

Catalogue of American Amphibians and Reptiles.

Heyer, W.R. and M.M. Heyer. 2006. *Leptodactylus knudseni*.

***Leptodactylus knudseni* Heyer
Knudsen's Thin-toed Frog**

Leptodactylus pentadactylus: Beebe 1925:123. First unambiguous use of this name for *L. knudseni*.

Leptodactylus knudseni Heyer 1972:3. Type-locality, "Limoncocha, 0° 24'S, 76° 37' W, Provincia de Napo, Ecuador, elevation 260 m." Holotype, Los Angeles County Museum (LACM) 72117, juvenile female, collected by K.A. Berven and W.R. Heyer on 3 August 1970.

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

• **DEFINITION.** Adult *Leptodactylus knudseni* are large, the head is as wide as long or usually wider than long, and the hind limbs are moderately long (Table 1; Heyer and Thompson 2000 provided definitions of adult size and leg length categories for *Leptodactylus*). Male vocal sacs are not visible externally or are weakly expanded as a single sac. Sexually active males have hypertrophied forearms (impressively so in some specimens), one large black spine on each thumb (occasionally some of the largest males have a low, black, keratinized prepollical bump), and a pair of large black chest spines. Usually a pair of dorsolateral folds, either complete or interrupted, originates behind the eye and extends posteriorly between one-quarter body length to the full distance to the sacrum. These folds rarely extend past the sacrum to the groin. Flank folds (diverging from the supratympanic fold at the uppermost posterior portion of the tympanum and extending as far as the lower flank at the mid-flank level) are usually absent entirely or only represented by an elongate dark spot/wart in the area where the fold rarely occurs in some specimens. A lateral fold from above the tympanum (diverging at the same point with the flank fold) extends straight back to the groin in some well-preserved individuals. The toe tips are rounded and either the same width or barely wider than the toes immediately behind the tips. The toes often have weak lateral ridges and a trace of webbing between toes II-III, II-III-IV, or I-II-III-IV. Metamorphic or slightly larger specimens lack any indication of lateral toe ridges or webbing. The upper shank and outer tarsal surfaces usually have a few to several scattered black or white tubercles, some specimens also are shagreened, although others have entirely smooth surfaces. The sole of the foot is usually smooth, although occasional specimens exhibit a shagreen or a few white tubercles.

The upper lip lacks a distinct light stripe and usually has a series of dark triangular marks, one or two of which are elongated and approach or reach the lower eyelid. The dorsum usually bears a series of two or



Figure 1. *Leptodactylus knudseni*, Manaus, Amazonas, Brazil (Photo courtesy of the late Adão J. Cardoso).

more transverse bands or chevrons in addition to an interorbital band or chevron, which may or may not be confluent laterally. Rarely, the dorsum is uniform light or dark brown. The supratympanic fold is dark brown. The dorsolateral folds may or may not be outlined with dark brown. The species lacks middorsal stripes. The belly is uniform light, uniform dark, mottled, or dark with small light spots or vermiculations. The posterior surface of the thigh is dark, usually with small to large light vermiculations or spots.

Larvae are elongate facultative carnivores 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, entire (not emarginated), and has a broad anterior gap lacking marginal papillae. A single row of marginal papillae is present, often the lateral and ventrolateral papillae are arranged such that they alternately point in opposite directions, making it difficult to determine whether a single or double row of papillae is present. Submarginal papillae are lacking. The tooth row formula is 2(2)/2-3(1). The interrupted A-2 row is very short and situated laterally beneath row A-1. Row P-3, when present, may be slightly shorter than P-1 and P-2 or very short. The spiracle is sinistral and the vent tube is median. The dorsal fin originates on the second to fourth tail myotome. Larval total length at Gosner stage 36-40 ranges from 55-76 mm. Body length of late stage 25-40 larvae ranges from 13-24 mm. Tail length is 66-72% of total length. Eye diameter is 8-12% of body length. The width of the oral disk is 17-21% of body length. The dorsum of the body is tan to brown. The sides of the body are uniform tan or mottled with shades of tan. The venter of the body is scattered with melanophores on the anterior half (usually) or anterior two-thirds. The tail musculature is lightly to heavily mottled tan to brown and cream. The tail fins are faintly to darkly mottled with brown melanophores.

The advertisement call consists of a single note per call, given at a rate of 16-66/min. Call duration ranges from 0.16-0.43 s. Calls have 6-14 pulses with a rate of 26-38 pulses/s (values are mean rates for

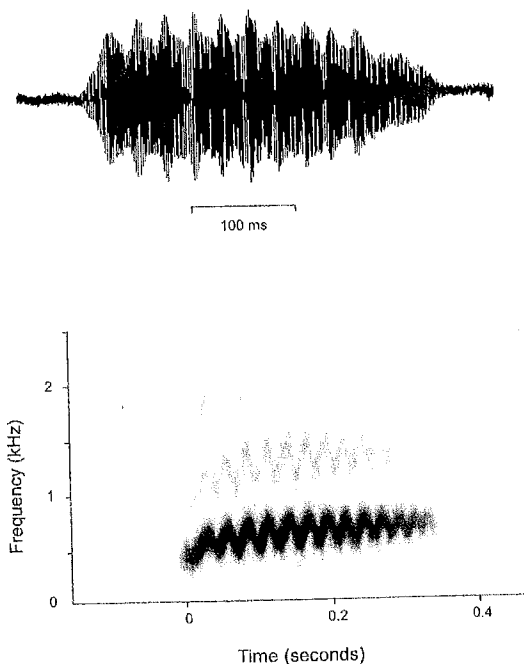


Figure 2. Wave form and audiospectrogram displays of the advertisement call of *Leptodactylus knudseni* (USNM recording 228, cut 1) from Usina Kararahô, 27 km from Altamira, Pará, Brazil, voucher specimen ZUEC 7232. Canary software was used to produce the figure.

11 recordings). The call, a rising whoop, is frequency modulated in two ways: (1) initial frequencies range from about 250–550 Hz with a final frequency ranging from about 30–300 Hz above the beginning frequency, (2) each pulse has rising and falling frequencies with mid-call pulses having a range of about 400–800 Hz between lowest and highest frequencies. The call is weakly intensity modulated, essentially loud from beginning to end, with the first half of the call slightly louder than the second half and the second half demonstrating a gradual decline in intensity to the end of the call. The dominant frequency is the fundamental frequency and ranges between about 340–700 Hz. The call has a well-developed harmonic structure.

• **DIAGNOSIS.** Adult specimens of *Leptodactylus knudseni* are large (94–170 mm SVL). The toes lack lateral fringes (although the toes sometimes have lateral ridges, these 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 (some individuals of) *L. fallax*, *L. flavopictus*, *L. labyrinthicus*, *L. laticeps*, *L. myersi*, *L. pentadactylus*, *L. stenodema*, *L. vastus*, and undescribed species (Heyer 2005) from Middle America, the Pacific versant of Colombia and adjacent Ecuador, the Pacific versant of Ecuador, the State of Pará in Brazil, and northern Venezuela. *Leptodactylus flavopictus* has a distinct light stripe on the upper lip, *L.*

knudseni lacks a lip stripe. *Leptodactylus laticeps* has a distinct tile-like dorsal pattern of black squares and triangles 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), *L. knudseni* does not have a tile-like dorsal pattern. The dorsolateral folds of *L. knudseni* originate just behind the eye and extend above the tympanum toward the sacrum, the dorsolateral folds of *L. stenodema* originate posterior to the tympanum. The dorsolateral folds of *L. knudseni* are almost always entire, the dorsolateral folds of *L. labyrinthicus*, *L. myersi*, *L. vastus*, the undescribed species from Pará, and the undescribed species from northern Venezuela usually have interrupted dorsolateral folds or lack folds altogether. The dorsolateral folds of *L. knudseni* almost always extend no farther than from the eye to the sacrum, and reproductively active males have a large black spine on each thumb and a pair of black multi-cusped spines on the chest, *L. fallax*, *L. pentadactylus*, and the undescribed species from the Pacific versant of Colombia have dorsolateral folds that often extend beyond the sacrum to the groin, and reproductively active males lack chest spines. Large black thumb spines are also lacking in *L. pentadactylus* and the undescribed species from the Pacific versant of Colombia. Adult specimens of *L. knudseni* can not be distinguished from the undescribed species from Middle America. Juvenile *L. knudseni* often have some green coloration in life, whereas juveniles of the undescribed species from Middle America never have any green coloration in life.

Table. Summary measurement data for *Leptodactylus knudseni* (means are in parentheses).

Measurement	Males	Females
SVL (mm)	94–170 (131.4)	103–154 (132.0)
Head length/ SVL (%)	32–40 (36)	32–46 (35)
Head width/ SVL (%)	34–44 (38)	34–42 (37)
Thigh length/ SVL (%)	35–46 (41)	35–45 (40)
Shank length/ SVL (%)	38–48 (42)	38–46 (42)
Foot length/ SVL (%)	38–51 (44)	40–50 (44)

• **DESCRIPTIONS.** Heyer's (1979) detailed descriptions of adult female and male morphological features include color in life. Bartlett and Bartlett (2003) recorded the colors of adults and juveniles. Fugler and Walls (1979) provided a color record of living and preserved males of *L. knudseni*. The morphology and living and preserved colors of the juvenile female holotype were described by Heyer (1972). Duellman (1978, as *L. pentadactylus*) described the tadpole,

Hero (1990) provided larval color notes, and Wassersug and Heyer (1988) delineated larval internal oral features. Cocroft et al. (2001) and Marty and Gaucher (2000) featured the advertisement call of *L. knudseni* on their compact discs. Karyotypic information is in Heyer (1972, 1979).

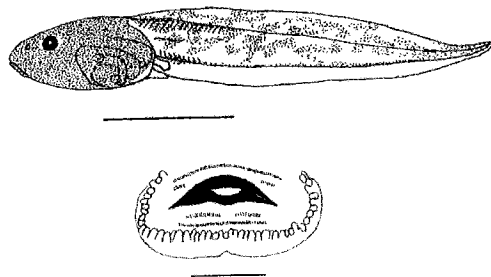
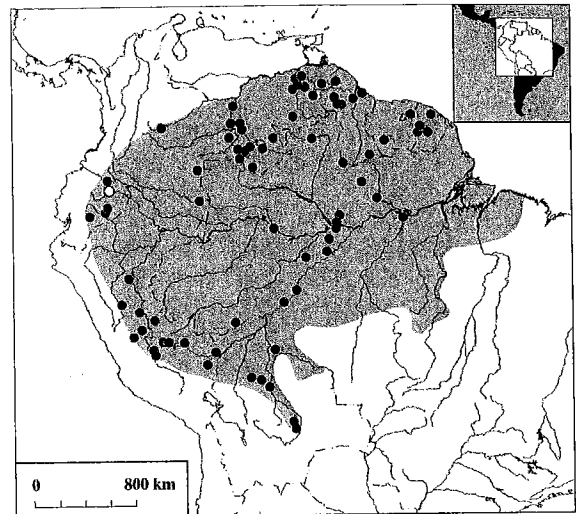


Figure 3. Tadpole of *Leptodactylus knudseni* (semi-agrammatic drawings from USNM 560922) from Dubulay Ranch, East Berbice, Guyana, Gosner stage 31. Lateral view bar = 10 mm, oral disk bar = 1 mm.

• **ILLUSTRATIONS.** Color photographs of adults are found in Bartlett and Bartlett (2003, as *L. pentadactylus*), Cocroft et al. (2001), Coloma and Ron (2001, as *L. pentadactylus*, fig. 50, p. 53), De la Riva et al. (2000), Duellman (2005), Gorzula and Señaris (1999), Gremone et al. (1986), Hennessey (2002), Kornacker and Dederichs (1998, as *L. pentadactylus*), Lescure and Marty (2000), Murphy (1997), and Rodríguez and Duellman (1994). Lehr (2002) and Rodríguez and Duellman (1994) included color photos of juveniles. Photos of foam nests and foam nesting pairs of *L. knudseni* are in Hermann (2001), Hödl (1990, 1993, 1996, 2000), Lehtinen and Nussbaum (2003), and Zug et al. (2001). Duellman's (1978, p. 109, Figure 71, lower photo) photograph is of *L. knudseni*, and Schulte's (1984) photo of *L. pentadactylus* appears to be *L. knudseni*. Heyer (1972) included photographs of juvenile paratypes. The color drawing of *L. knudseni* in Crump (2002) appears to be a juvenile *L. pentadactylus*. SEM micrographs of larval oral cavities are in Wassersug and Heyer (1988). Illustrations of larval characteristics are found in Hero (1990) and Larson and de Sá (1998). An audiospectrogram is depicted in Hero and Galatti (1990) and an audiospectrogram and an oscillogram are in Heyer (1979). Heyer (1979) provided a distribution map. Photos of the karyotype and the type locality are in Heyer (1972). A photograph of flies attacking a larva is in Hödl (1993).

• **DISTRIBUTION.** *Leptodactylus knudseni* is found in the Gran Sabana of Venezuela and neighboring Lavrado open formation in northern Brazil, and in mesic, tropical habitats of southern Venezuela south to Bolivia and Brazil extending eastward from Ecuador, Colombia, and Peru, through Guyana, Surinam, and French Guiana to Trinidad. Duellman (1999) tabulated its natural region distribution as Amazon Basin-Guiana lowlands, and Heyer (1979) and Les-



Map. Distribution of *Leptodactylus knudseni*. The type-locality is indicated by a circle. Dots mark other localities. A dot may represent more than one site. The only voucher specimen for Trinidad (MCZ 8663) has no specific locality data and is not shown on the map. Published locality data should be considered as secondary sources of information, as we did not confirm all specimen identifications. The locality data from which the map was generated can be found at <http://learning.richmond.edu/Leptodactylus>.

cure (1986) labeled it an Amazon Basin species. Harding (1983) listed its distribution by countries in the New World.

Leptodactylus knudseni inhabits primary and secondary forests (Martins 1998, O'Shea 1990, Tocher 1998) and cleared areas (Heyer 1972, Tocher 1998). The species may be found at elevations from 50 m to 1000 m asl (Acosta-Galvis 2000, Amézquita and Hödl 2004, Cadle et al. 2002, Cisneros-Heredia 2003, Duellman 1995, 2005, Fugler and Walls 1979, Heyer 1972, 1979, Heyer and Bellin 1973, Hödl 1990, Icochea et al. 1998, 1999, Lehr 2001, Morales and McDiarmid 1996, Rodríguez and Emmons 1994, Ruiz-Carranza et al. 1996).

The following references to distribution and localities are listed by country: **Bolivia** (De la Riva 1990, De la Riva et al. 2000, Heyer 1979, Köhler 2000, Lavilla et al. 1996, and Reichle 1997); **Brazil** (Avila-Pires and Hoogmoed 1997, Azevedo-Ramos 1995, Azevedo-Ramos et al. 1999, Buchacher 1993, Cardoso and Souza 1996, Estupiñán and Galatti 2000, Estupiñán et al. 2002, Galatti 1999, Hero 1990, Hero and Galatti 1990, Heyer 1977 [as *L. "pentadactylus"*], 1979, Hödl 1990, Hoogmoed 1993, Magnusson and Hero 1991, Martins 1998, Neckel-Oliveira et al. 2000, O'Shea 1990, Tocher 1998, Vanzolini 1986, Vogt and Bernhard 2003, Wassersug and Heyer 1988, Zimmerman 1991, Zimmerman and Rodrigues 1990, and Zimmerman and Simberloff 1996); **Colombia** (Acosta-Galvis 2000, Cochran and Goin 1970 (USNM specimens 144847 and 147272 identified as *L. pentadactylus* are *L. knudseni*), Heyer 1979, Lynch and Vargas R. 2000, and Ruiz-Carranza et al. 1996);

Ecuador (Almendáriz 1991, Cisneros-Heredia 2003, Coloma 1991, Duellman, 1978 [as *L. pentadactylus* in part], Fugler and Walls 1979, Heyer 1979, and Heyer and Bellin 1973); French Guiana (Boistel and Pauwels 2002, Born and Gaucher 2001b, Gottsberger and Gruber 2004, Heyer 1979, Hoogmoed and Avila-Pires 1991, Kok 2000, Lescure 1986, and Lescure and Marty 2000); **Guyana** (Crawford and Jones 1933 [as *L. pentadactylus*, probably *L. knudseni*], Heyer 1979); Peru (Cadle et al. 2002, Doan and Arizábal Arriaga 2002, Duellman 1989, 1990, 1995, 2005, Duellman and Salas 1991, Heyer 1979, Icochea et al. 1998, 1999, 2001, Lehr 2001, 2002, Morales and McDiarmid 1996, Rodríguez 1987, 1994, Rodríguez and Cadle 1990, Rodríguez and Duellman 1994, and Rodríguez and Emmons 1994); **Surinam** (Heyer 1979); **Trinidad** (Heyer 1979, Maclean et al. 1977, and Murphy 1996, 1997); **Venezuela** (Amézquita and Hödl 2004, Barrio Amarós 1998, Gorzula and Señaris 1999, Gremone et al. 1986, Heyer 1979, La Marca 1992, and McDiarmid and Paolillo O. 1988).

• **FOSSIL RECORD.** None.

• **PERTINENT LITERATURE.** Heyer (1972, 1979) published the most complete accounts of the species. The literature below is listed by topic; the symbol (M) indicates the species is mentioned and (S) means a secondary source: **auditory physiology** (Machens et al. 2004); **bibliographic information and lists** (La Marca 1992, Liner 1992, Morales 1995, Péfaur 1992, and Walley 2000); **biogeography** (Doan and Arizábal Arriaga 2002, Donnelly et al. 2005, Harvey 1998, Heyer 1988, Heyer and Maxson 1982a,b, Hoogmoed 1979 [probably based on specimens of both *L. knudseni* and *L. pentadactylus*], Köhler 2000, Lehr 2002, Lynch 1979, 1988, Murphy 1997, Péfaur and Rivero 2000, Péfaur and Sierra 1995, Rivero-Blanco and Dixon 1979 [information based on both *L. knudseni* and *L. pentadactylus*], and Zimmerman and Simberloff 1996); **call and call parameters** (Hero and Galatti 1990, Lescure and Marty 2000, Schneider 1984, and Zimmerman and Rodrigues 1990); **checklists** (De la Riva et al. 2000, Duellman and Salas 1991, Henle 1992, Hoogmoed and Avila-Pires 1991, Lescure 1976 [information based on both *L. knudseni* and *L. pentadactylus*], Miyata 1982, Morales 1995, Morales and McDiarmid 1996, O'Shea 1990, Péfaur 1992, Péfaur and Rivero 2000, and Rodríguez 1987); **conservation** (Estupiñán and Galatti 2000, Péfaur and Rivero 2000, Tocher et al. 1997, Vanzolini 1986, and Young et al. 2004); **ecology, natural history, and reproduction** (Amézquita and Hödl 2004 (M), Avila-Pires and Hoogmoed 1997, Azevedo-Ramos 1995, Azevedo-Ramos et al. 1999, Bartlett and Bartlett 2003, Beebe 1925, 1946 [both as *L. pentadactylus*], Boistel and Pauwels 2002, Born and Gaucher 2001a,b, Buchacher 1993, Cardoso and Souza 1996, Croft et al. 2001, Crombie and Heyer 1983, Crump 1974 [information based on both *L. knudseni* and *L. pentadactylus*], 1992, Duellman 1978 [probably based on specimens of both *L. knudseni* and *L. pentadactylus*], 1989, 1990, 1995, 2005, Duellman and

Lizana 1994, Duellman and Salas 1991, Estupiñán et al. 2002, Estupiñán and Galatti 2000, Galatti 1992 (M), 1999, Gascon 1991a,b, 1992 (M), 1994, 1995 (S), Gorzula and Señaris 1999, Gossmann et al. 2002 (M), Gottsberger and Gruber 2004, Heatwole 1982, Hero 1990, Hero and Galatti 1990, Hero et al. 1998, Hero et al. 2001, Heyer 1972, Heyer and Bellin 1973, Hödl 1988, 1990, 1992, 1993, 2000, 2002, Kornacker and Dederichs 1998 [as *L. pentadactylus*], Lehr 2002, Lescure 1975 [as *L. pentadactylus*], 1986, Lescure and Marty 2000, Magnusson 1997 (M), Magnusson and Hero 1991, Martins 1998, Morales and McDiarmid 1996, O'Shea 1990, Petranka and Kennedy 1999 (S), Parmelee 1999 [as *L. pentadactylus*, identified as *L. knudseni* by Duellman 2005], Pough et al. 1992, Prado et al. 2002, Rodríguez and Cadle 1990, Schneider 1984, Silva et al. 2005, Tocher et al. 1997, Wassersug and Heyer 1988, Zimmerman 1991, Zimmerman and Rodrigues 1990, Zimmerman and Simberloff 1996, and Zug et al. 2001 (M)(S); **evolution** (Heyer 1979); **faunal accounts** (Beebe 1925 [as *L. pentadactylus*], Fugler and Walls 1979, La Marca 1992, Lescure 1986, Martins 1998, Rodríguez and Cadle 1990, and Zimmerman and Rodrigues 1990); **habitat** (Allmon 1991, Avila-Pires and Hoogmoed 1997, Azevedo-Ramos et al. 1999, Bartlett and Bartlett 2003, Born and Gaucher 2001b, Cadle et al. 2002, Crawford and Jones 1993 [as *L. pentadactylus*, probably *L. knudseni*], Duellman 1989, 1990, Duellman and Salas 1991, Estupiñán et al. 2002, Estupiñán and Galatti 2000, Fugler and Walls 1979, Galatti 1999, Gascon 1991b, Hero 1990, Hoogmoed and Avila-Pires 1991, Jim 1980 (M), Kok 2000, Lescure 1986, Lynch and Vargas R. 2000, Morales and McDiarmid 1996, Neckel-Oliveira et al. 2000, O'Shea 1990, Rodríguez 1994, Rodríguez and Cadle 1990, Tocher 1998, Tocher et al. 2001, Zimmerman 1991, and Zimmerman and Rodrigues 1990); **inventory** (Avila-Pires and Hoogmoed 1997, Icochea et al. 1999, Icochea et al. 1998, Kok 2000, Lavilla et al. 1996, Vanzolini 1986, and Zimmerman and Rodrigues 1990); **karyotype** (Amaro-Ghildardi et al. 1999, 2004, and Kuramoto 1990 (S)); **keys** (Hero 1990, Heyer 1972, 1979, Lescure and Marty 2000, and Murphy 1997); **morphology** (Bartlett and Bartlett 2003, Crawford and Jones 1933 [as *L. pentadactylus*, probably *L. knudseni*], Fugler and Walls 1979, Hero and Galatti 1990, Hoogmoed and Avila-Pires 1991, Larson and de Sá 1998, Pough et al. 1992); **nomenclature and taxonomy** (Heyer 1974, 1979, Heyer and Peters 1971 [based on both *L. knudseni* and *L. pentadactylus*], and Spieler et al. 1999 (M)); **non-technical accounts** (Bartlett and Bartlett 2003, Crump 2002, Hödl 1992, 2002, and Oliveira 1996); **relationships and systematics** (Chipman et al. 2001, Crother 1999 (M), Eterovick and Szazima 2000, Heyer 1979, Heyer and Diment 1974, Larson and de Sá 1998, Lescure 1987 (M); MacCulloch et al. 1996, Maxson and Heyer 1988, Nuin and Val 2005, Savage 2002 (M), Wassersug and Heyer 1988, and Zimmerman and Simberloff 1996); **speciation** (Heyer et al. 2005); **species accounts** (Duellman 1978 [based on specimens of both *L. knudseni* and *L. pentadactylus*],

2005, Gorzula and Señaris 1999, Heyer 1979, Lescure and Marty 2000, Murphy 1997, and Rodríguez and Duellman 1994); **species comparisons** (Bartlett and Bartlett 2003, Fabrezi and Vera 1997 (M), Gorzula and Señaris 1999, Hero and Galatti 1990, Heyer 1972, 1979, Lescure and Marty 2000, McCranie et al. 1980, Murphy 1997, Péfaur and Sierra 1993 (M), Pyburn and Heyer 1975, and Wassersug and Heyer 1988); **species or taxonomic lists** (Acosta-Galvis 2000, Ananjeva et al. 1988, Barrio Amarós 1996, Born and Gaucher 2001b, Cisneros-Heredia 2003, Donnelly et al. 2005, Duellman 2003, Frost 1985, Galatti 1999, Glaw et al. 2000, Heyer 1977 [as *L. pentadactylus*]), La Marca 1995, 1997, Lehr 2002, Rodríguez et al. 1993, and Ruiz-Carranza 1996); **techniques** (Chen and Combs 1999 and Hayek and Heyer 2005).

• **NOMENCLATURAL HISTORY.** *Leptodactylus knudseni* was identified as *L. pentadactylus* prior to its description as a new species in 1972. Duellman (1978) synonymized *L. knudseni* with *L. pentadactylus* and Heyer (1979) demonstrated that *L. knudseni* is a distinct species.

• **REMARKS.** *Leptodactylus knudseni* is a member of the *L. pentadactylus* species group as defined in Maxson and Heyer (1988). Barrio Amarós (1998) indicated that the common name for *L. knudseni* is "Sapo-toro amazónico." Bartlett and Bartlett (2003) called it the "Rose-sided jungle frog." Boistel and Pauwels (2002) termed it "Knudsen's Bullfrog," Frank and Ramus (1995) used "Knudsen's Frog," while Hödl (1992, 2002) called it the "South American Bull Frog." Lescure et al. (1980) provided the Wayãpi name "Yuwai" and noted that *L. knudseni* is a food resource for the Wayãpi of French Guiana. Lescure and Marty (2000) determined that French Guianian Creole names for *L. knudseni* include "Krapo-lapli" (Crapaud la Pluie) and "Apel-lapli" (Appelle la Pluie). Finally, O'Shea (1990) referred to the frog as "Rã-pimenta" and "Knudsen's bullfrog."

• **ETYMOLOGY.** Heyer (1972) named the species for Jens W. Knudsen, who initiated WRH in the excitement of biological research and inspired him as an undergraduate to attend graduate school rather than to pursue a career as a high school teacher.

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