

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 extotrophic, 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

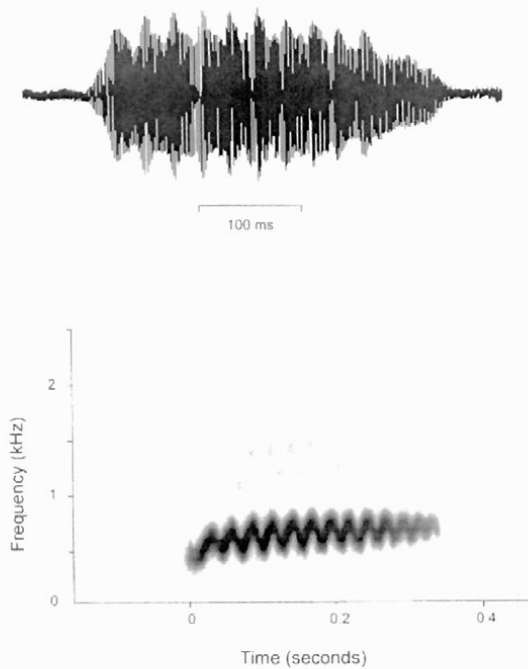


Figure 2. Wave form and audiospectrogram displays of the advertisement call of *Leptodactylus knudseni* (USNM recording 228, cut 1) from Usina Kararahô, 27 km from Altamira, Pará, Brazil, voucher specimen ZUEC 7232. Canary software was used to produce the figure.

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).

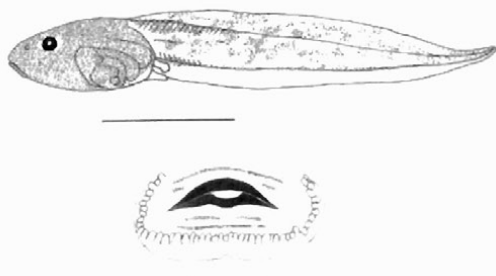
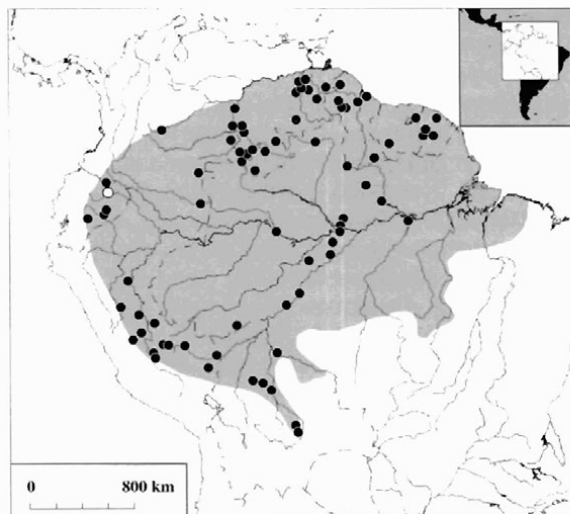


Figure 3. Tadpole of *Leptodactylus knudseni* (semidiagrammatic drawings from USNM 560922) from Dubulay Ranch, East Berbice, Guyana, Gosner stage 31. Lateral view bar = 10 mm, oral disk bar = 1 mm.

• **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** (Avilla-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 Arizabal 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 Arizabal 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, Petranksa 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-Ghilardi 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 Sazima 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 Amorós 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).

• **NOMENCLATURE 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 Amorós (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 Wayapi name "Yuwai" and noted that *L. knudseni* is a food resource for the Wayapi 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 "Räpimenta" 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.

• **ACKNOWLEDGMENTS.** Janalee Caldwell reviewed the manuscript. Staff of the Natural History Branch Library of the Smithsonian Institution, Claire Catron, Ron Lindsey, Leslie Overstreet, Martha Rosen, Courtney Shaw, David Steere, and Wanda West obtained some of the rarer publications cited in this manuscript. Research for this account was supported by NSF awards 981587 and DEB-03429 to Rafael O. de Sá and WRH.

LITERATURE CITED

- Acosta-Galvis, A.R. 2000. Ranas, salamandras y caecilias (Tetrapoda: Amphibia) de Colombia. *Biota Colombiana* 1:289–319.
- Allmon, W.D. 1991. A plot study of forest floor litter frogs, Central Amazon, Brazil. *Journal of Tropical Ecology* 7:503–522.
- Almendáriz, A. 1991. Anfíbios y reptiles. *Politécnica* 16:89–162.
- Amaro-Ghilardi, R.C., R.P. Oliveira, and Y. Yonenaga-Yassuda. 1999. Padrões de distribuição de seqüências teloméricas (TTAGGG)_n em espécies de *Bufo*, *Leptodactylus* e *Hyla* (Amphibia - Anura) [Abstract]. *Genetics and Molecular Biology* 22 (supplement):64–65.
- , M.T. Rodrigues, and Y. Yonenaga-Yassuda. 2004. Chromosomal studies after differential staining and fluorescence in situ hybridization using telomeric probe in three *Leptodactylus* species (Leptodactylidae, Anura). *Caryologia* 57:53–65.
- Amézquita, A. and W. Hödl. 2004. How, when, and where to perform visual displays: the case of the Amazonian frog *Hyla parviceps*. *Herpetologica* 60:420–429.
- Ananjeva, N., L.J. Borkin, I.S. Darevsky, and N.L. Orlov. 1988. Dictionary of Animal Names in Five Languages. Amphibians and Reptiles. Latin, Russian, English, German, French. 12126 Names. Russky Yazyk Publishers, Moscow.
- Avila-Pires, T.C.S. and M.S. Hoogmoed. 1997. The herpetofauna, p. 389–401. *In* P.L.B. Lisboa (organizer), Caxiuanã. Museu Paraense Emílio Goeldi, Belém.
- Azevedo-Ramos, C. 1995. Ecologia de comunidade de girinos às margens do rio Tapajós em uma região de savana amazônica. Doctoral Thesis, Universidade Estadual de Campinas.
- , W.E. Magnusson, and P. Bayliss. 1999. Predation as the key factor structuring tadpole assemblages in a savanna area in central Amazonia. *Copeia* 1999:22–33.
- Barrio Amorós, C.L. 1996. Anfíbios de Venezuela: Visión aproximativa. *Reptilia* 6:24–32.
- . 1998. Sistemática y biogeografía de los anfíbios (Amphibia) de Venezuela. Systematics and biogeography of the amphibians (Amphibia) of Venezuela. *Acta Biológica Venezuelica* 18:1–93.
- Bartlett, R.D. and P.P. Bartlett. 2003. Reptiles and Amphibians of the Amazon. An Ecotourist's Guide. University Press of Florida, Gainesville.
- Beebe, W. 1925. Studies of a tropical jungle: one quarter of a square mile of jungle at Kartabo, British Guiana. *Zoologica* 6:4–193.
- . 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. *Zoologica* 31: 11–52 + plates I–XIII.
- Boistel, R. and O.S.G. Pauwels. 2002. Natural history notes: *Leptodactylus knudseni* (Knudsen's Bullfrog). *Predation. Herpetological Review* 33: 303.
- Born, M. and P. Gaucher. 2001a. Distribution and life histories of amphibians and reptiles, p. 167–184. *In* F. Bongers, P. Charles-Dominique, P.-M. Forget, and M. Théry (eds), Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical

- Rainforest. Monographiae Biologicae 80, Kluwer Academic Publishers, Dordrecht, Boston, London.
- and –. 2001b. Appendix 5. Amphibian and reptile species at the Nouragues Nature Reserve, p. 371–379. In F. Bongers, P. Charles-Dominique, P.-M. Forget, and M. Théry (eds), Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest. Monographiae Biologicae 80, Kluwer Academic Publishers, Dordrecht, Boston, London.
- Buchacher, C.O. 1993. Field studies on the small Surinam toad, *Pipa arrabali*, near Manaus, Brazil. *Amphibia-Reptilia* 14:59–69.
- Cadle, J., J. Icochea, J.P. Zúñiga, A. Portilla, and C. Rivera. 2002. Anexo 3. Listado de especies registradas para el Santuario Nacional Pampas del Heath, p. 101–104. In J.R. Montambault (ed.), Informes de las Evaluaciones Biológicas Pampas del Heath, Perú, Alto Madidi, Bolivia y Pando, Bolivia. RAP (Rapid Assessment Program) Bulletin of Biological Assessment (24).
- Cardoso, A.J. and M.B. Souza. 1996. Distribuição temporal e espacial de anfíbios anuros no Seringal Catuaba, Estado do Acre, Brasil, p. 271–291. In J.E. Péfaur (compiler), Herpetología Neotropical. Actas de II Congreso Latinoamericano de Herpetología. II Volumen. Universidad de Los Andes, Consejo de Publicaciones, Mérida.
- Chen, M.H. and C.A. Combs. 1999. An alternative anesthesia for amphibians: Ventral application of benzocaine. *Herpetological Review* 30:34.
- Chipman, A.D., O. Khaner, A. Haas, and E. Tchernov. 2001. The evolution of genome size: what can be learned from anuran development? *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 291:365–374.
- Cisneros-Heredia, D.F. 2003. Herpetofauna de la Estación de Biodiversidad Tiputini, Amazonía Ecuatoriana: Ecología de una comunidad taxonómicamente diversa, con comentarios sobre metodologías de inventario. In S. De la Torre and G. Reck (eds.), *Ecología y Ambiente en el Ecuador: Memorias del I Congreso de Ecología y Ambiente, Ecuador País Megadiverso*. Compact Disc, Universidad San Francisco de Quito, Quito.
- Cochran, D.M. and C.J. Goin. 1970. Frogs of Colombia. *United States National Museum Bulletin* (288):xii + 655 p.
- Cocroft, R., V.R. Morales, and R.W. McDiarmid. 2001. Frogs of Tambopata, Peru. Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York (includes compact disc).
- Coloma, L.A. 1991. Anfíbios del Ecuador: lista de especies, ubicación altitudinal y referencias bibliográficas. *EcoCiencia, Reportes Técnicos* 2:1–46 + errata.
- and S.R. Ron. 2001. Ecuador megadiverso. Megadiverse Ecuador. Anfíbios, reptiles, aves, mamíferos. Amphibians, reptiles, birds and mammals. Museo de Zoología, Pontificia Universidad Católica del Ecuador, Serie de Divulgación (1):1–139.
- Crawford, S.C. and E.P. Jones. 1933. Field notes on some amphibians from British Guiana. *Copeia* 1933:88–92.
- Crombie, R.I. and W.R. Heyer. 1983. *Leptodactylus longirostris* (Anura: Leptodactylidae): advertisement call, tadpole, ecological and distributional notes. *Revista Brasileira de Biologia* 43:291–296.
- Crother, B.I. 1999. Evolutionary relationships, p. 269–334. In B.I. Crother (ed.), *Caribbean Amphibians and Reptiles*. Academic Press, San Diego and other cities.
- Crump, M.L. 1974. Reproductive strategies in a tropical anuran community. University of Kansas Museum of Natural History, Miscellaneous Publication (61):1–68.
- . 1992. Cannibalism in amphibians, p. 256–276. In M.A. Elgar and B.J. Crespi (eds.), *Cannibalism: Ecology and Evolution Among Diverse Taxa*. Oxford University Press, Oxford and New York.
- . 2002. Amphibians, p. 79–96, 272–291. In D.L. Pearson and L. Beletsky (eds.), *Brazil: Amazon and Pantanal. The Ecotraveller's Wildlife Guide*. Natural World, Academic Press, San Diego and other cities.
- 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.
- , 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.
- Doan, T.M. and W. Arizábal Arriaga. 2002. Microgeographic variation in species composition of the herpetofaunal communities of Tambopata Region, Peru. *Biotropica* 34:101–117.
- Donnelly, M.A., M.H. Chen, and G.G. Watkins. 2005. The Iwokrama herpetofauna: an exploration of diversity in a Guyanan rainforest, p. 428–460. In M.A. Donnelly, B.I. Crother, C. Guyer, M.H. Wake, and M.E. White (eds.), *Ecology & Evolution in the Tropics. A Herpetological Perspective*. The University of Chicago Press, Chicago and London.
- Duellman, W.E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. University of Kansas Museum of Natural History, Miscellaneous Publication (65):1–352.
- . 1989. Tropical herpetofaunal communities: patterns of community structure in Neotropical rainforests, p. 61–88. In M.L. Harmelin-Vivien and F. Bourlière (eds.), *Ecological Studies, Vol. 69, Vertebrates in Complex Tropical Systems*. Springer-Verlag, New York and other cities.
- . 1990. Herpetofaunas in Neotropical rainforests: comparative composition, history, and resource use, p. 455–505. In A.H. Gentry (ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven and London.
- . 1995. Temporal fluctuations in abundances of anuran amphibians in a seasonal Amazonian rainforest. *Journal of Herpetology* 29:13–21.
- . 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.
- . 2003. Amphibians species list, p. 456–489. In M. Hutchins, W.E. Duellman, and N. Schlager (eds.), *Grzimek's Animal Life Encyclopedia*, 2nd Edition. Volume 6, Amphibians. Gale Group, Farmington Hills, Michigan.
- . 2005. *Cusco Amazónico. The Lives of Amphibians and Reptiles in an Amazonian Rainforest*. Comstock Publishing Associates, Cornell University Press, Ithaca and London.
- and M. Lizana. 1994. Biology of a sit-and-wait predator, the leptodactylid frog *Ceratophrys cornuta*. *Herpetologica* 50:51–64.
- and A.W. Salas. 1991. Annotated checklist of the amphibians and reptiles of Cuzco Amazónico, Peru. *University of Kansas Museum of Natural History, Occasional Papers* (143):1–13.
- Estupiñán, R.A. and U. Galatti. 2000 (“1999”). La fauna Anura en áreas con diferentes grados de intervención antrópica de la Amazonia Oriental Brasileña. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 23 (Suplemento especial):275–286.
- , J.A.R. Bernardi, and U. Galatti. 2002. Fauna Anura, p. 541–553. In P.L.B. Lisboa (organizer), *Caxiuanã. Populações Tradicionais, Meio Físico e Diversidade Biológica*. Museu Paraense Emílio Goeldi, Belém.
- Eterovick, P.C. and I. Sazima. 2000. Description of the tadpole of *Leptodactylus syphax*, with a comparison of morphological and ecological characters of tadpoles and adults of the species in the *L. pentadactylus* group (Leptodactylidae, Anura). *Amphibia-Reptilia* 21:341–350.
- Fabrezi, M. and R. Vera. 1997. Caracterización morfológica de larvas de anuros del noroeste argentino. *Cuadernos de Herpetología* 11:37–49.
- 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.
- 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. and A.B. Walls. 1979. The Anura (Amphibia) of Rio Upano valley of eastern Ecuador. *Journal of the Tennessee Academy of Science* 54:149–156.
- Galatti, U. 1992. Population biology of the frog *Leptodactylus pentadactylus* in a central Amazonian rainforest. *Journal of Herpetology* 26:23–31.
- . 1999. Avaliação Ecológica Rápida Reserva Biológica Estadual Rio Ouro Preto, Guajará-Mirim RO. Inventário da Herpetofauna da Reserva Biológica Rio Ouro Preto, Rondônia. Programa das Nações Unidas para o Desenvolvimento – PNUD, Plano Agropecuário e Florestal de Rondônia – PLANAFLORO.
- Gascon, C. 1991a. Breeding of *Leptodactylus knudseni*: responses to rainfall variation. *Copeia* 1991: 248–252.
- . 1991b. Population- and community-level analyses of species occurrences of central Amazonian rainforest tadpoles. *Ecology* 72:1731–1746.
- . 1992. Spatial distribution of *Osteocephalus taurinus* and *Pipa arrabali* in a central Amazonian forest. *Copeia* 1992:894–897.
- . 1994. Bottom-nets as a new method for quantitatively sampling tadpole populations (Amphibia, Anura). *Revista Brasileira de Zoologia* 11:355–359.
- . 1995. Natural history notes on frogs from Manaus, Amazonas. *Revista Brasileira de Zoologia* 12:9–12.
- 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).
- Gorzula, S. and J.C. Señaris. 1999 (“1998”). Contribution to the herpetofauna of the Venezuelan Guyana I. A data base. *Scientia Guaianae* (8):xviii + 268 p. + 129 color photographs + 4 annex maps.
- Gossmann, V., S. Lötters, F. Obame, and W. Böhme. 2002. Zur Herpetofauna Gabuns. *Herpetofauna (Germany)* 24:19–33.
- Gottsberger, B. and E. Gruber. 2004. Temporal partitioning of reproductive activity in a neotropical anuran community. *Journal of Tropical Ecology* 20:271–280.
- Gremone, C., F. Cervigón, S. Gorzula, G. Medina, and D. Novoa. 1986. *Fauna de Venezuela. Vertebrados*. Editorial Biosfera, Caracas.
- Harding, K.A. 1983. *Catalogue of New World Amphibians*. Pergamon Press, Oxford and other cities.
- 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 Paper* (10):1–372 + 1 map. (Spanish version, p.154–166).
- Hayek, L.C. and W.R. Heyer. 2005. Determining sexual dimorphism in frog measurement data: integration of statistical significance, measurement error, effect size and biological significance. *Anais da Academia Brasileira de Ciências* 77:45–76.
- Heatwole, H. 1982. A review of structuring in herpetofaunal assemblages, p. 1–19. In N.J. Scott, Jr. (ed.), *Herpetological Communities. A Symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League*, August 1977. United States Department of the Interior, Fish and Wildlife Service, Wildlife Research Report (13):iv + 1–239.
- Henle, K. 1992. Zur Amphibienfauna Perus nebst Beschreibung eines neuen *Eleutherodactylus* (Leptodactylidae). *Bonner Zoologische Beiträge*

- 43:79–129.
- Hennessey, A.B. 2002. *Leptodactylus knudseni*, p. 34. In R. Márquez, I. De la Riva, J. Bosch, and E. Matheu (eds.), *Guía Sonora de las Ranas y Sapos De Bolivia. Sounds of Frogs and Toads of Bolivia*. Alosa, Museo Nacional de Ciencias Naturales, Fonoteca Zoológica, Madrid.
- Hero, J.-M. 1990. An illustrated key to tadpoles occurring in the central Amazon rainforest, Manaus, Amazonas, Brasil. *Amazoniana* 11:201–262.
- and U. Galatti. 1990. Characteristics distinguishing *Leptodactylus pentadactylus* and *L. knudseni* in the central Amazon rainforest. *Journal of Herpetology* 24:226–228.
- , C. Gascon, and W.E. Magnusson. 1998. Direct and indirect effects of predation on tadpole community structure in the Amazon rainforest. *Australian Journal of Ecology* 23:474–482.
- , W.E. Magnusson, C.F.D. Rocha, and C.P. Catterall. 2001. Antipredator defenses influence the distribution of amphibian prey species in the central Amazon rain forest. *Biotropica* 33:131–141.
- Herrmann, H.-J. 2001. Terrarien Atlas. Band 1. Kulturgeschichte, Biologie und Terrarienhaltung von Amphibien, Schleichenlurche, Schwanzlurche, Froschlurche (Erster Teil). Mergus Verlag GmbH, Melle, Germany.
- Heyer, W.R. 1972. The status of *Leptodactylus pumilio* Boulenger (Amphibia, Leptodactylidae) and the description of a new species of *Leptodactylus* from Ecuador. *Natural History Museum of Los Angeles County, Contributions in Science* (231): 1–8.
- . 1974. Relationships of the *marmoratus* species group (Amphibia, Leptodactylidae) within the subfamily Leptodactylinae. *Natural History Museum of Los Angeles County, Contributions in Science* (253):1–46.
- . 1977. Taxonomic notes on frogs from the Madeira and Purus rivers, Brasil. *Papéis Avulsos de Zoologia* 31:141–162.
- . 1979. Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology* (301):1–43.
- . 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.
- . 2005. Variation and taxonomic clarification of the large species of the *Leptodactylus pentadactylus* species group (Amphibia: Leptodactylidae) from Middle America, northern South America, and Amazonia. *Arquivos de Zoologia* (37):269–348.
- and M.S. Bellin. 1973. Ecological notes on five sympatric *Leptodactylus* (Amphibia, Leptodactylidae) from Ecuador. *Herpetologica* 29:66–72.
- , R.O. de Sá, and A. Rettig. 2005. Sibling species, advertisement calls, and reproductive isolation in frogs of the *Leptodactylus pentadactylus* species cluster, p. 35–39. In N. Ananjeva and O. Tsinenko (eds.), *Herpetologia Petropolitana. Proceedings of the 12th Ordinary Meeting of the Societas Europaea Herpetologica*, August 12–16, 2003, St. Petersburg. *Russian Journal of Herpetology* 12 (Supplement).
- and M.J. Diment. 1974. The karyotype of *Vanzolinus discodactylus* and comments on usefulness of karyotypes in determining relationships in the *Leptodactylus*-complex (Amphibia, Leptodactylidae). *Proceedings of the Biological Society of Washington* 87:327–336.
- and L.R. Maxson. 1982a. Neotropical frog biogeography: paradigms and problems. *American Zoologist* 22:397–410.
- and –. 1982b. 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 J.A. Peters. 1971. The frog genus *Leptodactylus* in Ecuador. *Proceedings of the Biological Society of Washington* 84:163–170.
- and A.S. Thompson. 2000. *Leptodactylus rugosus*. *Catalogue of American Amphibians and Reptiles* (708):1–5.
- Hödl, W. 1988. *Physalaemus ephippifer* (Leptodactylidae): Schaumnestbildung. Begleitveröffentlichungen zu wissenschaftlichen Filmen, Film C 1891 des Österreichisches Bundesinstitut für den Wissenschaftlichen Film (Wien), Nr. 38/39:29–35.
- . 1990. Reproductive diversity in Amazonian lowland frogs, p. 41–60. In W. Hanke (ed.), *Fortschritte der Zoologie*, 38. *Biology and Physiology of Amphibians*. Gustav Fischer Verlag, Stuttgart.
- . 1992. Amazonian frogs, p. 90–97. In H.-U. Bernard (ed.), *Insight Guides. Amazon Wildlife*. APA Publications (HK) Ltd., Singapore.
- . 1993. Amazonien aus der Froschperspektive. *Kataloge des OÖ. Landesmuseums N.F.* (61): 499–546.
- . 1996. Zur Fortpflanzungsbiologie von Fröschen, p. 71–85. In *Frösche Kröten Unken: aus der Welt der Amphibien*. Stapfia (47), zugleich Kataloge des OÖ. Landesmuseums, N.F. (107):1–271.
- . 2000. Amphibian foam nests, p. 152–153. 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).
- . 2002. Amazonian frogs, p. 83–87. In M. Lord (ed.), *Insight Guides. Amazon Wildlife*. Fourth Edition. APA Publications, Singapore.
- Hoogmoed, M.S. 1979. The herpetofauna of the Guianan region, p. 241–279. In W.E. Duellman (ed.), *The South American Herpetofauna: Its Origin, Evolution, and Dispersal*. Monograph of the Museum of Natural History, The University of Kansas (7):3 unnumbered + 485 p.
- . 1993. The herpetofauna of floating meadows, p. 199–213. In P.E. Ouboter (ed.), *Freshwater Ecosystems of Suriname*. Kluwer Academic Publishers, The Netherlands.

- and T.C.S. Avila-Pires. 1991. Annotated checklist of the herpetofauna of Petit Saut, Sinnamary River, French Guiana. *Zoologische Mededelingen* 65: 53–88.
- Icochea, J., A. Portilla, E. Quispitupac, C. Aguilar, E. Ponce, and R. Fernandez. 1999. Amphibians and reptiles: biodiversity assessment at the Pagoreni well site, p. 99–115. *In* A. Alonso and F. Dallmeier (eds.), *Biodiversity Assessment and Monitoring of the Lower Urubamba Region, Peru. Pagorini Well Site: Assessment and Training. Smithsonian Institution Monitoring & Assessment of Biodiversity Program Series (3):*xxxiv + 333 p.
- , E. Quispitupac, and A. Portilla. 1998. Amphibians and reptiles: biodiversity assessment in the lower Urubamba region, p. 125–142. *In* A. Alonso and F. Dallmeier (eds.), *Biodiversity Assessment and Monitoring of the Lower Urubamba Region, Peru. Cashiriari–3 Well Site and the Camisea and Urubamba Rivers. Smithsonian Institution Monitoring & Assessment of Biodiversity Program Series (2):*xliv + 298 p.
- , –, and E. Ponce. 2001. Assessment of amphibians and reptiles of the lower Urubamba region, Peru, p. 129–142. *In* A. Alonso, F. Dallmeier, and P. Campbell (eds.), *Urubamba: The Biodiversity of a Peruvian Rainforest. Smithsonian Institution Monitoring & Assessment of Biodiversity Program Series (7):*x + 204 p.
- Jim, J. 1980. Aspectos Ecológicos dos Anfíbios Registrados na Região de Botucatu, São Paulo (Amphibia, Anura). *Doutor em Ciências Tese, Universidade de São Paulo.*
- Köhler, J. 2000. Amphibian diversity in Bolivia: a study with special reference to montane forest regions. *Bonner Zoologische Monographien* (48): 1–243.
- Kok, P.J.R. 2000. A survey of the anuran fauna of Montagne Belvédère, county of Saül, French Guiana: field list with comments on taxonomy and ecology. *British Herpetological Society Bulletin* 71:6–26.
- Kornacker, P.M. and U. Dederichs. 1998. *Herpetologische Eindrücke einer Venezuelareise – Teil 2: Die Llanos. Elaphe* 6:68–73.
- Kuramoto, M. 1990. A list of chromosome numbers of anuran amphibians. *Bulletin of Fukuoka University of Education* 39:83–127.
- La Marca, E. 1992. Catálogo taxonómico, biogeográfico y bibliográfico de las ranas de Venezuela. *Cuadernos Geográficos* (9):1–197.
- . 1995. Crisis de biodiversidad en anfibios de Venezuela: estudio de casos, p. 47–70. *In* M.E. Alonso (ed.), *La Biodiversidad Neotropical y la Amenaza de las Extinciones. Cuadernos de Química Ecológica* (4):1–160.
- . 1997. Lista actualizada de los anfibios de Venezuela, p. 103–120. *In* E. La Marca (ed.), *Vertebrados Actuales y Fósiles de Venezuela. Catálogo Zoológico de Venezuela. Vol. 1. Museo de Ciencia y Tecnología de Mérida, Mérida, Venezuela.*
- Larson, P.M. and R.O. de Sá. 1998. Chondrocranial morphology of *Leptodactylus* larvae (Leptodactylidae: Leptodactylinae): its utility in phylogenetic reconstruction. *Journal of Morphology* 238:287–305.
- Lavilla, E.O., L. Gonzáles A., and I. Fernández S. 1996. Informe sobre la herpetofauna del Parque Nacional Amboró y áreas aledañas. *In* D. Rumiz (ed.), *Componente Fauna del Plan de Manejo del Parque Nacional Amboró. Informe FAN–TNC, Santa Cruz de la Sierra, Bolivia.*
- Lehr, E. 2001. New records for amphibians and reptiles from Departamentos Pasco and Ucayali, Peru. *Herpetological Review* 32:130–132.
- . 2002. Amphibien und Reptilien in Peru. *Die Herpetofauna entlang des 10. Breitengrades von Peru: Arterfassung, Taxonomie, ökologische Bemerkungen und biogeographische Beziehungen. Natur-und Tier - Verlag GmbH, Münster.*
- Lehtinen, R.M. and R.A. Nussbaum. 2003. Parental care: a phylogenetic perspective, p. 343–386. *In* B.G.M. Jamieson (ed.), *Reproductive Biology and Phylogeny of Anura, Volume 2. Reproductive Biology and Phylogeny. Science Publishers, Inc., Enfield, New Hampshire, Plymouth, United Kingdom.*
- Lescure, J. 1975. Observations écologiques sur les amphibiens dans l'Amazonie du Nord-Ouest, leur place dans l'environnement humain, p. 65–69. *In* C. Savary (ed.), *Culture sur Brûlis et Évolution du Milieu Forestier en Amazonie du Nord-Ouest. Bulletin de la Société Suisse d'Ethnologie, Numero Special.*
- . 1976. Contribution à l'étude des amphibiens de Guyane française, VI. Liste préliminaire des anoures. *Bulletin du Muséum National d'Histoire Naturelle, 3e série, (377), Zoologie* (265):475–525.
- . 1986. Les amphibiens anoures de la forêt Guyanaise (région de Trois Sauts, Guyane Française). *Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Série, Série A, Zoologie* 132:43–52.
- . 1987. Le peuplement en reptiles et amphibiens des Petites Antilles. *Bulletin de la Société Zoologique de France* 112:327–342.
- , F. Grenand, and P. Grenand. 1980. Les amphibiens dans l'univers Wayäpi. *Journal d'Agriculture Traditionnelle et de Botanique Appliquée* 27:247–261.
- and C. Marty. 2000. Atlas des amphibiens de Guyane. *Patrimoines Naturels* (45):1–388.
- 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.
- Lynch, J.D. 1979. The amphibians of the lowland tropical forests, p. 189–215. *In* W.E. Duellman (ed.), *The South American Herpetofauna: Its Origin, Evolution, and Dispersal. Monograph of the Museum of Natural History, The University of Kansas* (7):3 unnumbered + 485 p.
- . 1988. Refugia, p. 311–342. *In* A.A. Myers and P.S.

- Giller (eds.), *Analytical Biogeography. An Integrated Approach to the Study of Animal and Plant Distributions*. Chapman and Hall, London and New York.
- and M.A. Vargas R. 2000. Lista preliminar de especies de anuros del Departamento del Guainía, Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 24:579–589.
- MacCulloch, R.D., D.E. Upton, and R.W. Murphy. 1996. Trends in nuclear DNA content among amphibians and reptiles. *Comparative Biochemistry and Physiology* 113B:601–605.
- Machens, C.K., M.S. Wehr, and A.M. Zador. 2004. Linearity of cortical receptive fields measured with natural sounds. *The Journal of Neuroscience* 24: 1089–1100.
- Maclean, W.P., R. Kellner, and H. Dennis. 1977. Island lists of West Indian amphibians and reptiles. *Smithsonian Herpetological Information Service* (40):1–47.
- Magnusson, W.E. 1997. Biogeography of frogs: history as the magic bullet. *Journal of Biogeography* 24:251–252.
- and J.-M. Hero. 1991. Predation and the evolution of complex oviposition behaviour in Amazon rain-forest frogs. *Oecologia* 86:310–318.
- Martins, M. 1998. The frogs of the Ilha de Maracá, p. 285–306. *In* W. Milliken and J.A. Ratter (eds.), *Maracá: The Biodiversity and Environment of an Amazonian Rainforest*. John Wiley & Sons Ltd., Chichester, New York, Weinheim, Brisbane, Singapore, Toronto.
- Marty, C. and P. Gaucher. 2000. *Sound Guide to The Tailless Amphibians of French Guiana*. Centre de Bioacoustique Alpin, Paris (includes compact disc).
- Maxson, L.R. and W.R. Heyer. 1988. Molecular systematics of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Fieldiana, Zoology, New Series* (41):iii + 1–13.
- McCranie, J.R., L.D. Wilson, and L. Porras. 1980. A new species of *Leptodactylus* from the cloud forests of Honduras. *Journal of Herpetology* 14:361–367.
- McDiarmid, R.W. and R. Altig. 1999. Research: materials and techniques, p. 7–23. *In* R.W. McDiarmid and R. Altig (eds.), *Tadpoles: The Biology of Anuran Larvae*. University of Chicago Press, Chicago and London.
- and A. Paolillo O. 1988. Herpetological collections - Cerro de la Neblina. Updated January 1988, p. 667–670. *In* C. Brewer-Carias (ed.), *Cerro de la Neblina. Resultados de la Expedición 1983–1987*. Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales, Caracas.
- Miyata, K. 1982. A check list of the amphibians and reptiles of Ecuador with a bibliography of Ecuadorian herpetology. *Smithsonian Herpetological Information Service* (54):1–70.
- Morales, V.R. 1995. Checklist and taxonomic bibliography of the amphibians from Perú. *Smithsonian Herpetological Information Service* (107):1–20.
- and R.W. McDiarmid. 1996. Annotated checklist of the amphibians and reptiles of Pakitza, Manu National Park Reserve Zone, with comments on the herpetofauna of Madre de Dios, Peru, p. 503–522. *In* D.E. Wilson and A. Sandoval (eds.), *Manu. The Biodiversity of Southeastern Peru. La Biodiversidad del Sureste del Perú*. Office of Biodiversity Programs, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
- Murphy, J.C. 1996. Crossing Bond's line: the herpetofaunal exchange between the eastern Caribbean and mainland South America, p. 207–216. *In* R. Powell and R.W. Henderson (eds.), *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz*. *Contributions to Herpetology* (12):1–457.
- . 1997. *Amphibians and Reptiles of Trinidad and Tobago*. Krieger Publishing Co., Malabar, Florida.
- Neckel-Oliveira, S., W.E. Magnusson, A.P. Lima, and A.L.K. Albernaz. 2000. Diversity and distribution of frogs in an Amazonian savanna in Brazil. *Amphibia-Reptilia* 21:317–326.
- Nuin, P.A.S. and F.C. Val. 2005. Phylogenetic analysis of the subfamily Hylodinae (Anura, Leptodactylidae) based on morphological characters. *Amphibia-Reptilia* 26:139–147.
- Oliveira, J.J. 1996. *Manual de Identificação de Rãs Nativas Brasileiras e Rã-Touro Gigante*. Instituto Brasileiro de Meio Ambiente e dos Recursos Naturais Renováveis, Brasília.
- O'Shea, M. 1990 (“1989”). The herpetofauna of Ilha de Maracá, State of Roraima, northern Brazil, p. 51–72. *In* J. Coote (ed.), *Reptiles: Proceedings of the 1988 U.K. Herpetological Societies Symposium on Captive Breeding*. British Herpetological Society, London.
- Parmelee, J.R. 1999. Trophic ecology of a tropical anuran assemblage. *Natural History Museum, The University of Kansas, Scientific Papers* (11): 1–59.
- Péfaur, J.E. 1992. Checklist and bibliography (1960–85) of the Venezuelan herpetofauna. *Smithsonian Herpetological Information Service* (89):1–54.
- and J.A. Rivero. 2000. Distribution, species-richness, endemism, and conservation of Venezuelan amphibians and reptiles. *Amphibian & Reptile Conservation* 2:42–70.
- and N.M. Sierra. 1993. Estatus de *Leptodactylus pentadactylus* en Venezuela [Abstract]. III Congreso Latino-Americano de Herpetología. Instituto de Biología da Universidade Estadual de Campinas, Campinas:246.
- and –. 1995. Status of *Leptodactylus labyrinthicus* (Calf Frog, Rana Ternero) in Venezuela. *Herpetological Review* 26:124–127.
- Petranka, J.W. and C.A. Kennedy. 1999. Pond tadpoles with generalized morphology: is it time to reconsider their functional roles in aquatic communities? *Oecologia* 120:621–631.
- Pough, F.H., W.E. Magnusson, M.J. Ryan, K.D. Wells, and T.L. Taigen. 1992. Behavioral energetics, p. 395–436. *In* M.E. Feder and W.W. Burggren (eds.), *Environmental Physiology of the Am-*

- phibians. The University of Chicago Press, Chicago.
- Prado, C.P. de A., M. Uetanabaro, and C.F.B. Hadad. 2002. Description of a new reproductive mode in *Leptodactylus* (Anura, Leptodactylidae), with a review of the reproductive specialization toward terrestriality in the genus. *Copeia* 2002: 1128–1133.
- Pyburn, W.F. and W.R. Heyer. 1975. Identity and call of the frog, *Leptodactylus stenodema*. *Copeia* 1975:585–587.
- Riechle, S. 1997. Frösche des Savannengebietes der Estación Biológica del Beni (EBB), Bolivien. Teil I: Einleitung, Untersuchungsgebiet, Artenliste der Anuren des Schutzgebietes und die Familien Bufonidae und Pseudidae. *Herpetofauna (Germany)* 19(106):5–11.
- Rivero-Blanco, C. and J.R. Dixon. 1979. Origin and distribution of the herpetofauna of the dry lowland regions of northern South America, p. 281–298. *In* W.E. Duellman (ed.), *The South American Herpetofauna: Its Origin, Evolution, and Dispersal*. Monograph of the Museum of Natural History, The University of Kansas (7):3 unnumbered + 485 p.
- Rodríguez, L. 1987. Parque Nacional del Manu: lista preliminar de los batracios anuros de Cocha Cashu. *Boletín de Lima* (53):88–90.
- . 1994. Herpetofauna of the Ccolpa de Guacamayos, p. 50–51. *In* R.B. Foster et al. (eds.), *The Tambopata-Candamo Reserved Zone of Southeastern Perú: A biological assessment*. Rapid Assessment Program Working Papers (6):1 unnumbered page + 1–184.
- and J.E. Cadle. 1990. A preliminary overview of the herpetofauna of Cocha Cashu, Manu National Park, Peru, p. 410–425. *In* A.H. Gentry (ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven and London.
- , 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, Zoología* (45):1–22.
- and W.E. Duellman. 1994. Guide to the frogs of the Iquitos region, Amazonian Peru. The University of Kansas Natural History Museum, Special Publication (22):vi + 80 p. + 12 plates + 1 map.
- and L.H. Emmons. 1994. Appendix 8. Amphibians and reptiles in the Tambopata-Candamo Reserved Zone, p. 150–153. *In* R.B. Foster et al. (eds.), *The Tambopata-Candamo Reserved Zone of Southeastern Perú: a biological assessment*. Rapid Assessment Program Working Papers (6):1 unnumbered page + 1–184.
- Ruiz-Carranza, P.M., M.C. Ardila-Robayo, and J.D. Lynch. 1996. Lista actualizada de la fauna de Amphibia de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 20:365–415.
- Savage, J.M. 2002. *The Amphibians and Reptiles of Costa Rica. A Herpetofauna between Two Continents, between Two Seas*. The University of Chicago Press, Chicago and London.
- Schneider, H. 1984. Der Südamerikanische Ochsenfrosch und seine Brutfürsorge. *Aquarien Magazin* 18:60–62.
- Schulte, R. 1984. Frösche und Kröten. Tropische und einheimische Froschlurche im Terrarium. Second edition. Verlag Eugen Ulmer, Stuttgart.
- Silva, W.R., A.A. Giaretta, and K.G. Facure. 2005. On the natural history of the South American pepper frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura: Leptodactylidae). *Journal of Natural History* 39:555–566.
- Spieler, M., F. Skiba, A. Müllner, and A. Pfrommer. 1999. Untersuchungen zur Herpetofauna des Überschwemmungswaldes im Cuyabeno Reservat in Ecuador. Teil 2: Anuren. *Herpetofauna (Germany)* 21:5–15.
- Tocher, M.D. 1998. Diferenças na composição de espécies de sapos entre três tipos de floresta e campo de pastagem na Amazônia central, p. 219–232. *In* C. Gascon and P. Moutinho (eds.), *Floresta Amazônica: Dinâmica, Regeneração e Manejo*. Ministério da Ciência e Tecnologia, Instituto Nacional de Pesquisa da Amazônia, Manaus.
- , C. Gascon, and B. Zimmerman. 1997. Fragmentation effects on a central Amazonian frog community: a ten-year study, p. 124–137. *In* W.F. Laurance and R.O. Bierregaard, Jr. (eds.), *Tropical Forest Remnants. Ecology, Management, and Conservation of Fragmented Communities*. The University of Chicago Press, Chicago and London.
- , –, and J. Meyer. 2001. Community composition and breeding success of Amazonian frogs in continuous forest and matrix habitat aquatic sites, p. 235–247. *In* R.O. Bierregaard, Jr., G. Gascon, T.E. Lovejoy, and R.C.G. Mesquita (eds.), *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. Yale University Press, New Haven and London.
- Vanzolini, P.E. 1986. Levantamento herpetológico da área do estado de Rondônia sob a influência da rodovia BR 364. Conselho Nacional de Desenvolvimento Científico e Tecnológico, Assessoria Editorial, Brasília, Programa Polonoroeste, Subprograma Ecologia Animal, Relatório de Pesquisa (1):1–50.
- Vogt, R.C. and R. Bernhard. 2003. Biodiversidade e biogeografia de répteis e anfíbios da Amazônia. *Caderno de Ciência, Instituto Amazônia* (1):1–40 (unnumbered).
- 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.
- Wassersug, R.J. and W.R. Heyer. 1988. A survey of internal oral features of leptodactylid larvae (Amphibia: Anura). *Smithsonian Contributions to Zoology* (457):iv + 1–99.
- Young, B.E., S.N. Stuart, J.S. Chanson, N.A. Cox, and T.M. Boucher. 2004. *Disappearing Jewels: The Status of New World Amphibians*. Nature-

Serve, Arlington, Virginia.

- Zimmerman, B.L. 1991. Distribution and abundance of frogs in a central Amazonian forest. Ph.D. Dissertation, The Florida State University, Tallahassee.
- and M.T. Rodrigues. 1990. Frogs, snakes, and lizards of the INPA–WWF Reserves near Manaus, Brazil, p. 426–454. *In* A.H. Gentry (ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven and London.
- and D. Simberloff. 1996. An historical interpretation of habitat use by frogs in a central Amazonian forest. *Journal of Biogeography* 23:27–46.
- Zug, G.R., L.J. Vitt, and J.P. Caldwell. 2001. *Herpetology. An Introductory Biology of Amphibians and Reptiles*. Second Edition. Academic Press, San Diego.

W. Ronald Heyer and **Miriam Muedeking Heyer**,
Smithsonian Institution, PO Box 37012, NHB W-201,
MRC 162, Washington, DC, 20013–7012, USA (heyerr@si.edu).

Primary editor for this account, Twan Leenders.

Published 15 February 2006 and Copyright © 2006
by the Society for the Study of Amphibians and
Reptiles.
