

AMPHIBIA: ANURA: LEPTODACTYLIDAE

LEPTODACTYLUS ELENÆ

Catalogue of American Amphibians and Reptiles.

Heyer, W.R. and M.M. Heyer. 2002. *Leptodactylus elenae*.

Leptodactylus elenae Heyer

Leptodactylus elenae Heyer 1978:45. Type locality, "Argentina; Salta, Embarcación." Holotype, Los Angeles County Museum (LACM) 92096, adult female, collected by K.A. Berven, L.M. Heyer, M.H. Heyer, and W.R. Heyer on 4 January 1972 (examined by WRH).

Leptodactylus helenae: Cei 1982:215, 224, 226. *Lapsus*.

• **CONTENT.** The species is monotypic.

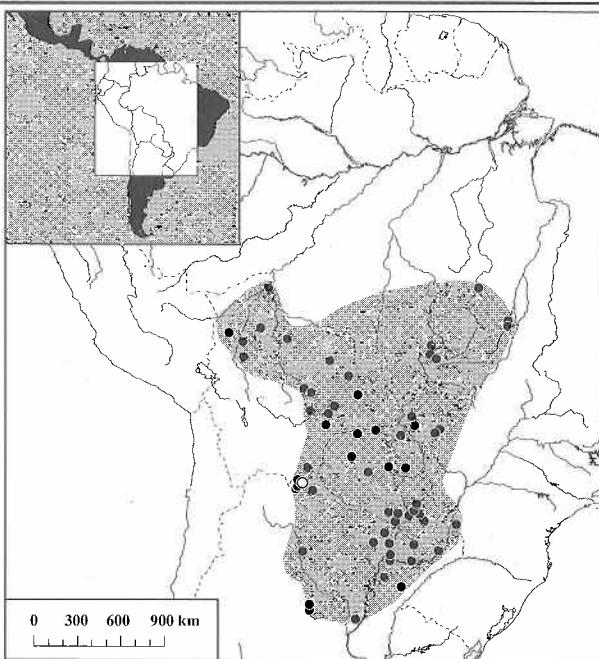
• **DEFINITION.** Adult *Leptodactylus elenae* males are of moderate size, females are moderately small, the head is not as wide as long, and the hind limbs are moderate in length (see Table; Heyer and Thompson 2000 provided definitions of adult size and leg length categories for *Leptodactylus*). Male vocal sacs are modestly expanded laterally and are usually at least moderately darkly pigmented. Male forearms are not hypertrophied. Males lack asperities on the thumbs and chest. Two distinct pairs of dorsolateral folds (indicated by dark/light outlining in indifferently preserved specimens) are present: one pair extends from behind the eye at the level above the posterior edge of the tympanum to the upper groin, and a second pair extends from the top of the tympanum level, posterior to the parotoid gland, to the groin along the flanks. The toe tips are rounded or very slightly swollen. The toes generally lack fringes or lateral fleshy ridges; some individuals have vestigial basal lateral ridges and toe webbing between toes I, II, and III. The upper shank is usually smooth, rarely with weak longitudinal folds. The outer tarsus usually has at least one or two to many white tubercles, but is smooth in some individuals. The sole of the foot has many or scattered white fleshy tubercles.

The upper lip has a distinct (77%) or indistinct (23%) light stripe. No dark suborbital bar is present. An interorbital bar is irregularly shaped. The dorsum ranges from almost uniform tan/brown to a pattern of parallel series of small darker spots, which may be coalesced longitudinally in some individuals, or to one or two small chevrons in the mid-scapular and mid-sacral regions. The dorsolateral folds are usually highlighted by a distinct light pin-stripe, more so posteriorly than anteriorly. The upper pair of dorsolateral folds is usually bordered below by a noticeably darker stripe, which is sometimes quite broad. The species lacks light middorsal stripes. The belly is immaculate or with a few indistinct dark spots or mottling on its lateralmost extent. The posterior thigh surfaces have distinct light horizontal stripes on their lower aspects. The dorsal surface of the shank has irregularly shaped crossbands.

Larvae have not been described.

TABLE. Summary measurement data for *Leptodactylus elenae* (means are in parentheses). Heyer and Thompson (2000) provided definitions of adult size and leg length categories for *Leptodactylus*.

Measurement	Males	Females
SVL (mm)	38–46 (43.1)	39–49 (43.5)
Head length/SVL (%)	35–40 (38)	36–39 (38)
Head width/SVL (%)	31–37 (34)	30–37 (34)
Thigh length/SVL (%)	36–47 (41)	33–46 (41)
Shank length/SVL (%)	44–53 (48)	42–52 (48)
Foot length/SVL (%)	45–57 (50)	45–54 (49)



MAP. Distribution of *Leptodactylus elenae*. The type locality is indicated by a circle. Dots mark other localities. Published locality data used to generate the map should be considered as secondary sources of information, as we did not confirm all specimen identities.



FIGURE 1. *Leptodactylus elenae*. Mucuñucu, Santa Cruz, Bolivia, field number JK 0612 (photograph courtesy of Jörn Köhler).

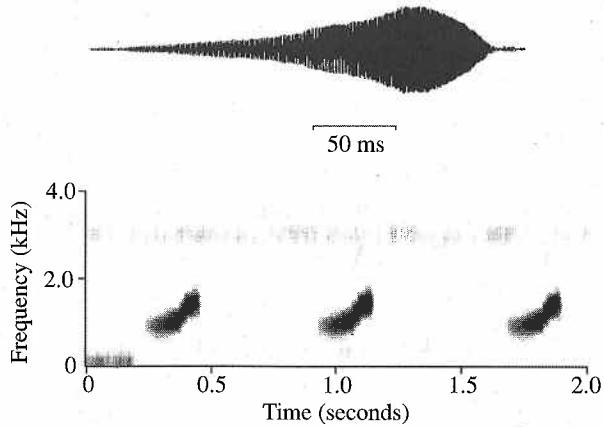


FIGURE 2. Wave form and audiospectrogram displays of the advertisement call of *Leptodactylus elenae* (USNM recording 180, cut 7) from El Tirol, near Encarnación, Itapúa, Paraguay.

The advertisement call consists of a single note per call, given at a rate of 64–120/min. Call duration ranges from 0.2–0.3 s. The call is either unpulsed or with very weak pulses in mid-call. The call is frequency modulated, rising very slowly in the first 1/3–1/2 of the call, then rising rapidly, and finally reaching a plateau at the end of the call. The call is intensity modulated, reaching the loudest intensity about 3/4–4/5 of the call duration, then decreasing rapidly for the rest of the call. The dominant frequency is the fundamental frequency. The dominant frequency ranges from 700–870 Hz at the beginning of the call and from 1370–1500 Hz at the end of the call. Harmonics are either absent (calls analyzed for this account) or present (Barrio 1965).

• **DIAGNOSIS.** Adult *Leptodactylus elenae* have the toes free of webbing or lateral fringes, one or two pair of distinct dorsolateral folds, a light stripe on the lower portion of the posterior face of the thigh, and the sole of the foot covered with obvious light tubercles. These features are shared with (at least some individuals of) *L. albilabris*, *L. didymus*, *L. fragilis*, *L. latinasus*, *L. mystaceus*, *L. notoaktites*, and *L. spixi*. *Leptodactylus elenae* lacks white tubercles on the dorsal surface of the shank, differing from *L. albilabris*, *L. fragilis*, *L. latinasus*, and *L. spixi*. *Leptodactylus elenae* usually has white tubercles on the posterior tarsus; the tarsus is smooth in *L. didymus*, *L. mystaceus*, and *L. notoaktites*.

• **DESCRIPTIONS.** Heyer (1978) provided morphological characteristics of the species and of the holotype. Detailed character descriptions of adults including color patterns are in Cei (1987), De la Riva (1993), and Gallardo (1987). Morphology and color were described by Cei (1980, as *L. mystaceus*), Gallardo (1964, as *L. mystaceus*), Méhely (1904, as *L. mystaceus*), and Proctor (1921, as *L. longirostris*). Mercolli et al. (1995) discussed sexually dimorphic color. Descriptions of advertisement calls are in Gallardo (1987), Gallardo and Valera de Olmedo (1992), Heyer et al. (1996), and Marquez et al. (1995), and as *L. mystaceus* in Barrio (1965, reiterated by Straughan and Heyer 1976). A cassette recording was provided by Straneck et al. (1993). An incomplete description of the karyotype is in Heyer (1978).

• **ILLUSTRATIONS.** Color photographs of adults are in De La Riva et al. (2000), Couturier (1985, as *L. mystaceus*), and Moravec and Aparicio (2000). Other photographs are in Cei (1987), Gallardo (1964, as *L. mystaceus*), and Heyer (1978). Figure drawings of adult specimens are in Cei (1980, as *L. mystaceus*), Di Tada et al. (1976, as *L. mystaceus*), Gallardo (1987), and Straneck et al. (1993). Limeses (1969, as *L. mystaceus*) and Limeses et al. (1972, as *L. mystaceus*) provided drawings of anatomical features. Audiospectrograms of the advertisement call are in Barrio (1965, as *L. mystaceus*), Heyer et al. (1996), Marquez et al. (1995), and Straneck et al. (1993). A wave form of the advertisement call is figured in Heyer et al. (1996).

• **DISTRIBUTION.** *Leptodactylus elenae* is a wide-ranging species that inhabits semi-arid Chaco, cerrado, caatinga, and dry forest regions from the eastern slopes of Bolivia to Mato Grosso, Brazil and south through Paraguay to north-central Argentina. Mercolli et al. (1995) and Strüssman et al. (2000a) found the species in forested formations and De La Riva (1993), Harvey (1998), Heyer and Maxson (1982), and Köhler (2000) noted that it preferred open habitats. Duellman (1999) tabled its distribution as Southwest Amazon Basin-Guiana lowlands and Caatinga-Cerrado-Chaco. Harding (1983) listed its distribution by countries in the New World. The Peruvian locality

for *L. elenae* of Tocache Nuevo, Río Huallaga, San Martin reported by Heyer (1978) and mentioned by Henle (1992) and Morales (1995) was questioned by Rodriguez et al. (1993). The juvenile specimens (USNM 195998–195999) are not *L. elenae* but probably an undescribed species of the *L. mystaceus* complex (W.R. Heyer, pers. obs.). A distributional map was provided by Heyer (1978).

Additional references to distribution and localities are listed by country: **Argentina** (Alvarez et al. 1996; Barrio 1965, as *L. mystaceus*; Berg 1896, as *L. mystaceus*; Boulenger 1889, as *L. poecilochilus*; Blair 1976, as *L. mystaceus*; Blair et al. 1976, as *L. mystaceus*; Bosso and Céspedes 1995; Cei 1955, 1980, as *L. mystaceus*, and 1987; Céspedes et al. 1995; Di Tada et al. 1976, as *L. mystaceus*; Duellman and Veloso 1977, as *L. mystaceus*; Freiberg 1942, as *L. mystaceus*; Gallardo 1964, 1966, 1974, as *L. mystaceus*, and 1987; Heyer 1978; Lajmanovich 1991; Laurent 1973, as *L. mystaceus*; Lavilla and Scrocchi 1991, 1999; Lavilla et al. 1992, 2000b; Mares et al. 1977, as *L. mystaceus*; Martori and Aun 1995; Mercolli et al. 1995; Montanelli and Acosta 1991; Straneck et al. 1993; Vaira 2001a; Vellard 1948, as *L. mystaceus*); **Bolivia** (Aparicio 1992; De la Riva 1990, 1993, 1995; De la Riva et al. 2000; Fugler 1983, 1984, 1988; Gallardo 1964, as *L. mystaceus*; Gans 1960, as *L. mystaceus*; González A. 1998; Harvey 1998; Harvey et al. 1998; Heyer 1978; Köhler 2000; Köhler and Löters 1999; Middendorf and Reynolds 2000; Moravec and Aparicio 2000; Padial et al. 2000; Parker 1928, as *L. mystaceus*; Peracca 1897, as *L. poecilochilus*); **Brazil** (Baumann 1912, as *L. poecilochilus* in part; Carvalho 1939, as *L. mystaceus*; Gallardo 1964, as *L. mystaceus*; Gans 1960, as *L. mystaceus*; Heyer 1978; Strüssman et al. 2000c); and **Paraguay** (Aquino 1986; Aquino et al. 1996; Bertoni, 1914, 1939, as *L. poecilochilus*; Heyer et al. 1996; Méhely, 1904 as *L. mystaceus*; Peracca 1895, as *L. poecilochilus*; Scott and Lovett 1975).

• FOSSIL RECORD. None.

• **PERTINENT LITERATURE.** The most comprehensive works on the species are those of Gallardo (1964, as *L. mystaceus*) and Heyer (1978). Additional literature is listed by topic: **bibliographic information and lists** (Lavilla and Cei 2001, Liner 1992, Walley 2000); **call and call parameters** (Barrio 1965, as *L. mystaceus*; De la Riva 1993; Heyer et al. 1996; Marquez et al. 1995; Straughan and Heyer 1976, as *L. mystaceus*); **checklists** (Contreras and Contreras 1982, as *L. mystaceus*; De la Riva et al. 2000); **conservation** (Anonymous 1997; Lavilla 2001; Lavilla et al. 2000a); **ecology, natural history, reproduction** (De la Riva 1993, 1995; Fugler 1986, 1988; Mercolli et al. 1995; Moravec and Aparicio 2000; Perotti 1994; Strüssman et al. 2000b; Vaira 2001b); **evolution** (Heyer 1978); **habitat** (De la Riva 1993; González A. 1998; Köhler 2000; Mercolli et al. 1995; Moravec and Aparicio 2000); **lists of specimens in individual collections** (Aquino et al. 1996; Avila and Martori 1991; Elter 1981, as *L. mystaceus*; Gavetti and Andreone 1993, as *L. mystaceus*; Quijada B. 1914, as *L. poecilochilus*; Tedesco et al. 1993; Yanosky et al. 1993, as *L. mystaceus*); **morphology** (Cei 1980, as *L. mystaceus*; Fabrezi 1993; Gallardo 1964, as *L. mystaceus*; Heyer et al. 1996; Limeses 1969, as *L. mystaceus*; Limeses et al. 1972, as *L. mystaceus*; Perotti 1994; Ponssa 1999; Strüssman et al. 2000b); **parasite host** (Baker and Vaucher 1984, 1985, 1986, 1988); **relationships** (Heyer 1978, Heyer and Maxson 1982, Maxson and Heyer 1988); **species accounts and systematics** (Berg 1896, as *L. poecilochilus*; Cei 1956, 1980, as *L. mystaceus*, and 1987; Di Tada et al. 1976, as *L. mystaceus*; Freiberg 1942, as *L. mystaceus*; Gallardo and Valera de Olmedo 1992; Heyer 1983; Heyer et al. 1996); **species or taxonomic lists** (Frost 1985; Glaw et al. 2000; Gorham 1966, as *L. mystaceus* in part; Lavilla 1992; Lavilla and Cei

2001; Nieden 1923, as *L. mystaceus* in part); and zoogeography (De la Riva 1993; Duellman and Thomas 1996; Gallardo 1966, as *L. mystaceus*; Harvey 1998; Heyer 1978, 1988; Heyer and Maxson 1982).

• **NOMENCLATURAL HISTORY.** *Leptodactylus elenae* was identified as *L. longirostris*, *L. mystaceus*, and *L. poecilochilus* prior to its recognition as a distinct species in 1978.

• **REMARKS.** The common name for *Leptodactylus elenae*, Rana Marmolada (Straneck et al. 1993), was translated to Marbled Frog by Frank and Ramus (1995).

• **ETYMOLOGY.** Heyer (1978) named the species for his daughter, Elena.

• **ACKNOWLEDGMENTS.** Ismael Di Tada, Marissa Fabrezi, Paulo C.A. Garcia, Esteban O. Lavilla, Norman J. Scott, Jr., and P.E. Vanzolini shared their knowledge in resolving queries that arose during the preparation of the account. Jörn Köhler provided the photograph of *Leptodactylus elenae*. Esteban O. Lavilla critically reviewed the manuscript. Work on this account was supported in part by the Neotropical Lowlands Research Program, Smithsonian Institution (Richard P. Vari, Principal Investigator) and the National Science Foundation (award 9815787 to Rafael de Sá and WRH).

LITERATURE CITED

- Alvarez, B.B., J.A. Céspedes, M.L. Lions, A. Hernando, and R. Aguirre. 1996. Herpetofauna de las provincias de Corrientes, Chaco y Formosa (Argentina). *Facena* 12:119–134.
- Anonymous. 1997. Aspectos ecológicos dos vertebrados terrestres e semiaquáticos no Pantanal, p. 197–433. In Plano de Conservação da Bacia do Alto Paraguai, Diagnóstico dos Meios Físico e Biótico, Meio Biótico. Volume II, Tomo III. Empresa Brasileira de Pesquisa Agropecuária, Projeto Pantanal, Programa Nacional de Meio Ambiente, Brasília, Brasil.
- Aparicio, J. 1992. Herpetofauna, p. 113–119. In H. Salm and M. Marconi (eds.), Reserva Nacional Amazônica Manupipi-Heath: Programa de Liga de Defensa del Medio Ambiente. Reestructuración (Fase II). LIDEMA, Cordeando: La Paz, Bolivia.
- Aquino, A.L. 1986. Anfibios del Arroyo Mina. Boletín el Inventario Biológico Nacional (Paraguay) (8):4.
- Aquino, A.L., N.J. Scott, and M. Motte. 1996. Lista de anfibios y reptiles del Museo Nacional de Historia Natural del Paraguay (Marzo, 1980–Setiembre, 1995), p. 331–400. In O.R. Martínez (ed.), Colecciones de Flora y Fauna del Museo Nacional de Historia Natural del Paraguay. Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Paraguay.
- Avila, L.J. and R. Martori. 1991. La colección herpetológica de la orientación zoología de vertebrados (Dto. Cs. Naturales) de la Universidad Nacional de Río Cuarto. Boletín de la Asociación Herpetológica Argentina 7:19–20.
- Baker, M.R. and C. Vaucher. 1984. Parasitic helminths from Paraguay VI: *Cosmocerca* Diesing, 1861 (Nematoda: Cosmocercoidea) from frogs. *Revue Suisse de Zoologie* 91:925–934.
- and —. 1985. Parasitic helminths from Paraguay VII: Systematic position of *Oxyascaris* Travassos, 1920 (Nematoda: Cosmocercoidea). *Revue Suisse de Zoologie* 92:303–310.
- and —. 1986. Parasitic helminths from Paraguay XII: *Aplectana* Railliet and Henry, 1916 (Nematoda: Cosmocercoidea) from frogs. *Revue Suisse de Zoologie* 93:607–616.
- and —. 1988. Parasitic helminths from Paraguay XV: Atractidae (Nematoda: Cosmocercoidea) from frogs. *Revue Suisse de Zoologie* 95:421–431.
- Barrio, A. 1965. Afinidades del canto nupcial de las especies cavícolas del género *Leptodactylus* (Anura-Leptodactylidae). *Physis* 25:401–410.
- Baumann, F. 1912. Brasilianische Batrachier des Berner Naturhistorischen Museums nebst Untersuchungen über die geographische Verbreitung der Batrachier in Brasilien. *Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere*, Jena 33:87–172 + 3 plates.
- Berg, C. 1896. Batracios argentinos. Enumeración sistemática, sinonímica y bibliográfica de los batracios de la República Argentina (con un cuadro sinóptico de clasificación). *Anales del Museo Nacional de Buenos Aires* 5:147–226.
- Bertoni, A. de W. 1914. Fauna Paraguaya. Catálogos sistemáticos de los vertebrados del Paraguay. Peces, batracios, reptiles, aves y mamíferos conocidos hasta 1913, p. 17–86. In M.S. Bertoni (ed.), *Descripción Física y Económica del Paraguay. Numeración Novenal*, 59:I. Establecimiento Gráfico M. Brossa, Asunción.
- . 1939. Catálogos sistemáticos de los vertebrados del Paraguay. Mamíferos, aves, reptiles, batracios y peces comprobados hasta 1937. *Revista de la Sociedad Científica del Paraguay* 4:5–59.
- Blair, W.F. 1976. Adaptation of anurans to equivalent desert scrub of North and South America, p. 197–222. In D.W. Goodall (ed.), *Evolution of Desert Biota*. University of Texas Press, Austin.
- , A.C. Hulse, and M.A. Mares. 1976. Origins and affinities of vertebrates of the North American Sonoran Desert and the Monte Desert of northwestern Argentina. *Journal of Biogeography* 3:1–18.
- Bosso, A. and J. Céspedes. 1995. Listas actualizadas de los anfibios de la áreas protegidas nacionales de nordeste argentino (Provincias de Misiones, Corrientes, Chaco y Formosa). XI Reunión de Comunicaciones Herpetológicas, Asociación Herpetológica Argentina, 11 al 13 de Octubre de 1995:5–6.
- Boulenger, G.A. 1889. On a collection of batrachians made by Prof. Charles Spiegazzini at Colonia Resistencia, South Chaco, Argentine Republic. *Annali del Museo Civico di Storia Naturale di Genova*, ser. 2, VII:246–249 + plate II.
- Carvalho, A.L. 1939. Observações e lista dos batráquios. *Boletim Biológico* (N.S.) 4:279–280.
- Cei, J.M. 1955. Chacoan batrachians in central Argentina. *Copeia* 1955: 291–293.
- . 1956. Nueva lista sistemática de los batracios de Argentina y breves notas sobre su biología y ecología. *Investigaciones Zoológicas Chilenas* 3:31–68 + 9 plates.
- . 1980. Amphibians of Argentina. *Monitore Zoologico Italiano* (N.S.) Monograph (2):1–609 + xii.
- . 1982. Reliquias y refugios, al sur del tropico, de la herpetofauna austral Pleistocénica Sudamericana, p. 213–227. In P.J. Salinas (ed.), *Zoología Neotropical*. Tomo I. Actas del VIII Congreso Latinoamericano del Zoología, Venezuela.
- . 1987. Additional notes to "Amphibians of Argentina:" An update, 1980–1986. *Monitore Zoologico Italiano* (N.S.) 21:209–272.
- Céspedes, J.A., R.H. Aguirre, and B.B. Alvarez. 1995. Composición y distribución de la anfibiofauna de la provincia de Corrientes (Argentina). *Facena* 11:25–49.
- Contreras, J.R. and A.N. Ch. de Contreras. 1982. Características ecológicas y biogeográficas de la batracofauna del noreste de la Provincia de Corrientes, Argentina. *Ecosur* 9:29–66.
- Couturier, G. 1985. La rana criolla, p. 1–32. In M.A. Palermo (ed.), *Fauna Argentina: Anfibios y Reptiles* 1. Centro Editor de América Latina, Buenos Aires.
- De la Riva, I. 1990. Lista preliminar comentada de los anfibios de Bolivia con datos sobre su distribución. *Bollettino del Museo Regionale di Scienze Naturali Torino* 8:261–319.
- . 1993. Ecología de una comunidad neotropical de anfibios durante la estación lluviosa. Ph.D. Thesis, Universidad Complutense de Madrid.
- . 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.
- , J. Köhler, S. Lötters, and S. Reichle. 2000. Ten years of research on Bolivian amphibians: updated checklist, distribution, taxonomic problems, literature and iconography. *Revista Española de Herpetología* 14:19–164.
- Di Tada, I.E., M.M. Salusso, and R.A. Martori. 1976. Lista de los batracios de Córdoba (con notas sobre su historia natural). *Boletín de la Academia Nacional de Ciencias, Córdoba*, Argentina 51:325–362.
- Duellman, W.E. 1999. Distribution patterns of amphibians in South America, p. 255–328. In W.E. Duellman (ed.), *Patterns of Distribution of Amphibians. A Global Perspective*. The Johns Hopkins University Press, Baltimore and London.
- and R. Thomas. 1996. Anuran-amphibians from a seasonally dry

- forest in southeastern Peru and comparisons of the anurans among sites in the upper Amazon basin. Occasional Papers of the Natural History Museum, University of Kansas (180):1–34.
- and A. Velo M. 1977. Phylogeny of *Pleurodema* (Anura: Leptodactylidae): A biogeographic model. Occasional Papers of the Museum of Natural History, University of Kansas (64):1–46.
- Elter, O. 1981. La collezione erpetologica del Museo di Zootologia dell' Università di Torino. Museo Regionale di Scienze Naturali, Torino Cataloghi (5):1–116.
- Fabrezi, M. 1993. The anuran tarsus. *Alytes* 11:47–63.
- Frank, N. and E. Ramus. 1995. A Complete Guide to Scientific and Common Names of Reptiles and Amphibians of the World. NG Publishing, Inc., Pottsville, Pennsylvania.
- Freiberg, M.A. 1942. Enumeración sistemática y distribución geográfica de los batracios argentinos. *Physis* 19:219–240.
- Frost, D.R. (ed.). 1985. Amphibian Species of the World: A Taxonomic and Geographical Reference. Allen Press Inc. and the Association of Systematics Collections, Lawrence, Kansas.
- Fugler, C.M. 1983. Lista preliminar de los anfibios y reptiles de Tumi Chucua. Museo Nacional de Historia Natural (Bolivia) Comunicación (2):4–11.
- . 1984. Tercera contribución a la fauna herpetológica del oriente Boliviano. *Ecología en Bolivia* 5:63–72.
- . 1986. La estructura de una comunidad herpetológica en las selvas benianas en la estación de sequía. *Ecología en Bolivia* 8:1–20.
- . 1988. Consideraciones sobre la herpetofauna de las selvas tropicales bolivianas. Museo Nacional de Historia Natural (Bolivia) Comunicación (6):3–12.
- Gallardo, J.M. 1964. *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.
- . 1966. Zoogeografía de los anfibios chaqueños. *Physis* 26:67–81.
- . 1974. Anfibios de los Alrededores de Buenos Aires. Editorial Universitaria de Buenos Aires, Buenos Aires.
- . 1987. Anfibios Argentinos: Guía para su Identificación. Biblioteca Mosaico, Buenos Aires.
- and E. Valera de Olmedo. 1992. Anfibios de la República Argentina: Ecología y comportamiento. Fauna de Agua Dulce de la República Argentina 41:1–116.
- Gans, C. 1960. Notes on a herpetological collecting trip through the southeastern lowlands of Bolivia. *Annals of Carnegie Museum* 35: 283–314.
- Gavetti, E. and F. Andreone. 1993. Revised catalogue of the herpetological collection in Turin University. I. Amphibia. Museo Regionale di Scienze Naturali, Torino Cataloghi (10):1–185.
- Glaw, F., J. Köhler, R. Hofrichter, and A. Dubois. 2000. Amphibian systematics: List of recent families, genera, and species, p. 252–258. In R. Hofrichter (ed.), *Amphibians: The World of Frogs, Toads, Salamanders and Newts*. Firefly Books, Buffalo, New York (originally published in German in 1998 by Weltbild Verlag GmbH, Augsburg, Germany).
- González A., L. 1998. La herpetofauna del Izozog. *Ecología en Bolivia* 31:45–52.
- Gorham, S.W. 1966. Liste der rezenten Amphibien und Reptilien: Ascaphidae, Leiopelmatidae [sic!], Pipidae, Discoglossidae, Pelobatidae, Leptodactylidae, Rhinophryidae. *Das Tierreich* (85):1–222 + xvi.
- Harding, K.A. 1983. Catalogue of New World Amphibians. Pergamon Press, Oxford.
- Harvey, M.B. 1998. Reptiles and amphibians of Parque Nacional Noel Kempff Mercado, p. 144–153. In T.J. Killeen and T.S. Schulenberg (eds.), *A Biological Assessment of Parque Nacional Noel Kempff Mercado, Bolivia*. Rapid Assessment Program, Working Papers (10): 1–372.
- , J. Aparicio E., C. Cortez, L. González A., J.F. Guerra S., M.E. Montaño, and M.E. Pérez B. 1998. Appendix 4. Reptile and amphibian species of Parque Nacional Noel Kempff Mercado, p. 348–355. In T.J. Killeen and T.S. Schulenberg (eds.), *A Biological Assessment of Parque Nacional Noel Kempff Mercado, Bolivia*. Rapid Assessment Program, Working Papers (10):1–372.
- Henle, K. 1992. Zur Amphibienvauna Perus nebst Beschreibung eines neuen *Eleutherodactylus* (Leptodactylidae). *Bonner zoologische Beiträge* 43:79–129.
- 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.
- . 1983. Clarification of the names *Rana mystacea* Spix, 1824, *Leptodactylus amazonicus* Heyer, 1978 and a description of a new species, *Leptodactylus spixii* (Amphibia: Leptodactylidae). *Proceedings of the Biological Society of Washington* 96:270–272.
- . 1988. On frog distribution patterns east of the Andes, p. 245–273. In P.E. Vanzolini and W.R. Heyer (eds.), *Proceedings of a Workshop on Neotropical Distribution Patterns Held 12–16 January 1987*. Academia Brasileira de Ciências, Rio de Janeiro.
- and L.R. Maxson. 1982. Distributions, relationships, and zoogeography of lowland frogs: The *Leptodactylus* complex in South America, with special reference to Amazonia, p. 375–388. In G.T. Prance (ed.), *Biological Diversification in the Tropics*. Columbia University Press, New York.
- and A.S. Thompson. 2000. *Leptodactylus rugosus*. Catalogue of American Amphibians and Reptiles (708):1–5.
- , J.M. García-López, and A.J. Cardoso. 1996. Advertisement call variation in the *Leptodactylus mystaceus* species complex (Amphibia: Leptodactylidae) with a description of a new sibling species. *Amphibia-Reptilia* 17:7–31.
- Köhler, J. 2000. Amphibian diversity in Bolivia: A study with special reference to montane forest regions. *Bonner Zoologische Monographien* (48):1–243.
- and S. Lötters. 1999. Annotated list of amphibian records from the Departamento Pando, Bolivia, with description of some advertisement calls. *Bonner Zoologische Beiträge* 48:259–273.
- Lajmanovich, R.C. 1991. Batracofauna del valle de inundación del Paraná. *Revista de la Asociación de Ciencias Naturales del Litoral* 22:69–78.
- Laurent, R.F. 1973. Comportamiento territorial en *Phyllomedusa hypochondrialis* (Daudin). *Acta Zoológica Lilloana* 26:315–316.
- Lavilla, E.O. 1992. Tipos portadores de nombre y localidades tipo de anfibios de Argentina. *Acta Zoológica Lilloana* 42:61–100.
- . 2001. Amenazas, declinaciones poblacionales y extinciones en anfibios argentinos. *Cuadernos de Herpetología* 15:59–82.
- and J.M. Cei. 2001. Amphibians of Argentina. A second update, 1987–2000. *Museo Regionale di Scienze Naturali Torino, Monografie* (28): 1–177 + 8 plates.
- and G.J. Scrocchi. 1991. Aportes a la herpetología del Chaco Argentino I. Lista comentada de los taxa colectados por la Expedición PRHERP 1985. *Acta Zoológica Lilloana* 40:21–32.
- and —. 1999. Anfibios y reptiles de Tariquía, p. 83–92. In J.A. González, G.J. Scrocchi, and E.O. Lavilla (eds.), *Relevamiento de la Biodiversidad de la Reserva Nacional de Flora y Fauna Tariquía (Tarija, Bolivia)*. Serie Conservación de la Naturaleza (14):1–134.
- , —, and L.J. Avila. 1992. Clave para la identificación de los anfibios de la Provincia de Córdoba (Argentina). *Asociación Herpetológica Argentina, Serie de Divulgación* (7):1–18.
- , M.L. Ponssa, D. Baldo, N. Basso, A. Bosso, J. Céspedes, J.C. Chebez, J. Faivovich, L. Ferrari, R. Lajmanovich, J.A. Langone, P. Peltzer, C. Úbeda, M. Vaira, and F.V. Candioti. 2000a. Categorización de los anfibios de Argentina, p. 11–34. In E.O. Lavilla, E. Richard, and G.J. Scrocchi (eds.), *Categorización de Los Anfibios y Reptiles de la República Argentina*. Asociación Herpetológica Argentina, San Miguel de Tucumán.
- , M. Vaira, M.L. Ponssa, and L. Ferrari. 2000b. Batracofauna de las Yungas Andinas de Argentina: Una síntesis. *Cuadernos de Herpetología* 14:5–26.
- Limeses, C.E. 1969. Las especies Argentinas del género *Leptodactylus* (Anura, Leptodactylidae). Algunos aspectos anatómicos de posible significación taxonómica. Parte I. *Physis* 28:457–470.
- , I. Vignes, and M. Tio. 1972. Las especies Argentinas del género *Leptodactylus* (Anura, Leptodactylidae). Algunos aspectos anatómicos de posible significación taxonómica. Parte II. *Physis* 31:631–652.
- Liner, E.A. 1992. Bibliography and scientific name index to amphibians and reptiles in the publications of the Biological Society of Washington Bulletin 1–8, 1918–1988 and Proceedings 1–100, 1882–1987. Smithsonian Herpetological Information Service (92):1–68.
- Mares, M.S., W.F. Blair, F.A. Enders, D. Gregor, A.C. Hulse, J.H. Hunt, D. Otte, R.D. Sage, and C.S. Tomoff. 1977. The strategies and community patterns of desert animals, p. 107–163, 269–285. In G.H. Orians and O.T. Solbrig (eds.), *Convergent Evolution in Warm Deserts: An Examination of Strategies and Patterns in Deserts of Argentina and the United States*. US/IBP Synthesis Series 3. Dowden,

- Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.
- Marquez, R., I. De la Riva, and J. Bosch. 1995. Advertisement calls of Bolivian Leptodactylidae (Amphibia Anura). *Journal of Zoology*, London 237:313–336.
- Martori, R. and L. Aun. 1995. Relevamiento de la herpetofauna de las Sierras Pampeanas del este en la provincia de Córdoba (Argentina) (registro de taxa y comentarios taxonómicos). *Acta Zoologica Lilloana* 43:87–97.
- Maxson, L.R. and W.R. Heyer. 1988. Molecular systematics of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Fieldiana, Zology, New Series* 41:1–13.
- Méhely, L. v. 1904. Investigations on Paraguayan batrachians. *Annales Historico-Naturales Musei Nationalis Hungarici* 2:207–232 + plate 13.
- Mercolli, C., A.A. Yanosky, and J.R. Dixon. 1995. The ecology of *Leptodactylus elenae* Heyer, 1978 (Anura: Leptodactylidae) in a protected area in subtropical Argentina. *Bulletin of the Maryland Herpetological Society* 31:130–142.
- Middendorf, G. and R. Reynolds. 2000. Herpetofauna of the Beni Biological Station Biosphere Reserve, Amazonian Bolivia: Additional information, and current knowledge in context, p. 151–169. In O. Herrera-MacBryde, F. Dallmeier, B. MacBryde, J.A. Comiskey, and C. Miranda (eds.), *Biodiversidad, Conservación y Manejo en la Región de la Reserva de la Biosfera Estación Biológica del Beni, Bolivia*. Smithsonian Institution MAB Series (4), Washington, D.C.
- Montanelli, S.B. and S. Acosta. 1991. Lista preliminar de la herpetofauna del Parque Nacional Iguazú. *Boletín de la Asociación Herpetológica Argentina* 7:9–10.
- Morales, V.R. 1995. Checklist and taxonomic bibliography of the amphibians from Perú. *Smithsonian Herpetological Information Service* (107):1–20.
- Moravec, J. and J. Aparicio. 2000. Amphibians and reptiles recently recorded from the surroundings of Riberalta (Departamento Beni, Bolivia). *Časopsis Národního muzea, Rada přírodevedená* 169:1–15 + 4 plates.
- Nieden, F. 1923. Amphibia. Anura I. Subordo Aglossa und Phaneroglossa, Sectio 1 Arcifera. *Das Tierreich* (46):xxxii + 1–584.
- Padial, J.M., S. Bielskis, and J. Castroviejo. 2000. Sobre los anfibios del pie de monte del Departamento de La Paz (Bolivia). *Boletín de la Asociación Herpetológica Española* 11:59–62.
- Parker, H.W. 1928. Notes on reptiles and batrachians from Matto Grosso and E. Bolivia. *Annals and Magazine of Natural History* (Ser. 10) 2: 96–99.
- Peracca, M.G. 1895. Viaggio del Dott. Alfredo Borelli nella Repubblica Argentina e nel Paraguay. Rettili ed Anfibi. *Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino* 10:1–32.
- . 1897. Viaggio del Dott. Alfredo Borelli nel Chaco boliviano e nella Repubblica Argentina. Rettili ed Anfibi. *Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino* 12:1–19.
- Perotti, M.G. 1994. Aportes preliminares sobre la reproducción en una comunidad de anuros chaqueños en Argentina. *Cuadernos de Herpetología* 8:39–50.
- Ponssa, M.L. 1999. Osteología comparada de las especies Argentinas del grupo *fuscus* del género *Leptodactylus* (Anura, Leptodactylidae) [Abstract], p. 97. In *Publicación Extra, Museo Nacional de Historia Natural, Montevideo-Uruguay* (50):1–137.
- Procter, J.B. 1921. On a small collection of reptiles and batrachians made by Mr. Goodfellow in E. Bolivia. *Annals and Magazine of Natural History* (Ser. 9) 7:189–192.
- Quijada B., B. 1914. Catálogo de las batracios chilenos i extranjeros conservados en el Museo Nacional. *Boletín del Museo Nacional de Chile* 7:319–326.
- Rodríguez, L.O., J.H. Córdova, and J. Icochea. 1993. Lista preliminar de los anfibios del Perú. *Publicaciones del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Serie A, Zoológica* (45):1–22.
- Scott, N.J. and J.W. Lovett. 1975. A collection of reptiles and amphibians from the Chaco of Paraguay. *The University of Connecticut Occasional Papers, Biological Science Series* 2:257–266.
- Straneck, R., E.V. de Olmedo, and G.R. Carrizo. 1993. *Catálogo de Voces de Anfibios Argentinos*. Tomo 1. Literature of Latin America, Buenos Aires (includes cassette recording).
- Straughan, I.R. and W.R. Heyer. 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.
- Strüessmann, C., C. P. de Almeida Prado, M. Uetanabaro, and V.L. Ferreira. 2000a. Amphibian and reptile survey of selected localities in the southern pantanal floodplains and surrounding cerrado, Mato Grosso do Sul, Brasil. *Rapid Assessment Program Bulletin of Biological Assessment* (18):98–102 + compact disk.
- , —, —, and —. 2000b. Appendix 9. Amphibians recorded during the AquaRAP survey, with natural history data. *Rapid Assessment Program Bulletin of Biological Assessment* (18):299–300 + compact disk.
- , —, —, and —. 2000c. Appendix 11. Anuran species recorded in each region. *Rapid Assessment Program Bulletin of Biological Assessment* (18):303–304 + compact disk.
- Tedesco, M.E., B.B. Alvarez, S. Bergna, A. Hernando, and R. Aguirre. 1993. Nota sobre la colección herpetológica Corrientes–Universidad Nacional del Nordeste (FACENA)–República Argentina. *Boletín de la Asociación Herpetológica Argentina* 9:4–6.
- Vaira, M. 2001a. Distribución especial de una comunidad de anuros de las Yungas Andinas de Argentina. *Cuadernos de Herpetología* 15:45–57.
- . 2001b. Breeding biology of the leaf frog, *Phyllomedusa boliviiana* (Anura, Hylidae). *Amphibia-Reptilia* 22:421–429.
- Vellard, J. 1948. Batracios del Chaco Argentino. *Acta Zoológica Lilloana* 5:137–174.
- Walley, H.D. 2000. Bibliography and scientific name index to amphibians and reptiles in the Occasional Papers of the Museum of Natural History, University of Kansas, Numbers 1–180, 1971–1995. *Smithsonian Herpetological Information Service* (128):1–45.
- Yanosky, A.A., J.R. Dixon, and C. Mercolli. 1993. The herpetofauna of El Bagual Ecological Reserve (Formosa, Argentina) with comments on its herpetological collection. *Bulletin of the Maryland Herpetological Society* 29:160–171.

W. RONALD HEYER and MIRIAM MUEDEKING HEYER, *Amphibians & Reptiles*, MRC 162, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0162, USA.

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