2010

*Leptodactylus savagei*

W. R. Heyer

Miriam M. Heyer

Rafael O. de Sá

*University of Richmond, rdesa@richmond.edu*

---

Follow this and additional works at: [http://scholarship.richmond.edu/biology-faculty-publications](http://scholarship.richmond.edu/biology-faculty-publications)

Part of the [Biology Commons](http://scholarship.richmond.edu/biology-commons), [Population Biology Commons](http://scholarship.richmond.edu/population-biology-commons), [Terrestrial and Aquatic Ecology Commons](http://scholarship.richmond.edu/terrestrial-and-aquatic-ecology-commons), and the [Zoology Commons](http://scholarship.richmond.edu/zoology-commons)

---

Recommended Citation


---

This Article is brought to you for free and open access by the Biology at UR Scholarship Repository. It has been accepted for inclusion in Biology Faculty Publications by an authorized administrator of UR Scholarship Repository. For more information, please contact [scholarshiprepository@richmond.edu](mailto:scholarshiprepository@richmond.edu).
AMPHIBIA: ANURA: LEPTODACTYLIDAE

Leptodactylus savagei


**Savage’s Thin toed Frog**

Cystignathus pentadactylus: Cope 1887:18.
Leptodactylus pentadactylus: Noble 1918:323.

**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.

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

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

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

The tadpole lacks 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.

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

**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.
The tooth row formula is 2(2)/3(1). The interrupted A-row posteriorly. There are no submarginal papillae.

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 302–50 Hz. The call has harmonic structure (Figure 3).

**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. peritoakties*, *L. rhodomerus*, *L. stenodema*, *L. turimiquestis*, 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. turimiquestis*, 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. peritoakties*, 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. knobndsens* 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).


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 spreadsheet at http://learning.richmond.edu/Leptodactylus.
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 2005; Barquero degen et al. 1999; Hawley 2008; Duellman 1967b; Franzen 1988; Gans 1958; Günther tella 2004; Donnelly 1994, 2003, 2006; Martínez Cortés and Rodríguez 2005; Méndez 1987; Muedeking and Heyer 1978; Myers and Rand 1969; Nemuras 1968; Park 1938; Park et al. 1940; Ponsssa 2005; Rand and Myers 1990; Rodríguez A. et al. 2005; 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.


**Remarks.** The following common names have been published for *Leptodactylus savagei*: “Sav-age’s Thin-toed Frog” proposed English common name at www.learning.richmond.edu/Leptodactylus, “Rá 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 (Mal'kin 1956), Central Amer-ican Bullfrog (Greene 1997; Guyer and Donnelly 2004 [2005]; Leenders 2001; Martínez Cortés and Rodríguez 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 (McCrane and Castañeda
2007a, as L. savagei), Rana Ternero (Barquero Rod-
riquez and Barquero Arroyo 2007 [as L. savagei];
Beletsky 1998; Buitrago Vannini 2003; Burger 2001;
Leenders 2001; Norman 1998; Pröhl 1997; Savage
1988; Wainwright 2000), Rana Toro (Beletsky 1998;
Cedeño et al. 2006; Höbel 2008; Leenders 2001;
Pröhl 1997; Rodríguez A. et al. 2005 [2004]), Sav-
age'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 refer-
ence only]; Guyer and Donnelly 2004 [2005]; Hayes
et al. 1989; Henderson 2002; Krywicki 2001; Lewis
2001; Norman 1998; Pounds 2000; Roth and Willis
1986; Wainwright 2000), South
American Bullfrog (Beletsky 1998; Green 1990;
Guyer and Donnelly 2004 [2005]; Höbel 2008; Hödl
Lewis 2001; Ryan 1985; Tárano 1998; Tuttle 1982);
Südamerikanische Ochsenfrosch (Hödl 1996);
Suklí'n (Malkin 1956).

• ETYMOLOGY. Leptodactylus savagei honors Dr.
Jay M. Savage whose work in Costa Rican herpetol-
ogy has inspired countless researchers and promot-
ed a comprehensive understanding of the Costa Ri-
can herpetofauna.

• ACKNOWLEDGMENTS. We thank Jay M. Sav-
age and James R. McCranie for reviewing the manu-
script. Research for this account was supported by
NSF award DEB-0342918 to RdS and WRH.

LITERATURE CITED

amphibian and reptiles check-list of Pacuare Na-
ture Reserve, Costa Rica. Boletín de la Asocia-

Acosta Galvis, A.R., C. Huertas-Salgado, and M.
Rada. 2006. Aproximación al conocimiento de los
anfibios en una localidad del Magdalena medio
(Departamento de Caldas, Colombia). Revista de
la Academia Colombiana de Ciencias Exactas,

Albert, R., W. Hödl, W. Huber, M. Ringler, P. Weish,
and A. Weissenhofer. 2005. The Amphibians and
Reptiles of the Golfo Dulce Region Costa Rica:
Corcovado National Park, Piedras Blancas Na-
tional Park, "Regenwald der Österreicher". W. Hu-
ber & A. Weissenhofer, Vienna.

tion, and predation, p. 240–278. In R.W. McDiarm-
mid, and R. Altig (eds.), Tadpoles: The Biology of
Anuran Larvae. The University of Chicago Press,
Chicago.

Altig, R. 1974 (1972). Defensive behavior in Rana
areolata and Hyla avivoca. Quarterly Journal of
the Florida Academy of Sciences 35:212–216.

diversity and evolution of egg and clutch structure in am-

–, M.R. Whiles, and C.L. Taylor. 2007. What do tad-
poles really eat? Assessing the trophic status of
an understudied and imperiled group of consum-
ers in freshwater habitats. Freshwater Biology
52:386–395.

Anastasi, A., G. Bertaccini, J.M. Cei, G. De Caro, V.
Erspamer, M. Impicciatore, and M. Roseghini.
1970. Presence of caerulein in extracts of the skin
of Leptodactylus pentadactylus labyrinthicus and
of Xenopus laevis. British Journal of Pharmacol-
ogy 38:221–228.

Archer, J. 2006. Program notes from the August CHS
meeting. Bulletin of the Chicago Herpetological
Society 41:171.

Asociación Nacional para la Conservación de la Na-
turaleza (ANCON) and The Nature Conservancy
(TNC). 1995a. Ecological Survey of the U.S. De-
partment of Defense Lands in Panama. Phase II:
Albrook Air Force Station, Corozal, Fort Clayton,
Fort Amador, Quarry Heights, Semaphore Hill,
Summit Radio Station Panama. The Nature Conser-
vancy, Legacy Resource Management, Aso-
ciación Nacional para la Conservación de la Na-
turaleza, Panama City.

–. 1995b. Ecological Survey of the U.S. Depart-
ment of Defense Lands in Panama. Phase IV: Fort
Davis and Fort Gulick, Panama. The Nature Conser-
vancy, Legacy Resource Management, Aso-
ciación Nacional para la Conservación de la Na-
turaleza, Panama City.

–. 1996a. Ecological Survey of the U.S. Depart-
ment of Defense Lands in Panama. Phase III: HORO-
KO, Empire Range and Balboa West Range, Pa-
nama. The Nature Conservancy, Legacy Resource
Management, Asociación Nacional para la Conser-
vación de la Naturaleza, Panama City.

–. 1996b. Ecological Survey of the U.S. Depart-
ment of Defense Lands in Panama. Phase IV: Fort
Sherman, Piña Range and Naval Security Group
Activity, Galeta Island, Panama. The Nature Conser-
vancy, Legacy Resource Management, Asociación
Nacional para la Conservación de la Naturaleza,
Panama City.

Austin, J.D., S.C. Lougheed, K. Tanner, A.A. Chek,
J.P. Bogart, and P.T. Boag. 2002. A molecular per-
npective on the evolutionary affinities of an enig-
matic neotropical frog, Allophryne ruthveni. Zoolo-
gical Journal of the Linnean Society 134:335–
346.

Auth, D.L. 1994. Checklist and bibliography of the
amphibians and reptiles of Panama. Smithsonian

Aycrigg, A.D., T.M. Farrell, and P.G. May. 1998. SOS:
Sounds of survival. Reptile & Amphibian Maga-


Dieguez, M., I. Domínguez, G. Ortega, A. Veces, Y.


Herpetological Information Service (119):1–44.
Meyer, J.R. 1969. A Biogeographic Study of the Am-


–. 2003. Anfibios del Museo de Vertebrados de la Universidad de Panamá, Catálogo. Museo de Vertebrados de la Universidad de Panamá, Panamá.


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).

Primary editor for this account, Andrew H. Price.

Published 15 January 2010 and Copyright © 2010 by the Society for the Study of Amphibians and Reptiles.