates. *Zoologischer Anzeiger, Leipzig* 57:38–42.

Müller L. 1926. Neue Reptilien und Batrachier der Zoologischen Sammlung des bayrischen Staates. *Zoologischer Anzeiger, Leipzig* 65:193–200.

Müller L. 1927. Amphibien und Reptilien der Ausbeute Prof. Bresslau's in Brasilien 1913–1914. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 40:259–304.

Müller P. 1968. Beitrag zur Herpetofauna der Insel Campeche (27°42'S, 48°28'W). (Ergebnisse einer Reise nach Brasilien im Jahre 1967). *Salamandra* 4:47–55.

Mullis K.B. 1990. The unusual origin of the polymerase chain reaction. *Scientific American* 262:56–61, 64–5. doi:10.1038/scientificamerican0490-56

Muniz K.P.R., da Silva W.R. 2005. *Leptodactylus labyrinthicus* (South American Pepper Frog). Predation. *Herpetological Review* 36:302–303.

Myers C.W., Paolillo O.A., Daly J.W. 1991. Discovery of a defensively malodorous and nocturnal frog in the family Dendrobatidae: Phylogenetic significance of a new genus and species from the Venezuelan Andes. *American Museum Novitates* 3002:1–33.

Nascimento A.C.C., Zanotta L.C., Kyaw C.M., Schwartz E.N.F., Schwartz C.A., Sebben A., …, Castro M.S. 2004. Ocellatins: new antimicrobial peptides from the skin secretion of the South American frog *Leptodactylus ocellatus* (Anura: Leptodactylidae). *The Protein Journal* 23:501–508. doi:10.1007/s10930-004-7877-z

Nascimento A.C.C., Chapeaurouge A., Perales J., Sebben A., Sousa M.V, Fontes W., Castro M.S. 2007. Purification, characterization and homology analysis of ocellatin 4, a cytolytic peptide from the skin secretion of the frog *Leptodactylus ocellatus. Toxicon* 50:1095–1104. doi:10.1016/j.toxicon.2007.07.014

Nieden F. 1923. Amphibia. Anura I. Subordo Aglossa und Phaneroglossa, Sectio 1 Arcifera. *Das Tierreich* 46: xxxii + 1–584.

Nixon K.C. 1999, The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15:407–414. doi:10.1111/j.1096-0031.1999.tb00277.x

Noble G.K. 1923. New batrachians from the Tropical Research Station, British Guiana. *Zoologica* 3:289–299.

Nuin P.A.S., Oliveira Filho F.C.V. 2005. Phylogenetic analysis of the subfamily Hylodinae (Anura, Leptodactylidae) based on morphological characters. *Amphibia-Reptilia* 26:139–147. doi:10.1163/1568538054253456

Oda F.A., Santos D.L., Gambale P.G., Campos V.A., Batista V.G., Affonso I.P., Strüssmann C. 2014. New Brazilian records of *Leptodactylus chaquensis* Cei, 1950, at the species' southern range limit. *Herpetozoa* 26:195–200.

Oliveira Filho J.C., Giaretta A.A. 2009. Reproductive behavior of *Leptodactylus mystacinus* (Anura, Leptodactylidae) with notes on courtship call of other *Leptodactylus* species. *Iheringia, Série Zoologia* 98:508–515. doi:10.1590/S0073-47212008000400015

Oliveira Filho J.C., Cardoso de Moura Costa H., Lobo Braga U.M. 2005. Egg-laying and foam-beating in *Leptodactylus fuscus* (Anura, Leptodactylidae). *Biota Neotropica* 5:1–2. doi:10.1590/S1676-06032005000300022

Oliveira Filho J.C., Giaretta A.A. 2006. *Leptodactylus mystacinus* (shovel-nosed frog). Parental care. *Herpetological Review* 37:204.

Orton G.L. 1951. The tadpole of *Leptodactylus melanonotus* (Hallowell). *Copeia* 1951:62–66. doi:10.2307/1438055

Padial J.M., de Sá R.O., De la Riva I. 2006. The distress calls of *Leptodactylus chaquensis* Cei, 1950 and *Leptodactylus elenae* Heyer, 1978 (Anura: Leptodactylidae). *Salamandra* 42:1–4.

Padial J.M., Grant T., Frost D.R. 2014. Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria. *Zootaxa* 3825:1–132. doi:10.11646/zootaxa.3825.1.1

Palumbi S.R. 1996. Nucleic acids II: the polymerase chain reaction. Pp. 205–247, in Hillis D.M., Moritz C., Mable B.K., (Eds.). Molecular Systematics, 2nd ed. Sinauer Associates, Sunderland.

Parker H.W. 1935. The frogs, lizards, and snakes of British Guiana. *Proceedings of the Zoological Society of London* 1935:505–530.

Peters J.A. 1952. Catalogue of type specimens in the herpetological collections of the University of Michigan Museum of Zoology. *Occasional Papers of the Museum of Zoology, University of Michigan* 539:1–55.

Peters W.C.H. 1862. Eine neue Gattung von Laubfröschen, *Plectromantis,* aus Ecuador vor. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* 1862:232–233.

Peters W.C.H. 1870. Über neue Amphibien (*Hemidactylus, Urosaura, Tropidolepisma, Geophis, Uriechis, Scaphiophis, Hoplocephalus, Rana, Entomoglossus, Cystignathus, Hylodes, Arthroleptis, Phyllobates, Cophomantis*) des Königlich zoologischen Museums. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1870:641–652 + 2 plates.

Peters W.C.H. 1872. Über die von Spix in Brasilien gesammelten Batrachier des Königl. Naturalienkabinets zu München. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* 1872:196–227.

Petranka J.W., Kennedy C.A. 1999. Pond tadpoles with generalized morphology: is it time to reconsider their functional roles in aquatic communities? *Oecologia* 120:621–631. doi:10.1007/s004420050898

Philibosian R., Ruibal R., Shoemaker V.H., Mcclanahan L.L. 1974. Nesting behavior and early larval life of the frog *Leptodactylus bufonius*. *Herpetologica* 30:381–386.

Philippi R.A. 1902. Suplemento a los batraquios Chilenos descritos en la Historia Física i Política de Chile de don Claudio Gay. Librera Alemana de José Ivens, Santiago.

Pisanó A., Barbieri F.D. 1965. Propiedades biológicas del dializado de espuma de *Leptodactylus bufonius*. *Archivos de Farmacia y Bioquímica* 12:65–74.

Pisanó A., Rengel D., Lavilla E.O. 1993. Le nid souterrain comme chambre nuptiale pour un amphibien d'Argentine. *Revue Française Aquariol* 19:125–126.

Ponssa M.L. 2001. Cuidado parental y comportamiento de cardumen de larvas en *Leptodactylus insularum* (Anura, Leptodactylidae). *Alytes* 19:183–195.

Ponssa M.L. 2006. On the osteology of a distinctive species of the genus *Leptodactylus: Leptodactylus laticeps* (Boulenger, 1917) (Anura, Leptodactylidae). *Zootaxa* 1188:23–26.

Ponssa M.L. 2008. Cladistic analysis and osteological descriptions of the species of the *L. fuscus* species group of the genus *Leptodactylus* (Anura, Leptodactylidae). *Journal of Zoological Systematics and Evolutionary Research* 46:249–266. doi:10.1111/j.1439-0469.2008.00460.x

Ponssa M.L., Barrionuevo J.S. 2008. Foam-generating behaviour in tadpoles of *Leptodactylus latinasus* (Amphibia, Leptodactylidae): significance in systematics. *Zootaxa* 1884:51–59.

Ponssa M.L., Barrionuevo J.S. 2012. Sexual dimorphism in *Leptodactylus latinasus* (Anura, Leptodactylidae): nasal capsule anatomy, morphometric characters, and performance associated with burrowing behavior. *Acta Zoologica* 93:57–67.

Ponssa M.L., Lavilla E.O. 1998. Osteology of *Leptodactylus latinasus* (Anura: Leptodactylidae) and the validity of its subspecies. *Bulletin of the Maryland Herpetological Society* 34:57–63.

Ponssa M.L., Jowers M.J., de Sá R.O. 2010. Osteology, natural history notes and phylogenetic relationships of the poorly known Caribbean frog *Leptodactylus nesiotus* (Anura: Leptodactylidae). *Zootaxa* 2646:1–25.

Ponssa M.L., Brusquetti F., Souza F.L. 2011. Morphological analysis of *Leptodactylus podicipinus* (Anura, Leptodactylidae) with different reproductive modes: Does morphology reflect burrowing habits? *Journal of Herpetology* 45:79–93.

Pough F.H., Magnusson W.E., Ryan M.J., Wells K.D., Taigen T.L. 1992. Behavioral energetics. Pp. 395–436, in Feder M.E., Burggren W.W. (Eds.). Environmental Physiology of the Amphibians. University of Chicago Press, Chicago.

Pramuk J.B. 2006. Phylogeny of South American *Bufo* (Anura: Bufonidae) inferred from combined evidence. *Zoological Journal of the Linnean Society* 146:407–452. doi:10.1111/j.1096-3642.2006.00212.x

Prado C.P.A., d'Heursel A. 2006. The tadpole of *Leptodacytlus elenae* (Anura: Leptodactylidae), with the description of the internal buccal anatomy. *South American Journal of Herpetology* 1:79–86. doi:10.2994/1808-9798(2006)1[79:TTOLEA]2.0.CO;2

Prado C.P.A., Haddad C.F.B. 2003. Testes size in leptodactylid frogs and occurrence of multimale spawning in the genus *Leptodactylus* in Brazil. *Journal of Herpetology* 37:354–362. doi:10.1670/0022-1511(2003)037[0354:TSILFA]2.0.CO;2

Prado C.P.A., Haddad C.F.B. 2005. Size-fecundity relationships and reproductive investment in female frogs in the pantanal, south-western Brazil. *Herpetological Journal* 15:181–189.

Prado C.P.A., Uentanabaro M., Lopes F.S. 2000. Reproductive strategies of *Leptodactylus chaquensis* and *L. podicipinus* in the Pantanal, Brazil. *Journal of Herpetology* 34:135–139.

Prado C.P.A., Uentanabaro M., Haddad, C.F.B. 2002. Description of a new reproductive mode in *Leptodactylus* (Anura, Leptodactylidae), with a review of the reproductive specialization toward terrestriality in the genus. *Copeia* 2002 4:1128–1133.

Prado C.P.A., Toledo L.F., Zina J., Haddad C.F.B. 2005. Trophic eggs in the foam nests of *Leptodactylus labyrinthicus* (Anura, Leptodactylidae): an experimental approach. *Herpetological Journal* 15:279–284.

Prado G.M., Bilate M., Wogel H. 2007. Call diversity of *Leptodactylus natalensis* Lutz, 1930 (Anura; Leptodactylidae). *Papéis Avulsos de Zoologia* 47:97–103.

Pregill G. 1981. Late Pleistocene herpetofaunas from Puerto Rico. *University of Kansas Museum of Natural History Miscellaneous Publications* 71:1–72. doi:10.5962/bhl.title.63988

Pugener L.A., Maglia A.M. 2007. Skeletal morphology and development of the olfactory region of *Spea* (Anura: Scaphiopodidae). *Journal of Anatomy* 211:754–768. doi:10.1111/j.1469-7580.2007.00826.x

Pyron R.A, Wiens J.J. 2011. A large-scale phylogeny of Amphibia with over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* 61:543–583. doi:10.1016/j.ympev.2011.06.012

Raddi G. 1823. Continuazione della descrizione dei rettili Brasiliani. *Memorie di Matematica e di Fisica della Società Italiana delle Scienze Residente in Modena* 19:58–73.

Reading C.J., Jofré G.M. 2003. Reproduction in the nest building vizcacheras frog *Leptodactylus bufonius* in central Argentina. *Amphibia-Reptilia* 24:415–427. doi:10.1163/156853803322763882

Reinhardt J., Lütken C.F. 1862 "1861". Bidrag til det vestindiske Øriges og navnligen de dansk-vestindiske Øers Herpetologie. *Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjöbenhavn* IV:153–291.

Rivero J.A. 1961. Salientia of Venezuela. *Bulletin of the Museum of Comparative Zoology at Harvard College* 126:1–207.

Rivero J.A., Esteves A.E. 1969. Observations on the agonistic and breeding behavior of *Leptodactylus pentadactylus* and other amphibian species in Venezuela. *Breviora* 321:1–14.

Rodrigues A.P., Giaretta A.A., da Silva D.R., Facure K.G. 2011. Reproductive features of three maternal-caring species of *Leptodactylus* (Anura: Leptodactylidae) with a report on alloparental care in frogs. *Journal of Natural History* 45:2037–2047. doi:10.1080/00222933.2011.574799

Rodrigues D.J., Menin M., Lima A.P. 2007. Redescription of the tadpole of *Leptodactylus rhodomystax* (Anura: Leptodactylidae) with natural history notes. *Zootaxa* 1509:61–67.

Rodrigues D.J., Uetanabaro M., Prado C.P.A. 2004. Seasonal and ontogenetic variation in diet composition of *Leptodactylus podicipinus* (Anura, Leptodactylidae) in the southern Pantanal, Brazil. *Revista Española de Herpetología* 2004:19–28.

Rodríguez L.O. 1992. Structure et organization du peuplement d'anoures de Cocha Cashu, Parc National Manu, Amazonie Péruvienne. *Revue Ecology* 47:151–197.

Rodríguez L.O., Duellman W.E. 1994. Guide to the Frogs of the Iquitos Region, Amazonian Peru. Kansas, The University of Kansas.

Rollins-Smith L.A., King J.D., Nielsen P.F., Sonnevend A., Conlon J.M. 2005. An antimicrobial peptide from the skin secretions of the mountain chicken frog *Leptodactylus fallax* (Anura: Leptodactylidae). *Regulatory Peptides* 124:173–178. doi:10.1016/j.regpep.2004.07.013

Rossa-Feres D.C., Nomura F. 2006. Characterization and taxonomic key for tadpoles (Amphibia: Anura) from the northwestern region of São Paulo State, Brazil. *Biota Neotropica* 6:26 unnumbered pages. doi:10.1590/S1676-06032006000100014

Ruibal R., Thomas E. 1988. The obligate carnivorous larvae of the frog, *Lepidobatrachus laevis* (Leptodactylidae). *Copeia* 3:591–604. doi:10.2307/14453

Sabaj Pérez M.H. (Ed.). 2010. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 2.0 (8 November 2010). American Society of Ichthyologists and Herpetologists, Washington, D.C. Accessible at www.asih.org

Sanchiz B. 1998. Salientia. Pp. 1–275, in: Wellnhofer P. (Ed.), Encyclopedia of Palaeoherpetology, Part 4. Verlag Dr. Friedrich Pfeil, Munich.

Sanger F.N.S., Coulson A.R. 1977. DNA sequencing with chain-terminating inhibitors. *Proceeding of the National Academy of Sciences USA* 74:5463–7. doi:10.1073/pnas.74.12.5463

Sankoff D. 1975. Minimal mutation trees of sequences. *SIAM Journal on Applied Mathematics* 28:35–42.

Santos E.M., Amorim F.O. 2005. Modo reprodutivo de *Leptodactylus natalensis* Lutz, 1930 (Amphibia, Anura, Leptodactylidae). *Revista brasileira Zoociências Juiz de Fora* 7:39–45.

Santos E.M., Amorim F.O. 2006. Cuidado parental em *Leptodactylus natalensis* (Amphibia, Anura, Leptodactylidae). *Iheringia, Série Zoologia* 96:491–494. doi:10.1590/S0073-47212006000400015

Savage J.M. 1974. Type localities for species of amphibians and reptiles described from Costa Rica. *Revista de Biología Tropical* 22:71–122.

Savage J.M. 2002. The Amphibians and Reptiles of Costa Rica. A Herpetofauna Between Two Continents, Between Two Seas. The University of Chicago Press, Chicago.

Sazima I. 1975. Hábitos reprodutivos e fase larvária de *Leptodactylus mystacinus* e *L. sibilatrix* (Anura, Leptodactylidae). Master's Thesis, Universidade de São Paulo, Brazil.

Sazima I., Bokermann W.C.A. 1978. Cinco novas espécies de *Leptodactylus* do centro e sudeste brasileiro (Amphibia, Anura, Leptodactylidae). *Revista Brasileira de Biologia* 38:899–912.

Schalk C.M. 2012. *Phylsalaemus biligonigerus*. Burrow use. *Herpetological Review* 43:123–124.

Schlaepfer M.A., Figeroa-Sandi R. 1998. Female reciprocal calling in a Costa Rican leaf-litter frog, *Eleutherodactylus podiciferus. Copeia* 1998:1076–1080. doi:10.2307/1447362

Schlüter A., Löttker P., Mebert K. 2009. Use of an active nest of the leaf cutter ant *Atta cephalotes* (Hymenoptera: Formicidae) as a breeding site of *Lithodytes lineatus* (Anura: Leptodactylidae). *Herpetology Notes* 2:101–105.

Schmidt K.P., Inger R.F. 1951. Amphibians and reptiles of the Hopkins-Branner Expedition to Brazil. *Fieldiana, Zoology* 31:439–465.

Schneider J.G. 1799. Historiae Amphibiorum Naturalis et Literariae. Fasciculus Primus continens *Ranas, Calamitas, Bufones, Salamandras et Hydros* in Genera et Species Descriptos Notisque suis Distinctos. Sumtibus Friederici Frommanni, Jena.

Schulze A., Jansen M. 2012. One species, two strategies? Oviposition site variation in a member of the *Leptodactylus pentadactylus* group (Amphibia: Anura: Leptodactylidae). *Studies on Neotropical Fauna and Environment* 47:183–191. doi:10.1080/01650521.2012.711102

Schwartz A., Thomas R. 1975. A check-list of West Indian amphibians and reptiles. *Carnegie Museum of Natural History, Special Publication* 1:1–216.

Scott E. 2005. A phylogeny of ranid frogs (Anura: Ranoidea: Ranidae), based on a simultaneous analysis of morphological and molecular data. *Cladistics* 21:507–574. doi:10.1111/j.1096-0031.2005.00079.x

Scott N.J. Jr. 1983. *Leptodactylus pentadactylus* (Rana ternero, Smoky Frog). Pp. 405–406, in D.H. Janzen (Ed.), Costa Rican Natural History. University of Chicago Press, Chicago.

Scott N.J. Jr., Aquino A.L. 2005. It's a frog-eat-frog world in the Paraguayan Chaco: Food habits, anatomy, and behavior of the frog-eating anurans. Pp. 243–59, in M.A. Donnelly, Crother B.I, Guyer C., Wake M.H., White M.E. (Eds.), Ecology and Evolution in the Tropics. A Herpetological Perspective. University of Chicago Press, Chicago.

Seba A. 1734. Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimis expressio, per universam physices historiam. Opus, cui, in hoc rerum genere, nullum par exstitit. Ex toto terrarum orbe collegit, digessit, descripsit, et depingendum curavit Albertus Seba. Tomus I. Janssonio-Waesbergios, and J. Wetstenium, and Gul. Smith, Amstelaedam.

Sebben A., Maciel N.M., Campos L.A., Kokubum M.N.C., da Silva H.R. 2007. Occurrence of a calcified pseudodontoid in *Leptodactylus troglodytes* (Anura: Leptodactylidae). *Journal of Herpetology* 41:337–340. doi:10.1670/0022-1511(2007)41[337:OOACPI]2.0.CO;2

Sexton O.J. 1962. Apparent territorialism in *Leptodactylus insularum. Herpetologica* 18:212–14.

Shepard D.B., Caldwell, J.P. 2005. From foam to free-living: ecology of larval *Leptodactylus labyrinthicus. Copeia* 2005:803–811. doi:10.1643/00458511(2005)005[0803:FFTFEO]2.0.CO;2

Shreve B. 1957. Reptiles and amphibians from the Selva Lacandona. *Bulletin of the Museum of Comparative Zoology at Harvard College* 116:242–248.

Silva A.P.Z., Garcia P.C.A., Martins V.G., Bacci M., Kasahara S. 2004. Chromosomal and molecular analyses of *Leptodactylus gracilis gracilis, L. gracilis delattini,* and *L. plaumanni* (Anura, Leptodactylidae); taxonomic implications. *Amphibia-Reptilia* 25:185–196. doi:10.1163/1568538041231193

Silva M.B., Juncá F.A. 2006. Oophagy in tadpoles of *Leptodactylus troglodytes* (Amphibia, Anura, Leptodactylidae). *Sitientibus Série Ciências Biologicas* 2:89–91.

Silva R., Martins I.A., Rossa-Feres D.C. 2008. Bioacústica e sítio de vocalização em taxocenoses de anuros de área aberta no noroeste paulista. *Biota Neotropica* 8:123–134. doi:10.1590/S1676-06032008000300012

Simon M. 1983. The ecology of parental care in a terrestrial breeding frog from New Guinea. *Behavior Ecology and Sociobiology* 14:61–67.

Siqueira C.D.C., Marra R.V., Vrcibradic D., Van Sluys M. 2006. *Leptodactylus marambaiae* (Marambaia white-lipped frog). Death feigning. *Herpetological Review* 37:444–445.

Smith H.M., Taylor E.H. 1948. An annotated checklist and key to the Amphibia of Mexico. *United States National Museum Bulletin:* iv + 1–118.

Smith H.M., Taylor E.H. 1950. Type localities of Mexican reptiles and amphibians. *University of Kansas Science Bulletin* 33, Part 2:313–380.

Smith H.M., Schneider T., Smith R.B. 1977. An overlooked synonym of the giant toad *Bufo marinus* (Linnaeus) (Amphibia, Anura, Bufonidae). *Journal of Herpetology* 11:423–425.

Solano H. 1987. Algunos aspectos de la biología reproductiva del sapito silbador *Leptodactylus fuscus* (Schneider) (Amphibia: Leptodactylidae). *Amphibia-Reptilia* 8:111–128. doi:10.1163/156853887X00388

Sousa J.C., Berto R.F., Gois E.A., Fontenele-Cardi N.C., Honório J.E.R., Konno K., …, Carvalho K.M. 2009. Leptoglycin: a new glycine/leucine-rich antimicrobial peptide isolated from the skin secretion of the South American frog *Leptodactylus pentadactylus* (Leptodactylidae). *Toxicon* 54:23–32. doi:10.1016/j.toxicon.2009.03.011

Souza M.B. de, Haddad C.F.B. 2003. Redescription and reevaluation of the generic_Status of *Leptodactylus dantasi* (Amphibia, Anura, Leptodactylidae) and description of its unusual advertisement call. *Journal of Herpetology* 37:490–497. doi:10.1670/259-01A

Spix J.B. 1824. Animalia Nova sive Species Novae Testudinum et Ranarum, quas in Itinere per Brasiliam Annis MDCCCXVII–MDCCCXX jussu et Auspiciis Maximiliani Josephi I. Bavariae Regis Suscepto Collegit et Descripsit Dr. J.B. de Spix. Franc. Seraph. Hübschmanni, Monachii, ii + 53 pp. + 22 plates.

Steffen G.A. 1815. De Ranis Nonnullis. Observationes Anatomicae. Joannis Friderici Starckii: Berlin.

Steindachner F. 1864. Batrachologische Mittheilungen. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 14:239–288 + plates IX–XVII.

Steindachner F. 1867. Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859. Amphibien. Kaiserlich-Königlichen hof-und Staatsdruckerei, Wien, 70 pp. + 101 figs.

Straughan I.R., Heyer W.R. 1976. A functional analysis of the mating calls of the neotropical frog genera of the *Leptodactylus* complex (Amphibia, Leptodactylidae). *Papéis Avulsos de Zoologia* 29:221–245.

Strüssman C., Ribeiro do Vale M.B., Meneghini M.H., Magnusson W.E. 1984. Diet and foraging mode of *Bufo marinus* and *Leptodactylus ocellatus*. *Journal of Herpetology* 18:138–46.

Swofford D.L., Maddison W.P. 1992. Parsimony, character-state reconstructions, and evolutionary inferences. Pp. 186–223, in Mayden R.L. (Ed.), Systematics, Historical Ecology, and North American Freshwater Fishes. Stanford University Press, Stanford.

Taylor E.H. 1937 "1936". New species of Amphibia from Mexico. *Transactions of the Kansas Academy of Science* 39:349–363.

Toft C.A., Duellman W.E. 1979. Anurans of the lower Rio Llullapichis, Amazonian Perú: a preliminary analysis of community structure. *Herpetologica* 35:71–77.

Toledo L.F., Tozetti A.M., Zina J. 2005. *Leptodactylus labyrinthicus* (Pepper Frog): repertoire of defensive behaviour. *The Herpetological Bulletin* 90:29–31.

Townsend D.S., Stewart M.M., Pough H. 1984. Male parental care and its adaptive significance in a Neotropical frog. *Animal Behavior* 32:421–431.

Tozetti A.M., Toledo L.F. 2005. Short-term movement and retreat sites of *Leptodactylus labyrinthicus* (Anura: Leptodactylidae) during the breeding season: A spool-and-Line tracking study. *Journal of Herpetology* 39:640–644. doi:10.1670/155-04N.1

Trewavas E. 1933. The hyoid and larynx of the Anura. *Philosophical Transactions of the Royal Society of London* 222:401–527. doi:10.1098/rstb.1932.0020

Trivers R.L. 1972. Parental investment and sexual selection. Pp. 136–179, in Campbell B. (Ed.), Sexual Selection and the Descent of Man. Adeline Press, Chicago.

Troschel F.H. 1848. Amphibien. Pp. 645–661, in M.R. Schomburgk (Ed.), Reisen in Britisch-Guiana in den Jahren 1840–1844. Im Auftrag Sr. Mäjestat des Königs von Preussen ausgeführt von Richard Schomburgk. Nebst einer Fauna und Flora Guiana's nach Vorlagen von Johannes Müller, Ehrenberg, Erichson, Klotzsch, Troschel, Cabanis und Andern. Mit Abbildungen und einer Karte von Britisch-Guiana aufgenommen von Sir Robert Schmoburgk. Dritter Theil. Versuch einer Fauna und Flora von Britisch-Guiana. Vol. 3. J.J. Weber, Leipzig.

Trueb L. 1973. Bones, frogs and evolution. Pp. 65–132, in Vial, J.L. (Ed.), Evolutionary Biology of the Anurans: Contemporary Research on Major Problems. The University Missouri Press, Columbia.

Trueb L., Pugener L.A., Maglia A.M. 2000. Ontogeny of the bizarre: an osteological description of *Pipa pipa* (Anura: Pipidae), with an account of skeletal development in the species. *Journal of Morphology* 243:75–104. doi:10.1002/(SICI)1097-4687(200001)243:1<75::AID-JMOR4>3.0.CO;2-L

Tschudi J.J. 1838. Classification der Batrachier, mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. Buchdruckerei von Petitpierre, Neuchâtel, 102 pp. + 6 plates.

Van der Meijden A., Vences M., Hoegg S., Boistel R., Channing A., Myer A. 2007. Nuclear gene phylogeny of narrow-mouthed toads (Family: Microhylidae) and a discussion of competing hypotheses concerning their biogeographical origins. *Molecular Phylogenetics and Evolution* 44:1017–1030. doi:10.1016/j.ympev.2007.02.008

Van Devender T.R., Rea A.M., Smith M.L. 1985. The Sangamon interglacial vertebrate fauna from Rancho la Brisca, Sonora, Mexico. *Transactions of the San Diego Society of Natural History* 21:23–55.

Vaira M. 1997. *Leptodactylus bolivianus* (NCN). Behavior. *Herpetological Review* 28:200.Varón A., Wheeler W.C. 2012. The tree alignment problem. *BMC Bioinformatics* 13:293. doi:10.1186/1471-2105-13-293

Varón A., Wheeler W.C. 2013. Local search for the generalized tree alignment. *BMC Bioinformatics* 14:66. doi:10.1186/1471-2105-14-66

Varón A., Vinh L.S., Wheeler W.C. 2010. POY version 4: phylogenetic analysis using dynamic homologies. doi:10.1111/j.1096-0031.2009.00282.x

Vaz-Ferreira R., Gehrau A. 1974. Protección de la prole en leptodactylidos. *Revista de Biologia del Uruguay* II:59–62.

Vaz-Ferreira R., Gehrau A. 1975. Comportamiento epimelético de la rana común *Leptodactylus ocellatus* (L.) (Amphibia, Leptodactylidae). I. Atención de la cría y actividades alimentarias relacionadas. *Physis (B)* 34:1–14.

Vaz-Ferreira R, Gerhau A. 1986. Comportamiento de los renacuajos gregarios de *Leptodactylus ocellatus*. División Publicaciones y Ediciones, Universidad de la República, Montevideo.

Vaz-Silva W., da Frota, J.G. 2003. *Leptodactylus labyrinthicus* (Labyrinth Frog). Diet. *Herpetological Review* 34:359.

Vellard J. 1947. *Leptodactylus laticeps* Blgr., un raro batracio del chaco argentino. *Acta Zoológica Lilloana* 4:463–491.

Vera Candioti M.F., Brusquetti F., Netto F. 2007. Morphological characterization of *Leptodactylus elenae* tadpoles (Anura: Leptodactylidae: *L. fuscus* group), from central Paraguay. *Zootaxa* 1435:1–17.

Verdade V.K. 2005. Relaçoes filogenéticas entre as espécies dos gêneros *Cycloramphus* Tschudi 1838 e *Zachaenus* Cope 1866 (Anura, Leptodactylidae). Ph.D. Dissertation, Universidade de São Paulo, Brazil.

Vergnaud-Grazzini C. 1968. Amphibiens Pleistocenes de Bolivie. *Bulletin de la Societe G´eologique de France* 7:688–695.

Vieira W.L.S., Santana G.G., Vieira K.S. 2007. Description of the tadpole of *Leptodactylus vastus* (Anura: Leptodactylidae). *Zootaxa* 1529:61–68.

Vizotto L.D. 1967. Desenvolvimento de anuros da região norte-ocidental do Estado de São Paulo. *Faculdade de Filosofia, Ciências e Letras de São José do Rio Prêto, Zoologia No. Especial:* 2 unnumbered + 1–161.

Wassersug R.J., Heyer W.R. 1988. A survey of internal oral features of leptodactyloid larvae (Amphibia: Anura). *Smithsonian Contributions to Zoology* 457:1–99.

Wagler J.G. 1829. Descriptiones et icones amphibiorum. *Isis von Oken* 22:68–70.

Wagler J.G. 1830. Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vögel. Ein Beitrag zur vergleichenden Zoologie. J.G. Cotta, München, Stuttgart.

Wake D.B., Wake M.H., Specht C.D. 2011. Homoplasy: From detecting pattern to determining process and mechanism of evolution. *Science* 331:1032–1035. doi:10.1126/science.1188545

Wallbaum [= Walbaum] J.J. 1784. Beschreibung eines Meerfrosches. *Schriften der Gesellschaft naturforschender Freunde zu Berlin* 5:230–245.

Wassersug R.J. 1976. A procedure for differential staining of cartilage and bone in hole formalin fixed vertebrates. *Staining Technology* 51:131–134.

Wassersug R.J., Duellman W.E. 1984. Oral structures and their development in egg-brooding hylid frog embryos and larvae: evolutionary and ecological implicactions. *Journal of Morphology* 182:1–37

Wells K.D. 1977. The social behavior of anuran amphibians. *Animal Behavior* 25:666–693. doi:10.1016/0003-3472(77)90118-X

Wells K.D. 2007. The Ecology and Behavior of Amphibians. University of Chicago Press, Chicago.

Wells K.D., Bard K.M. 1988. Parental behavior of an aquatic-breeding tropical frog, *Leptodactylus bolivianus*. *Journal of Herpetology* 22:361–364.

Werner F. 1893. Wissenschaftliche Mittheilungen. 1. Herpetologische Nova. *Zoologischer Anzeiger, Leipzig* 16:81–84.

Werner F. 1894. Bemerkungen über die nordamerikanischen *Rana*-Arten. *Jahresbericht und Abhandlungen des Naturwissenschaftlichen Vereins in Magdeburg* 1893–1894:123–136.

Werner F. 1899. Ueber Reptilien und Batrachier aus Columbien und Trinidad. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 49:470–484.

Wheeler W.C. 1996. Optimization alignment: the end of multiple sequence alignment in phylogenetics? *Cladistics* 12:1–9. doi:10.1111/j.1096-0031.1996.tb00189.x

Wheeler W.C. 2003a. Iterative pass optimization of sequence data. *Cladistics* 19:254–260. doi:10.1111/j.1096-0031.2003.tb00368.x

Wheeler W.C. 2003b. Implied alignment: a synapomorphy-based multiple sequence alignment method. *Cladistics* 19:261–268. doi:10.1111/j.1096-0031.2003.tb00369.x

Wheeler W.C., Aagesen L., Arango C.P., Faivovich J., Grant T., D'Haese C.A., …, Giribet G. 2006. Dynamic Homology and Phylogenetic Systematics: A Unified Approach Using POY. American Museum of Natural History, New York.

Wied-NeuwiedM.A.P.,Prinzzu.1824a.*AbbildungenzurNaturgeschichte Brasiliens. Heft 8.* Weimar: Landes-Industrie-Comptoir.

Wied-Neuwied M. 1824b. Verzeichniss der Amphibien, welche im zweiten Bande der Naturgeschichte Brasiliens vom Prinz Max von Neuwied werden beschrieben werden. (Nach Merrems Bersuch eines Systems der Amphibien). *Isis von Oken* 1824: Columns 661–673.

Wied-Neuwied M. 1825. Beitrage zur Naturgeschichte von Brasilien. I. Band. Verlage des Gr. H.S. priv. Landes-Industrie-Comptoirs, Weimar.

Wiens J.J., Kuczynski C.A., Duellman W.E., Reeder T.W. 2007. Loss and re-evolution of complex life cycles in marsupial frogs: does ancestral trait reconstruction mislead? *Evolution* 61:1886–1899. doi:10.1111/j.1558-5646.2007.00159.x

Wittenberger J.F. 1981. Animal Social Behavior. Duxbury Press, Boston.

Yanek K., Heyer W.R., de Sá R.O. 2006. Genetic resolution of the enigmatic Lesser Antillean distribution of the frog *Leptodactylus validus* (Anura, Leptodactylidae). *South American Journal of Herpetology* 1:192–201. doi:10.2994/1808-9798(2006)1[192:GROTEL]2.0.CO;2

Zimmerman B.L., Bogart J.P. 1988. Ecology and calls of four species of Amazonian forest frogs. *Journal of Herpetology* 22:97–108.

Zina J., Haddad C.F.B. 2005. Reproductive activity and vocalizations of *Leptodactylus labyrinthicus* (Anura: Leptodactylidae) in southeastern Brazil. *Biota Neotropica* 5:1–11. doi:10.1590/S1676-06032005000300008

APPENDIX 1. GENBANK ACCESSION NUMBERS

Below we list the GenBank accession numbers of the DNA sequences included in the phylogenetic analysis of *Leptodactylus*. New sequences are marked in boldface.

Terminal	12S	16S	Rhodopsin
Adenomera hylaedactyla 1	DQ283063	DQ283063	DQ283790
Adenomera hylaedactyla 2	AY943240.1	AY943227	**KM091505**
Adenomera lutzi		**KM091597**	
Adenomera sp.	AY364538	AY364538	
Allophryne ruthveni	AF364511, AF364512, AF843564	AF364511, AF364512, AF843564	AY844538
Alsodes gargola	AY843565	AY843565	AY844539
Amazophrynella minuta	AY843582	AY843582	AY844555
Atelognathus patagonicus	AY843571	AY843571	AY844545
Atelopus spurrelli	DQ502200	DQ502200	
Batrachyla leptopus	AY843572	AY843572	AY844546
Ceratophrys cranwelli	AY843575	AY843575	AY843797
Chacophrys pierottii	DQ283328	DQ283328	
Craugastor rhodopis	DQ283317	DQ283317	DQ283960
Crossodactylus schmidti	AY843579	AY843579	AY844780
Cycloramphus boraceiensis	DQ283097	DQ283097	DQ283813
Edalorhina perezi 1	AY843585	AY843585	AY844558
Edalorhina perezi 2	**KM091465**	**KM091581**	**KM091515**
Engystomops cf. *freibergi*	DQ337229	DQ337229	
Engystomops coloradorum	DQ337222	DQ337222	
Engystomops guayaco	DQ337220	DQ337220	
Engystomops montubio	DQ337224	DQ337224	
Engystomops petersi	EF011554	EF011554	
Engystomops pustulatus	DQ337215	DQ337215	
Engystomops pustulosus	DQ337235	DQ337235	
Engystomops randi	DQ337228	DQ337228	
Engystomops sp.B	DQ337216	DQ337216	
Engystomops sp.D	DQ337218	DQ337218	
Espadarana prosoblepon	AY364358, AY364379, AY843574	AY364358, AY364379, AY843574	AY364404
Eupsophus calcaratus	AY843587	AY843587	AY844560
Gastrotheca megacephala	AY843592	AY843592	AY844564
Hemiphractus helioi	AY843594	AY843594	AY844566
Hyalinobatrachium eurygnathum	AY843595		AY844567
Hyalinobatrachium fleischmanni	DQ283453	DQ283453	DQ284043
Hyalinobatrachium sp.	AY326024	AY326024	
Hydrolaetare caparu	**KM091473**	**KM091589**	**KM091526**
Hydrolaetare dantasi	**KM091474**	**KM091590**	**KM091527**
Hylodes phyllodes	DQ283096	DQ283096	DQ283812
Hypsiboas boans	AY843610	AY843610	AY844588
Lepidobatrachus laevis	DQ283152	DQ283152	DQ283851
Leptodactylus albilabris	**KM091460**	**KM091577**	**KM091506**
Leptodactylus bolivianus	**KM091461**	HQ232831	**KM091507**
Leptodactylus bufonius	AY943220	AY943233	**KM091508**
Leptodactylus camaquara	**KM091462**	**KM091578**	**KM091509**
Leptodactylus chaquensis	EF613179	EF632055	**KM091510**
Leptodactylus colombiensis	**KM091463**	**KM091579**	**KM091511**
Leptodactylus cunicularis	**KM091464**	**KM091580**	**KM091512**
Leptodactylus didymus	AY948953	AY948957	**KM091513**
Leptodactylus diedrus	AY943217	AY943230	**KM091514**
Leptodactylus discodactylus	AY943226	AY943239	

Terminal	12S	16S	Rhodopsin
Leptodactylus elenae	**KM091466**	**KM091582**	**KM091516**
Leptodactylus fallax	**KM091467**	**KM091583**	**KM091517**
Leptodactylus flavopictus	**KM091468**	**KM091584**	**KM091518**
Leptodactylus fragilis	**KM091469**	**KM091585**	**KM091519**
Leptodactylus furnarius	**KM091470**	**KM091586**	**KM091520**
Leptodactylus fuscus 1		AY911275	
Leptodactylus fuscus 2	AY905712	AY911281	**KM091523**
Leptodactylus fuscus 3	AY905715		**KM091522**
Leptodactylus fuscus 4	DQ283404	DQ283404	DQ284015
Leptodactylus fuscus 5		AY911284	
Leptodactylus fuscus 6	AY905702	AY911271	
Leptodactylus fuscus 7	AY905705	AY911274	
Leptodactylus fuscus 9	AY905706		**KM091521**
Leptodactylus gracilis	**KM091471**	**KM091587**	**KM091524**
Leptodactylus grisegularis	**KM091472**	**KM091588**	**KM091525**
Leptodactylus insularum	AY943222	AY943235	**KM091528**
Leptodactylus joyli AF465	**KM091475**	**KM091591**	**KM091529**
Leptodactylus knudseni	**KM091476**	**KM091592**	**KM091530**
Leptodactylus labrosus	**KM091477**	**KM091593**	**KM091531**
Leptodactylus labyrinthicus 1	AY947875	AY947861	
Leptodactylus labyrinthicus 2	AY947874	AY947860	
Leptodactylus labyrinthicus 3	**KM091478**		
Leptodactylus laticeps	**KM091479**	**KM091594**	**KM091532**
Leptodactylus latinasus	**KM091480**	**KM091595**	**KM091533**
Leptodactylus latrans 1	**KM091490**	**KM091605**	**KM091546**
Leptodactylus latrans 2	AY843688	AY843688	AY844681
Leptodactylus latrans HOLOTYPE	AY669856	**KM091606**	**KM091547**
Leptodactylus leptodactyloides	AY943223	AY943236	**KM091534**
Leptodactylus lithonaetes	**KM091482**		**KM091537**
Leptodactylus longirostris	**KM091483**	**KM091596**	**KM091536**
Leptodactylus macrosternum 1	**KM091485**	**KM091599**	
Leptodactylus macrosternum 2	**KM091484**	**KM091598**	**KM091538**
Leptodactylus marambaiae	**KM091486**	**KM091600**	**KM091539**
Leptodactylus melanonotus	AY943224	AY943237	**KM091540**
Leptodactylus myersi	**KM091487**	**KM091601**	**KM091541**
Leptodactylus mystaceus 1	AY905717	AY911286	**KM091542**
Leptodactylus mystaceus 2	AY948952	AY948956	**KM091576**
Leptodactylus mystaceus 3	AY948954	AY948958	**KM091575**
Leptodactylus mystacinus	AY905716	AY911285	**KM091543**
Leptodactylus natalenis	**KM091488**	**KM091602**	**KM091544**
Leptodactylus nesiotus 3	**KM091489**	**KM091603**	**KM091545**
Leptodactylus notoaktites	**KM091504**	**KM091604**	
Leptodactylus paraensis	AY947870	AY947856	**KM091549**
Leptodactylus pentadactylus	**KM091491**	**KM091607**	**KM091550**
Leptodactylus peritoaktites	AY947880	AY947864	**KM091551**
Leptodactylus petersii	**KM091492**	**KM091608**	**KM091552**
Leptodactylus plaumanni	**KM091493**	**KM091609**	**KM091553**
Leptodactylus podicipinus	EF613172	EF632048	**KM091555**
Leptodactylus poecilochilus	**KM091495**	**KM091611**	**KM091556**
Leptodactylus pustulatus	**KM091497**	**KM091613**	**KM091557**
Leptodactylus rhodonotus	**KM091498**	**KM091614**	**KM091559**
Leptodactylus riveroi	AY943218	AY943231	**KM091560**
Leptodactylus rugosus	**KM091499**	**KM091615**	**KM091561**
Leptodactylus savagei	AY943225	AY943238	**KM091562**

Terminal	**12S**	**16S**	**Rhodopsin**
Leptodactylus sertanejo		**KM091616**	
Leptodactylus silvanimbus	AY943219	AY943232	**KM091563**
Leptodactylus sp. *juvenile*	AY843561	AY843561	**AY844535**
Leptodactylus stenodema	**KM091500**	**KM091617**	**KM091564**
Leptodactylus syphax	**KM091501**	**KM091618**	**KM091565**
Leptodactylus tapiti	**KM091481**	**KM091619**	**KM091566**
Leptodactylus troglodytes	**KM091502**	**KM091620**	**KM091567**
Leptodactylus validus 1	EF613169	EF632029	**KM091569**
Leptodactylus validus 2	EF613164	EF632024	**KM091570**
Leptodactylus validus 3	EF613123	EF632033	**KM091568**
Leptodactylus validus continental	EF613170	EF632046	**KM091548**
Leptodactylus vastus	AY947873	AY947859	**KM091571**
Leptodactylus ventrimaculatus	**KM091503**	**KM091621**	**KM091572**
Leptodactylus viridis		**KM091622**	**KM091573**
Leptodactylus wagneri	EF613176	EF632053	**KM091574**
Leptodactyus fuscus 8	AY905698	AY911267	
Leptodactyus rhodomystax	AY947869	AY947855	**KM091558**
Limnomedusa macroglossa	AY843689	AY843689	AY844682
Lithodytes lineatus 1	AY943228	AY943241	**KM091535**
Lithodytes lineatus 2	AY843690	AY843690	AY844683
Megaelosia goeldii	DQ283072	DQ283072	DQ283797
Melanophryniscus klappenbachi	AY843699	AY843699	DQ283765
Nymphargus bejaranoi	AY843576	AY843576	AY844372
Nymphargus grandisonae	AY364540	AY364540	
Nymphargus sp.	AY326025	AY326025	
Odontophrynus achalensis	DQ283247, DQ283248	DQ283247, DQ283248	DQ283918
Paratelmatobius cardosoi	EU224402	EU224402	
Paratelmatobius gaigeae	EU224397	EU224397	
Paratelmatobius poecilogaster	EU224400	EU224400	
Paratelmatobius sp.1	DQ283098	DQ283098	DQ283814
Paratelmatobius sp.2	EU224412	EU224412	
Paratelmatobius sp.3	EU224411	EU224411	
Phyllomedusa vaillanti	AY549363	AY549363	AY844716
Physa albonotatus	DQ337210	DQ337210	
Physa barrioi	DQ337213	DQ337213	
Physa biligonigerus	DQ337212	DQ337212	
Physa cuvieri	AY843729	AY843729	AY844717
Physa enesefae	DQ337211	DQ337211	
Physa nattereri	DQ337208	DQ337208	
Physa riograndensis	AY326021	AY326021	
Physa signifer	DQ337209	DQ337209	
Physalaemus gracilis	DQ283417	DQ283417	DQ284022
Pleurodema brachyops 1	AY843733	AY843733	AY844721
Pleurodema brachyops 2	**KM091494**	**KM091610**	**KM091554**
Pseudopaludicola falcipes 1	AY843741	AY843741	AY844728
Pseudopaludicola falcipes 2	**KM091496**	**KM091612**	
Rhaebo haematiticus	DQ283167	DQ283167	DQ283861
Rhinoderma darwinii	DQ283324	DQ283324	DQ283963
Scythrophrys sawayae	DQ283099	DQ283099	DQ283815
Stefania evansi	AY843767	AY843767	AY844755
Telmatobius jahuira	DQ283041	DQ283041	DQ283771
Telmatobius marmoratus	AY843769	AY843769	AY844757
Thoropa miliaris	DQ283331	DQ283331	

APPENDIX 2. NON-MOLECULAR CHARACTERS USED IN THE ANALYSES

Below we list the 156 non-molecular characters included in the total evidence analysis of the phylogeny of *Leptodactylus*. Characters marked with an asterisk (*) are taken from Ponssa (2008). Characters 113–130 are from Larson and de Sá (1998).

Character 0: Broad longitudinal mid-dorsal stripe*. Additive. 0: absent; 1: present, from the vent to between or behind the eyes; 2: present, from the vent to the tip of the snout.

Character 1: Light stripe (or a line of light dots) on the posterior surface of the thigh*. 0: absent; 1: present.

Character 2: Longitudinal light lines on the dorsal surface of the tibia*. 0: absent; 1: present.

Character 3: Dorsolateral folds*. Additive. 0: absent; 1: 2–4; 2: 6; 3: 8.

Character 4: Shank texture (modified from Ponssa, 2008, who considered character 4 and 5 a single character). 0: smooth; 1: with spicules.

Character 5: Tarsal texture (modified from Ponssa, 2008, who considered character 4 and 5 a single character). 0: smooth; 1: with spicules.

Character 6: Foot surface texture*. 0: smooth; 1: with spicules.

Character 7: Mid-dorsal pin stripe*. 0: absent; 1: present.

Character 8: Gular region pattern. The gular pattern can be coincident or not with belly pattern. 0: completely unpigmented, or slightly spotted antero-laterally and 1: pigmented, different patterns evident in entire gular region.

Character 9: Dorsal body texture*. Additive. 0: without white spicules; 1: white spicules posteriorly (Ponssa et al., 2010: fig. 12A); 2: white spicules on all dorsal surfaces.

Character 10: Belly pattern. The variation observed in the belly pattern has been described previously (Heyer, 1973, 1994; 2005). 0: unpigmented or slightly spotted laterally (Heyer, 1973: fig. 7A); 1: pigmented, different patterns are evident: uniformly pigmented, labyrinthine, vermiculate, spotted (Heyer, 2005: fig. 13).

Character 11: Dark canthal stripe (modified from Ponssa, 2008, who considered character 11 and 12 a single character). Additive. 0: from tip of snout to eye; 1: from nostril to eye; 2: absent.

Character 12: Dark supratympanic stripe (modified from Ponssa, 2008, who considered character 11 and 12 a single character). Additive. 0: absent; 1: extending only above the tympanum; 2: extending above tympanum and continuing posterolaterally behind tympanum.

Character 13: Dark stripe on the outer surface of the forearm. 0: absent; 1: present (Ponssa et al., 2010: Fig. 12B).

Character 14: Light spot in center of dorsum* 0: absent; 1: present.

Character 15: Post-tympanic gland* 0: unpigmented; 1: pigmented in males.

Character 16: Ventral surfaces of thighs. The variation observed in the thigh pattern has been described previously (Heyer, 1973, 1994, 2005). 0: immaculate or with spots on margins; 1: pigmented, different patterns evident on entire ventral surface of thighs: uniformly pigmented, labyrinthine, vermiculate, spotted.

Character 17: White tubercles on head and/or arms*. 0: absent; 1: present, unevenly distributed (with areas of greater concentration of tubercles and other areas with few or no tubercles); 2: present, evenly distributed (same concentration of tubercles over entire dorsum).

Character 18: Toes. (modified from Ponssa, 2008). Additive. 0: no fringe or web; 1: weak basal fringe and/or web; 2: toes with fringes extending along length of toes except tips; 3: toes webbed.

Character 19: Tubercle in middle of posterior surface of tarsus (surface continuous with sole)*. 0: absent; 1: present.

Character 20: Light interscapular spot*. 0: absent; 1: present.

Character 21: Nuptial excrescences*. 0: absent; 1: thumb with one lateral keratinized spine; 2: thumb with two lateral keratinized spines (Ponssa et al., 2010: fig. 12B); 3: thumb with sandpaper-like nuptial callosities.

Character 22: Snout in lateral view*. 0: truncated; 1: protruding; 2: rounded.

Character 23: Light labial band above dark labial stripe. 0: distinct; 1: indistinct.

Character 24: Male chest spines. Variation of this character was analyzed previously for the *L. pentadactylus* group and, as they are deciduous seasonally, they are characteristic of sexually active males (Heyer, 2005). 0: absent; 1: present.

Character 25: Dorsolateral folds (modified from Heyer, 2005, who considered Characters 11 and 12 a single character). 0: continuous; 1: interrupted.

Character 26: Dorsolateral folds. Additive. 0: extending from eye, not reaching sacrum; 1: extending from eye to sacrum; 2: extending from eye to groin.

Character 27: Interorbital pattern (variation in dorsal patterns was reported in the *L. pentadactylus* group by Heyer, 2005). 0: same as rest of dorsal pattern; 1: with transverse band, chevron, or butterfly-like blotch.

Character 28: Thigh spicules. Distributed over the surface of the thigh but more common around the knee (Heyer, 1978). 0: absent; 1: present.

Character 29: Small, sometimes keratinized spines between fingers of sexually active males. This seasonally deciduous characteristic of sexually active males may not be visible in preserved specimens. 0: absent; 1: present.

Character 30: Dark band on anterior surface of thigh extending dorsally from groin to knee. 0: present, continuous or not; 1: absent.

Character 31: Conspicuous inguinal gland. This glandular area is distinguishable as a lengthened darker area, sometimes delimited by a ridge. 0: absent; 1: present.

Character 32: Spicules on flanks/chest/belly. White, sometimes keratinized spicules, a seasonal deciduous character characteristic of sexually active males. 0: absent; 1: present.

Character 33: Dark glandular area on posterior thigh delimited by a ridge. 0: absent; 1: present.

Character 34: Snout spatulate (either with sharp edge or glandular callosity). This character is associated with the construction of the nuptial chamber with the snout (Philibosian et al., 1974; Prado et al., 2002; Reading and Jofré, 2003; Kokubum and Giaretta, 2005, Ponssa and Barrionuevo, 2012). Additive. 0: absent; 1: present only in males (Ponssa and Barrionuevo, 2012: fig. 2; Angulo and Icochea, 2010: fig. 8); 2: present in females and males.

Character 35: Seasonally deciduous spicules on gular region characteristic of sexually active males. 0: absent; 1: present.

Character 36: Keratinized male tarsal fold. 0: absent; 1: present.

Character 37: Tympanum. 0: visible; 1: not visible.

Character 38: Pseudo-odontoid (hypertrophy of the mandibular symphysis)*, the calcified pseudo-odontoid was described as a fibro-cartilaginous structure in *L. troglodytes,* different from the dense connective tissue of other frogs (Fabrezi and Emerson; 2003; Scott, 2005). 0: absent; 1: present (Sebben et al., 2007: fig. 1).

Character 39: Dentary serrations (Sebben et al., 2007). 0: absent; 1: present (Sebben et al., 2007: fig. 1).

Character 40: Angle between mentomeckelian and angulosplenial. 0: acute angle between anterior tip of angulosplenial relative to a line drawn from anteromedial tip of mentomeckelian element to posteromedial tip of mentomeckelian element; 1: line drawn between anterior tip of angulosplenial is roughly parallel to line drawn from anterior and interior tip off mentomeckelian element to posterior and interior tip of mentomeckelian element.

Character 41: Alary process of premaxilla (similar to Scott's, 2005, character 78, Pramuk's, 2006, character 23, and Grant et al., 2006, character 131). Alary processes of premaxillae directed dorsally or posterodorsally was considered diagnostic for the genus *Leptodactylus* (Lynch, 1971), anterodorsally directed was found in the species of the *Engystomops pustulosus* species group. 0: posterodorsally directed; 1: directed dorsally (Ponssa and Barrionuevo, 2012: figs. 3B, 4); 2: directed anterodorsally.

Character 42: Base of alary process of premaxilla*. 0: narrower than or subequal to the dorsal extreme; 1: broader than the dorsal extreme.

Character 43: Pars facialis of maxilla* 0: ends anterior to palatines; 1: ends at level of palatines; 2: ends posterior to palatines.

Character 44: Pars facialis of maxilla (character similar to Grant et al., 2006, character 134). 0: separated from nasal, without antorbital process (Ponssa et al., 2010: fig. 2); 1: separated from nasal, with a modestly developed antorbital process; 2: contiguous with nasal, with well-developed antorbital process (Ponssa, 2006: fig. 2C); 3: contiguous with nasal, without a differentiated antorbital process; 4: continuous with nasal, with narrow, elongate antorbital process.

Character 45: Terminus of posterior area of the pars facialis of maxilla in lateral or dorsal view. 0: ends gradually; 1: ends abruptly.

Character 46: Pars palatina of premaxilla (similar to Scott's, 2005, character 46). 0: middle portion of shelf (M) equal to or slightly narrower than lateral portion (D) ($M/D < 0.1$); 1: middle portion of shelf (M) obviously narrower than lateral portion (D) ($M/D > 0.1$).

Character 47: Lateral extension of posterior distal pars palatina of premaxilla. 0: short (anterior and posterior distal projections of almost equal length); 1: elongate (noticeable postero-lateral projection of distal surface of pars palatina of premaxilla).

Character 48: Anterior tip of the maxillae. Additive. 0: straight; 1: with a ventrolateral projection that does not reach the base of the alary process of premaxilla; 2: a ventrolateral projection reaching the base of the alary process of premaxilla.

Character 49: Teeth. Extend anteriorly from the level of the anterior rami of pterygoid, whereas posteriorly two conditions are found. 0: not reaching the anterior tip of the quadratojugal; 1: reaching or even surpassing the anterior tip of the quadratojugal.

Character 50: Teeth. 0: absent, 1: present.

Character 51: Articulation of maxilla and quadratojugal (different states from those defined by Pramuk, 2006, and Grant et al., 2006). 0: broadly superimposed; 1: maxilla and quadratojugal hardly superimposed in their tips.

Character 52: Position of tectum nasi relative to alary processes of premaxillae*. Additive. 0: posterior; 1: at same level (Ponssa and Barrionuevo, 2012: fig. 6); 2: anterior.

Character 53: Prenasal process (anterior protrusion of the anterior wall of the septum nasi, similar to Faivovich's, 2002, character 7). 0: absent; 1: present.

Character 54: Tectum nasi and solum nasi*. 0: cartilaginous (Ponssa and Barrionuevo, 2012: fig. 4); 1: ossified (Ponssa and Barrionuevo, 2012: fig. 6B).

Character 55: Relationship between sphenethmoid and nasals in antero-posterior plane*. 0: nasals and sphenethmoid not overlapping; 1: sphenethmoid reaches the posterior edge of the nasals; 2: sphenethmoid reaches half the length of the nasals; 3: sphenethmoid reaches the posterior 2/3 of the nasals; 4: sphenethmoid and septum nasi fused, the relative position of nasals is indistinguishable (Ponssa and Barrionuevo, 2012: fig. 6B).

Character 56: Orbitosphenoid. 0: cartilaginous (Ponssa et al., 2010: fig. 3); 1: mineralized or ossified.

Character 57: Relationship between sphenethmoid and optic foramina. 0: separated (Ponssa et al., 2010: fig. 3); 1: sphenethmoid borders part of the optic foramina.

Character 58: Anterolateral side of prootic (= area bearing crista parotica). Additive. 0: anterolateral side not protruding beyond otic capsule edge; 1: anterolateral side just, but noticeably, extending beyond otic capsule body; 2: anterolateral side extending well beyond otic capsule body.

Character 59: Posterior epiotic eminence prominent or part of overall shape of otic capsule. Lynch (1971) diagnosed *Leptodactylus* as having well-defined epiotic eminences. 0: lacking a posterolateral extension beyond the otic capsule body; 1: extending laterally beyond the otic capsule body.

Character 60: Crista parotica. The crista parotica is located laterally on the otic capsule, connecting the otic capsule to the squamosal (similar to Scott's, 2005, character 67). 0: cartilaginous (Ponssa et al., 2011: fig. 9B); 1: mineralized (Ponssa et al., 2011: fig. 9A).

Character 61: Frontoparietal fontanelle*. 0: not completely covered by frontoparietals; 1: completely covered by frontoparietals.

Character 62: Posterolateral prolongations of frontoparietals*. 0: minimal projection or absent; 1: prominent projection (Ponssa, 2006: fig. 2B).

Character 63: Shape of anterior portion of the frontoparietals*. Additive. 0: gradually expanding towards posterior plane (width of the base of the anterior portion of frontoparietal/width of anterior side of this portion ≥ 0.60 mm); 1: approximately of uniform width (width of the base of the anterior portion of frontoparietal minus width of anterior side of this portion: between -0.60 and -0.60 mm); 2: gradually expanding toward the anterior plane (width of the base of the anterior portion of frontoparietal minus width of anterior side of this portion ≤ -0,60 mm).

Character 64: Nasals*. Additive. 0: separated (Ponssa et al., 2010: fig. 2); 1: adjacent or in contact to each other in the middle or anterior zone of the medial borders (Ponssa et al., 2011: fig. 1A); 2: adjacent or in contact to each other along its medial borders (Ponssa, 2006: fig. 2C).

Character 65: Anterolateral border of nasals*. Additive. 0: deeply concave (anterolateral border of nasals in angle ≤ 130°); 1: approximately or straight (anterior border of nasals in an angle > 130° ≤ 190°); 2: convex (anterior border of nasals in an angle > 190°).

Character 66: Maxillary process of nasals*. 0: weakly differentiated from nasal body; 1: well differentiated from nasal body.

Character 67: Postero-medial angle of nasals*. 0: separated from frontoparietals; 1: adjacent or in contact with frontoparietals (Ponssa, 2006: fig. 2D).

Character 68: Shape of nasals*. 0: triangular; 1: rhomboidal; 2: claw-shaped.

Character 69: Posterior extension of posteromedial border of nasals. 0: absent; 1: present.

Character 70: Posterior border of the nasals. 0: deeply concave: concavity outline < 160°; 1: moderately concave, or even straight: posterior border outline > 160°.

Character 71: Anterior extension of nasals. Anterior apex of nasal forming distinct protuberance. 0: absent; 1: present.

Character 72: Extension of cultriform process of parasphenoid*. 0: between palatines (Ponssa, 2006: fig. 2A); 1: not reaching the palatines.

Character 73: Shape of the cultriform process of parasphenoid (Scott, 2005). 0: rhomboidal or ovoid in shape: middle area expanded; 1: bottle-shaped: edges diverging toward the middle part, from the base and from the middle part continuing almost parallel to each other, the width of this portion less than that of the posterior portion; 2: triangular: base expanded.

Character 74: Alae of parasphenoid (similar to Pramuk's, 2006, character 51). 0: gradually expanded toward the lateral side; 1: uniform width.

Character 75: Position of alae of parasphenoid (similar to Pramuk's, 2006, character 30). 0: oriented posterolaterally; 1: perpendicular to axial axis of skull.

Character 76: Vomerine teeth*. 0: in a straight line; 1: in a shallowly arched series; 2: in a deeply arched series, with the vertex located centrally; 3: in a deeply arched series, with the vertex located toward the lateral side; 4: absent.

Character 77: Orientation of dentigerous processes of vomers. 0: horizontal or almost horizontal: the angle measured between the line crossing both ends of the series of teeth and the maximum deflection < 10.5°; 1: oblique: the angle measured between the line crossing both extremes of the series of teeth and the maximum deflection > 10.5°.

Character 78: Number of vomerine teeth*. Additive. 0: none; 1: 2 to 7; 2: more than 8.

Character 79: Anterior ala of vomers*.0: broad; 1: pointed.

Character 80: Relationships between palatines and vomers* 0: not overlapping; 1: vomers overlap palatines.

Character 81: Anterior ala of vomers. The anterior blunt process of the vomer extends anterolaterally to the premaxilla-maxilla articulation in different degree (similar to Scott's, 2005, character 39 and Pramuk's, 2006, character 10). 0: not reaching premaxillae or maxillae; 1: reaching premaxillae or maxillae (Ponssa and Barrionuevo, 2012: fig. 5).

Character 82: Degree of development of middle ala of vomer. This ala is the prechoanal process, which forms the anterior and medial margin of the aperture nasalis interna. Additive. 0: narrow, without prolongations or serrations; 1: narrow, with anterior convex prolongation or serrated prolongations; 2: robust, with anterior convex prolongation or serrated prolongations.

Character 83: Vomer. 0: wide; 1: narrow.

Character 84: Ridge on the ventral surface of the palatines (similar to Pramuk's, 2006, character 38). Lynch (1971) described the palatines in *Leptodactylus* as "sometimes bearing odontoid ridge." Additive. 0: absent; 1: present, superficial and hardly noticeable; 2: present, prominent and serrated.

Character 85: Palatines. These bones are slender, curved, and posteriorly concave. 0: arched, angle of posterior edge ≤ 165°; 1: slightly arched, angle of posterior edge > 165°.

Character 86: Basal process of middle ramus of pterygoid. The middle ramus of pterygoid abuts against the otic capsule through the basal process. 0: cartilaginous; 1: bony.

Character 87: Pterygoid. The anterior extension of the anterior ramus of pterygoid (character 49 of Scott, 2005). 0: not reaching the palatines; 1: contacting the palatines.

Character 88: Overlap between pterygoid and parasphenoid in antero-posterior plane. Lynch (1971) used this character in his diagnosis of *Leptodactylus*. 0: no overlap (present); 1: overlapping (present).

Character 89: Length of posterior ramus of pterygoid relative to medial ramus. Additive. 0: posterior ramus almost twice length of medial ramus; 1: posterior ramus slightly longer or equal to medial ramus; 2: posterior ramus shorter than medial ramus.

Character 90: Otic ramus of squamosal*. Additive. 0: not contacting crista parotica; 1: just reaching border of crista parotica; 2: overlapping crista parotica (Ponssa et al., 2011: fig. 9).

Character 91: Skull proportions. 0: wider than long: skull width (maximum distance between both sides of the maxillary arch)/maximum length of skull (from the right occipital condyle to the tip of the premaxilla on the same side) > 1.1; 1: almost equal in width and length or longer than wide: skull width/skull length < 1.1.

Character 92: Hyoid plate. 0: anteriorly broadened, margin gradually diverging anteriorly; 1: margins parallel or slightly convergent to each other anteriorly.

Character 93: Alary process of hyoid*. 0: narrow, stalk-like; 1: broad based; 2: wing-like.

Character 94: Anteromedial process of hyoid (similar to Scott's, 2005, character 83, Nuin and Oliveira Filho's, 2005, character 29, and Grant et al.'s, 2006, character 117). 0: absent; 1: present (Ponssa et al., 2010:4).

Character 95: Hyoid plate proportions (similar to Scott's, 2005, character 91). Additive. 0: longer than wide: width (distance between mid-point of both lateral margins)/length (distance between mid-point of anterior and posterior margins) ≤ 0; 1: slightly wider than long: width/length between 0 and 2; 2: conspicuously wider than long: width/length > 2.

Character 96: Depth of hyoglossal sinus (similar to Scott's, 2005, character 88). Additive. 0: hyoglossal sinus posteriorly not reaching level of anterior borders of alary processes; 1: hyoglossal sinus posteriorly extending to level of or immediately posterior to anterior borders of alary processes; 2: deep, hyoglossal sinus extending posteriorly to a distance of 2 mm from the anterior borders of alary processes; 3: very deep, hyoglossal sinus extending posteriorly to a distance greater than 2 mm to anterior borders of the alary processes.

Character 97: Tip of posterolateral process of hyoid*. 0: acute; 1: rounded dilatation; 2: expanded, ending with concavity oriented posteriorly or medially, pincer-shaped.

Character 98: Posteromedial process (thyrohyal) of hyoid (similar to Scott's, 2005, character 97). 0: distal end expanded; 1: uniform width throughout length.

Character 99: Arytenoids. The arytenoids consist of a pair of valve-shaped cartilages, triangular in lateral view. 0: with medially oriented swelling in the inferior side of the "triangle"; 1: without swelling in the inferior side of the "triangle."

Character 100: Sexual dimorphism in size of cricoid + arytenoid. Additive. 0: present, male structures moderately larger than female; 1: present, male structures larger than female, such that opening of posteromedial process is wider in males; 2: present, male structures noticeable larger than female, such that posteromedial process is curved in males.

Character 101: Cotylar arrangement (Lynch, 1971). 0: type I; 1: type II.

Character 102: Neural spine of vertebrae I-V*. Additive. 0: absent; 1: not imbricated; 2: imbricated.

Character 103: Anterior prolongations or ridges in anterior margins of the apophysis of the second vertebrae. 0: absent; 1: present.

Character 104: Position of occipital condyles relative to line drawn between posterior-most points of skull. This line can be drawn through either squamosals or maxillae, depending on which element is further posterior. 0: bases of occipital condyles posterior to line; 1: bases of occipital condyles anterior to or at same level as line.

Character 105: Number of the prepollical segments (Fabrezi, 2001; Scott 2005). Additive. 0: base + 3 segments; 1: base + 2 segments; 2: base + 1 segment.

Character 106: Number of carpal elements*. 0: five; 1: six.

Character 107: Humeral crest in males (modified from Ponssa, 2008). Lynch (1971) noted that the development of humeral flange is uncommon in leptodactylid, and is most pronounced in *Leptodactylus*. Additive. 0: crista medialis well developed, constituting a large crest along length of humerus (Lynch, 1971: fig. 41B); 1: crista medialis moderately developed, present only on distal half or two-thirds of humerus (Ponssa et al., 2010: fig. 13A); 2: crista medialis absent.

Character 108: Femur: tibiafibula ratio. 0: tibiafibula larger than femur: femur/tibiafibula ≤ 0.95; 1: tibiafibula approximately equal length to femur: > 0.95.

Character 109: Terminal phalanges*. 0: rounded or knobbed; 1: rounded and bifurcate: dilated with a split that defines two lobules; 2: T-shaped (Ponssa et al., 2010: fig. 13B).

Character 110: Mesosternum. This character refers to the anterior portion of the mesosternum, which is expanded, triangular, and two conditions are observed. 0: undivided; 1: divided.

Character 111: Area of junction between scapula and coracoid. 0: cartilaginous; 1: mineralized; 2: both elements contiguous, junction being bone-to-bone.

Character 112: Sesamoid in the lateral surface of each sacral diapophysis, in the area of iliosacral articulation. 0: absent; 1: present.

Character 113: Fusion of suprarostral corpus and ala. 0: not fused; 1: fused dorsal only; 2: fused ventrally only; 3: fused dorsally and ventrally.

Character 114: Contact between the suprarostral corpora. 0: contact along nearly entire length; 1: narrowly separated; 2: widely separated.

Character 115: Length of cornua trabeculae relative to chondrocranial length. 0: 25%; 1: 20%; 2: 10–15%.

Character 116: Planum trabeculare anticum. 0: wide; 1: narrow.

Character 117: Frontoparietal fenestra in tadpoles. 0: open; 1: posterior half closed.

Character 118: Otic capsules. 0: than 30% of chondrocranial length; 1: 30% of chondrocranial length.

Character 119: Processus anterolateralis of crista parotica. 0: small and triangular; 1: large and triangular; 2: long finger-like projection; 3: large and rectangular; 4: absent.

Character 120: Projection of posterolateral curvature of palatoquadrate. 0: absent; 1: present.

Character 121: Processus posterolateralis of crista parotica. 0: distinct; 1: reduced.

Character 122: Attachment of the processus ascendens. 0: low; 1: intermediate.

Character 123: Processus pseudopterygoideus. 0: absent; 1: present.

Character 124: Pars articularis quadrati. 0: distinct from processus muscularis; 1: indistinct from the muscularis.

Character 125: Processus muscularis. 0: large; 1: small.

Character 126: Commissura quadratoorbitalis. 0: absent; 1: present.

Character 127: Infrarostral cartilages. 0: large, anteriorly notched; 1: small, notched anteriorly; 2: small, thick, rounded anteriorly; 3: small, slender, anteriorly notched.

Character 128: Anterior process of hypobranchial plate. 0: absent; 1: present.

Character 129: Processus branchialis. 0: open; 1: closed.

Character 130: Hyoquadrate process. 0: small, triangular; 1: large, rounded.

Character 131: Female call. Emerson and Boyd (1999) estimated that the female mating vocalization is more common than originally assumed; therefore, they proposed that the calls of female frogs might have evolved by co-opting the pre-existing advertisement calling pathway common to both sexes, an adaptation for mate location that is present in most species. Lescure (1979) reported that the magnitude of the difference between the call of both sexes in *L. fallax* is bigger than the difference between this species and *Leptodactylus pentadactylus*. In *L. troglodytes* was described a reciprocation call (Kokubum et al., 2009), this kind of call is not initiated by the females, but rather they respond vocally to the call of males (Schlaepfer and Figeroa-Sandí, 1998). 0: absent; 1: present.

Character 132: Aggressive call. This call can be displayed in different situations, e.g., as part of territorial interaction (Kokubum et al., 2005), or of parental care (Vaz-Ferreira and Gerhau, 1975; Vaira, 1997; Ponssa, 2000). 0: absent; 1: present.

Character 133: Calling site. 0: water; 1: rocks; 2: open ground; 3: land, among vegetation; 4: basin; 5: subterranean chamber; 6: land from branches or trunks of trees.

Character 134: Amplexus site. 0: water; 1: on ground; 2: basin; 3: subterranean chamber.

Character 135: Oviposition site. 0: lotic water, river or streams; 1: lentic water, pond or marsh; 2: on ground; 3: natural depressions; 4: constructed depressions; 5: incubation chambers.

Character 136: Shape of incubation chamber (Giaretta and Kokubum, 2004: fig. 6; Oliveira Filho and Giaretta, 2009: figs. 1–6). 0: spherical; 1: elliptical; 2: pyriform; 3: ovoid.

Character 137: Tunnel to access incubation chamber. 0: absent; 1: present.

Character 138: Covering of incubation chamber. 0: open; 1: closed.

Character 139: Incubation chambers connected by additional gallery or constriction. 0: absent, only one chamber; 1: present, more than one chamber (Arzabé and Prado, 2006: fig. 1).

Character 140: Sex that build burrow or chamber. Most commonly constructed by males, in some *Leptodactylus* both males and females participate in chamber construction (Cei, 1949; Martins, 1988; Oliveira Filho et al., 2005; da Silva et al., 2005; Arzabe and Prado 2006; Lucas et al., 2008:9). 0: male; 1: both sexes participate at different times in construction of the chamber.

Character 141: Body part used in the construction of the burrow or chamber. Emerson (1976) proposed two patterns of burrowing in frogs: (1) hind limb-first digging, and (2) headfirst digging. She stated that anurans use both their head and hind limbs when burrowing. Although in the generalized characterization of the *L. fuscus* group of the genus has been considered that the incubation chamber is built with the snout, some species have been observed using both snout and hind limbs during the excavation (e.g., *L. natalensis, L. bufonius, L. labyrinthicus;* Philibosian et al., 1974; Pisanó et al., 1993; Santos and Amorim, 2005; da Silva et al., 2005). 0: snout; 1: hind limbs; 2: both snout and hind limbs are used in different moments of the construction of the burrow or chamber.

Character 142: Timing of chamber construction. 0: prior to pair formation; 1: following pair formation.

Character 143: Egg pigmentation. 0: not pigmented, yellow; 1: pigmented, grey or black.

Character 144: Larvae. 0: exotrophic; 1: endotrophic.

Character 145: Parental care. Additive. The term "parental care" was introduced by Trivers (1972), who defined it as any investment by the parents to a particular offspring that increases the survival probability of this offspring and, hence, reproductive success, at the expense of the capacity of the parent to invest in other offspring. Many authors have analyzed the behavior patterns associated with this term, such as the relationship between external or internal fertilization and parental care by males and/or females and the advantages or disadvantage to the parents and offspring (Gross and Shine, 1981; Gross and Sargent, 1985; Simon, 1983; Smith, 1977; Townsend et al., 1984; Wells, 1977; Wittenberger, 1981). 0: absent; 1: present, care of nest; 2: present, care of nest and larvae.

Character 146: Sex of parent that provides parental care. 0: male; 1: female; 2: both sexes participate simultaneously in parental care.

Character 147: Aggressive behavior associated with parental care. The functions of parental care include aeration of aquatic eggs, manipulations and/or moistening of terrestrial eggs, removal of dead or infected eggs, and protection against predators (summary in Duellman and Trueb, 1986). Thus, as part of this last function, aggressive behavior directed toward potential predators has been reported in some species (Ponssa, 2001; Vaz-Ferreira and Gehrau, 1975; Vaira, 1987). 0: absent; 1: present.

Character 148: Mode of communication between parent and the larvae during parental care. 0: pumping movements (physical and/or chemical communication between the adult and the aquatic larvae), 1: low-frequency vocalizations.

Character 149: Foam-generating behavior by larvae. *Leptodactylus* tadpoles produce foam quite similar in all the species described, involving the release of bubbles through the mouth while the tadpoles wriggle up to the foam surface (Kokubum and Giaretta, 2005). Some species of the genus start reproducing early in the wet season, when temporary water bodies are still dry. As such, the foam generated by tadpoles is important to avoid desiccation when dry season lasts longer (Caldwell and Lopez, 1989; Downie, 1984, 1990; Downie and Smith, 2003; Ponssa and Barrionuevo, 2008). 0: absent; 1: present (Downie, 1984: fig. 1; Ponssa and Barrionuevo, 2008: fig. 8).

Character 150: Trophic eggs. Anuran eggs may represent an important food item for tadpoles (Hero and Galatti, 1990; Magnusson and Hero, 1991; Prado et al., 2005; da Silva and Giaretta, 2008). Thus, this predatory behavior may represent a strategy to occupy low-productive habitats (Heyer et al., 1975; Petranka and Kennedy, 1999) or opportunistically use an abundant and nutritive food source (da Silva et al., 2005). The tadpole can prey on con- or heterospecific eggs and even small larvae (Shepard and Caldwell, 2005). In *L. labyrinthicus,* females do not return to nests to resupply them with unfertilized eggs; the nests are provisioned with eggs only at the time of oviposition (Shepard and Caldwell, 2005; da Silva and Giaretta, 2008). In contrast, *L. fallax* females return to the nest to deposit trophic eggs (Gibson and Buley, 2004). 0: absent; 1: present.

Character 151: Territoriality. 0: absent; 1: present.

Character 152: Aggressive behavior between males. 0: absent; 1: present (da Silva et al., 2005: fig. 6).

Character 153: Multi-male spawning. As well in *Leptodactylus,* the multiple spawning is reported in other foam nest-building rhacophorids, such as *Chiromantis xerampelina* (Jennions et al., 1992), *Polypedates leucomystax* (Feng and Narins, 1991), *Rhacophorus schlegelii* (Fukuyama, 1991). Furthermore, simultaneous polyandry is phylogenetically widespread among frog families, which exhibit different reproductive modes, and reproductive activity patterns, suggesting convergent evolution (Prado and Haddad, 2003). 0: absent; 1: present (Prado and Haddad, 2003: figs. 1, 2).

Character 154: Site where tadpoles complete development. 0: lentic water, ponds or marshes; 1: lotic water, streams or watercourses; 2: basin or incubation chamber.

Character 155: Seismic signals. Anurans possess a structurally unique saccule, providing them with seismic sensitivity greater than that observed in any other terrestrial vertebrates. The species of *Leptodactylus,* where this character has been reported, produce thumps or impulsive seismic signals simultaneously with their advertisement calls. The signals have sufficient amplitude to be sensed by the frog's saccule. This evidence suggests that these frogs might use the seismic channel in intraspecific communication, probably as an alternative to the airborne channel (Lewis et al., 2001). 0: absent; 1: present.

APPENDIX 3. SPECIES EXAMINED FOR MORPHOLOGICAL DATA COLLECTION

Below we list the specimens examined for morphological data. Asterisks (*) indicate cleared and double stained specimens or dry-skeleton preparations; a superscript "r" (^{r}) denotes X-rayed specimens.

Adenomera andreae: MCZ 93762, 109841, 111698, 111699, 111703; QCAZ 6189, 6209*, 6192*; USNM 247992*, 247289*; MZUSP 129677, 129694–129695, 129698.

Adenomera hylaedactylus: AMNH 100634, 167127; MCZ 85707, 85792, 93766, 93770, 93773, 96789; MNRJ 31203–31204; MZUSP 13258, 27770, 27786, 31203–31204*, 61437, 69548, 69556, 82278.

Adenomera lutzi: USNM 546152.

Adenomera marmoratus: MNRJ 28282–28283, 28287, 28289; MZUSP 24304–24305, 24307, 24309, 28289*, 63549– 63552*; MCZ 11689, 12900–12901, 15582, 15584; USNM 247586*, 292478–292480*.

Adenomera martinezi: AMNH 158106; MCZ 100140; USNM 200619–200621.

Lithodytes lineatus: MCZ 7608–7609; MZUSP 13431*–13432, 63094*; QCAZ 5735, 6046, 6058*,10815*; USNM 196824*, 216795–216797, 291081, 99908, 227602*, 227606*.

Engystomops pustulosus: FML 12175–12178, 12179–12183*.

Paratelmatobius lutzi: KU 92981*, MCZ 64345; USNM 207948, 207950, 207952–207956, 523810–525811.

Leptodactylus albilabris: AMNH 20958, 20952, 20963, 34405, 34408, 52654– 52656, 95698, 95708; MZUSP 23999; USNM 192332*, 221219*, 221094*, 221674–221681*.

Leptodactylus bolivianus: USNM 202438, 202446, 219764*, 227571*, 298939*, 317995*; MZUSP 65784, 66319.

Leptodactylus bufonius (Boulenger, 1894): FML 589*, 672* (6 specimens), 1921, 3568 (2 specimens)*, 3890* (2 specimens), 4366 (2 specimens)*, 4366 (9 specimens), 4410, 4908 (7 specimens)*, 5309, 5362, 5364, 5367, 12126, 12128–12144, 12155, 9779–09792*; MZUSP 65016*.

Leptodactylus camaquara: MZUSP 56838–56840, 56843–56845, 73693, 74229, 74248–74249, 74291–74296, 56759*, 56841–56842*; MCZ 100140; USNM 217647, 218140, 218136, 218134–218135, 218139.

Leptodactylus caatingae: USNM 547844^{r}–547845^{r}.

Leptodactylus chaquensis: FML 12127, 12156–12157, 12201–12204, 12097–12101*.

Leptodactylus colombiensis: MCZ 16277, 96975–96976, 96979–96980; USNM 148800–148802, 148804*, 148806*, 148808*, 148810–148811*, 148813*, 148815.

Leptodactylus cunicularis: MCZ 100141; MZUSP 56756, 73685, 74179–74184, 74223–74225, 74228, 74270–74271, 74273, 86578, 56756–56757*, 58030*, 76443*; USNM 218145–218146, 218150–218151, 218153.

Leptodactylus didymus: MZUSP 68986–68987, 68989–68990, 68988*, 68991*; USNM 314910*, 314911–314914.

Leptodactylus diedrus: AMNH 115695; MZUSP 24008, 24857, 24861; USNM 307106.

Leptodactylus discodactylus: QCAZ 14932*, 14933–14934; MCZ 90385, 94884–94885; USNM 196877*.

Leptodactylus elenae: FML 1274, 9326, 09590–09591, 11913–11917*, 11954–11955*, 11956*, 12113–12118*, 12161–12163, 12674–12676, 12677–12680, 12681–12684, 12113–12117*, 13737.

Leptodactylus fallax: AMNH 76218–76219*, 76220, 03793, 76221; MCZ 2182, 19711, 81149, 81153–81154; USNM 162244.

Leptodactylus flavopictus: USNM 24105, 24119, MZUSP 24105*, 24119*.

Leptodactylus fragilis: MCZ 24974–24976, 24982–24983; MZUSP 56607–56608, 58851–58853, FML 12317*, 12721–12728*; USNM 227574–257575*.

Leptodactylus furnarius: MCZ 15849, 22951–22952, 22955–22956; MZUSP 09034, 11328, 00130, 13516, 24136, 24138–24139, 25467, 04275, 58019, 70453, 73678, 74226–74227, 74230–74231, 74297–74300, 74330–74331, 74415, 81974, 82466, 82948, 82973, 82467*, 83271*.

Leptodactylus fuscus: FML 4788*, 4790*, 9581, 9583–09589, 12151–12154, 12237–12239, 04788*, 11939–11948*, 11961–11962*, 12349–12354*; MACN 08316–8, 08739, 09752–09756, 13422–3, 18887–902, 22364, 26787, 26949, 29792, 32307–10, 34710, 34965–34968; MCZ 7637, 30030–30031; MZUSP 12511, 14906, 16917–16999, 21596–21597, 21849–21853, 21874, 22711–22713, 2294, 2440–2442, 24627, 24628–24646, 24670–24671, 24973–24974, 25160–25161, 25277–25281, 25340–25342, 25496, 28552, 35805, 04606–12; 04614–15; 04617–26, 04993, 51965–51969, 51999, 52106, 52351, 52375–52377, 52427, 52545, 52488, 54128–54135, 54752, 56541–56542, 56543–56578, 57461–57465, 58377–58378, 58456–58457, 58836, 59440, 59876, 59968–59972, 60368, 60495, 60548–60549, 60871–60872, 61022–61023, 61051, 62106–62109, 62226–62228, 63070–63071, 63074, 65061–65094, 65295–65296, 65439, 65493–65494, 65587, 65627–65636, 65673–65674, 65746, 65806, 65824–65832, 66009–66012, 66540, 66700, 66735, 66833, 67273–67274, 67533, 68797–68798, 68799–68804, 69664, 69861–69867, 69954–69956, 70074, 70493, 70914–70916, 71105, 71531, 71791, 72463, 72577, 07512–07513, 9035–9037, 52405*, 52395*, 66042*.

Leptodactylus gracilis: FML 4784 (2 specimens), 2984*, 11949–11953*, 12259; MACN 00072 (2 specimens), 00223, 13108–9, 17369, 24019, 24238, 24448–51, 25156, 25488, 25679–25711, 29783, 29860, 32053, 32058–32059, 32790, 32939, 33828–29, 34120–121, 35537, 8312–15; MZUSP 22640–22641, 22926, 56589, 56591, 57543, 57889.

Leptodactylus griseigularis: MCZ 196021, 196023–196024; USNM 196021*, 196023*, 196024.

Leptodactylus insularum: MZUSP 150749*; USNM 53984*, 150743*, 150749*.

Leptodactylus jolyi: MZUSP 42621, 73726, 74100–74108, 74255, 74265, 47621*; USNM 210831.

Leptodactylus knudseni: MCZ 22821–22822, 44560; MZUSP 15907, 25169, 53743–53744, 54667, 60404, 61556, 71187, 80655–80659, 80661–80662, 80869, 87667, 106690; USNM 193875*, 193881*, 290870*, 193875*, 193881*.

Leptodactylus labialis: FML 12317, 12721–12728*; MCZ 50707, 89759, 93257; USNM 227574–227575*.

Leptodactylus labrosus: AMNH 07549, 07550, 71024, 16241, 16206; MCZ 5269–5270, 5272–5173, 5281, 5284, 94889, 95639–95640. MZUSP 56373–6375, 76619–76620, 76939–76940, 82987, 76937–76938*; USNM 227578*.

Leptodactylus labyrinthicus: FML 00740, 00742, 00825 (4 specimens), 00829 (4 specimens), 00830, 00943, 02220–02201, 04376, 06720, 09669–09670; MCZ 28290; MLP A577*; MNRJ 30726*; MZUSP 5987, 56605, 58016, 4461, 19812, 54753–54754, 129286, 52286, 25951, 56398, 50187.

Leptodactylus latinasus: FML 1429*, 2410/1–2410/3*, 2410–5*, 2410–7*, 2410/9–2410/10*, 3539*, 3886 (2 specimens)*, 3891*, 4808, 6284*, 8583*, 11900*, 11901*, 11902*, 11909*, 11910–11912*, 12041–12061, 12166–12171, 12184–12196, 12205–12210, 12212–12214, 12240–12247, 12255–12258, 12260, 12316*; MACN 6280–6285*; MCZ 28426, 28427.

Leptodactylus laticeps: USNM 227605*, 253711*–253712*.

Leptodactylus latrans: MACN 29425–7, 299430, 29568, 29570–2, 20247–50, L 309, L314–315.

Leptodactylus lauramiriamae: CHUNB 11921; MZUSP 132773, MZUSP uncataloged specimens [LTT 39, 95, 101, 103, 105, and T 01]; USNM 509521^{r}.

Leptodactylus leptodactyloides: MCZ 75022–75023, 90819, 90831, 90834; USNM 227602*, 227606*, 247372*, 247380–247381*, 247382, 247393, 247409*; MZUSP 40432, 40434, 40442.

Leptodactylus lithonaetes: USNM 216795^{r}–216797^{r}.

Leptodactylus longirostris: AMNH 23168, 90318, 133838, 118789, 118788; MCZ 97301–97302, 97304–97305; MZUSP 15869–15870, 24880, 28401–28404, 4470936, 53975–53979, 59023, 62537, 63777–63781, 59024–59025*, 65779*, 65792–65793*.

Leptodactylus macrosternum: MNRJ 26191; MZUSP 29972*, 32258*.

Leptodactylus magistris: USNM 216804^{r}.

Leptodactylus marambaie: MNRJ 3932, 20088, 26144*.

Leptodactylus melanonotus: AMNH AK708, 64402, 283471, 283477, 283491, 283495, 283519; MCZ 29220, 96639, 44310, 29218–29229; USNM 114232–114233, 114264, 114266–114267, 227580*–227585*, 227590*–227594*, 319201*.

Leptodactylus myersi: AMNH 128021, 18515; USNM 302066*; MZUSP 54114.

Leptodactylus mystaceus: AMNH 166393, 166390, 166387, 166392, 18415, 93175, 39658, 39593; MCZ 56309, 56312, 92357, 92365, 97874, 111178, 124844; MZUSP 01358, 21835, 21876, 23492, 24941, 24946, 25005, 25014, 25029, 25347–25348, 25493–25494, 28400, 29937, 36837, 36886, 37919, 50549, 52000, 56062, 56069–56074, 56609, 57353–57356, 57996, 58219–58222, 58251, 60076, 60128, 60130–60131, 60158–60159, 60369, 61144, 62555, 63089–63090, 63355, 63827, 64220–64248, 65522–65526, 65644, 65696, 65702, 65734, 65737, 65814, 65939, 68191–68199, 68737, 69329–69330, 69755, 70002, 70366–70369, 70370–70372, 71535–71542, 72155–72159, 63431, 56065–56068*, 60158–60159*, 65676*, 65696*, 65702*, 70336–70337*; QCAZ 379*, 8960; USNM 227570*.

Leptodactylus cf. *mystaceus:* MZUSP 63292–63293.

Leptodactylus mystacinus: FML 1272 (3 specimens)–1273 (2 specimens), 1473 (3 specimens), 2188 (3 specimens), 2356 (2 specimens), 3529 (2 specimens), 3661*, 3890*, 3883*, 4806 (4 specimens), 5709 (2 specimens), 9708–9710, 9582, 12236, 12266–12267*, 12314–12316*, 12343–12347*; MACN 00087, 00179, 03280, 06913, 09495, 12231–12232, 12314, 13111, 18316, 19273 (2 specimens), 19440–41, 20055, 20995, 23704–709, 24219–24020, 24226–24232, 25175–25176, 26388–391, 27589–90, 29585, 29591, 30274–30275, 32258, 35111, 36675, 37028, 36093, MZUSP 14907, 15800, 15877, 16048–16049, 21688–21689, 22640–22641, 24155, 25069, 25423–25426, 25456, 25478, 27307–27308, 50220, 53034–53035, 53203–53215, 63292–63293, 64755, 07132, 71543, 08694–08696, MZUSP 53033*, 65236*.

Leptodactylus natalensis: MNRJ 27929*, 27888*, 34987–34988; MZUSP 37853, 37877, 63103–63104.

Leptodactylus nesiotus: USNM 558321–558322*.

Leptodactylus notoaktites: MZUSP 00459, 10378, 24149–24150, 25420, 25428, 55927–55930*; USNM 217791–217792, 217795, 303189, 303192.

Leptodactylus paraensis: USNM 523765, 559809^{r}, 523765^{r}, 313875.

Leptodactylus pascoensis: USNM 40664^{r}.

Leptodactylus pentadactylus: AMNH 42888*, MCZ 57944, 57949, 96857, 97262, 116664; MZUSP 56779, 64253, 127572, 106102, 58437, 38956, 129673, 98326, 128241, 128243, 86210–86211, 100955, 87966–87967, 98633, 83182, 22126; USNM 539175*, 539395*.

Leptodactylus peritoaktites: USNM 196739^{r}–196740, 285391^{r}.

Leptodactylus petersii: MCZ 96209, 85777, 90822, 93781, 112256, 136406; MZUSP 69036*, 71546*, 71563.

Leptodactylus plaumanni: FML 9341*, 9345*, 11957*, 12112*; MACN 2837, 30155, 33057, 5778, 5793, 5816, 5860, 6188, 6221, 06274, 06283, 06288, 06316, 06353, 06780.

Leptodactylus podicipinus: FML 3577 (7 specimens)*, 3577/1–5, 10, 12, FML 4312 (three specimens*), 4312(4 specimens)/48, 71: Laguna - km 1141 - Ruta Nacional 95, Cte. Fernandez, Chaco, Argentina; FML 760/1, 2*, 3–4, 6–8, 9*, 10, 13, 19: Isla Antequera-Resistencia, San Fernando, Chaco, Argentina; ZUFM 478/1*, 478/2–5, 467/1–2*, 4*, 467/3, 5: Base de Estudos do Pantanal-BEP-, Fazenda Corumba, Mato Grosso do Sul, Brazil; 760–2, 760–9, 12198–12200; ZUFM 470/1–5: Fazenda Nhumirim, Corumba, Mato Grosso do Sul, Brazil; ZUFM 421/1–3; Passo do Lontra, Corumba, Mato Grosso do Sul, Brazil; ZUFM 243/1–2: 4u ponte, Corixa˜ o, MS-184, Abobral, Corumba´, Mato Grosso do Sul, Brazil; IIBP-H 403, 405*, 406, 415, 420: Distrito Emboscada, Cabaña Las Marías, Cerro Vy, Cordillera, Paraguay. IIBP-H 259–260: Costa del Río, Pilar, Ñeembucú, Paraguay; IIBP-H 278*, 284, 286, 293*, 342, 347, 350, 359: Estancia San José, Ñeembucú, Paraguay; ZUFM 467–1–0467–2*, 467–4*, 478–2*.

Leptodactylus poecilochilus: AMNH 88742, 88741, 18931, 41022, 18931, 18946; KNHM 32353*, 32369*; MZC 9161, 10036, 24880, 89585, 89586; MZUSP 83277; USNM 227600–227601*.

Leptodactylus pustulatus: MCZ 373; MNRJ 23839–23840; MZUSP 23839*, 83775, 83794.

Leptodactylus rhodomerus: USNM 109148–109149.

Leptodactylus rhodomystax: MNRJ 4560–4561; USNM 531567–531568*, 539176*; MZUSP 70373–70374, 64255, 83305, 88197, 75606, 85169, 76339, 111253, 8463, 70966, 60088–63091, 70864, 69532, 64255; USNM 311568*, 531567*, 539176*, 1568*, 531567*.

Leptodactylus rhodonotus: AMNH 6129, 42311, 42874, 91927, 133792; MCZ 4780, 4789, 118049, 136356; USNM 196003–196005*, 196998–196009*.

Leptodactylus riveroi: AMNH131119–131120*, 131091*; MCZ 65966; MZUSP 60340*.

Leptodactylus rugosus: AMNH 18884, 133789, 133788, 133786, 133793, 133795*,18887, 133796; MCZ 6960.

Leptodactylus sabanensis: AMNH 39753.

Leptodactylus savagei: AMNH A6972*, AMNH 40435*; MCZ 9169, 21259, 29134, 96080; USNM 227599*, 297785*.

Leptodactylus silvanimbus: USNM 226386*.

Leptodactylus spixi: MCZ 1298; MZUSP 00834, 01295, 58679, 63755, 63669–63671*; 47066.

Leptodactylus stenodema: AMNH 39753, 42379, 71023, 90835*, 90836, 93704; MZUSP 60160.

Leptodactylus syphax: MNRJ 26191*, 34313*, 35558, 25968, 26197, 26189, 4562, 26191*, 34313*; MZUSP 71805*–71806, 71812*, 71808, 66693, 71575, 73851, 71802; USNM 71805*, 71812*.

Leptodactylus tapiti: CHUNB 49535*, 49537*, 49539*, 49543*.

Leptodactylus troglodytes: MCZ 100146; MZUSP 10715, 13589, 20441–20442, 24694, 25017, 38167, 38278, 51771–51772, 51775, 51961–51962, 51997–51998, 52268–52272, 52276–52279, 54760, 57578, 60370, 61998, 63064, 63080–63082, 63119, 69839, 70478, 71017–71020, 51963*, 52273–52275*, 65341*.

L. turimiquensis: AMNH 70667, 70668.

Leptodactylus validus: MCZ 2968, 11777, 31555, 71920–71921, 71940; MZUSP 25725, 24744; USNM 14566*, 192762*, 197494*, 319191*.

Leptodactylus ventrimaculatus: MCZ 91220, 98191, 104469, 106989; MZUSP 77040–77042, 56776*; QCAZ 750*, 1308, 3977; USNM 121300, 167494–167496, 192762, 196765*, 216080, 524082–524083*, 524085–524087, 524091, 524096, 534010.

Leptodactylus viridis: USNM 501176^{r}.

Leptodactylus wagneri: MCZ 56397, 56431, 75021, 88303, 119097; MZUSP 36192–36193*, 36224*; USNM 283836*, 283838*, 283839, 283845–283446*, 283858*, 283870–283871*, 283873*.

PLATES

Plate 1. *Leptodactylus fuscus* species group. **(A)** *Leptodactylus albilabris* (S.B. Hedges). **(B)** *L. bufonius* (R.A. Brandão). **(C)** *L. caatingae* (R.O. de Sá). **(D)** *L. camaquara* (I. Sazima). **(E)** *L. cunicularius* (C.F.B. Haddad). **(F)** *L. cupreus* (J.L.R. Gasparini).

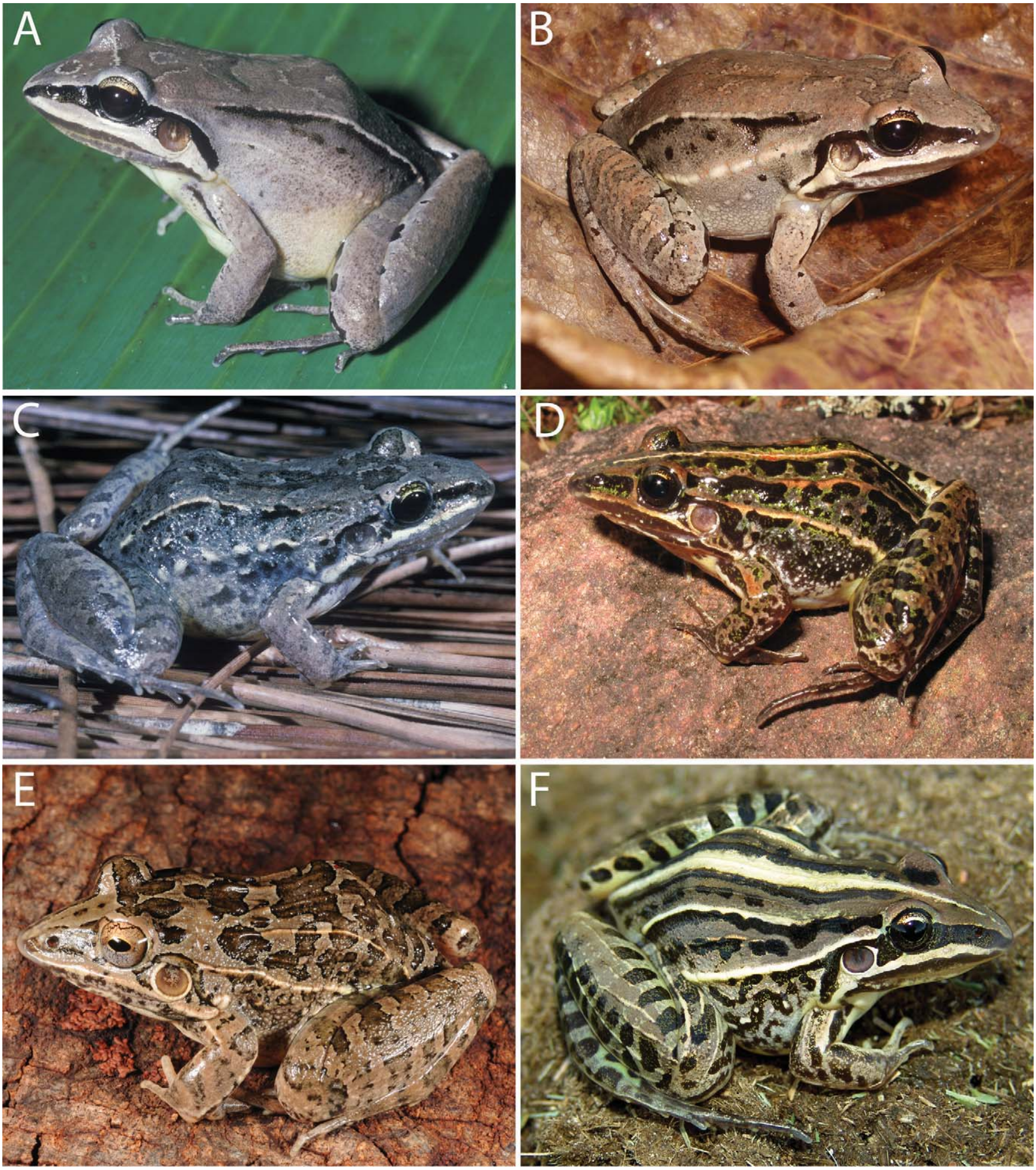

Plate 2. *Leptodactylus fuscus* species group. **(A)** *Leptodactylus didymus* (R.W. McDiarmid). **(B)** *L. elenae* (A. Pansonato). **(C)** *L. fragilis* (J.R. McCranie). **(D)** *L. furnarius* (C.F.B. Haddad). **(E)** *L. fuscus* (J.P. Pombal Jr.). **(F)** *L. gracilis* (D. Loebmann).

Plate 3. *Leptodactylus fuscus* species group. **(A)** *Leptodactylus jolyi* (J.P. Pombal Jr.). **(B)** *L. labrosus* (C. Koch). **(C)** *L. laticeps* (E.O. Lavilla). **(D)** *L. latinasus* (R. Maneyro) **(E)** *L. longirostris* (A. Garda). **(F)** *L. marambaiae* (M. Franco).

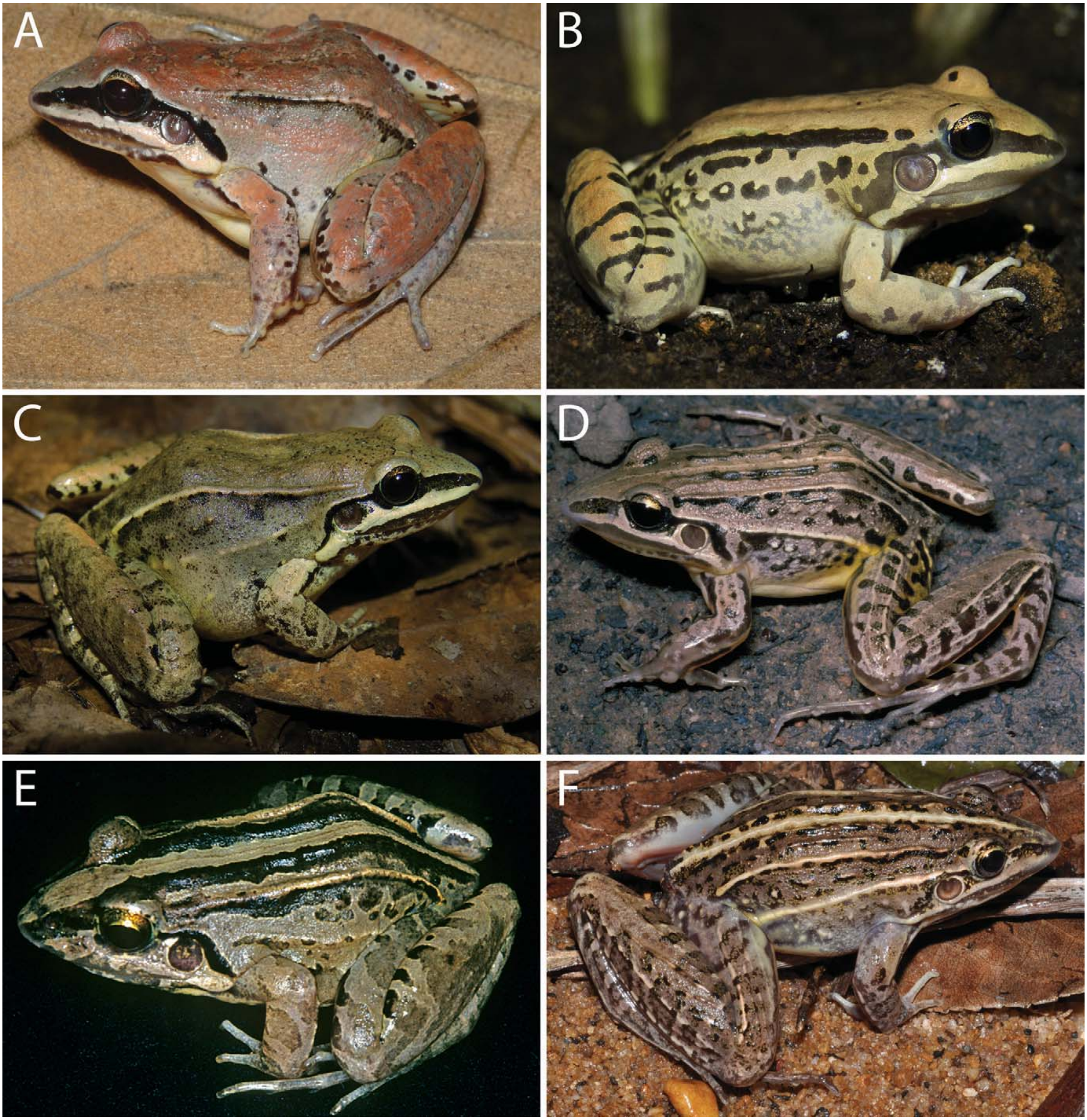

Plate 4. *Leptodactylus fuscus* species group. **(A)** *Leptodactylus mystaceus* (C.F.B. Haddad). **(B)** *L. mystacinus* (D. Loebmann). **(C)** *L. notoaktites* (D. Loebmann). **(D)** *L. plaumanni* (A.J. Cardoso) **(E)** *L. poecilochilus* (W.E. Duellman). **(F)** *L. sertanejo* (A. Giaretta).

Plate 5. *Leptodactylus fuscus* (A–E) and *L. pentadactylus* **(F)** species groups. Plate 5. **(A)** *Leptodactylus spixi* (J.L.R. Gasparini). **(B)** *L. syphax* (R.A. Brandão). **(C)** *L. tapiti* (R.A. Brandão). **(D)** *L. troglodytes* (R.O. de Sá) **(E)** *L. ventrimaculatus* (L. Coloma). **(F)** *L. fallax* (S.B. Hedges).

Plate 6. *Leptodactylus pentadactylus* species group. **(A)** *Leptodactylus flavopictus* (J.P. Pombal Jr.). **(B)** *L. knudseni* (R.A. Brandão). **(C)** *L. labyrinthicus*, juvenile (R.A. Brandão). **(D)** *L. labyrinthicus*, adult (R.A. Brandão). **(E)** *L. myersi* (J.-P. Vacher). **(F)** *L. paraensis* (A.J. Cardoso).

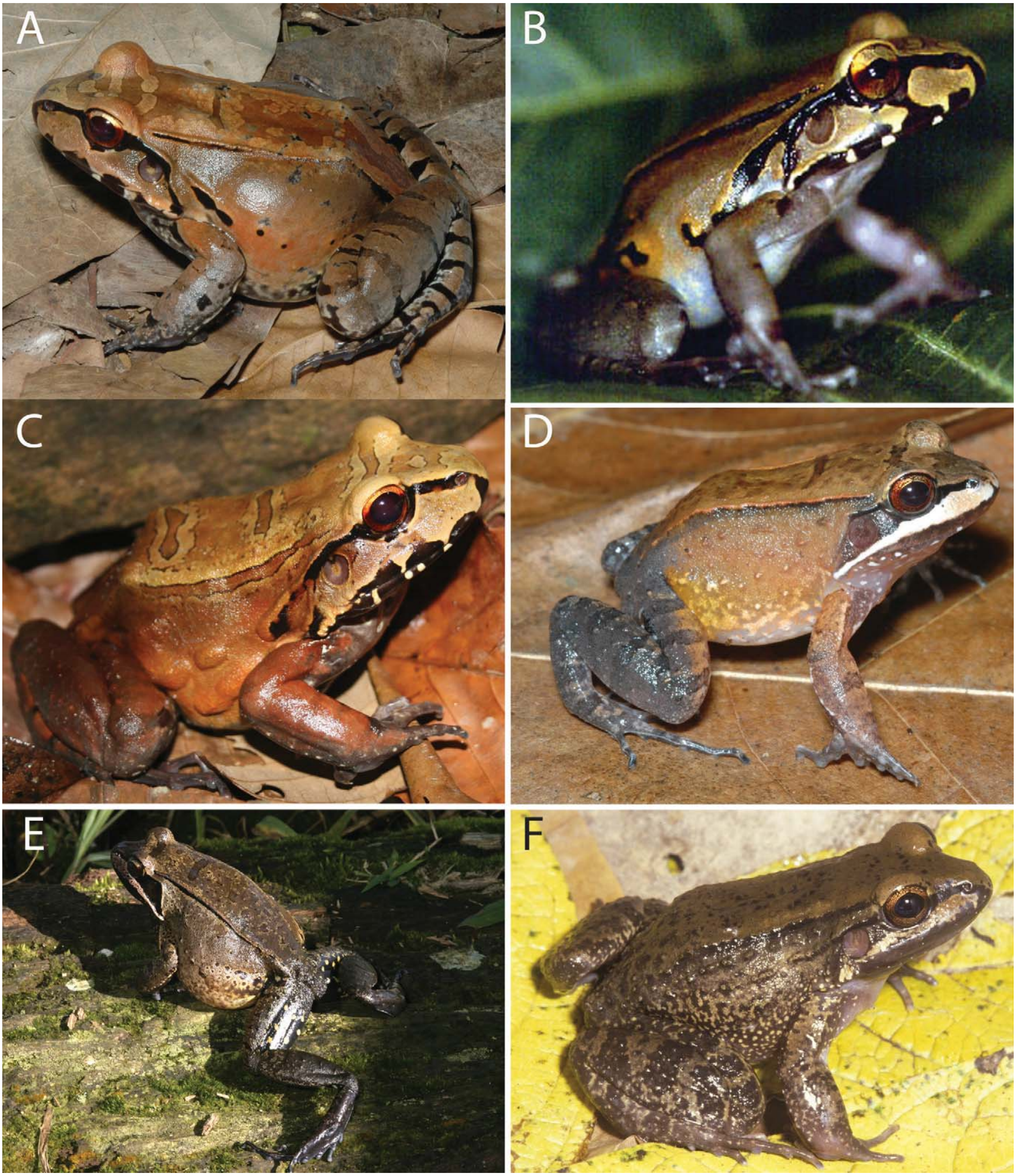

Plate 7. *Leptodactylus pentadactylus* species group. **(A)** *Leptodactylus pentadactylus* (C.F.B. Haddad). **(B)** *L. peritoaktites,* juvenile (R.O. de Sá). **(C)** *L. rhodomerus* (A. Acosta). **(D)** *L. rhodomystax,* juvenile (C.F.B. Haddad) **(E)** *L. rhodomystax,* adult (T. Grant). **(F)** *L. rhodonotus* (R. Cocroft).

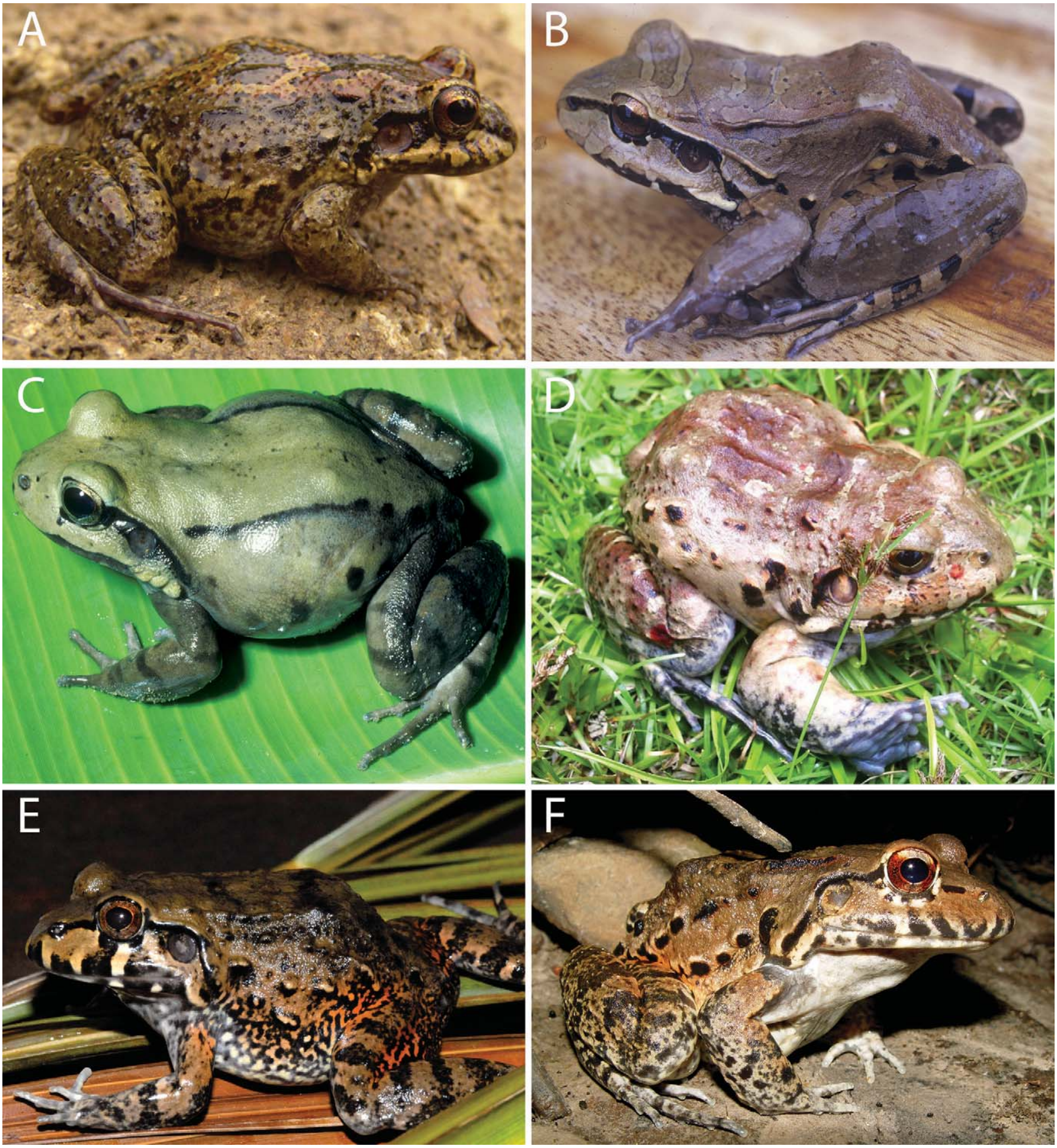

Plate 8. *Leptodactylus pentadactylus* species group. **(A)** *Leptodactylus rugosus* (C. Barrio-Amoros). **(B)** *L. savagei* (R.W. McDiarmid). **(C)** *L. stenodema* (R.W. McDiarmid). **(D)** *L. turimiquensis* (D. Flores); **(E)** *L. vastus,* juvenile (R.O. de Sá). **(F)** *L. vastus,* adult (D. Loebmann).

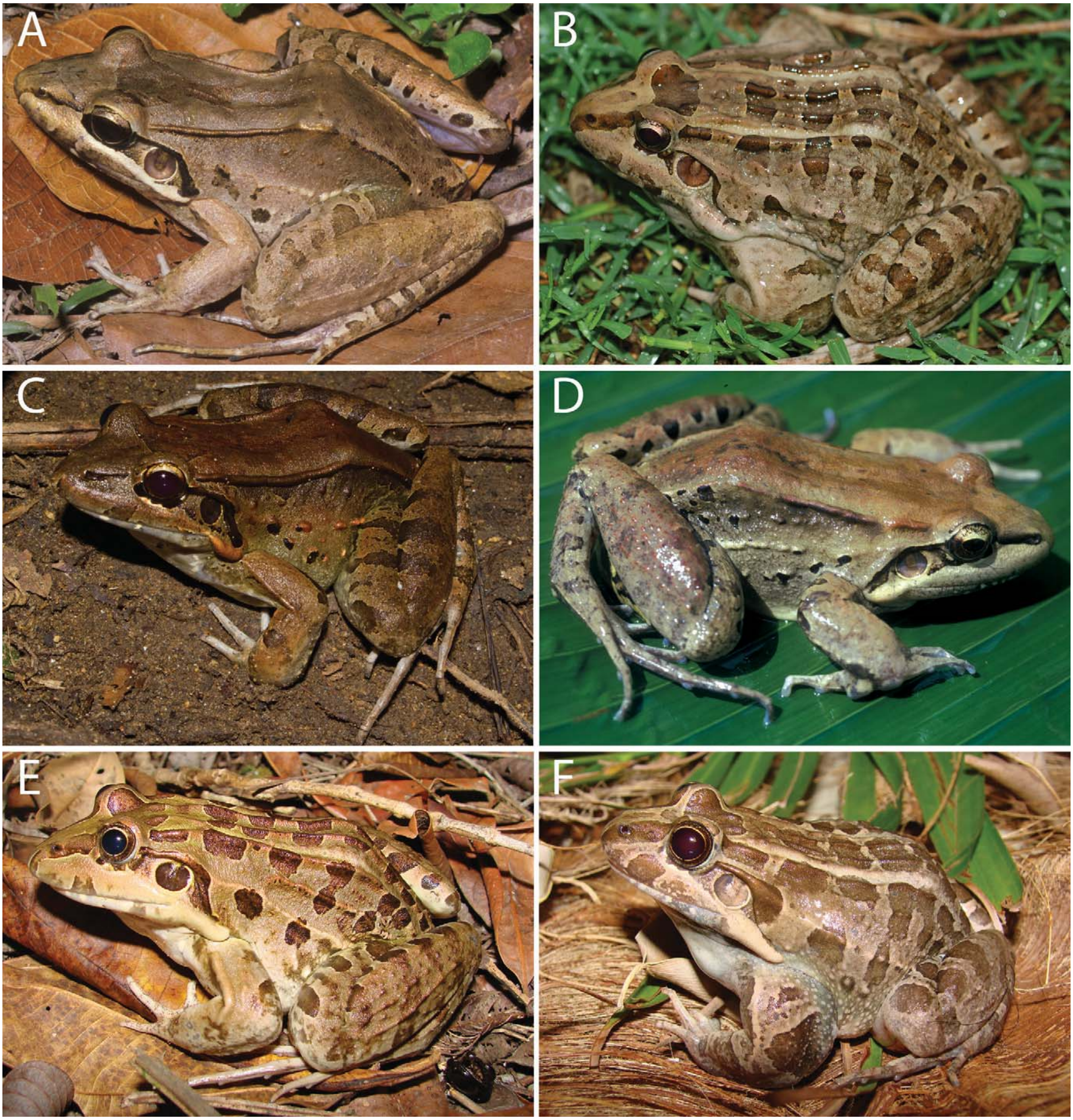

Plate 9. *Leptodactylus latrans* species group. **(A)** *L. bolivianus* (R.W. McDiarmid). **(B)** *L. chaquensis* (A. Giaretta). **(C)** *L. guianensis* (A. Fouquet). **(D)** *L. insularum* (R.W. McDiarmid). **(E)** *L. latrans* (R.A. Brandão). **(F)** *L. macrosternum* (R.A. Brandão).

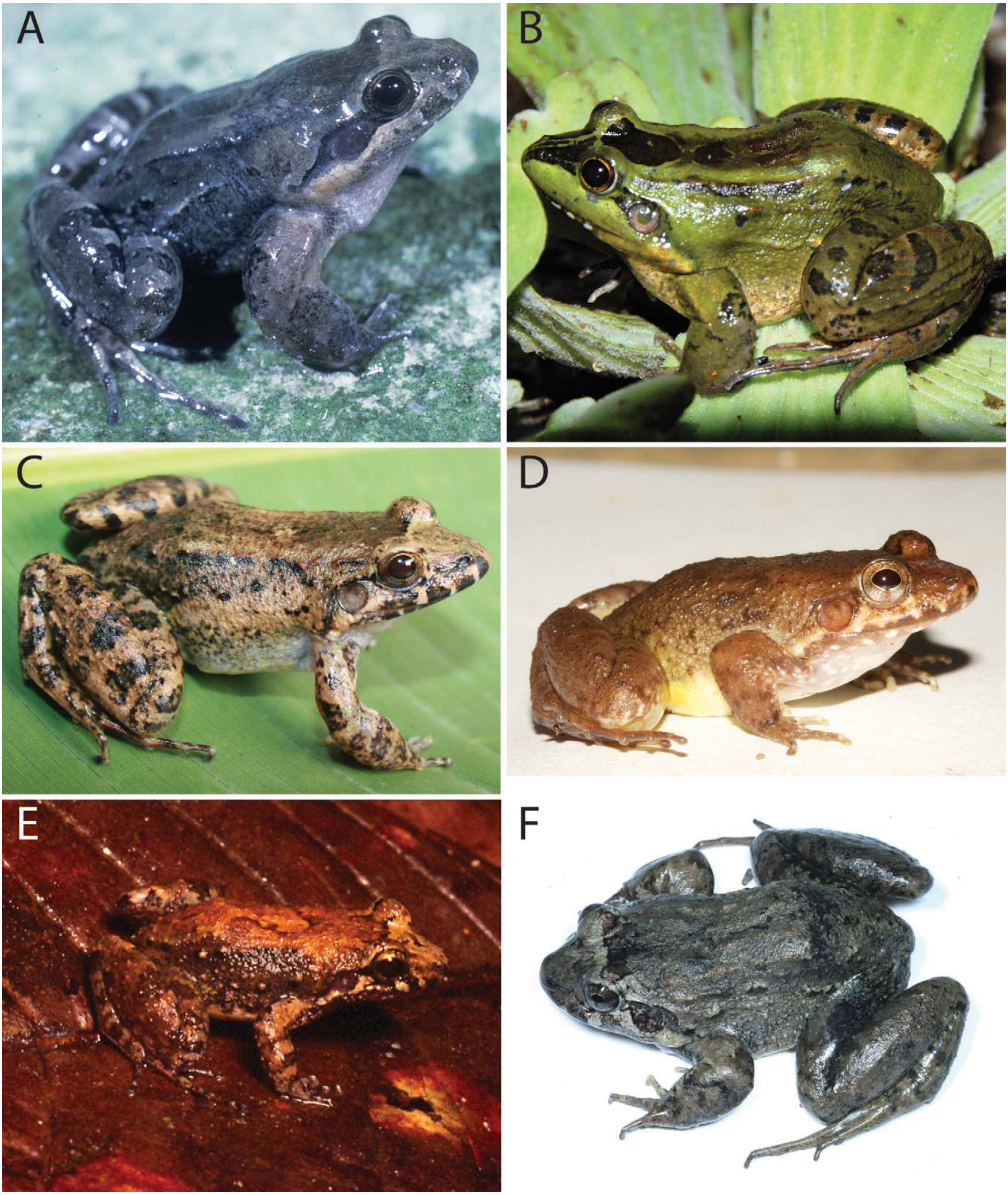

Plate 10. *Leptodactylus latrans* **(A–B)** and *L. melanonotus* **(C–F)** species groups. **(A)** *L. silvanimbus* (J.R. McCranie). **(B)** *L. viridis* (R.O. de Sá). **(C)** *L. colombiensis* (A. Acosta). **(D)** *L. diedrus* (S. Castroviejo). **(E)** *L. discodactylus* (F. Toledo). **(F)** *L. griseigularis* (S.B. Hedges).

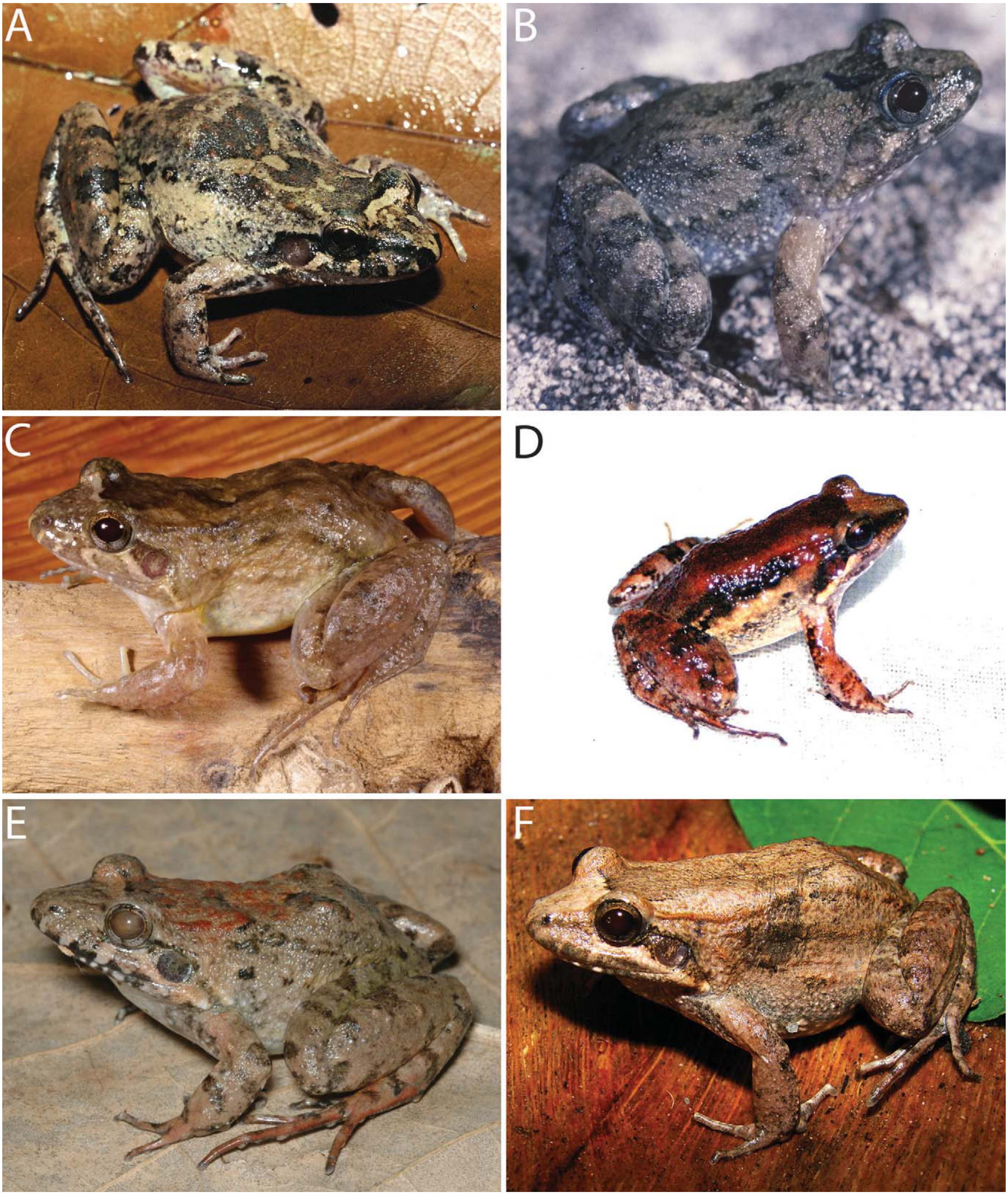

Plate 11. *Leptodactylus melanonotus* species group. **(A)** *L. leptodactyloides* (I. De La Riva) **(B)** *L. melanonotus* (A. Garcia). **(C)** *L. natalensis* (A. Garda). **(D)** *L. nesiotus* (M.J. Jowers). **(E)** *L. petersii* (C.F.B. Haddad). **(F)** *L. podicipinus* (R.O. de Sá).

Plate 12. *Leptodactylus melanonotus* species group **(A–E)** and unassigned species **(F)**. **(A)** *L. pustulatus* (R.A. Brandão). **(B)** *L. riveroi* (A.J. Cardoso). **(C)** *L. sabanensis* (J.A. Cardoso). **(D)** *L. validus* (J. Smith). **(E)** *L. wagneri* (J.P. Caldwell). **(F)** *L. lauramiriamae*, holotype (scale = 1 cm; image provided by the Museu de Zoologia, Universidade de São Paulo).