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Lepidobatrachus laevis

Lepidobatrachus laevis Budgett
Budgett's Frog

Lepidobatrachus laevis Budgett, 1899: 329. Type locality, "Paraguayan Chaco." [Holotype not stated; designated by J. S. Budgett, Natural History Museum, London, BMNH 1919.4.23.2, renumbered as BMNH 1947.2.17.32 (Jeffrey Streicher, Natural History Museum, personal communication, 3 February 2015), an adult female (80 mm SVL), collected by J. S. Budgett in 1899 (not examined by authors)] See **Remarks**.

Ceratophrys laevis Boulenger, 1919:533.

Ceratophrys (*Lepidobatrachus*) *laevis* Parker, 1931:289.

Lepidobatrachus asper Vellard, 1948:164.

Lepidobatrachus laevis Barrio, 1968a:445.

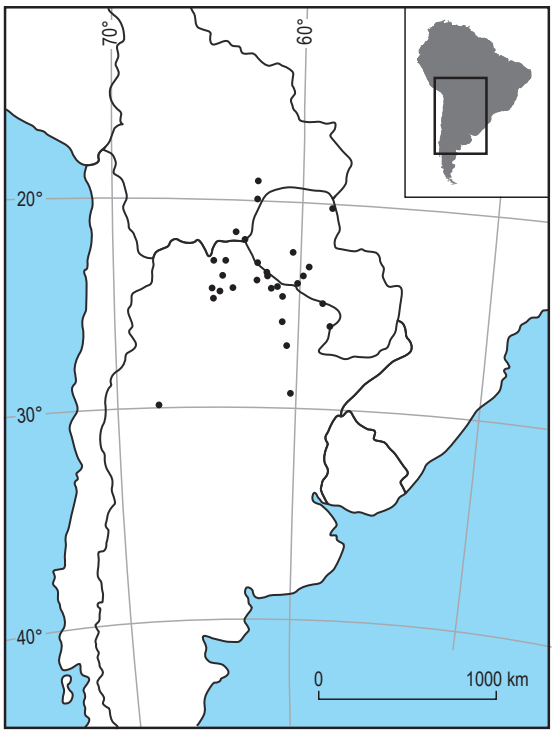
Lepidobatrachus laveis Moreira Sugai et al., 2013:133. *Lapsus*.

CONTENT. No subspecies are recognized.

DESCRIPTION. *Lepidobatrachus laevis* is a large ceratophryid frog with adult snout-vent length (SVL) ranging between 60–130 mm. The species is sexually dimorphic with females larger than males (Table 1). Besides overall body size, there is no sexual dimorphism in limb proportions. The head is wider than long, with head width being over half of body length. On average, head length is over 40% SVL and is rounded in front, with a wide mouth. The eyes typically have a round pupil and stick up almost vertically from the flattened top of the head. The mouth is characterized by vomerine teeth in two groups between the choanae, and two fang-like projections of the dentary bone at the front midline of the mouth. Body shape is round and flat, with short fore limbs (approximately half of the SVL) and hind limbs (approximately 40% of the SVL). Thigh and shank lengths are a little over a third of the SVL, while the foot-tarsal length is over half of the SVL. Fingers are free, but toes are webbed for approximately two-thirds of their length with large metatarsal tubercles. No vertebral shield is present. There is a double row of glands on the dorsum, arranged in the shape of a V with its base above the cloaca. Dorsal color ranges from gray to brown to green, sometimes with lighter yellowish, irregular vein-like patterning. Venter is white. Males possess lateral, dark vocal sacs.

Figure 1. Adult female *Lepidobatrachus laevis* from Yande Yari, Parque Nacional Kaa-Iya del Gran Chaco, Provincia Cordillera, Departmento de Santa Cruz, Bolivia. Photo by Christopher M. Schalk.

The tadpole of *Lepidobatrachus laevis* is a member of the carnivorous ecomorphological guild (Altig and McDiarmid 1999a). Tadpoles range between 16–19 mm total length at four days of development (Gosner stage 26–27; Gosner 1960) and 87 mm total length around 20 days after egg deposition (Gosner stage 40+). They possess a broad head, a wide mouth, and a symmetrical pair of branchial openings. They have a single row of keratinous denticles on each jaw, covered by a scalloped anterior labium with approximately 20 labial papillae. The posterior labium is curved, with 4–9 papillae. Their skin is transparent where it comprises the opercular flaps, and above



Map 1. Distribution of *Lepidobatrachus laevis*. The locality of the holotype was listed as the "Paraguayan Chaco" by Budgett (1899), but its exact location is unknown. These locality data should be considered secondary sources because we did not confirm the identifications of specimens from all localities.

the buccopharyngeal and branchial regions, but the ventral surface is opaque. The dorsum varies in color depending on the background upon which tadpoles are raised. They possess a comparatively short but well-developed intestinal tract.

The advertisement call of *Lepidobatrachus laevis* was described by Barrio (1968b) as 1300 ms bursts of unpulsed sound with a 1700 ms internote interval. This species was described as having 20 calls/minute with a dominant frequency ranging between 800–1400 Hz, and a second harmonic of 2500–2900 Hz (Barrio 1968b). We were unable to obtain a recording of the call to analyze because *Lepidobatrachus laevis* calls at low densities and is rarely heard (N. J. Scott Jr., personal communication).

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

Measurement	Males (n=16)	Females (n=14)
SVL (mm)	63-83 (76)	79-124 (93)
HW/SVL (%)	54-66 (61)	53-61 (58)
HL/SVL (%)	36-50 (42)	26-47 (41)
FL/SVL (%)	44-57 (50)	40-53 (49)
ThL/SVL (%)	28-45 (36)	31-42 (36)
SL/SVL (%)	30-38 (35)	29-36 (33)
FTL/SVL (%)	46-67 (58)	49-58 (53)

DIAGNOSIS. *Lepidobatrachus laevis* has a Chacoan distribution and is sympatric with the ceratophryids *Ceratophrys cranwelli*, *Chacophrys pierottii*, *Lepidobatrachus asper*, and *Lepidobatrachus llanensis*. Though similar in size to *Ceratophrys cranwelli* (80–130 mm SVL), *Lepidobatrachus laevis* lacks the 'horns' present on the upper eyelids of *Ceratophrys cranwelli*. The skin is smoother in *Lepidobatrachus laevis*, which tends to be primarily grey or brown in color; the skin of *Ceratophrys cranwelli* is rougher and is green, patterned with dark brown blotches. *Lepidobatrachus laevis* is consistently much larger than *Chacophrys pierottii* (55 mm average SVL), which has granular skin and is typically green with dark spots. *Lepidobatrachus laevis* also has a flatter body shape with a wide head, while *Chacophrys pierottii* has a more rounded, erect posture and a narrower head. *Lepidobatrachus laevis* is larger than both adult *Lepidobatrachus llanensis* (65–100 mm SVL; both sexes) and *Lepidobatrachus asper* (70–90 mm SVL; both sexes). *Lepidobatrachus laevis* lacks the bony dorsal vertebral

shield that is present in *Lepidobatrachus asper* and *Lepidobatrachus llanensis*. Additionally, *Lepidobatrachus asper* has rougher skin with more dorsal tubercles; *Lepidobatrachus laevis* has smoother skin and fewer dorsal tubercles. Only *Lepidobatrachus laevis* has a V-shaped double row of glands on its dorsum. *Lepidobatrachus llanensis* possesses elliptical pupils, whereas the pupils of *Lepidobatrachus laevis* are rounded. Tadpoles of *Lepidobatrachus* have paired spiracles and lack a keratinous jaw sheath. This is in contrast to the single spiracle and keratinized jaw sheaths with denticle teeth present in *Ceratophrys cranwelli* and *Chacophrys pierottii*, though the denticle teeth often are lost in tadpoles of *Ceratophrys* spp. (Altig and McDiarmid 1999a). Tadpoles of *Lepidobatrachus laevis* also lack the nasal appendage present in tadpoles of *Chacophrys pierottii*. The tadpoles of the three species of *Lepidobatrachus* are similar morphologically, though the tadpoles of *Lepidobatrachus laevis* can reach longer total lengths (maximum length = 87 mm; Ruibal and Thomas 1988) than those of *Lepidobatrachus asper* (46 mm; Cei 1968) and *Lepidobatrachus llanensis* (56 mm; Cei 1968). In later stages of development, *Lepidobatrachus asper* and *Lepidobatrachus llanensis* begin developing the dorsal shields that distinguish adult individuals, and *Lepidobatrachus laevis* develops its characteristic V-shaped glandular pattern on its dorsum.

PHYLOGENETIC RELATIONSHIPS. *Lepidobatrachus laevis, Lepidobatrachus asper*, and *Lepidobatrachus llanensis* are the three recognized species in the monophyletic genus *Lepidobatrachus*, with *Lepidobatrachus laevis* hypothesized to be the sister taxon of *Lepidobatrachus llanensis* (Faivovich et al. 2014). *Lepidobatrachus* was initially placed in the subfamily Ceratophryinae in the family Ceratophryidae (Lynch 1982; Frost 1985; Frost et al. 2006; Pyron and Wiens 2011), but subsequent researchers found no support for the subfamily divisions within this clade (Faivovich et al. 2014; Frost 2016). Within Ceratophryinae, the *Ceratophrys* lineage diverged simultaneously with sister genera *Lepidobatrachus* and *Chacophrys* separating later (Fabrezi 2006; Faivovich et al. 2014; Maxson and Ruibal 1988).

PUBLISHED DESCRIPTIONS. Aside from the original description by Budgett (1899), descriptions of the adults were provided by Barrio (1968a, 1968b), Boulenger (1919), Cei (1980), Gallardo (1987), Freiberg (1954 [as *Lepidobatrachus asper*]), Hutchins et al. (2003), Nieden (1923), Mattison (2007a, 2007b), Norman (1994), Uchiyama (1997, 1999), and Weiler et al. (2013). Further descriptions of generic synapomorphies present in *Lepidobatrachus laevis* were provided by Lynch (1971, 1972). A partial description of the tadpole was provided by Barrio (1963), Cei (1980), and Parker (1931). Detailed and thorough descriptions of the tadpole and its anatomy were provided by Ruibal and Thomas (1988) and Wassersug and Heyer (1988). The only known description of the advertisement call was provided by Barrio (1968b). The distress call was discussed by Gallardo (1994).

ILLUSTRATIONS. Color photographs of the adult were provided by Alt and Alt (1992), Bartlett and Bartlett (1996), Coborn (1992), De la Riva et al. (2000), Earley (2014), Fabrezi and Lobo (2009), Faivovich et al. (2014), Gonzales et al. (2006), Hennessy (2010, 2016), Lavilla et al. (1995a), Malkmus (1998, 2000a, 2000b), Mattison (2007a, 2007b, 2011, 2014, 2015), Norman (1994), Scott and Aquino (2005), Schalk et al. (2013), Starosta and Moncuit (2006), Uchiyama (1997, 1999), Wang et al. (2015), and Weiler et al. (2013). A color photograph of a metamorph was published by Fabrezi et al. (2014a) and Weiler et al. (2013) and color photos of the tadpole were provided by Alt and Alt (1992), Fabrezi (2011), and Fabrezi et al. (2014a). A color photo of an adult in its cocoon was provided by Faivovich

et al. (2014). A color photo of the embryo was provided by Bloom et al. (2013). Color photos of additional morphological features were published by Bloom et al. (2013: tadpole gut), Fabrezi (2006: stained hyoid apparatus and vertebral column; 2011: hind and fore feet), Fabrezi and Quinzio (2011: suspensoriohyoideus), Fabrezi et al. (2014a: dorsal and ventral views of musculature, thigh musculature, tadpole caudal muscle), Fabrezi et al. (2014b: stained tadpole hyobranchial, teeth, stained cross-section of the skin), and Perchez and Carroll (1996: oviduct). **Color drawings** of the adult(s) were provided by Barraclough (2008, 2009, 2010), Duellman (2003), Flannery and Schouten (2004), The Encyclopedia of Animals (2004), The Encyclopedia of Reptiles, Amphibians & Invertebrates (2006), and Twist (2005a, 2005b); color drawings of additional features were published by Fabrezi et al. (2014b). **Black-and-white photographs** of the adult were published by Barrio (1968a, 1968b), Cei (1955, 1956 [as *Lepidobatrachus asper*]; 1980 [as *Lepidobatrachus laevis*]), Cochran (1961 [as *Lepidobatrachus asper*]), Malkmus (1998, 2000a, 2000b), Reig and Cei (1963), and Ziegler et al. (2002). Black-and-white photos of the tadpole were provided by Hanken (1992), Ruibal and Thomas (1988), and Ziermann et al. (2013). A black-and-white photo of a fossilized adult skull published by Tomassini et al. (2011) was initially described as *Lepidobatrachus laevis*, but was subsequently redescribed as *Lepidobatrachus australis* by Nicoli (2015). Black-and-white micrographs of the egg cortex, jelly layers, and egg envelopes were provided by Carroll et al. (1991b, 1991c) and Peavy and Carroll (1993). Additional black-and-white photos were published by Altig and McDiarmid (1999b: tadpole rectus abdominus muscle), Barrio (1968a: x-ray of skull, pupil, and hind foot), Bloom et al. (2013: tadpole gut), Carroll et al. (1991a: cross-sections of the tadpole stomach mucosa), Fabrezi (2001a: teeth), Fabrezi (2001b: cartilage in tadpole foot), Fabrezi and Quinzio (2008: cavum cranii, nerves, dorsal skin, feet, diaphyseal levels), Fritsch et al. (1987: rhombencephalic alar plate and neuromast cross section), Quinzio and Fabrezi (2012: cross-sections of dorsal and ventral skin), Ruibal and Thomas (1988: tadpole body cross-section), and Waggener and Carroll (1998b: spermatozoa). **Black-and-white drawings** of the adult was provided by Gallardo (1987) and Halliday (2010, 2016). Black-and-white drawings of the tadpole were published by Cei (1980), Fabrezi and Quinzio (2008), and Parker (1931) and a black-and-white drawing of an embryo was produced by Bloom et al. (2013). Black-and-white drawings of additional morphological features were provided by Cei (1980: dorsal view of the adult, pupil, hind foot, and hand), Fabrezi and Emerson (2003: mandible), Fabrezi and Lobo (2009: adult hyoid and related muscles), Fabrezi and Quinzio (2008: chondrocranium), Frazer (1973: front and lateral views of tadpole mouth), Limeses (1964 and 1968: musculature), Lynch (1971: skull; 1982: hind foot, eye profile, and upper eyelid of the adult), Perchez and Carroll (1996: oviduct), Ruibal and Thomas (1988: larval musculature, cartilaginous structures, and a cross-section of the body of the tadpole), Wassersug and Heyer (1988: buccal and pharyngeal cavities of the tadpole), and Ziermann et al. (2013: skull and transverse sections of the tadpole).

DISTRIBUTION. The species is distributed across the Gran Chaco ecoregion and can be found in western and northern Paraguay, northern Argentina, and southeastern Bolivia (Map 1).

FOSSIL RECORD. A partial skull from Miocene-Pliocene sediments of the Monte Hermosa Formation in Buenos Aires Province, Argentina was identified as *Lepidobatrachus laevis* by Tomassini et al. (2011). The geographically anomalous position of the fossil relative to the modern distribution of the species is striking, but any need for explanation was removed recently when the specimen was

redescribed as a new species, *Lepidobatrachus australis*, by Nicoli (2015). The phylogenetic affinities of the new species with respect to extant species of *Lepidobatrachus* remain unresolved.

PERTINENT LITERATURE. The most comprehensive sources for the species are Barrio (1968a, 1968b) and Cei (1980). Other information is listed by topic: **biogeography** (Bridarolli and di Tada 1994; Cei 1955, 1956; De la Riva et al. 2000; Duellman 1999; Faivovich 1994; Gallardo 1966; Lynch 1982); **call** (Barrio 1968b; Duellman 2003; Gallardo 1994); **checklists and catalog lists** (Álvarez et al. 1996, 2002; Aquino et al. 1996; Aquino-Shuster et al. 1991; Barrio 1968b; Brusquetti and Lavilla 2006; Céspedez et al. 2004; Cruz et al. 1992; De la Riva et al. 2000; Duellman 1999; Faivovich 1994; Gorham 1974; Gallardo 1966; Glaw et al. 1998, 2000a, 2000b; Gonzales et al. 2006; Harding 1983; Hutchins et al. 2003; Köhler 1997; Kacoliris et al. 2006; Lavilla 1994; Lavilla and Cei 2001; Lavilla et al. 1995a, 1995b; Martinez 1996; Modesto and Noss 2000; Schalk et al. 2013; Slavens 1988; Slavens and Slavens 2000; Weiler et al. 2013; Ziegler et al. 2002); **conservation** (Álvarez et al. 2002; Aquino-Shuster et al. 1991; Bertonatti 1994; De la Riva and Reichle 2014; Duellman 1999; Hutchins et al. 2003; Lavilla 2001; Lavilla and Cei 2001; Lavilla and Brusquetti 2010; Lavilla and Heatwole 2010; Lavilla et al. 2000, 2004; Motte et al. 2009; Stuart et al. 2008; Weiler et al. 2013); **diet** (Scott and Aquino 2005; Scott et al. 1983); **ecology** (Cei 1980; Freiberg 1954 [as *Lepidobatrachus asper*]; Gallardo 1987; Gallardo and Varela de Olmedo 1992; Hutchins et al. 2003; Mattison 2007a, 2007b, 2011; Norman 1994; Parker 1931; Perotti 1997; Reig and Cei 1963; Schalk et al. 2014; Scott and Aquino 2005; Weiler et al. 2013); **evolution** (Blair 1970; Fabrezi 2006, 2011, 2012; Fabrezi and Emerson 2003; Fabrezi and Quinzio 2008; Fabrezi et al. 2014a, 2014b; Faivovich et al. 2014; Hanken 1992; Lynch 1982); **fossils** (Tomassini et al. 2011; Nicoli 2015); **karyotypes** (Barrio and de Chieri 1970; Green and Sessions 2007); **keys** (Cei 1980; Nieden 1923; Weiler et al. 2013); **larvae and larval characteristics** (Alt and Alt 1992; Altig and Johnson 1986, 1989; Altig and McDiarmid 1999a, 1999b; Barraclough 2008, 2009, 2010; Barrio 1963; Burggren and Just 1992; Carr and Altig 1992; Carroll 1996; Carroll et al. 1991b; Cei 1980; Crump 2015; Duellman 2003; Fabrezi 2001b, 2011; Fabrezi and Quinzio 2008; Faivovich and Carrizo 1992; Frazer 1973; Gallardo 1987; Hanken 1992; Larsen 1992; Parker 1931; Ruibal and Thomas 1988; Ulloa Kreisel 2001; Wassersug and Heyer 1988; Ziermann et al. 2013); **morphology and development** (Altig and McDiarmid 1999b; Burggren and Just 1992; Barrio 1968a, 1968b; Bloom et al. 2013; Burton 1998; Cannatella 1999; Carr and Altig 1992; Emerson 1985; Fabrezi 2001a, 2001b, 2006, 2011, 2012; Fabrezi and Barg 2001; Fabrezi and Emerson 2003; Fabrezi and Lobo 2009; Fabrezi and Quinzio 2008; Fabrezi et al. 2014a, 2014b; Freiberg 1954 [as *Lepidobatrachus asper*]; Fritzsch 1988; Fritzsch et al. 1987; Hanken 1992; Limeses 1963, 1964, 1965, 1968; Lynch 1971; Mattison 1993; Parker 1931; Quinzio and Fabrezi 2012; Ruibal and Shoemaker 1984; Scott and Aquino 2005; Starosta and Moncuit 2006; Viertel and Richter 1999; Wassersug and Heyer 1988; Ziermann et al. 2013); **parasites** (de Chambrier and Pertierra 2012; González and Hamann, 2013; Vucetich and Giacobbe 1949 [as *Lepidobatrachus asper*]); **physiology and biochemistry** (Burggren and Just 1992; Carroll 1996; Carroll et al. 1991a, 1991b, 1991c; Fritsch et al. 1987; Larsen 1992; Peavy and Carroll 1993; Perchez and Carroll 1996; Waggener and Carroll 1998a, 1998b; Wang et al. 2015); **popular press books** (Barraclough 2008, 2009, 2010; Bartlett and Bartlett 1996; Coborn 1992; Earley 2014; Flannery and Schouten 2004; Halliday 2010, 2016; Hennessy 2010, 2016; Malkmus 1998, 2000a, 2000b; Mattison 1987 [and reprints, e.g., 1989 and 1994], 1993, 2007a, 2007b, 2011, 2014, 2015; Starosta and Mon-

cuit 2006; The Encyclopedia of Animals 2004; The Encyclopedia of Reptiles, Amphibians & Invertebrates 2006; Twist 2005a, 2005b; Uchiyama 1997, 1999); **reproductive biology** (Alt and Alt 1992; Barraclough 2008, 2009, 2010; Carroll et al. 1991a, 1991c; Crump 2015; de Vosjoli and Mailloux 1989; Duellman 2003; Mattison 1993; Peavy and Carroll 1993; Perchez and Carroll 1996; Perotti 1994, 1997; Waggener and Carroll 1998a, 1998b); **taxonomy, systematics, and phylogenetics** (Barrio 1968a, 1968b; Boulenger 1919 [as *Ceratophrys laevis*]; Cei 1965, 1987; De Sá et al. 2014; de Vosjoli 1990; Fabrezi 2006; Fabrezi and Quinzio 2008; Fabrezi and Lobo 2009; Faivovich et al. 2014; Frank and Ramus 1995; Frost 1985, 2016; Frost et al. 2006; Lynch 1982; Maxson and Ruibal 1988; Nicoli 2015; Parker 1931 [as *Ceratophrys* (*Lepidobatrachus*) *laevis*]; Plötner et al. 2007; Reig and Cei 1963 [as *Lepidobatrachus asper*]; Sokolov 1988; Vellard 1948 [as *Lepidobatrachus asper*]; Zhao et al. 1998).

REMARKS. The description of *Lepidobatrachus laevis* predates the usage of the term holotype, thus a holotype was never explicitly designated in the original description. The description of *Lepidobatrachus laevis* was based on a single specimen (designated XXIV.c by Budgett 1899), but because only a single specimen is mentioned in the original description this is equivalent to designating it as a holotype. Based on the measurement data and registrar information at the Natural History Museum, this is the same specimen as BMNH 1947.2.17.32 (Jeffrey Streicher, Natural History Museum, personal communication, 13 February 2015). Thus, J. S. Budgett is listed as having designated the holotype of *Lepidobatrachus laevis*. All of the type specimens, including the holotype of *Lepidobatrachus laevis*, at the Natural History Museum were renumbered following World War II (Darrel Frost, American Museum of Natural History, personal communication, 29 January 2015). This renumbering of the type specimen resulted in the holotype of *Lepidobatrachus laevis* possessing two specimen numbers; the original number of BMNH 1919.4.23.2 was renumbered as BMNH 1947.2.17.32 (Jeffrey Streicher, Natural History Museum, personal communication, 3 February 2015).

ETYMOLOGY. There were no comments on the etymology of the species in the original description (Budgett 1899). Presumably *lepido* from the Latin *lepidus* (= pleasant) for the perpetually 'smiling' mouth of this species, *batrachus* from the modern Latin *batrachia* (= amphibian) or the Greek βατρακηοσ (= frog or toad), and *laevis* from the Latin *lēvis* (= slight or light) from the Greek λειοσ (= smooth). Compared to the other species in the genus, *Lepidobatrachus laevis* has smooth skin.

ADDITIONAL VERNACULAR NAMES. Guaraní, Kururú chiní (Duellman 2003); Hippo Frog, Wide-mouth Frog (Halliday 2016).

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