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Leptodactylus bufonius.

***Leptodactylus bufonius* Boulenger**
Oven Frog

Leptodactylus bufonius Boulenger 1894a: 348. Type locality, "Asunción, Paraguay." Lectotype, designated by Heyer (1978), Museum of Natural History (BMNH) 1947.2.17.72, an adult female collected by G.A. Boulenger (not examined by authors). See **Remarks**.

Leptodactylus buffonis Vogel, 1963: 100. *Lapsus*.

CONTENT. No subspecies are recognized.

DESCRIPTION. *Leptodactylus bufonius* is a moderately-sized species of the genus (following criteria established by Heyer and Thompson [2000]) with adult snout-vent length (SVL) ranging between 44–62 mm (Table 1). Head width is generally greater than head length and hind limbs are moderately short (Table 1). *Leptodactylus bufonius* lacks distinct dorsolateral folds. The tarsus contains white tubercles, but the sole of the foot is usually smooth. Mature males have a strongly sloped, spatulate snout. Sexually mature males lack both thumb and chest spines. The dorsum is grey and may contain black spots or irregular shaped splotches; black bars are present on the tibia and the venter is white. This species lacks a white stripe on its posterior thigh and tarsus. A middorsal stripe and light lip stripe are absent. Males possess a pair of black bilateral gular spots, but a single vocal sac. Juveniles and adults have a similar color pattern.

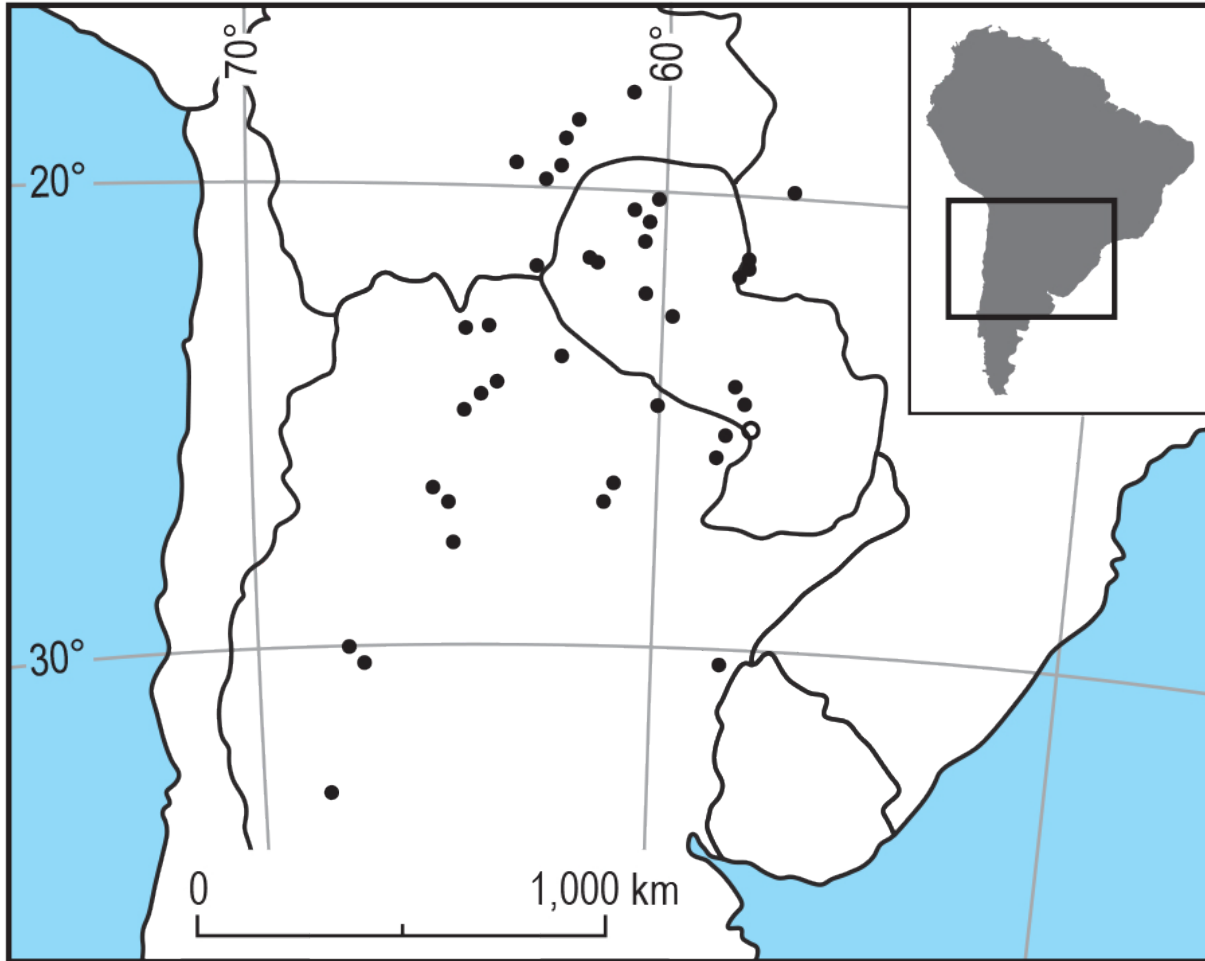
Larvae are exotrophic, lentic, benthic guild members (Altig and McDiarmid 1999). The body is ovoid-shaped and color can vary from brown to a grayish color. Eyes are dor-



FIGURE 1. Calling male *Leptodactylus bufonius* in Cordillera, Santa Cruz, Bolivia. Photograph by Christopher M. Schalk.

sally positioned. The oral disc is ventrally positioned. The tooth row formula is 2(2)/3(1). The oral disc is slightly emarginated, surrounded with marginal papillae, and possesses a dorsal gap. A row of submarginal papillae is present. The spiracle is sinistral and the vent tube is median. The tail fins originate at the tail-body junction. The tail fins are transparent, almost unspotted (Cei 1980). Individuals collected from the Bolivian Chaco possessed tail fins that were darkly pigmented with melanophores, especially towards the terminal end of the tail (Christopher M. Schalk, personal observation).

Two advertisement calls have been documented in *Leptodactylus bufonius*. Advertisement call type 1 (Figure 2A) consists of a single note. To the human ear, the call sounds like a metallic "huinc, hunic" (Cei 1980). Call duration is approximately 0.5 seconds; calls/minute, 38; maximum call energy, 2 kHz; average dominant frequency, 1.488 kHz, frequency range, 1.25–2.0 Hz. Advertisement call type 2 (Figure 2B) consists of three notes. Call duration is 0.39 seconds with each note lasting 0.13 seconds; calls/minute, 16; maximum call energy, 1.75 kHz; average dominant frequency, 1.567 kHz, frequency range, 1.0–2.0 kHz.



MAP 1. Distribution of *Leptodactylus bufonius*. The lectotype is designated by the white circle. These locality data should be considered secondary sources because we did not confirm the identifications of specimens from all localities.

DIAGNOSIS. Adult *Leptodactylus bufonius* lack toe fringes and dorsolateral folds, two traits found in *Leptodactylus fragilis*, *Leptodactylus labyrinthicus*, *Leptodactylus laticeps*, *Leptodactylus latinus*, *Leptodactylus lithonaetes*, *Leptodactylus myersi*, *Leptodactylus rugosus*, *Leptodactylus syphax*, *Leptodactylus turimiquensis*, and *Leptodactylus troglodytes*. However, *Leptodactylus bufonius* has a Chacoan distribution and is found in sympatry with *Leptodactylus chaquensis*, *Leptodactylus elenae*, *Leptodactylus fuscus*, *Leptodactylus lacticeps*, *Leptodactylus latinus*, *Leptodactylus leptodactyloides*, and *Leptodactylus mystacinus*.

Leptodactylus bufonius is smaller than *Leptodactylus chaquensis* (female SVL: 68.1–97.6 mm; male SVL: 65.4–94.3 mm; de Sá et al. 2014), *Leptodactylus labyrinthicus* (female SVL: 141.8±12.3 mm; male SVL: 148.9±16.3 mm; Heyer 1979), *Leptodactylus laticeps* (female SVL: 88.0–117.0 mm; male SVL: 94.2–109.7 mm; de Sá et al. 2014), *Leptodactylus myersi* (female SVL: 78.9–112.9 mm; male SVL: 74.2–123.4 mm; Heyer 2005), and *Leptodactylus turimiquensis* (female SVL: 122.4–128.0 mm; male SVL: 127.2–160.0 mm; Heyer 2005), but generally larger than *Leptodactylus elenae* (female SVL: 42.8 ± 3.1 mm; male SVL: 42.7 ± 2.5 mm; Heyer 1978),

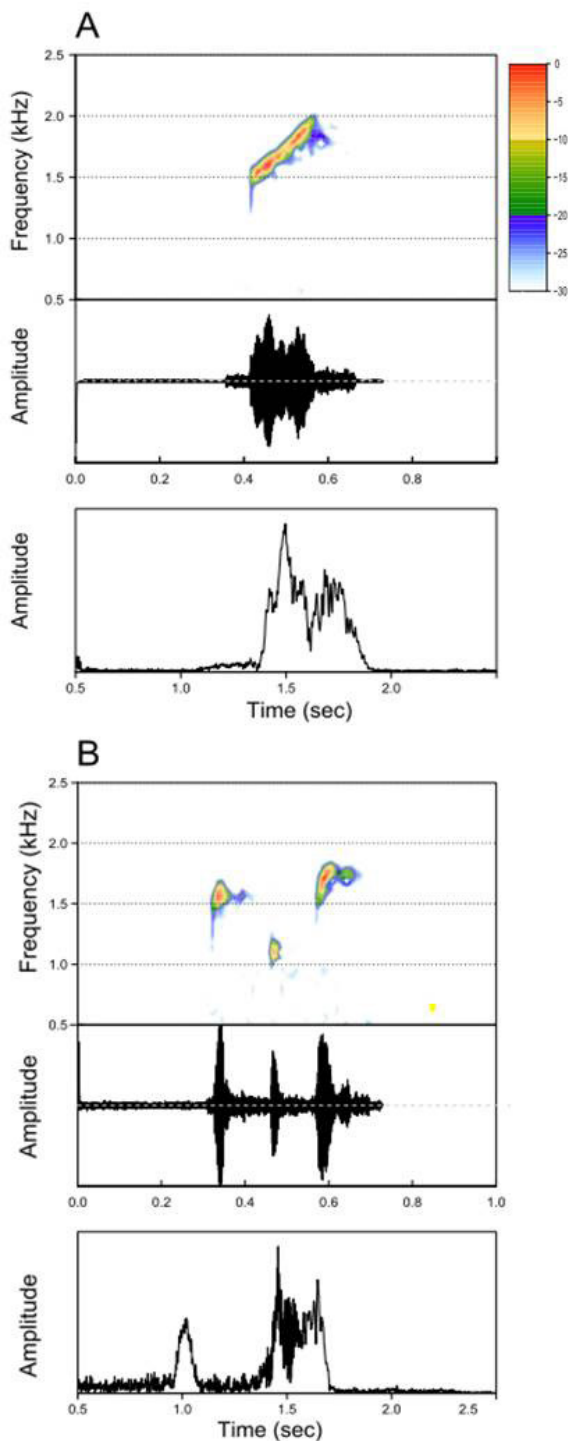


FIGURE 2. Audiospectrogram (top) wave form (center), and expanded waveform (bottom) of the advertisement calls A) type 1 (recorded at 23:00h at 30.3°C) and B) type 2 (recorded at 21:00h at 27.9°C) of *Leptodactylus bufonius* recorded by a SM2 Song Meter in Cordillera, Santa Cruz, Bolivia. No voucher specimens.

Leptodactylus fuscus (female SVL: 43.6 ± 4.4 ; male SVL: 42.8 ± 4.0 ; Heyer 1978), *Leptodactylus latinasus* (female SVL: 33.0 ± 1.9 mm; male SVL: 31.2 ± 1.7 mm; Heyer 1978), and *Leptodactylus leptodactyloides* (female SVL: 34.8–56.2 mm; male SVL: 28.3–47.9 mm; Heyer 1994). Distinct dorsolateral folds are lacking in *Leptodactylus bufonius*, but one pair of folds is present in *Leptodactylus labyrinthicus*; one or two pair of folds are present in *Leptodactylus elenae*, *Leptodactylus leptodactyloides*, and *Leptodactylus mystacinus*; three pair of folds are found in *Leptodactylus fuscus*, and four pair of folds are present in *Leptodactylus chaquensis*.

The dorsum of *Leptodactylus bufonius* contains dark spots or irregular shaped splotches, often black against a grey-colored dorsum. The colors are duller compared to *Leptodactylus laticeps*, which contains a tile-like pattern of aposematic colors of black and red rectangles against white (in life). *Leptodactylus bufonius* lacks a white stripe on the posterior surface of the thigh, but this stripe is present in *Leptodactylus elenae*, *Leptodactylus fragilis*, *Leptodactylus fuscus*, *Leptodactylus latinasus*, and generally in *Leptodactylus leptodactyloides*. Longitudinal dorsal stripes are present in *Leptodactylus chaquensis* and *Leptodactylus latinasus*, but absent in *Leptodactylus bufonius*. A middorsal white stripe is sometimes present in *Leptodactylus fuscus*, but always absent in *Leptodactylus bufonius*. The venter is solid white in *Leptodactylus bufonius*, but melanophores are almost always present on the venter of *Leptodactylus leptodactyloides*.

White tubercles are present on the foot of *Leptodactylus elenae*, *Leptodactylus fragilis*, and *Leptodactylus latinasus*, but these are generally absent in *Leptodactylus bufonius*, which tend to have a smooth foot. The shank of *Leptodactylus lithonaetes* has a few to many black and/or white tubercles, but the shank of *Leptodactylus bufonius* is smooth. Thumb spines are absent in sexually mature males of *Leptodactylus bufonius*, but one pair of spines

TABLE 1. Summary measurements for adult specimens of *Leptodactylus bufonius*. Ranges of trait/SVL proportions are presented with the average values in parentheses. Individuals measured for this table were from museum specimens and captured-and-released individuals from localities in the Gran Chaco of Bolivia. Abbreviations: SVL = snout-vent length, HW = head width, HL = head length, TL = thigh length, SL = shank length, FTL = foot and tarsal length.

Measurement	Males (n=38)	Females (n=48)
SVL (mm)	44–57 (52)	47–62 (54)
HW/SVL (%)	33–38 (36)	33–40 (35)
HL/SVL (%)	29–37 (36)	27–40 (32)
TL/SVL (%)	30–45 (35)	27–44 (35)
SL/SVL (%)	37–48 (41)	38–46 (41)
FTL/SVL (%)	47–67 (54)	46–60 (53)

are present in *Leptodactylus labyrinthicus*, *Leptodactylus leptodactyloides*, *Leptodactylus lithonaetes*, and *Leptodactylus myersi*; two pair of thumb spines are present in *Leptodactylus chaquensis*, *Leptodactylus laticeps*, and *Leptodactylus syphax*.

Adult *Leptodactylus bufonius* are most similar to *Leptodactylus troglodytes* that are similar in size, and lack both toe fringes and distinct dorsolateral folds (Heyer 1978). However, these species are not sympatric; *Leptodactylus troglodytes* occur in northeastern Brazil, whereas *Leptodactylus bufonius* is restricted to the Gran Chaco ecoregion.

PHYLOGENETIC RELATIONSHIPS. *Leptodactylus bufonius* is a member of the *fuscus* species group, which is the largest species group of the five recognized species groups of genus *Leptodactylus* (Barrio 1973; de Sá et al. 2014; Heyer 1969; Ponssa 2008). While the *fuscus* species group has undergone revisions (Heyer 1978, 1998), *Leptodactylus bufonius* has remained in the *fuscus* species group since its initial designation by Heyer (1969). Support for the monophyly of the *fuscus* spe-

cies group was provided by Ponssa (2008) in a cladistic analysis using external morphology, osteology, larval morphology, and behavior; *Leptodactylus troglodytes* was the sister species of *Leptodactylus bufonius* (Ponssa 2008). A more recent phylogenetic analysis of molecular and non-molecular characters by de Sá et al. (2014) also supports the monophyly of the *fuscus* species group. *Leptodactylus bufonius* is part of the basal clade in the *fuscus* species group that includes *Leptodactylus troglodytes* and *Leptodactylus mystacinus* as sister taxa (de Sá et al. 2014). These three species comprise the sister clade to the remaining species in the *fuscus* group (de Sá et al. 2014).

PUBLISHED DESCRIPTIONS. Descriptions of *Leptodactylus bufonius* were provided by Achenbach (1962), Andersson (1906), Berg (1896), Boulenger (1894a), Budgett (1899), Cei (1980), de Sá et al. (2014), Gallardo (1987), Gallardo and Varela de Olmedo (1992), Heyer (1978), Lutz (1930), Mertens (1929), Müller and Hellmich (1936), Neiden (1923), Norman (1994), Straneck et al. (1993), and Weiler et al. (2013). A description of the tadpole was published by Cei (1980). Audiospectrograms and descriptions of the call were provided by Heyer (1978), Heyer and Scott (2006), Straneck et al. (1993), and Straughan and Heyer (1976). Márquez et al. (2002) and Straneck (1992) provide recordings of the call.

ILLUSTRATIONS. Color photographs of the adult were provided by De la Riva et al. (2000), de Sá et al. (2014), Gonzales et al. (2006), Heyer and Scott (2006), Lavilla et al. (1995a), Márquez et al. (2002), Norman (1994), Pansonato et al. (2011), Ponssa and Medina (2016), and Weiler et al. (2013). A color photograph of a metamorph being consumed during a predation event was published by Schalk (2010a). Color photographs of stained skeletal features were published by Vera and Ponssa (2014). Color photographs of the nest were published by Crump (2015),

Faggioni et al. (2017), and Weiler et al. (2013). **Black-and-white photographs** of adults can be found in Achenbach (1962), Bogart (1974), Cei (1949a), Cei (1956), Pisanó et al. (1993), Reading and Jofré (2003); black-and-white photographs of the tadpole were published by Pisanó' (1965b), Pisanó' (1966), and Pisanó and Barbieri (1965). Black-and-white photographs of the nest were provided by Cei (1949a), Cei (1956), Crump (1995, 2010), Eisentraut (1932), Pisanó' (1965b), Pisanó et al. (1993), and Reading and Jofré (2003). A black-and-white photograph of the karyotype was published by Bogart (1974); a black-and-white photograph of the chromosome and sperm was published by Barbieri (1950). Black-and-white photographs of the prepollex of an adult and primary carpal cartilages of a tadpole were published in Fabrezi (2001). Pisanó' (1966) provided a black-and-white photograph cross-sections of the mesonephros of the tadpole. A black-and-white drawing of the jaw musculature was presented by Manzano et al. (2003). **Color illustrations** of adult *Leptodactylus bufonius* were published by Cei (1980), The Encyclopedia of Animals (2004), and The Encyclopedia of Reptiles Amphibians & Invertebrates (2006a, 2006b). **Black-and-white illustrations** of adult *Leptodactylus bufonius* were published by di Tada et al. (1976), Gallardo (1987), Heyer (1978), Lutz (1930), Müller and Hellmich (1936), and Straneck et al. (1993). Black-and-white illustrations of the tadpole were provided by Cei (1949a) and Cei (1980). Black-and-white illustrations of the musculature were published by Limeses (1964). Black-and-white illustrations of the nest were provided by Eisentraut (1932) and Norman (1994). Black-and-white illustrations of the nesting behavior were published by Faggioni et al. (2017) and a black-and-white illustration of the calling site was published by Straneck et al. (1993).

DISTRIBUTION. *Leptodactylus bufonius* is one of the most common and abundant spe-

cies of anurans in the Gran Chaco ecoregion of South America. Oven Frogs are known from southeastern Bolivia to northern Argentina, Paraguay, the Brazilian Chaco, and the northwestern Pantanal of Brazil.

FOSSIL RECORD. None.

PERTINENT LITERATURE. Relevant citations are listed by topic: **biogeography** (Álvarez et al. 1996; Alvarez et al. 2002; Blair et al. 1976; Bridarolli and di Tada 1994; Cei 1955a, 1957, 1980, 1982; Contreras and Contreras 1982; Duellman 1999; Gallardo 1966, 1979, 1985; Gonzales et al. 2006; Heyer 1988; Heyer and Maxson 1982a, 1982b; Roig and Contreras 1975), **call and call parameters** (Barrio 1965b; Cei 1980; de Sá et al. 2014; Eggermont 1988; Gingras and Fitch 2013; Heyer 1978; Heyer and Scott 2006; Kerr 1950; Márquez et al. 2002; Straneck 1992; Straneck et al. 1993; Straughan and Heyer 1976), checklists and catalog lists (Álvarez et al. 1996, 2009; Alvarez et al. 2002; Aquino et al. 1996; Aquino-Schuster et al. 1991; Avila et al. 1998; Avila and Carrizo 2003; Berg 1896; Bertoni 1914, 1939; Boulenger 1894a, 1894b, 1898; Briguera et al. 2006; Brusquetti and Lavilla 2006; Bucher 1980; Budgett 1899; Cei 1955a, 1955b, 1956, 1957, 1960; Cei and Roig 1964; Cespedez and Klein 2002; Cespedez et al. 1995, 2004; Contreras 1982; Cruz et al. 1992; De la Riva 1990; De la Riva et al. 2000; di Tada et al. 1976, 1996; Doria et al. 2001; Duellman 1999; Elter 1981; Freiberg 1942; Gavetti and Andreone 1993; Glaw et al. 1998, 2000a, 2000b; Godoy 1963; Gonzales 1998; Gonzales et al. 2006; Gorham 1963, 1966, 1974; Harding 1983; Hutchins et al. 2003; Jofré et al. 2013; Kacoliris et al. 2006; Köhler 2000; Lanza et al. 2006; Laurent and Teran 1981; Lavilla and Cei 2001; Lavilla and Scrocchi 1991; Lavilla et al. 1995a, 1995b, 2000a, 2000b; Manzano et al. 2004; Martori and Aun 1995; Müller and Hellmich 1936; Padial et al. 2003; Pansonato et al. 2011; Peracca 1895 [and 2007a reprint], 1897 [and 2007b reprint]; Pérez Iglesias and

Natale 2013; Reichle 2004; Sanabria and Quiroga 2009; Schalk et al. 2013; Scott and Lovett 1975; Soria Modesto and Noss 2000; Souza et al. 2010; Vellard 1948; Vogel 1963, 1964a, 1964b; Weiler et al. 2013; Wrobel 2004; Yanosky et al. 1993; Ziegler 2002), **conservation** (Briguera et al. 2006; Brusquetti and Lavilla. 2006; Crump 2005; De la Riva and Reichle 2014; Duellman 1999; Lavilla 2001; Lavilla and Brusquetti 2010; Lavilla and Cei 2001; Lavilla and Heatwole 2010; Lavilla et al. 2000a, 2000b, 2004; Stuart et al. 2008; Weiler et al. 2013), **ecology** (Blair 1970, 1976a, 1976b; Bucher 1980, 1982; Cei 1949a, 1953, 1955b, 1956, 1980; Cei and Roig 1964; Contreras and Contreras 1982; di Tada et al. 1976; Duré and Kehr 2004; Gallardo and Varela de Olmedo 1992; Heyer 1969; Jofré et al. 2010; Lutz 1969; Mares et al. 1977; Mattison 1987 [and reprints, e.g., 1989 and 1994]; Perotti 1997; Pisanó et al. 1993; Ponssa and Medina 2016; Reading and Jofré 2003; Sanabria and Quiroga 2009; Schalk 2016; Schalk and Saenz 2016; Schalk and Sezano 2014; Schalk et al. 2013; Schalk et al. 2017; Straneck et al. 1993; Vellard 1948), **evolution** (Blair 1970, 1976a, 1976b; Emerson 1976; Heyer 1969), **genetics and karyotypes** (Barbieri 1950; Bogart 1967, 1974; Brum-Zorrilla and Saez 1968; Faggioni et al. 2014; Green and Sessions 2007; Heyer and Diment 1974; Maxson and Heyer 1988; Morescalchi 1979; Rabello 1970), **keys** (Berg 1896; Cei 1980; Heyer 1978; Lavilla et al. 1993; Nieden 1923; Weiler et al. 2013), **larvae and larval characteristics** (Cei 1980; Crump 2015; De La Riva 1995; de Sá et al. 2014; Duellman and Trueb 1986, 1994; Faivovich and Carrizo 1992; Langone and de Sá 2005; Larson and de Sá 1998; McClanahan 1975; Motte et al. 2004; Pisanó 1965a; Pisanó 1965b; Pisanó and del Rio 1968; Pisanó and Rengel 1967; Schalk 2016; Schalk et al. 2017; Shoemaker and McClanahan 1973; Vera and Ponssa 2014), **morphology and development** (Andersson 1906; Fabrezi 1992, 1996, 2001, 2012; Fabrezi and Barg 2001; Goin 1959; Hayek and Heyer 2005; Heyer 1978; Larson and de Sá 1998; Limeses 1964, 1968; Limeses et al. 1972; Manzano et al. 2003; Medina et al. 2013; Peracca 1895 [and 2007a reprint]; Pisanó 1965a; Pisanó 1966; Pisanó and Barbieri 1965; Pisanó and del Rio 1968; Pisanó and Rengel 1967; Ponssa 2008; Ponssa and Medina 2016; Ponssa and Vera Candiotti 2012; Schalk 2016; Sebben et al. 2007; Vera and Ponssa 2014; Viertel and Richter 1999), **physiology and biochemistry** (Barrio 1965a; Bertini and Rathe 1962; Cei and Erspamer 1965, 1966; Cei et al. 1961, 1967; Duellman and Trueb 1986, 1994; Erspamer et al. 1964; Fernández and Fernández 1975; McClanahan 1975; Montero 1986; Rastogi et al. 2005; Shoemaker and McClanahan 1973; Warburg 1997; Wells 2007), **popular press books** (Mattison 1987 [and reprints, e.g., 1989 and 1994]; The Encyclopedia of Animals 2004), **predators and parasites** (Baker 1987; Baker and Vaucher 1984, 1986; Durette-Desset et al. 1985; González and Hamann 2006, 2014, 2015; Hamann et al. 2012a, 2012b; Heyer and Scott 2006; Hulse 1978; Lent et al. 1946; Schalk 2010a, 2010b, 2016; Schalk and Montaña 2012; Schalk et al. 2014; Scott and Aquino 2005; Senzano and Schalk 2013; Smales 2007; Vucetich and Giacobbe 1949), **reproductive biology** (Barbieri 1950; Budgett 1899; Cei 1949a, 1949b; Crump 1995, 2005, 2010, 2015; Duellman and Trueb 1986, 1994; Eisentraut 1932; Faggioni et al. 2011, 2017; Klingelhöffer 1956; Lavilla et al. 2000b; Pérez Iglesias and Natale 2013; Perotti 1994, 1997; Philibosian et al. 1974; Pisanó 1962, 1965a; Pisanó 1965b; Pisanó and Barbieri 1965; Pisanó et al. 1993; Rastogi et al. 2005; Reading and Jofré 2003; Ridley 1978; Schalk 2016; Schalk and Saenz 2016; Schalk et al. 2013; Shoemaker et al. 1973; Weiler et al. 2013; Wells 2007), and **taxonomy, systematics, and phylogenetics** (Barrio 1973; Cei 1987; Cei and Erspamer 1965, 1966; Cei et al. 1967; De la Riva 1996; de Sá et al. 2005, 2014; Frank and Ramus 1995; Frost 1985, 2017; Heyer 1978, 1995, 1998; Larson and de Sá 1998; Lavilla 1992; Limeses et al. 1972; Maxson and Heyer 1988; Montero 1986; Ponssa

2008; Sokolov, 1988; Zhao et al. 1998).

ADDITIONAL VERNACULAR NAMES.

Rana de los hormigueros (di Tada et al. 1976), Vizcacheras' White-lipped Frog (Faggioni et al. 2011; The Encyclopedia of Animals 2004; The Encyclopedia of Reptiles Amphibians & Invertebrates 2006a, 2006b).

ETYMOLOGY. There were no comments on the etymology of the species in the original description (Boulenger 1894a). The word *bufo* is Latin for toad, and Budgett (1899) stated the species name "*bufonius*" refers to the presence of the spots. Presumably *Leptodactylus bufonius* is considered more toad-like as compared to other species of *Leptodactylus*, referring to the small wart-like bumps present on the dorsum.

REMARKS. In the original description, there was no holotype designated by Boulenger (1894a). Boulenger (1894a) reported the SVL measurement of the specimen in his description as 48 mm. Parker (1931) reexamined the type series (n = 4) and reassigned the smallest two of the series to *Leptodactylus diptyx*. The four syntypes collected by Boulenger (1894a) were examined by Heyer (1978). The first specimen of the series, BMNH 1947.2.17.72, had an SVL of 46.4 mm, the closest measurement to Boulenger's (1894a) description, and is likely the specimen upon which Boulenger's description was based. This specimen was designated as the lectotype by Heyer (1978).

SPECIMENS EXAMINED. All *Leptodactylus bufonius* specimens examined were collected in Bolivia and are housed in the Herpetology Collection in the Museo de Historia Natural Noel Kempff Mercado (MNKA): MNKA 399, 452, 505, 1363, 1365, 1365, 1366, 1367, 1370, 1987, 4646, 4655, 4656, 5239, 5558, 5559, 5560, 5612, 5613, 5614, 5615, 5644, 5645, 5694, 5907, 7537, 7571, 8483, 8484, 8507, 8526.

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