Catalogue of American Amphibians and Reptiles.

Heyer, W.R., M.M. Heyer, and R.O. de Sá. 2010. *Leptodactylus savagei*.

Leptodactylus savagei Heyer
Savage's Thin-toed Frog

Cystignathus pentadactylus: Cope 1887:18.
Leptodactylus pentadactylus: Noble 1918:323.
Leptodactylus pentadactylus dengleri: Taylor 1952: 649.
Leptodactylus pentadactylus pentadactylus: Gans 1958:1.
Leptodactylus dengleri: Goin 1959:136.
Leptodactylus pendactylus: Savage and Villa R. 1986:23. *Lapsus*.
Leptodactylus pentadcactylus: Savage and Villa R. 1986:104. *Lapsus*.
Leptodactylus savagei Heyer 2005:330. Type-locality, "Rincon de Osa, Puntarenas, Costa Rica, 08º 42'N, 83º29'W." Holotype, National Museum of Natural History, Smithsonian Institution (USNM) 227652, adult male, collected by Miriam H. Heyer and W. Ronald Heyer on 11 June 1973.

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

• **DEFINITION.** Adult *Leptodactylus savagei* are large, the head is as wide as long or usually wider than long, and the hind limbs are moderate in length (Table 1; Heyer and Thompson (2000) provided definitions of adult size and leg length categories for *Leptodactylus*). Male vocal sacs are not visible externally. Sexually active males have hypertrophied forearms, usually 1 large black spine on each thumb, rarely with 1 large spine and a prepollical bump, and a pair of black chest spines. A pair of entire dorsolateral folds extend anteriorly from at least one-half to full distance from eye to groin, the dorsolateral folds are rarely interrupted. Flank folds (diverging from the supratympanic fold at the uppermost posterior portion of the tympanum and extending as far as the lower flank at mid-body level) range from entire (often) to only a dark spot/wart (rarely) in the area where the fold would be between the tympanum and shoulder. Lateral folds are not distinguishable. The toe tips are rounded and either barely wider than or of equal width as the toes immediately behind the tips. The toes have weak to noticeable lateral ridges and either lack any web or (usually) have vestigial webbing between toes I-II-III or I-II-III-IV. Metamorphic and slightly larger juveniles lack webbing and either have very weak lateral ridges or lack them. The upper shank surfaces almost always have some texture, including a shagreen and/or small black or white tubercles. The outer surface of the tarsus may either be smooth or with a shagreen or small black or white tubercles. The sole of the foot is typically smooth, lacking texture.

TABLE 1. Summary measurement data for *Leptodactylus savagei* (means are in parentheses).

Measurement	Males	Females
SVL (mm)	106–156 (133.2)	110–164 (137.1)
Head length/SVL (%)	33–40 (38)	34–40 (37)
Head width/SVL (%)	36–44 (39)	33–42 (38)
Thigh length/SVL (%)	37–47 (42)	37–46 (42)
Shank length/SVL (%)	40–49 (44)	39–48 (44)
Foot length/SVL (%)	38–51 (46)	40–51 (46)

FIGURE 1. *Leptodactylus savagei*, Rincon de Osa, Puntarenas, Costa Rica. Photograph by Roy W. McDiarmid.

The upper lip lacks a distinct light stripe and usually has dark triangular marks, 1 or 2 of them elongate and approaching or entering the lower eye; the upper lip is rarely uniformly light. The dorsal pattern is quite variable, usually with irregular quadrangular or rectangular markings of equal or alternating lighter/darker intensity, confluent laterally or not, or the dorsum often is uniform light or dark, or uniform light with one or two well-defined narrow transverse dark bands, or the dorsum rarely has more than two dark transverse bands of equal intensity in addition to an interorbital band, sometimes with the transverse bands confluent laterally. The supratympanic fold is dark brown. The dorsolateral folds are outlined with dark brown. There are no middorsal stripes. The belly is dark with large or small light vermiculations, or dark with small or large discrete light spots. The pattern of the posterior

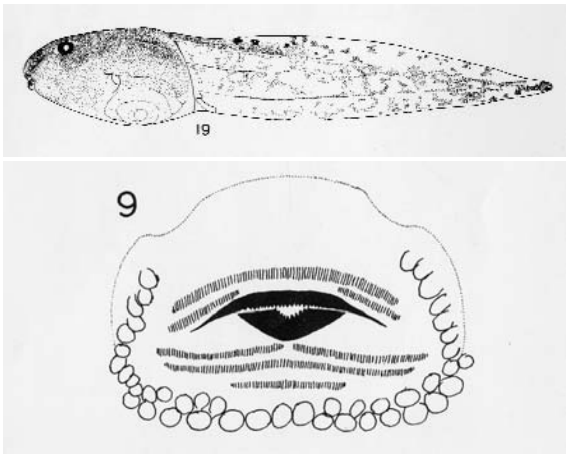


FIGURE 2. Tadpole of *Leptodactylus savagei*, figures 9 and 19 in Heyer (1970 [1968]), based on a specimen from Costa Rica. Tadpole length 41.3 mm, width of oral disk 2.7 mm. Tail myotomes not illustrated.

surface of the thigh is variable, including dark with small to large distinct light vermiculations (vermiculations sometimes coalesced in part), or a dark back ground with contrasting large and light irregular blotches/spots extending from light dorsal transverse bars. The rest of the thigh is dark with light vermiculations, or rarely labyrinthine, or rarely mostly distinctly light with a few irregular dark marks.

Juveniles are often mistaken as a different species by individuals in the field for their first time, as the mid-dorsal areas are much more red/brown than adults (J.M. Savage pers. comm.; Heyer 2005:283).

The facultatively carnivorous larvae are elongate and have characteristics of both the lentic exotrophic, carnivorous and lentic suspension feeder guilds (McDiarmid and Altig 1999, guilds 5 and 7). The oral disk is positioned almost completely anteriorly and entire (not emarginate). There is a single row of marginal papillae laterally, a broad rostral gap lacking papillae, and various combinations of a single and/or double row posteriorly. There are no submarginal papillae. The tooth row formula is 2(2)/3(1). The interrupted A-2 row consists of two short rows of teeth. Row P-3 is about half the length of row P-2. The spiracle is sinistral and the vent tube is median. The dorsal fin originates at the tail/body juncture or at the first or second tail myotome. The lateral line system is visible under magnification on the dorsal and lateral head-body region. Larval total length at Gosner stages 29–30 ranges from 32.2–34.8 mm; stages 34–36 range from 53.6–63.8 mm. Body length of stage 29–30 larvae ranges from 9.0–9.8 mm, stage 34–36 from 13.0–14.1 mm. Eye diameter is 10–11% of body length. The width of the oral disk is 17–20% of body length. The dorsum is tan to brown with denser concentrations of melanophores posteromedially to the nostrils and on either side of the tail musculature on the body. The oral disk is suffused with melanophores or not; if melanophores are present, they extend posteriorly to the midventer. The anal tube has few or no melanophores. The tail fins and musculature are blotched.

The advertisement call consists of a single note per call, given at rates of 40–49 calls/min. Call duration ranges from 0.24–0.42 s. Calls have 5–13 pulses/call, with a mean pulse rate among individuals of 31–46 pulses/s. The call is intensity modulated, starting and ending quietly. The call is frequency modulated, a rising whoop, with a mean initial frequency among individuals of about 300–345 Hz. The mean dominant frequency among individuals ranges from 350–520 Hz. The call has harmonic structure (Figure 3).

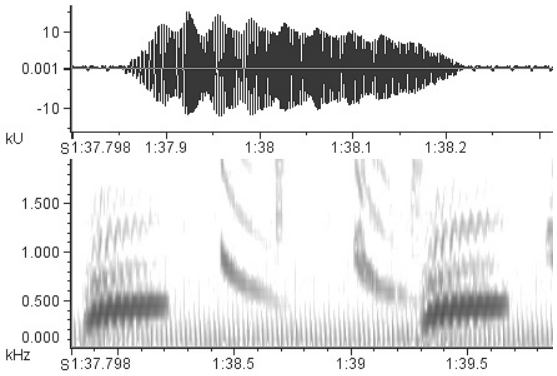


FIGURE 3. Wave form and audiospectrogram display of the advertisement call of *Leptodactylus savagei*, USNM recording 89 cut 6. Wave form of first call in audiospectrogram. Recording by Roy W. McDiarmid, Rincon de Osa, Puntarenas, Costa Rica, 11 June 1973, 20:35 h, 74–76°F (no specimen voucher).

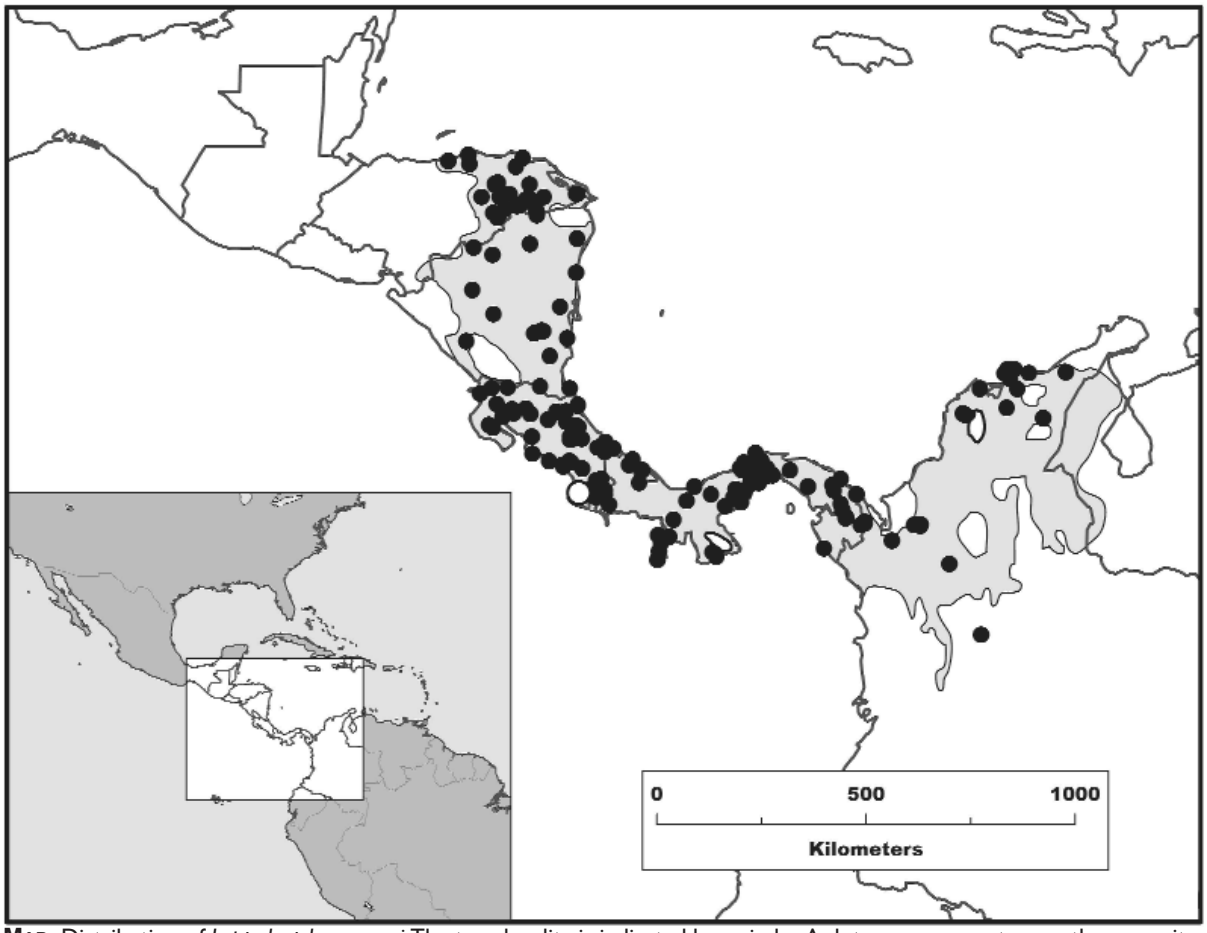
• **DIAGNOSIS.** Adult specimens of *Leptodactylus savagei* are large (106–164 mm SVL). The toes lack lateral fringes (the toes sometimes have lateral ridges that are not developed into moveable fringes). A single pair of distinct dorsolateral folds is present, and the head is relatively broad. These features are shared with (at least some individuals of) *L. fallax, L. flavopictus, L. knudseni, L. labyrinthicus, L. laticeps, L. myersi, L. paraensis, L. pentadactylus, L. peritoaktites, L. rhodomerus, L. stenodema, L. turimiquensis*, and *L. vastus*. *Leptodactylus flavopictus* has a distinct light stripe on the upper lip, whereas *L. savagei* lacks a lip stripe. *Leptodactylus laticeps* has a distinct tile-like dorsal pattern of black squares and rectangles with whitish areas within and between the black markings (in life the black squares and rectangles each have a red center and are separated from one another by a yellow background), whereas *L. savagei* does not have a tile-like dorsal pattern. The dorsolateral folds of *L. savagei* originate just behind the eye and extend above the tympanum toward the sacrum, whereas the dorsolateral folds of *L. stenodema* originate posterior to the tympanum. The dorsolateral folds of *L. savagei* are almost always entire, whereas the dorsolateral folds of *L. labyrinthicus, L. myersi, L. paraensis, L. turimiquensis*, and *L. vastus* usually have interrupted dorsolateral folds or lack dorsolateral folds altogether. Female, sub-adult, and juvenile male *L. savagei* cannot consistently be differentiated morphologically from *L. fallax, L. knudseni, L. pentadactylus, L. peritoaktites*, or *L. rhodomerus*. Adult male *L. savagei* have a pair of chest spines, whereas *L. fallax, L. pentadactylus*, and *L. rhodomerus* males lack chest spines. Adult specimens of *L. savagei* cannot be distinguished from adult *L. knudseni*. Larval *L. savagei* have 9 filter rows per plate on ceratobranchial IV, whereas *L. knudseni* larvae have 7 rows. Juvenile *L. savagei* are never green in life, whereas juvenile *L. knudseni* are often green. *Leptodactylus savagei* is the only species being compared that occurs in Middle America. *Leptodactylus savagei* also occurs on the Caribbean versant of Colombia.

• **DESCRIPTIONS.** Heyer (2005) provides a comprehensive description of the holotype of *L. savagei*. Other detailed descriptions of adults may be found in Heyer (1970 [1968], as *L. pentadactylus*, 2005), Savage (2002, as *L. pentadactylus*), and Taylor (1952, as *L. pentadactylus dengleri*). Larval descriptions are in Heyer (1970 [1968], as *L. pentadactylus*, 2005), and Savage (2002, as *L. pentadactylus*). Recordings of the advertisement call of *L. savagei* appear on compact discs by Bradbury and Budney (2001, as *L.*

pentadactylus) and Ibáñez D. et al. (1999b, as *L. pentadactylus*). Advertisement call characterizations are provided by Heyer (2005) and Straughan and Heyer (1976, Costa Rica and Panama examples only, as *L. pentadactylus*).

• **ILLUSTRATIONS.** The following photographs or illustrations of *L. savagei,* unless noted by (*), were referred to by the authors as *L. pentadactylus*: Albert et al. (2005), Bartlett (1996), Buitrago Vannini (2003), Card (1995), Cuentas Montalvo et al. (2002), De la Riva (1997b), Guyer and Donnelly (2004 [2005], as Smoky Jungle Frog), Hawley (2008*), Henderson (2002, as Smoky Jungle Frog), Heyer (1970 [1968]), Heyer (2005*), Höbel (2004b, 2008), Ibáñez D. et al. (1999b), Köhler (2001), Krywicki (2001), Leenders (2001), Martínez Cortés and Rodriguez (2005), McCranie and Castañeda (2007a*), McCranie et al. (2006), McCranie and Wilson (2002), Mendez (1987), Noble (1918), Norman (1998), Park (1938), Pröhl (1997), Renjifo and Lundberg (1999), Rodríguez A. et al. (2005 [2004]), Ryan (1985), Savage (2002), Scott (1983), Taylor (1952, as *L. pentadactylus dengleri*), van Santen (2006), Villa (1972), Villa et al. (1988), Vinton (1938, genus omitted, as Smoky and Smoky Jungle Frog), and Wainwright (2000).

Other illustrations include the following: **audiospectrograms** (Bernal et al. 2007; Heyer 1979, 2005*; Ibáñez D. et al. 1999a; Kime et al. 2000; Wollerman and Wiley 2002), **defensive behavior** (Villa 1969 [1967], 1972), **foam nests** (Breder 1946; Heyer and Rand 1977; Mertens 1960), **habitat** (Cuentas Montalvo et al. 2002; McCranie and Castañeda 2007a*), **morphology** (Bhaduri 1953), **photomicrographs of the female urogenital system** (Burton 1998a), **palmar and dorsal musculature of the hand** (Heyer 1969b), **dorsal and ventral views of the skull** (Larson and de Sá 1998), **suprarostral cartilages, dorsal, ventral, and lateral views of the chondrocranium, ventral view of the hyobranchial apparatus** (Leenders 2001), **male secondary sexual characteristics** (Lynch 1971; Savage 2002; Villa 1972), **maxilla-pterygoid articulation, dorsal, ventral, lateral, and median views of the right septomaxilla, posterior and dorsal views of the skull, vertebral column, middle ilium, thumb bones, and prepollices of male** (Norman 1998), **upper lip** (Taylor 1952), **lateral head view, thumb spine** (Vinton 1938, as Smoky and Smoky Jungle Frog, x-ray of abdomen with prey), **oocytes** (Davidson and Hough 1969), **larvae** (Breder 1946; Heyer 1970 [1968]; Kluge 1981; Savage 2002; Villa 1972). Altig et al.



Map. Distribution of *Leptodactylus savagei*. The type-locality is indicated by a circle. A dot may represent more than one site. Predicted distribution modified from a BIOCLIM analysis. Published locality data used to generate the map should be considered as secondary sources of information, as we did not confirm identifications for all specimen localities. The locality coordinate data and sources are available on a spread-sheet at http://learning.richmond. edu/Leptodactylus.

(2007) provided an illustration of a tadpole preying on a smaller tadpole.

• **DISTRIBUTION.** *Leptodactylus savagei* occurs in mesic areas of Honduras, Nicaragua, Costa Rica, Panama and scattered localities in the Caribbean versant of Colombia, from sea level to 1385 m. The following references to distribution, localities, and altitude when provided, are organized by country; all references listed referred to this species as *Leptodactylus pentadactylus* unless indicated by (*****). (**S**) indicates a secondary source: **Colombia** (Acosta-Galvis et al. 2006*****; Bernal and Lynch 2008*****; Cuentas Montalvo et al. 2002; Renjifo and Lundberg 1999; Romero-Martínez et al. 2008*****; Ruthven 1922), **Costa Rica** (Abella et al. 2008; Albert et al. 2005; Barquero Rodríguez 1994; Barquero Rodríguez and Barquero Arroyo 2007*****; Bartlett 1996; Blankenship 1992; Bringsøe 2003, 2004; Card 1995; Darst and Cannatella 2004; Donnelly 1994; Donnelly and Guyer 1994; Duellman 1967b; Franzen 1988; Gans 1958; Günther 1900, 1902; Guyer and Donnelly 2004 [2005]; Hartdegen et al. 1999; Hawley 2008*****; Hayes et al. 1989; Heatwole and Sexton 1966; Henderson 2002; Heyer 1967, 1970 [1968], 1979, 2005*****; Heyer et al. 1975; Höbel 2000, 2008; Hödl 1996; Johanboeke 1974, 1977 [1976]; Kratzer et al. 1990; Kubicki 2008; Krywicki 2001; Laurencio 2009*****; Leenders 2001; Lewis 2001; Lieberman 1986; Lips and Savage 1996; Malmström 1993; McDiarmid and Savage 2005; Minton and Smith 1960; Norman 1998; Palmer 1992; Pounds 2000 (as Smoky Jungle Frog); Pounds and Fogden 2000; Pounds et al. 1997; Pröhl 1997; Roberts 1997; Sasa and Solórzano 1995; Savage 1973a,b, 1980a,b,c, 2002; Savage and Villa 1986; Scott 1983; Scott and Starrett 1974; Scott et al. 1983; Straughan and Heyer 1976; Taylor 1952, p. 589 (**S**), p. 651 [as *L. pentadactylus dengleri*]; Valerio 1971; Villa 1969 [1967]; Villa et al. 1982; Wainwright 2000; Wassersug and Heyer 1988; Weimer et al. 1994; Weimer et al. 1993a,b; Wollerman and Wiley 2002; Zelmer and Brooks 2000), **Honduras** (Heyer 1979; House et al. 2002; Köhler et al. 2000; Lynch and Fugler 1965 (as *L. pentadactylus dengleri*); McCranie 2006*****, 2007*****; McCranie and Castañeda 2007a,b; McCranie et al. 2002; McCranie et al. 2006; McCranie and Wilson 2002; Meyer 1969; Meyer and Wilson 1971; Nicholson et al. 2000; Wilson 1983; Wilson and McCranie 1994, 2004 [2003]; Wilson et al. 2001; Wilson and Townsend 2006), **Nicaragua** (Brattstrom and Howell 1954; Buch 1994; Buitrago Vannini 2003; Gaige et al. 1937; Heyer 1979; Köhler 1998, 1999, 2001; Köhler and Seipp 1998; Noble 1918; Villa 1971, 1972, 1983), **Panama** (Asociación Nacional para la Conservación de la Naturaleza (ANCON) and The Nature Conservancy (TNC) 1995a,b, 1996a,b; Barbour 1923; Bernal 2006; Bernal et al. 2007; Bhaduri 1953; Brattstrom 1961, 1968; Breder 1925, 1927, 1946; Brem and Lips 2008*****; Caballero y C. 1955; Cabrera-Gúzman et al. 2007 (p. 97 only); Cedeño et al. 2006; Davidson and Hough 1969; De la Riva 1997a,b; de Sá et al. 2006 [2005]; Dieguez et al. 2006; Dunn 1931a,b, 1933b; Gray and Rand 1997; Heyer 1979; Heyer and Rand 1977; Ibáñez D. et al. 1995 [1994], 1997 [1995], 1999a,b, 2001; Jaeger and Hailman 1981; Jaramillo et al. 1994; Kaufmann 1962; Kluge 1981; Kourany et al. 1970; Leigh 2002; Lips et al. 2003, 2006; Martínez Cortés and Rodriguez 2005; Mendez 1987; Muedeking and Heyer 1976; Myers and Rand 1969; Nemuras 1968; Park 1938; Park et al. 1940; Ponssa 2005 [2004]; Rand and Myers 1990; Rodríguez A. et al. 2005 [2004]; Schmidt 1933; Sexton et al. 1964; Sousa and Arosemena 1991; Summers 2002; Swanson 1945; Tejera Nuñez and Dupuy Loo 1994, 2003; Vinton 1938, 1951; Weaver and Bauer 2004; Wells 1979; Young et al. 1999; Zetek and Wetmore 1951).

• **FOSSIL RECORD.** None.

• **PERTINENT LITERATURE.** Inclusive accounts of the species are found in Heyer 2005, McCranie and Wilson 2002 (as *L. pentadactylus*), and Savage 2002 (as *L. pentadactylus*). The following literature is listed by topic; all references listed referred to this species as *Leptodactylus pentadactylus* unless indicated by (*****), which signifies *L. savagei*. The symbol (**M**) indicates the species is only mentioned and (**S**) indicates that all the species information represents a secondary source: **bibliographic information and lists** (Campbell 1999; Cochran 1940 [Vinton 1938 reference only]; Hardouin 1997; Liner 1994 [Sexton et al. 1964 reference only], 1997, 1998, 2009; Liner and Gans 2004; Lips and Savage 1996; Savage 1980a,c, 2002; Savage and Villa 1986 [p. 23, Heyer 1970b, as CR spp., Scott 1983m as *L. pendactylus* {sic}, and p. 104 as *L. pentadcactylus* {sic}]; Toledo et al. 2007 (**S**) [Roberts 1997a citation only; Villa et al. 1988 [except Breen 1974, Cochran and Goin 1970, Duellman 1978, Duellman and Trueb 1986, and most information in Heyer 1979 except Central American localities]; Vizotto 1964 [p. 389 only]; Walley 1997), **biogeography** (Lynch 1971; Maxson and Heyer 1982; Wilson and McCranie 1998), **book reviews and articles** (Eckerlin 1971; Wilson and Meyer 1972), **call and call parameters** (Aycrigg et al. 1998 (**S**); Bernal 2006; Bernal et al. 2007; Breder 1927, 1946; Duellman 1967a; Duellman and Trueb 1966; Dunn 1933a, b; Fouquette 1960; Gray and Rand 1997; Höbel 2008; Johanboeke 1974, 1977 [1976]; Kime et al. 2000; Kluge 1981 (**S**); LeVering 1999 [p. 52 and as experimental animal throughout]; Park 1938; Park et al. 1940; Rose et al. 1988; Ryan 1985; Scott and Limerick 1983; Straughan and Heyer 1976 [p. 228, Costa Rican and Panamanian information, and p. 232; Toledo and Haddad 2009*****; Wollerman and Wiley 2002; Zelick et al. 1991), **checklists** (Abella et al. 2008; Auth 1994; Bernal and Lynch 2008*****; Burger 2001; Leenders 2001; McDiarmid and Savage 2005; Myers and Rand 1969; Palmer 1992; Savage 1973a, b, 1980b; Savage and Bolaños 2009*****; Savage and Villa 1986; Scott et al. 1983; Villa 1971, 1983), **conservation** (Asociación Nacional para la Conservación de la Naturaleza (ANCON) and The Nature Con-

servancy (TNC) 1995a,b, 1996a,b; Dieguez et al. 2006; McCranie et al. 2006; McCranie and Wilson 2002; Weimer et al. 1994; Wilson and McCranie 2004 [2003]; Wilson and Townsend 2006; Young et al. 1999), **development** (Barquero Rodríguez and Barquero Arroyo 2007*****; Blankenship 1992; Breder 1946; Gallardo 1958; Savage 2002; Vinton 1951; Vizotto 1967 (**S**)), **dictionaries and encyclopedias** (Marx and Heath 1992 (as burka and la rana mugidora come-pollo)), **distribution** (Campbell 1999; Cei 1968 [as *L. pentadactylus dengleri*]; Lynch and Fugler 1965 (**S**); McCranie et al. 2006; McCranie and Wilson 2002; Meyer 1969), **ecology, natural history, reproduction** (Alford 1999 (**S**); Altig 1974 [1972]; Altig and McDiarmid 2007; Altig et al. 2007; Barbour 1923; Barlow 1998 (**S**) [Heyer et al. 1975 citation only]; Barquero Rodríguez 1994; Behler and Behler 2005 [p. 52 only]; Bernal 2006; Bernal et al. 2007; Borteiro and Kolenc 2007 (**S**); Brattstrom and Howell 1954; Breder 1925, 1927, 1946; Brodie et al. 1978 (**S**); Caldwell 1992 (**S**); Card 1995; Cardoso and Sazima 1997 (**S**); Conzemius 1932 [as burka and burki]; Cooke 1984; Cooke et al. 2008; Cramer et al. 2001 (**S**); Crossland 1998 (**S**); Crossland and Azevedo-Ramos 1999 (**S**); Crump 1992 (**S**); Cuentas Montalvo et al. 2002; Davidson and Hough 1969; De la Riva 1993 [p. 109 Muedeking and Heyer 1976, citation only, and p. 110 1997a,b]; Dent 1956 (**S**); Dixon et al. 1993; Donnelly 1994; Downie 1984 (**S**); Downie et al. 1995; Downie and Smith 2003 (**S**); Duellman 1966; Duellman and Trueb 1966, 1986 [pp. 75 (**S**), 162 (**S**), 244 (**S**), 273 (**S**), 281 (**S**); Dunn 1954; Gibson and Buley 2004 [p. 133 Hödl citation only], Green 1990; Greene 1988, 1997; Gregory 1983 (**S**); Gunzburger and Travis 2005 [p. 561 Heyer et al. citations only, and pp. 563 and 570 only]; Heyer 1967; Heyer et al. 1975; Heyer and Rand 1977; Heyer and Scott 2006 (**S**); Höbel 2000, 2004a,b, 2008; Hödl 1988 (**S**), 1990a (**S**), b (**S**) [Breder 1946 and Heyer and Rand 1977 citations only], 1992 (**S**); Ibáñez D. et al. 1997 [1995], 1999a; Jaeger 1978 (**S**); Jaeger and Hailman 1981; Johanboeke 1974, 1977 [1976]; Kaufmann 1962; Kluge 1981; Kotiaho 2001 (**S**); Kubicki 2008; Lebron et al. 1995 (**S**); Leigh 2002; LeVering 1999 [p. 52 and as experimental animal throughout]; Lieberman 1986; Lips et al. 2003; Lutz 1947 (**S**); Malkin 1956; Magnhagen 1991 (**S**); Manzanilla Puppo et al. 2005 (**S**); McCranie et al. 2006; McCranie and Wilson 2002; Meyer 1969; Mudde and van Dijk 1983; Muedeking and Heyer 1976; Nemuras 1968; Noble 1918, 1927; Park 1938; Petranka et al. 1994 (**S**); Petranka and Kennedy 1999 (**S**); Polis and Myers 1985 (**S**); Ponssa 2005 [2004]; Ponssa and Barrionuevo 2008*****; Pough et al. 1996 (**S**); Pounds 2000 (**S**) [as Smoky Jungle Frog]; Prado et al. 2005 (**S**) [Vinton 1951 and Muedeking and Heyer 1976 citations only]; Prado et al. 2002 (**S**) [Breder 1946, Heyer et al. 1975, Muedeking and Heyer 1976, and Vinton 1951 citations only]; Rand 1983 [p. 412], Rand and Myers 1990; Roberts 1997; Rodrigues et al. 2007 (**S**)*****; Rodrigues et al. 2005 [2004] (**S**); Roth and Willis 1960; Noble 1918; Ruibal and Thomas 1988 (**S**); Ryan 1985; Ryan and Tuttle 1983 (**S**); Ryan et al. 1981; Sasa and Solórzano 1995; Savage 2002; Scott and Limerick 1983 [Breder 1946, Villa 1967, 1972, and Vinton 1951 citations only]; Sherratt and Harvey 1989 (**S**); Silva and Juncá 2006 (**S**); Silva and Giaretta 2009*****; Silva et al. 2005 (**S**) [Heyer and Rand 1977 and Muedeking and Heyer 1976 citations only]; Tárano 1998; Tejedo 1991 (**S**); Toft 1985 (**S**); Toft et al. 1982 (**S**); Toledo et al. 2007 (**S**) [p. 172 only]; Toledo et al. 2005 (**S**) [Villa 1969 citation only]; Tuttle and Ryan 1981; Veloso 1977 (**S**); Vera Candioti 2004, 2005 (**S**), 2006 (**S**); Villa 1969 [1967], 1972; Villa et al. 1982 [Costa Rican example and Muedeking and Heyer 1976 citations only]; Vinton 1938, 1951; Vizotto 1967 (**S**); Wassersug and Heyer 1988; Wells 1979, 2007 (**S**) [pp. 293, 341, 573, 661, 663 only]; Wilson and McCranie 2004 [2003]; Wilson et al. 2001; Wunder 1932 (**S**); Zelick et al. 1991; Zina and Haddad 2005 (**S**)), **evolution** (Heyer 1969a [Breder 1946 citation only]; Heyer and Liem 1976 (**S**); Lynch 1971; Silva and Giaretta 2009*****), **faunal lists** (Mendez 1987; Park et al. 1940; Zetek and Wetmore 1951), **field guides** (Beletsky 1998 [except plate 4, as Smoky Jungle Frog]; De la Riva 1997b; Henderson 2002; Leenders 2001; McCranie and Castañeda 2007a*****; Norman 1998; Renjifo and Lundberg 1999; Wainwright 2000), **habitat** (Acosta Galvis et al. 2006*****; Asociación Nacional para la Conservación de la Naturaleza (ANCON) and The Nature Conservancy (TNC) 1995a,b, 1996a,b; Burger 2001; Campbell 1999; Cuentas Montalvo et al. 2002; Dunn 1931a, 1933b; House et al. 2002; Ibáñez D. et al. 1995 [1994], 1997 [1995], 1999a; Kubicki 2008*****; Laurencio 2009*****; Lieberman 1986; McCranie et al. 2006; McCranie and Wilson 2002; Park 1938; Pounds and Fogden 2000; Pounds et al. 1997; Rand and Myers 1990; Ruthven 1922; Sasa and Solórzano 1995; Savage 2002; Sexton et al. 1964; Tejera Nuñez and Dupuy Loo 2003; Wells 2007 (**S**) [p. 98 only]; Wilson and McCranie 1998; Wilson et al. 2001; Wilson and Townsend 2006), **inventories** (Asociación Nacional para la Conservación de la Naturaleza (ANCON) and The Nature Conservancy (TNC) 1995a,b, 1996a,b; Cedeño et al. 2006; De La Riva 1997a; Laurencio 2009*****; Lewis 2001; McCranie et al. 2002; Nicholson et al. 2000; Rodríguez A. et al. 2005 [2004]), **karyotypes** (Morescalchi 1973 (**S**); Morescalchi and Gargiulo 1968; Rabello 1970 (**S**) [Morescalchi and Gargiulo citations only]); **keys** (Breder 1946; Cuentas Montalvo et al. 2002; Dunn 1931a; Guyer and Donnelly 2004 [2005]; Heyer 1970 [1968]; Köhler 1999, 2001; Lips and Savage 1996; McCranie and Castañeda 2007a*****; McCranie et al. 2006; McCranie and Wilson 2002; Meyer and Wilson 1971; Nemuras 1968; Romero-Martínez et al. 2008*****; Savage 1980a, c, 2002; Savage and Villa 1986; Taylor 1952 [as *L. pentadactylus dengleri*]; Villa 1972; Wilson and McCranie 1993), **lists of specimens in collections** (Cope 1887; Tejera Nuñez and Dupuy Loo 1994, 2003), **miscellaneous mention** (Jara 2008a,b; Jungfer 1988; Mudde and van Dijk 1985; Vizotto 1984 (**S**)), **morphology** (Bhaduri 1953; Burton

1998a,b, 2004; Cardozo 2004 (**S**); Fabrezi and Vera 1997; Fox 1984 (**S**); Goin 1959 [as *L. pentadactylus dengleri*]; Hayek and Heyer 2005; Jaslow 1985, 1987; Johanboeke 1977 [1976]; Kluge 1981; Larson and de Sá 1998; Lynch 1971; McCranie and Wlson 2002; Miranda and Ferreira 2008 (**S**) [Wassersug and Heyer 1988 citation]; Muedeking and Heyer 1976; Palavecino 1997 (**S**); Prado and d'Heursel 2006 (**S**); Rodrigues et al. 2007 (**S**)*****; Savage 2002; Scott and Limerick 1983; Silva and Mendelson 1999; Starrett 1968 [Costa Rican specimens only]; Vera Candioti 2006 (**S**); Vera Candioti et al. 2007 [Larson and de Sá 1998 and Wassersug and Heyer 1988 information only]; Vieira et al. 2007 (**S**) [Muedeking and Heyer 1976, Savage 2002, Vizotto 1967, Wassersug and Heyer 1988, and Central American *L. pentadactylus* citations only]; Villa 1972; Villa et al. 1982 (**S**) [Villa 1969, 1972 citations only]; Wassersug and Heyer 1988; Wells 2007 (**S**) [pp. 577 and 661 only]), **nomenclature and taxonomy** (McCranie and Wilson 2002; Smith 1987), **parasites and diseases** (Brem and Lips 2008*****; Caballero y C. 1955; Cabrera-Guzmán et al. 2007 [p. 97 only]; Duellman and Trueb 1986 [p. 243 only]; Hartdegen et al. 1999; Johnston 1975 [p. 530 only]; Kourany et al. 1970; Lamothe-Argumedo and Jaimes Cruz 1982; Lamothe-Argumedo et al. 1997; Lips et al. 2006; Metcalf 1923 [p. 408 only, Panamanian specimen]; Suriano 1970 [p. 218 only]*****; Taylor et al. 2001 (**S**) [Kourany et al. 1970 citation only]; Thatcher 1993 [p. 183 only]; Villa 1984 (**S**) [Villa et al. 1982 citation only]; Villa et al. 1982 [Costa Rican example and Muedeking and Heyer 1976 citation only]; Wells 2007 (**S**) [p. 835 only]*****; Yamaguti 1971 [p. 341 only]; Zelmer and Brooks 2000 [p. 1114, column 1 only]), **physiology** (Brattstrom 1961, 1968; Valerio 1971), **popular literature** (Archer 2006; Bartlett 1988, 1996; Behler and Behler 2005 [pp. 52 and 105 only]; Echternacht 1977; Mendez 1987; Nemuras 1976; Pröhl 1997; Tuttle 1982; Vinton 1938), **relationships, systematics and phylogeny** (Austin et al. 2002; Cei et al. 1967 [as *L. pentadactylus dengleri*]; Darst and Cannatella 2004; de Sá et al. 2006 [2005]; Dutta et al. 2004; Grant et al. 2006; Graybeal 1997; Hedges et al. 2008; Hedges and Heinicke 2007; Heinicke et al. 2007; Heyer 1995, 1998; Heyer and Maxson 1982 [p. 401 figure 6 as *L. pentadactylus*, Panama only]; Larson and de Sá 1998; Larson et al. 2003; Leistikow 2001 (**S**); [as Costa Rican population of *L. pentadactylus*]; Lourenço et al. 2008 (**S**); Lynch 1971; Maxson and Heyer 1982, 1988 [antigen sample from Panama only]; Miyamoto 1981; Ponssa and Barrionuevo 2008*****, Wassersug and Heyer 1988), **skin secretions** (Anastasi et al. 1970 [as *L. pentadactylus dengleri*]; Cei 1969 [as *L. pentadactylus dengleri*], 1972, 1980 [both as *L. dengleri*]; Cei and Erspamer 1965, 1966 [both as *L. pentadactylus dengleri*]; Cei et al. 1967 [as *L. pentadactylus dengleri*]; G. Erspamer and Cei 1970 [as *L. pentadactylus dengleri*]; V. Erspamer 1971 [as *L. pentadactylus dengleri*]; V. Erspamer et al. 1963 [as *L. pentadactylus dengleri*]; Erspamer and Erspamer 1965 [as *L. pentadactylus dengleri*]; V. Erspamer et al. 1986 [as *L. pentadactylus dengleri*]; V. Erspamer et al. 1964 [p. 1089 only as *L. pentadactylus dengleri*]; V. Erspamer et al. 1964, 1967 [both as *L. pentadactylus dengleri*]; Flier et al. 1980; Roseghini et al. 1986) [as *L. pentadactylus dengleri*], **species accounts** (Albert et al. 2005; Beletsky 1998; Buitrago Vannini 2003; Cuentas Montalvo et al. 2002; Günther 1900; Henderson 2002; Heyer 1970 [1968], 2005*****; Ibáñez D. et al. 1999a [see Heyer et al. in prep. *Leptodactylus pentadactylus* for clarification of references in this species account]; Köhler 1999, 2001; Leenders 2001; Martínez Cortés and Rodriguez 2005; McCranie and Castañeda 2007a*****; McCranie et al. 2006; McCranie and Wilson 2002; Mendez 1987; Noble 1918; Norman 1998; Pröhl 1997; Renjifo and Lundberg 1999; Rodríguez A. et al. 2005 [2004]; Savage 2002; Scott 1983 [Heyer 1979 citation]; Taylor 1952 [as *L. pentadactylus dengleri*]; Villa 1972; Weimer et al. 1993b), **species comparisons** (Dunn 1940; Heyer 2005 [as Middle American Unit]; Heyer and Heyer 2006 [as undescribed species from Middle America]; Savage 2002; Skuk et al. 2007; Vieira et al. 2007 (**S**) [Muedeking and Heyer 1976, Savage 2002, Vizotto 1967, Wassersug and Heyer 1988, and Central American *L. pentadactylus* citations only]; Villa 1972; Wassersug and Heyer 1988), **species or taxonomic lists** (Cuentas Montalvo et al. 2002; Dunn 1931b; Gans 1958 [as *L. pentadactylus pentadactylus*]; Hayes et al. 1989; House et al. 2002; Ibáñez D. 2005; Ibáñez D. et al. 1995 [1994], 1997 [1995], 1999a, 2001; Köhler 1999, 2001; Köhler et al. 2000; Köhler and Seipp 1998; Krywicki 2001; Kubicki 2008*; Laurencio 2009*; Lewis 2001; Malmström 1993; Martínez Cortés and Rodriguez 2005; McCranie and Castañeda 2007b; Noble 1918; Pounds et al. 1997; Romero-Martínez et al. 2008*****; Ruiz Pérez and Buitrago Vannini 2003; Schmidt 1933; Sousa and Arosemena 1991; Villa 1972; Weaver and Bauer 2004; Weimer et al. 1994; Weimer et al. 1993a; Wilson 1983; Wilson and McCranie 1994, 1998, 2004 [2003]; Wilson et al. 2001; Wilson and Townsend 2006; Young et al. 1999).

• **REMARKS**. The following common names have been published for *Leptodactylus savagei*: "Savage's Thin-toed Frog" proposed English common name at www.learning.richmond.edu/Leptodactylus, "Rã-de-dedos-delgados-de-Savage" proposed Portuguese common name at www.learning.richmond.edu/Leptodactylus, and "Rana de dedos delgados de Savage" proposed Spanish common name at www.learning.richmond.edu/Leptodactylus. Other cited common names are as follows; all references listed referred to this species as *Leptodactylus pentadactylus* unless otherwise indicated: **Bûrh** (Green 1999), **Burka** (Conzemius 1932; House et al. 2002; Marx and Heath 1992; McCranie et al. 2006), **Burki** (Conzemius 1932), **Burxká** (Malkin 1956), **Central American Bullfrog** (Greene 1997; Guyer and Donnelly 2004 [2005]; Leenders 2001; Martínez Cortés and Rodriguez 2005), **La Rana Mugidora Come-Pollo** (Marx and Heath 1992), **Rana Comepollos** (Guyer

and Donnelly 2004 [2005]), **Rã de dedos delgados de Savage** (Heyer 2005, as *L. savagei*), **Rana de dedos delgados de Savage** (Heyer 2005, **Rana Grande de la Selva** (McCranie and Castañeda 2007a, as *L. savagei*), **Rana Ternero** (Barquero Rodríguez and Barquero Arroyo 2007 [as *L. savagei*]; Beletsky 1998; Buitrago Vannini 2003; Burger 2001; Guyer and Donnelly 2004 [2005]; Köhler 1999, 2001; Leenders 2001; Norman 1998; Pröhl 1997; Savage 2002; Villa 1969 [1967], 1971, 1972, 1983; Villa et al. 1988; Wainwright 2000), **Rana Toro** (Beletsky 1998; Cedeño et al. 2006; Höbel 2008; Leenders 2001; Pröhl 1997; Rodríguez A. et al. 2005 [2004]), **Savage's Thin Toed Frog** (Heyer 2005 as *L. savagei*), **Smoki Jungle Frog** (Savage 2002), **Smoky** (Vinton 1938), **Smoky Frog** (Beletsky 1998), **Smoky Jungle Frog** (Bartlett 1988, 1996; Behler and Behler 2005, p. 52 only); Beletsky 1998; Bernal 2006; Blankenship 1992; Burger 2001; Cochran 1940 [Vinton 1938 reference only]; Guyer and Donnelly 2004 [2005]; Hayes et al. 1989; Henderson 2002; Krywicki 2001; Lewis 2001; Norman 1998; Pounds 2000; Roth and Willis 1960; Vinton 1938, 1951; Wainwright 2000), **South American Bullfrog** (Beletsky 1998; Green 1990; Guyer and Donnelly 2004 [2005]; Höbel 2008; Hödl 1992; Johanboeke 1974, 1977 [1976]; Leigh 2002; Lewis 2001; Ryan 1985; Tárano 1998; Tuttle 1982); **Südamerikanische Ochsenfrosch** (Hödl 1996); **Sukli'n** (Malkin 1956).

• **ETYMOLOGY.** *Leptodactylus savagei* honors Dr. Jay M. Savage whose work in Costa Rican herpetology has inspired countless researchers and promoted a comprehensive understanding of the Costa Rican herpetofauna.

• **ACKNOWLEDGMENTS.** We thank Jay M. Savage and James R. McCranie for reviewing the manuscript. Research for this account was supported by NSF award DEB 0342918 to RdS and WRH.

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W. Ronald Heyer, **Miriam Muedeking Heyer**, Smithsonian Institution, P.O. Box 37012, NHB W-201, MRC 162, Washington, DC, 20013–7012, USA (heyerr@si.edu) and **Rafael O. de Sá**, Department of Biology, University of Richmond, Richmond, VA 23173, USA (rdesa@richmond. edu).

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Primary editor for this account, Andrew H. Price.