

Studies on the genus *Leptodactylus* (Amphibia: Leptodactylidae). II. Diagnosis and distribution of the *Leptodactylus* of Costa Rica

by

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This paper serves a dual purpose. It is an updating of TAYLOR'S (17, 18) evaluation of the diagnosis and distribution of the *Leptodactylus* of Costa Rica. Many new locality records are available; the specimens at hand indicate re-evaluations of certain species' status, and the tadpoles of all Costa Rican forms are now known. Second, the analysis of intra- and inter-population morphological variation forms part of the groundwork of my projected long-term study on the biosystematics of the genus *Leptodactylus*.

Adults of the genus *Leptodactylus* are distinguished from members of other frog families found in Costa Rica as follows (*Leptodactylus* characters in parentheses): representatives of the families Centrolenidae and Hylidae usually have a membranous web between the toes, and all phalanges terminate in an expanded disk (no toe webbing, no disks); members of the Bufonidae and Atelopodidae have a fleshy web between the toes, members of the Ranidae have a membranous web between the toes (no toe webbing); the representatives of the Dendrobatidae are distinguished by the presence of pairs of dermal scutes above the expanded finger and toe disks (no scutes, no disks); the representatives of the family Microhylidae of Costa Rica usually have an obvious amount of toe webbing and always have a fleshy fold across the palate (no web, no palatal fold); the monotypic Rhinophrynidae has four toes on each foot (five).

From other genera of leptodactylids, the genus *Leptodactylus* is distinguished as follows: *Engystomops* lacks vomerine teeth, and has a prominent tubercle on the mid-tarsus (vomerine teeth present, no tarsal tubercle); almost

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all *Eleutherodactylus* have webs between the toes and/or expanded digital disks (no webbing, no disks); species of *Eleutherodactylus* which lack webs and disks are difficult to distinguish from members of the genus *Leptodactylus* by use of external morphological characters. Technically, all *Leptodactylus* can be distinguished from all *Eleutherodactylus* by having the mesosternum with a bony style instead of a broad cartilaginous (may be calcified) plate.

Leptodactylus larvae are distinguished from other known larvae of Costa Rican families as follows: larvae of the family Microhylidae have a median spiracle (sinistral in *Leptodactylus*); tadpoles of the families Hylidae and Ranidae have a dextral anus (median); the only known *Atelopus* tadpole has a large sucking disk extending onto the belly (mouthparts not involving belly); bufonid tadpoles have an anterior and posterior oral papilla gap (anterior break only); centrolenid tadpoles have a posteriorly placed spiracle (near mid-body, not noticeably posterior); dendrobatid tadpoles may lack tooth rows, have lateral indentations of the oral disk, have a confluence of anterior and posterior (to beak) tooth rows, and are often found on the backs of adults (tooth rows present, basically emarginate oral disk, anterior and posterior tooth rows separate, larvae not found on back of adults); *Rhinophrynus* tadpoles lack tooth rows and a horny beak (present). Members of the genus *Eleutherodactylus* undergo direct development. *Engystomops* tadpoles have a median or dextral anus (variable within some populations [KU 104276]) and a laterally indented oral disk (median anus, basically emarginate oral disk).

MATERIAL AND METHODS

Morphological features were examined for series of specimens of each species, based largely on material at the University of Southern California (CRE). Definitions of characters and techniques follow PETERS (14), except for the following: *Adults*. All measurements were taken with either dividers and metric rule or metric calipers; head length was measured from the angle of the jaw to the tip of the snout; head width was taken as the widest portion of the head; for purposes of comparing finger lengths, the first (thumb) and second digits were measured from their confluence to the respective digital tips, fingers three and four were measured from their confluence to the respective digital tips; the femur and tibia were measured (when possible) while the right leg was held as a Z, the femur at a right angle to the body, the tibia folded next to the femur; the femur was measured from mid-anus to the extremity, the tibia was measured as the greatest tibial length when the leg was positioned as above; the foot was measured from the posterior edge of the inner metatarsal tubercle to the tip of the fourth toe; snout-vent length is given in millimeters, the first number being the minimum, the second the median, the last the maximum measured; all measurements except snout-vent are given as percentages of the snout-vent length in the same manner. *Larvae*. Tadpoles were staged following GOSNER (9); all measurements were made with either a micrometer in a Wild stereoscopic microscope or dividers and metric rule, depending on the size of the tadpole;

eye diameter was taken as the greatest horizontal diameter; body length was measured ventrally, from the tip of the snout to the joining of the anal tube with the body, or the posterior confluence of the legs if the anal tube had been resorbed; body width was taken ventrally as the greatest width of the body; body height was taken vertically as the greatest depth of the body; oral disk width was taken ventrally (or more or less head-on depending on the position of the mouthparts) as the greatest width of the oral disk; the oral papilla gap was measured between the dorsal origins of the oral papillae; measurements are given in the manner indicated for adults; rows of papillae are given in formulae, such as 1-2-3-2 (Fig. 6), 1 indicates a single row of papillae anteriorly, 2 indicates a change to a double row of papillae anterolaterally, 3 indicates a change to three papillae rows in width laterally, and 2 indicates a change to a double row of papillae posteriorly on the oral disk.

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SPECIES ACCOUNTS

Leptodactylus bolivianus Boulenger

1898. *Leptodactylus bolivianus* Boulenger: 4-5 (Holotype: Genoa Mus. 28875 A, Bolivia: Barraca and Misiones Mosevenes); 1954, Taylor: 617-620 (redescription).

DIAGNOSIS - Adult: From all *Leptodactylus* of Costa Rica except *L. melanonotus*, *L. bolivianus* is distinguished by the extensive fringing on the sides of the toes. *L. melanonotus* is a small robust frog (*L. bolivianus* resembles *Rana pipiens*), has vomerine teeth in transverse series posterior to the choanae (arched, partly between), and reaches 45 mm standard length (95 mm).

Larva: Only *L. melanonotus* sometimes shares the characteristic of entire

tooth rows (formula 2/3). From *L. melanonotus*, *L. bolivianus* is distinguished by a narrow anterior gap in the oral papillae (21-31% of oral disk width in *L. bolivianus*, 40-60% in *L. melanonotus*).

SUMMARY OF CHARACTERISTICS - Adult: Snout subovoid to subelliptical from above, rounded to rounded acute in profile; tympanum distinct, horizontal diameter just over $\frac{1}{2}$ to $\frac{2}{3}$ eye diameter; male vocal slits elongate, arise laterally to tongue, almost parallel to jaw; single internal vocal sac in males; vomerine teeth in arched series, extend from between choanae posteriorly; head length greater than or equal to width, 35-37.0-39% standard length; head width 32-34.4-37% standard length; first finger much longer than second, first shorter than third, second longer than fourth; two horny spines on male thumb; male arm hypertrophied; back and upper femur smooth to tuberculate, upper tibia tuberculate; one pair of dorsolateral folds from back of eye to sacrum, supra-tympanic fold extends to shoulder, lateral folds from tympanum to groin developed or not; gland present at angle of jaw; post-tympanic gland present; diffuse glands ventrolaterally on body and back of limbs developed or not; toes with well-developed lateral fringes; metatarsal ridge present; inner tarsal fold well-developed from below tibio-tarsal articulation to the inner metatarsal tubercle; lower tarsus moderately to heavily covered with small, black-tipped tubercles; sole of foot moderately covered with small, black-tipped tubercles; dark canthal stripe extends posteriorly from eye along the supratympanic fold; interorbital dark blotch sometimes continuing as broad dark dorsal band to axillary region or beyond; dorsolateral folds dark, continuous or broken; posterior portion of lateral band light, rest of dorsal body more or less ocellated; posterior face of arm dark, upper surface may be uniform or spotted; upper legs with oblong spots appearing as barred; chin suffused with melanophores; rest of ventral surfaces almost immaculate to mottled; posterior thigh mottled to almost spotted; standard length of males to 94 mm, females to 88 mm; femur shorter than or equal to tibia, 38-47.4-51% standard length; tibia shorter than foot, 48-51.2-54% standard length; foot longer than femur, 49-53.2-57% standard length (Fig. 1).

Larva: Nostril midway between anterior edge of eye and tip of snout or slightly nearer eye; internareal distance slightly less than interorbital distance; eye small, diameter 5-7-10% of body length; mouth subterminal; oral papillae rows 1-2-3-2; oral disk entire; oral disk width 20-24.3-28% of body length; oral papilla gap 21-26.2-31% of oral disk width; tooth row formula 2/3, all tooth rows equal length; tooth row anterior to beak usually with more denticles (130-200) than row just posterior to beak (120-185); beak teeth small, blunt; dorsal tail fin origin at tail-body juncture; tail height just greater than body height; tail tip bluntly pointed; extensive to moderate suffusion of brown or black melanophores dorsally; concentration of melanophores posteromedially to nostrils; light spot under eye; lighter areas over tail musculature on body; side may be reticulated or uniformly suffused with melanophores; lateral line system not evident; few melanophores on oral papillae; no melanophores just posterior to mouthparts, otherwise anterior venter lightly suffused with melano-

phores; belly with few or no melanophores; anal tube with a few scattered melanophores or not; tail generally suffused with melanophores, with scattered light specks; total length largest specimen, stage 34, 32 mm; body length 32-39.1-44% of total length. (Figs. 6, 11, 16).

LOCALITIES: GUANACASTE: Río Bebedero, 5 km S Bebedero, 5 m; 0.8 km E Finca Jiménez along Río Higuerón, 11 m; Finca Taboga, 9.7 km S and 8.0 km W of Cañas, 4 m; PUNTARENAS: 1.6 km E of Volcán de Buenos Aires, Cone Finca, 400 m; 9.6 km W Buenos Aires at Río Volcán, 400 m; Coto, km 47 on Rail from Golfito, 75 m; Esterillos Oeste, 15 km SE Jacó, 10 m; Golfito, 5 m; 3 km E, 9.6 km ESE Golfito, 10 m; Palmar Norte, 20 m; Palmar Sur, 16 m; 5.6 km SE, 7 km SE Palmar Sur, 15 m; 3-5 km W Palmar Norte on rd. to Puerto Cortés, 10 m; 39 km E Palmar Norte, 4 km E Río La Vieja, 150 m; Parrita, La Julieta, Finca La Ligia, 5 m; Quebrada, 1 km NW of Pochotol, Playa Hermosa, 2m; Rincón, vic. Camp Seattle, 50 m; 2.4 km WSW Rincón de Osa; 24-32 km W San Isidro de El General; Villa Neily, 75 m; 14.5 km NW Villa Neily at Río Claro, 60 m (Fig. 22).

REMARKS: I tentatively allocate the Costa Rican population to *L. bolivianus* Boulenger rather than *L. insularum* Barbour. A re-examination of the *ocellatus*-complex is needed to clarify the species limits within the group. Until that time, I follow RIVERO (16) rather than MINTON & SMITH (13) in regarding *L. insularum* a synonym of *L. bolivianus*, instead of recognizing two species.

The prominent toe-fringing of this species and *L. melanonotus* is evident in late stage tadpoles (stage 40 on) and persists throughout the remaining developmental stages.

Leptodactylus labialis (Cope)

1877. *Cystignathus labialis* Cope: 90 (Holotype: USNM 31302, Mexico?)

1881. *Leptodactylus labialis*, Brocchi: 20 (Cites Cope's record); 1954, Taylor: 613-617 (redescription).

DIAGNOSIS - Adult: The light longitudinal stripe on the posterior thigh distinguishes *L. labialis* from *L. bolivianus*, *L. melanonotus*, and *L. pentadactylus*. *L. poecilochilus* has a smooth ventral tarsus and foot; the tarsus and foot of *L. labialis* is white tuberculate.

Larva: The blotched tail of *L. labialis* distinguishes it from larvae of *L. bolivianus* and *L. melanonotus*. *L. labialis* larvae have subterminal mouthparts and a light spot immediately posterior to the oral disk, distinguishing them from *L. pentadactylus* larvae which have almost terminal mouthparts and lack a distinct light spot behind the mouthparts. *L. labialis* larvae are difficult to distinguish from *L. poecilochilus* larvae (*L. poecilochilus* characteristics in parentheses): *L. labialis* larvae are uniformly patterned (dark-flecked); are blunt snouted (snout elongately rounded); are large eyed, horizontal diameter 12-16% of body length (eye moderate, 9-14% body length); lack a light mid-dorsal stripe (present or absent); and have few denticles in the tooth rows just anterior and posterior to the beak, 46-101 and 59-104 respectively (64-142 and 92-152).

SUMMARY OF CHARACTERISTICS - Adult: Snout subelliptical to pointed from above; snout acutely rounded to almost sharply pointed in profile in males, rounded in females; tympanum distinct, horizontal diameter about $\frac{3}{5}$ eye diameter; male vocal slits elongate, from lateral to base of tongue to angle of jaw; moderate, paired, lateral, external, vocal sacs in males; vomerine teeth in transverse series, posterior to choanae; head longer than wide; head length 36-37.7-39% standard length; head width 32-33.6-35% standard length; first finger much longer than second, first equal to third, second equal to fourth; no spine on male thumb; male arm not hypertrophied; no chest spines on male; back smooth to warty; upper femur usually smooth, sometimes slightly warty; upper tibia tuberculate; usually four well-developed dorsolateral folds; jaw angle gland developed; may be small diffuse lumbar gland; no ventral glands; toes with small lateral ridges or not; no metatarsal fold; inner tarsal fold weakly developed, usually a tuberculate ridge; lower tarsus and foot with prominent white tubercles; light stripe from tip of snout to just under eye to angle of jaw more or less developed; dorsum more or less ocellated; some kind of dark interorbital bar or spots; sides of body and legs marbled with dorsal and ventral colors; dorsal limbs barred or striped; chin bordered with pigment; chest and belly lacking melanophores, ventral limbs may or may not be dark-spotted; posterior thigh mottled with distinct light longitudinal line, line may be partially broken, but distinct in all specimens at hand; standard length of males to 36 mm, females to 40 mm; femur shorter than tibia, 34-40.3-44% standard length; tibia shorter than foot, 39-44.6-48% standard length; foot longer than femur, 46-50.2-53% standard length (Fig. 2).

Larva: Nostril slightly closer to tip of snout than to anterior edge of eye; internareal distance $\frac{1}{2}$ or slightly greater than $\frac{1}{2}$ of interorbital distance; eye large, horizontal diameter 12-13.4-16% of body length; mouth subterminal; oral papillae rows 1-2 or 1-2-1; oral disk entire; oral disk width 17-19.6-22% of body length; oral papilla gap 53-63.4-67% of oral disk width; tooth row

formula: $\frac{1}{1-1}$, large gap in tooth row just anterior to beak, a gap in tooth row

$\frac{2}{2}$ just posterior to beak, most posterior tooth row from just shorter to $\frac{2}{3}$ length of anterior two tooth rows; more denticles in divided tooth row just posterior to beak (59-104) than in divided tooth row just anterior to beak (46-101); beak teeth moderate, pointed; dorsal tail fin origin at tail-body juncture, or on tail, just posterior to tail-body juncture; tail height usually less than body height, sometimes equal to or just greater than body height; tail tip bluntly pointed, sharply pointed, or tapering to filament; dorsum uniformly suffused with melanophores, greater concentration posteromedially to nostrils; two light lateral areas at mid-body; spiracle lighter or not much lighter than surroundings; lateral line system evident or not; mouthparts with a few scattered melanophores or not; absence of melanophores just posterior to mouthparts or not, rest of anterior venter with scattered melanophores; rest of belly and anal tube lacking melanophores or with very few scattered melanophores; tail with scattered groupings of

melanophores forming blotched patterns; total length largest specimen, stage 41, 41 mm; body length 31-35.9-40% of total length (Figs. 7, 12, 17).

LOCALITIES: ALAJUELA: Los Chiles, 70 m; GUANACASTE: Arenal, 520 m; 3.9 km N Bagaces; Río Bebedero, 2-5 km S Bebedero, 5 m; Cañas; 2 km NE Cañas, 100 m; 6.4 km N Cañas; 50 km S Cañas, 180 m; 12.2 km S La Cruz; Hacienda Mojica, 3.2 km S, 17.7 km W Cañas, 10 m; Las Huacas, 42 m; 4 km W Liberia; 7.2 km W Liberia, 270 m; 7.4 km N Liberia; 7.7 km WSW Liberia, 100 m; Liberia, 5 km N and 4½ km W, Hacienda La Norma, on Río Colorado, 150 m; 12.5 km W Liberia on rd. to Playa del Coco; 14.3 km N Liberia; 15.3 km N Liberia; 34.1 km SW Liberia, Hiway N^o 21; 38 km SE Liberia (5 km NW Cañas), 48 m; 57.1 km N Liberia; 1.6-3.2 km S Nicoya; 5.9 km N Nicoya; 3-11 km E Playa del Coco, 45 m; 1.6 km S Santa Cruz; Tenorio; 4 km NE Tilarán; Finca Taboga, 9.6 km S and 8.0 km W of Cañas, 4 m; PUNTARENAS: Barranca, 5 m; Boca de Barranca, nr. Puntarenas; Río Barranca on W side of Inter-Am. Hwy., 25 m; 5 km WNW Barranca; Río Barú, 5 km NW Dominical, 10 m; Coto, 10 m; 4 km WNW Esparta, 45 m; 12 km WNW Esparta, 30 m; Esterillos Oeste, 15 km SE Jacó; Golfito, 10 m; Orotina, 213 m; 6.1 km NE mouth of Río Grande de Tárcoles; 4 km ESE Palmar Sur, 15 m; base of Peninsula along side of road, 5 m; 12.1 km N and 2.4 km E Puntarenas, 30 m; Villa Neily, 75 m; 21.8 km NW Villa Neily. (Fig. 23).

REMARKS - Just transformed individuals have noticeable lateral toe ridges. These ridges are never as developed as the fringes of comparably-staged *L. bolivianus* and *L. melanonotus*, and the ridges disappear by the time an individual is 25-30 mm standard length. All recently transformed *L. labialis* have a longitudinal light posterior thigh stripe, but it is not always distinct. The characteristic white foot and tarsal tubercles of the adults are not present in late larval metamorphosing stages. In all transformed material at hand, the tubercles are present.

Most Costa Rican tadpole lots of *L. labialis* and *L. poecilochilus* are very distinctive and offer no difficulty in identification, as are all the available Panamanian lots. A few lots from the Costa Rican Pacific Wet Lowlands appear intermediate in almost all characters that separate the species. The parentage is not known for any of the tadpole lots, and they had previously been identified by means of the adults which were present at the time of collection, a dangerous practice. In addition, nothing is known of characteristics that are environmentally produced. Obviously, additional sampling is needed to establish the limits of species variation in larval *L. labialis* and *L. poecilochilus*. The number of denticles appears diagnostic (Fig. 21). I have assumed that the variation in denticle number in *L. labialis* and *L. poecilochilus* represents environmentally-induced variation within the genetic limits of the species.

Leptodactylus melanonotus (Hallowell)

1881. *Leptodactylus melanonotus*, Brocchi: 20 (cites Hallowell's record); 1952, Taylor: 652-655 (redescription).

1952. *Leptodactylus maculilabris*, Taylor: 657-660 (misidentification, redescription).

DIAGNOSIS - Adult: Prominent lateral toe fringes separate *L. melanonotus* from *L. labialis*, *L. pentadactylus*, and *L. poecilochilus*. *L. melanonotus* is a small, robust frog (*L. bolivianus* resembles *Rana pipiens*), has vomerine teeth in transverse series posterior to the choanae (arched, partly between), reaching 45 mm (95 mm).

Larva: The uniform or barely noticeable light-speckled larvae of *L. melanonotus* can only be confused with *L. bolivianus*. *L. melanonotus* larvae usually have a divided tooth row just anterior to the beak (always continuous in *L. bolivianus*); and have a wide anterior oral papilla gap, 40-60% of the mouthpart width (21-31% in *L. bolivianus*).

SUMMARY OF CHARACTERISTICS - Adult: Snout subovoid, subelliptical, or almost pointed from above, rounded in profile; tympanum distinct, horizontal diameter $\frac{1}{2}$ - $\frac{2}{3}$ eye diameter; male vocal slits elongate, arise lateral to tongue and extend almost to the angle of the jaw; single, internal vocal sac in male; vomerine teeth in transverse series, posterior to choanae; head longer than broad; head length 35-37.1-41% standard length; head width 31-34.6-38% standard length; first finger longer than second, third longer than first, second, and fourth, second equal to fourth; two spines on male thumb; male arm not hypertrophied; male lacking chest spines; dorsum tuberculate; supratympanic fold extending to shoulder only; jaw angle gland developed or not; post-tympanic gland developed in largest specimens only; ventral and ventrolateral glands almost non-existent to almost entirely covering lower body surfaces, from very diffuse to well-defined; toes with prominent lateral fringes; metatarsal fold distinct or not well-developed, tuberculate or not; inner tarsal fold well-developed, from below tibio-tarsal articulation to just outside inner metatarsal tubercle, suffused or not with melanophores, tuberculate or not; lower tarsus always with black tubercles; foot usually with numerous black tubercles, not apparent in some specimens; upper lip with distinct or obscure bars; dark interorbital triangle; rest of dorsum dark, with various obscure markings; limbs distinctly barred or not; venter mottled or almost uniformly light; posterior thigh mottled, no distinct light stripe; standard length of males to 44 mm, females to 45 mm; femur longer than, equal to, or shorter than tibia, 40-41.6-45% standard length; tibia shorter than foot, 40-42.3-46% standard length; foot longer than femur, 45-49.0-53% standard length (Fig. 3).

Larva: Nostril median or slightly closer to tip of snout than to anterior edge of eye; internareal distance about $\frac{2}{3}$ interorbital distance; eye small, horizontal diameter 5-7.8-10% of body length; mouth subterminal; oral papillae rows 1-2, 1-2-3-2, 1-2-3-2-1, or 1-2-1; oral disk entire; oral disk width 15-18.9-24% body length; oral papilla gap 40-50.1-59% of oral disk width;

tooth row formula: $\frac{1}{3}-1$ or 2/3, tooth row just anterior to beak continuous or just divided, most posterior tooth row noticeably to slightly shorter than the anterior two rows; more denticles in the single or divided tooth row just anterior to beak (total 110-146) than in tooth row just posterior to beak (90-137); beak teeth small, blunt; dorsal tail fin origin at tail-body juncture or on tail, just posterior to tail-body juncture; tail equal to or just greater than body height; tail tip bluntly rounded; uniform light to heavy suffusion of melanophores dorsally, greater concentration of melanophores posteromedially to nostrils and on either side of tail musculature on body or not; lighter areas lateral to eyes; spiracle lighter than surroundings or not; lateral line system not evident; entire venter heavily to lightly suffused with melanophores, if a light suffusion, more anteriorly; anal tube suffused with melanophores; tail uniformly suffused with melanophores, scattered small light specks or not; total length largest specimen, stage 40, 40 mm; body length 38-41.3-46% of total length (Figs. 8, 13, 18).

LOCALITIES: ALAJUELA: Cariblanco, 800 m; 0.5 km S Cariblanco, 820 m; Cascajal, 105 m; Los Chiles, 70 m; Punta Cortéz, 8 km E Los Chiles, 70 m; Río Sardinal, 5 km W Cariblanco, 850 m; CARTAGO: Cervantes, 1441 m; IICA, Turrialba, 600 m; La Suiza, 616 m; Turrialba, 620 m; GUANACASTE: Arenal, 520 m; 4.8 km NW Arenal; Bebedero, 6 m; Río Bebedero, 2-5 km S Bebedero, 5 m; Cañas at Río Cañas, 88 m; 16 km SSE Cañas, 60 m; 9.6 km S, 12.2 km S La Cruz; Las Flores; Las Huacas, 42 m; Río Lagarto at Inter. Am. Hwy, 100 m; 2 km W Liberia; 4 km W Liberia; 6.4 km WSW Liberia, 100 m; Liberia, 9 km N and 4 km E Inter. Am. Hwy. on Río Colorado; 14.8 km S Liberia, 90 m; 45 km SW Liberia, Hwy. N° 21; Hacienda Mojica, 3.2 km S and 17.7 km W Cañas, 10 m; Hacienda La Norma, 5 km N and 4½ km W Liberia on Río Colorado, 150 m; 3-11 km E Playa del Coco, 45 m; Finca San Bosco de Tilarán, 640 m; 3.2 km W Santa Cruz on the Playa del Tamarindo rd.; Santa Cruz, Río Diría, 50 m; 4.8 km N Santa Rosa; Silencio de Tilarán, 825-850 m; Tenorio; 0.5 km NW Tilarán, 530 m; 3 km NE, 5 km NW, Tilarán; 5 km NE Tilarán, 600 m; 5½ km NE Tilarán, 560 m; 6 km NE Tilarán, 550 m; Finca Taboga, 9.6 km S and 8.0 km W Cañas, 4 m; HEREDIA: Puerto Viejo, 100 m; 6.5 km W, 7.5 km W Puerto Viejo, 100 m; LIMON: Batán, 15 m; La Castilla, 10 m; Los Diamantes, 300 m; 2.4 km E Los Diamantes, 260 m; Guápiles, 262 m; Monteverde de Limón, 40 m; nr. Peralta, Lake Bonilla, 400 m; El Tigre, 680 m; PUNTARENAS: Barranca, 20 m; 1.5 km W Barranca, 20 m; 5 km WNW Barranca; 10 km WNW Esparta, 30 m; Golfito, 5 m; 9.6 km ESE Golfito, 10 m; 4 km ESE Palmar Sur, 15 m; Puntarenas, 10.4 km N and 2.4 km E, 30 m; Puntarenas, 12 km N and 3.2 km W, 30 m; Puntarenas, at junct. of rd. and rail line (Base of Peninsula), 5 m; San Isidro de El General, 703 m; 3.2 km E San Isidro de El General; SAN JOSE: 15 km SW San Isidro de El General, 865 m; 19-24 km WSW San Isidro de El General. (Fig. 24).

REMARKS - *L. maculilabris* Boulenger is a strict synonym of *L. poecilochilus* (Cope). Taylor's specimens identified as *L. maculilabris* are *L. melanonotus*.

Leptodactylus pentadactylus (Laurenti)

1768. *Rana pentadactyla* Laurenti: 32 (Indies).
 1872. *Cystignathus pentadactylus*, Peters: 198 (synonymy).
 1882. *Leptodactylus pentadactylus*, Boulenger: 241-242 (records, redescription); 1952, Taylor: 649-652 (redescription).

DIAGNOSIS - Adult: The lack of prominent lateral toe fringes separates *L. pentadactylus* from *L. bolivianus* and *L. melano-notus*. The lack of a distinct light longitudinal stripe on the posterior thigh further distinguishes *L. pentadactylus* from *L. labialis* and *L. poecilochilus*. *L. pentadactylus* is the largest *Leptodactylus* in Costa Rica, reaching 146 mm standard length.

Larva: *L. pentadactylus* larvae are the only *Leptodactylus* larvae in Costa Rica to have blotched tails and an almost terminal oral disk.

SUMMARY OF CHARACTERISTICS - Adult: Snout rounded to nearly semi-circular from above, rounded to rounded-obtuse laterally; tympanum distinct, horizontal diameter $\frac{1}{2}$ to $\frac{2}{3}$ eye diameter; male vocal slits elongate, originate at posterolateral tongue base, extend almost to angle of jaw; internal, single vocal sac in male; vomerine teeth in arched series, extend from between choanae posteriorly; head length greater than, equal to, or less than head width, 38-39.5-41% standard length; head width 37-40.1-43% standard length; first finger much longer than second, second equal to or just longer than fourth, first less than or equal to third in females, first equal to or greater than third in males; single horny spine on male thumb; male arm moderately to grossly hypertrophied; chest spines in male present or absent; back usually smooth, upper femur smooth, warty, or with scattered tubercles, upper tibia always with scattered tubercles; one pair of dorsolateral folds from behind eye to sacrum, another fold complex from corner of eye over tympanum, divides over tympanum, one branch extends to shoulder region, the other branch extends posteriorly at least to shoulder region, sometimes to groin; jaw angle gland evident; distinct lumbar glands; entire lateral body may appear glandular; post-tympanic gland present or absent; no leg or ventrolateral glands; toes with small, distinct ridges; no metatarsal fold; well-developed tarsal fold, shallow sinuous curve extending $\frac{3}{4}$ distance of tarsus to inner metatarsal tubercle; lower tarsus usually scattered tuberculate to almost smooth; foot essentially smooth; dark well-developed canthal stripe, extending posterior to shoulder; upper lip barred or spotted; back uniform or pattern of spots and bars with faint dark outlines; groin and side of body uniform, mottled, or with dark warts; upper limbs uniform, mottled or distinctly barred or striped; venters with melanophores uniformly distributed to forming a mottled pattern; posterior thigh mottled to spotted, no light longitudinal stripe; standard length of males to 142 mm; females to 146 mm; femur shorter than, equal to, or longer than tibia, 43-45.1-47% standard length; tibia shorter than foot, 42-44.4-47% standard length; foot shorter than, equal to, or longer than femur, 44-46.6-49% standard length (Fig. 4).

Larva: Nostril usually slightly closer to anterior edge of eye than to tip of snout, median, or slightly closer to snout; internareal distance about 2/3 interorbital distance; eye moderate, horizontal diameter 7.9-8-13% of body length; mouth almost terminal; oral papillae rows 1, 1-2, 1-2-1, 1-2-1-2, or 1-2-1-2-1; oral disk entire, or indented midventrally; oral disk width 15-18-22% body length; oral papilla gap 50-66-74% of mouthpart width; tooth row

formula: $\frac{1}{1-1}$, large gap in tooth row just anterior to beak, barely a gap in tooth

row just posterior to beak, most posterior tooth row from 1/3 to 2/3 length of anterior two tooth rows; fewer denticles in divided tooth row just anterior to beak (total 45-67) than divided tooth row just posterior to beak (89-125); beak teeth small and blunt to moderate and sharp; dorsal tail fin origin at body-tail juncture or origin on tail, posterior to body-tail juncture; tail height equal to or just greater than body height; tail tip bluntly pointed to narrowly pointed; dorsum suffused with melanophores, denser concentrations posteromedially to nostrils and on either side of tail musculature on body; lateral line system well-developed; venter with gradient from almost no melanophores midventrally to dorsal concentration laterally; mouthparts suffused with melanophores or not, if present, extend posteriorly to midventer; anal tube with almost no melanophores or absent; tail blotched; total length largest specimen, stage 40, 83 mm; body length 28-31.2-39% of total length (Figs. 9, 14, 19).

LOCALITIES: ALAJUELA: Río La Fortuna at La Fortuna, 199 m; CARTAGO: 2 km, NE Jabillos, 900 m; Moravia de Chirripó, 1200 m; 1 km S Orosí, 1050 m; 4.3 km NE Río Reventazón bridge, Río Peralta, 945 m; La Suiza, 616 m; Tunel Camp. nr. Peralta, 400 m; Turrialba, 620 m; Turrialba, IICA, 600 m; Turrialba, 1 km. from 2nd bridge on road from Turrialba to Pavones; 6 km W Turrialba, 1050 m; GUANACASTE: 14.8 km S Liberia; 3.2 km S Nicoya; Silencio de Tilarán, 850 m; Silencio de Tilarán, laguna, 780 m; Tilarán, 560 m; 5 km NE Tilarán, 600 m; HEREDIA: Puerto Viejo, 100 m; 1.5 km N, 4.2 km W, 15.5 km N Puerto Viejo, 100 m; confluence of Ríos Sarapiquí and Puerto Viejo, 100 m; Finca La Selva, 100 m; LIMON: Alta Talamanca, confluence of Ríos Larí and Diparí about 21 km SW Amubri, 800 m; La Castilla, lower Reventazón, 10 m; Los Diamantes, 300 m; Guácimo, 103 m; Guápiles, 262 m; La Lola, 39 m; Pandora, on banks of Río Estrella, 100 m; Puerto Viejo, 5 m; Suretka, 60 m; PUNTARENAS: Agua Buena; 1.6 km S Agua Buena, 1150 m; 1.6 km E Volcán de Buenos Aires, Cone Finca, 400 m; 3.7 km E Esparta, 280 m; Golfito, 10 m; 3 km E, 9.6 km ESE Golfito, 10 m; 14.5 km ENE Golfito, 30 m; Gromaco; 7 km SE Piedras Blancas, 45 m; 21.8 km W San Ramón, 410 m; Rincón, 30 m; Rincón, Camp Seattle, 50 m; 3 km N Tambor; Villa Neily, 75 m; 1.6 km WNW Villa Neily, 45 m; 5.6 km NW Villa Neily, 60 m; SAN JOSE: El General, 704 m; 2 km W Santa Ana along Río de Oro, 810 m; San Isidro de El General, 703 m; 2 km E San Isidro de El General, 710 m; 24.1 km WSW San Isidro de El General (Fig. 25).

REMARKS - Metamorphosing young have pronounced lateral toe ridges which closely approach the condition of comparably staged *L. bolivianus* and *L. melanonotus*. Different growth stages at hand indicate a differential growth of this characteristic, with a relative diminishing of the ridges throughout the life of the individual. A ridge is still evident in juveniles up to 100 mm in standard length, but is not readily visible to the naked eye in adult specimens.

One male, CRE 505, has a small horn tip on the metacarpal projection forming a second subequal spine on the thumb.

Leptodactylus poecilochilus (Cope)

1862. *Cystignathus poecilochilus* Cope: 156-157 (Holotype: USNM 4347, Colombia: Antioquia; Turbo).
1882. *Leptodactylus poecilochilus*, Boulenger: 243-244 (records, redescription); 1940, Dunn: 106-107 (includes *L. quadrivittatus* and *L. maculilabris* in *L. poecilochilus*, range).
1893. *Leptodactylus quadrivittatus* Cope: 339-340 (type lost, Costa Rica: Puntarenas; Buenos Aires); 1940, Dunn: 106-107; 1952, Taylor: 655-657 (redescription).
1896. *Leptodactylus maculilabris* Boulenger: 404-405 (type locality Costa Rica: Guacacaste; Bebedero); 1940, Dunn: 106-107.

DIAGNOSIS - Adult: The presence of a light longitudinal stripe on the posterior thigh separates *L. poecilochilus* from *L. bolivianus*, *L. melanonotus*, and *L. pentadactylus*. From *L. labialis*, *L. poecilochilus* differs in having a smooth ventral tarsus and sole of foot (white tuberculate in *L. labialis*).

Larva: The blotched tail of *L. poecilochilus* distinguishes *L. poecilochilus* larvae from the uniformly patterned *L. bolivianus* and *L. melanonotus* larvae. *L. poecilochilus* larvae have sub-terminal mouthparts and a light spot immediately posterior to the oral disk, distinguishing them from *L. pentadactylus* larvae which have almost terminal mouthparts and lack a distinct light spot behind the mouthparts. *L. poecilochilus* larvae are difficult to distinguish from *L. labialis* larvae (*L. labialis* characteristics in parentheses): *L. poecilochilus* larvae have dark flecked patterns (uniform pattern); have elongately rounded snouts (snout blunt); have moderate eyes, horizontal diameter 9-14% of body length (eyes large, 12-16% of body length); may have a light mid-dorsal stripe (never a mid-dorsal stripe); have a moderate number of denticles in the tooth rows just anterior and posterior to the beak, 64-124 and 92-152 respectively (few denticles, 46-101 and 59-104).

SUMMARY OF CHARACTERISTICS - Adult: Snout subovoid to subelliptical from above, rounded to sharply acute in profile; tympanum distinct, horizontal diameter $1/2$ - $2/3$ eye diameter; male vocal slits elongate, arise lateral to tongue, extend almost to angle of jaw; paired, lateral vocal sacs in male; vomerine teeth in almost transverse to definitely arched series, usually entirely posterior to choanae, but may extend to just between choanae; head length greater than width,

head length 36-37.7-39% of standard length; head width 33-35.1-37% standard length; first finger longer than second, first shorter than, equal to, or longer than third, second longer than fourth; no horny spine on male thumb; male arm not hypertrophied; male chest lacking spines; dorsal texture essentially smooth; two to six dorsal folds, fold from posterior corner of eye to sacrum always present; distinct gland at angle of jaw; no parotoid gland; no ventrolateral or leg glands; toes with small, distinct ridges, not produced into flaps; very weak metatarsal fold present or absent, fold line usually indicated by a strip lacking pigment; tarsal fold present, a shallow sinuous curve $\frac{3}{4}$ tarsal length, extending to inner metatarsal tubercle, lighter than surrounding tarsus; no tarsal or foot tubercles; dark, broad canthal stripe present at least anteriorly, rest of upper jaw distinctly barred to spotted; dark supratympanic fold; back with indistinct pattern of spotting to distinct series of stripes; broad, light mid-dorsal stripe present to absent, if present may be surrounded by dark stripes; longitudinal folds may or may not be distinctly darker or lighter; side of body usually with dark spots; dark spotting in groin; anterior limbs with dark stripes anteriorly and posteriorly or obscured; may be light ulnar line; anterior femur and posterior tibia with large, distinct spots or obscured; upper legs distinctly barred, striped, or uniform; venter usually uniformly light, melanophores sometimes present on lateral belly, chin, and tarsus; posterior thigh with a distinct light longitudinal stripe; standard length of males to 49 mm, females to 50 mm; femur shorter than tibia, 38-44.3-49% standard length; tibia shorter than, equal to, or longer than foot, 47-50.6-57% standard length; foot longer than femur, 50-51.8-55% standard length (Fig. 5).

Larva: Nostril nearer tip of snout than to anterior edge of eye, or median; internareal distance about $\frac{1}{2}$ interorbital distance; eye moderately large, horizontal diameter 9-11.6-14% body length; mouth subterminal; oral papillae rows 1-2 or 1-2-3-2; oral disk usually entire, or with mid-ventral indentation; oral disk width 15-21.3-27% of body width; oral papilla gap 45-56.4-65% of oral disk width; tooth row formula: $\frac{1}{1-1}$ or $\frac{1}{1-1}$, moderate gap in tooth row

just anterior to beak, if tooth row just posterior to beak is divided, halves abut or are just separated, most posterior tooth row just shorter than anterior two tooth rows; fewer denticles in divided tooth row just anterior to beak (total 64-142) than in single or divided tooth row just posterior to beak (total 92-152); beak teeth small and blunt to moderately small and moderately pointed; dorsal tail fin origin at tail-body juncture; tail height noticeably less than body height to greater than body height; tail tip shape bluntly pointed to filamentous; dorsum with or without broad mid-dorsal light stripe; concentration of melanophores posteromedially to nostrils and lateral to tail musculature on body; sides with dark flecks; few melanophores on mouthparts; lack of melanophores just behind mouthparts, rest of anterior venter with few to many scattered melanophores; posterior belly with very few or no melanophores; anal tube with very few or no melanophores; tail blotched;

total length largest specimen, stage 41, 37 mm; body length 35-38.8-45% of total length (Figs. 10, 15, 20).

LOCALITIES: ALAJUELA: 3 km W La Fortuna; GUANACASTE: Arenal, 520 m; Playa del Coco, 5 m; Hacienda Coyolar, 4.8 km N and 4.0 km W Liberia; 7.2 km N, 6.4 km W Liberia, 274 m; Hacienda Mojica, 3.2 km S and 17.7 km W Cañas, 10 m; Río Bebedero, 0.5 km S Bebedero, 5 m; Río Tenorio, 4.8 km S and 16 km W Cañas, 3 m; 3.2 km W Santa Cruz; Tronadora, 520 m; PUNTARENAS: 1.6 km S Agua Buena, 1150 m; Quebrada Agua Buena, 2.7 km SW Rincón; Coto, 10 m; Golfito, 5 m; 4.6 km ESE Golfito, 10 m; 14.5 km ENE Golfito, 30 m; Gromaco; Finca Helechales, 15 km NE Potrero Grande, 1050 m; Palmar, 20 m; 7 km SE Piedras Blancas, 45 m; 8 km NE Potrero Grande; Puerto Cortés, 3 m; Rincón, Camp Seattle, 50 m; Ujarrás, 560 m; Villa Neily, 75 m; 4.2 km NW Villa Neily, 60 m; SAN JOSE: Pozo Azul de Pirrís, 100 m; 20.9 km WSW San Isidro de El General on Dominical road, 710 m (Fig. 26).

REMARKS - I find no differences, except those due to preservation and fading, between the type of *Cystignathus poecilochilus* and the representatives of the Costa Rican population at hand.

A lot of metamorphosing individuals from 2 km N Tocumen, Panamá, Panamá (KU 104225) and a series of adults from Camp Seattle, Rincón, Puntarenas, Costa Rica (CRE 705, 750) demonstrate the extreme and intermediate phases of a uniform to striped dorsal pattern. *L. quadrivittatus* Cope is based on the striped phase of *L. poecilochilus* (Cope).

All specimens above 15 mm standard length, with one exception (see below), have very distinct posterior thigh stripes. Metamorphosing individuals have small lateral toe ridges, but the ridges are essentially lost by 30 mm standard length.

A single male specimen from 3 km W La Fortuna, Alajuela (CRE 8078) is distinctive in several features: (i) no lateral vocal sacs are evident, (ii) the head is noticeably shorter than in the rest of the specimens at hand, (iii) the light longitudinal posterior thigh stripe is not clearly distinct, and (iv) the femur is noticeably shorter and the tibia longer than in other specimens. The only other example from Atlantic Costa Rica is from Arenal, Guanacaste (CRE 6254) and is typical *L. poecilochilus*. If CRE 8078 is typical of the population near La Fortuna, there is little doubt that the deme is genetically isolated from other *L. poecilochilus* in Costa Rica, and probably represents a distinct species. The peculiar features of the hindlimb may all represent an anomaly. Without further material, I regard the frog as an anomalous *L. poecilochilus*.

DISTRIBUTIONAL PATTERNS

All five species have overlapping geographic ranges. Two species, *L. melanonotus* and *L. pentadactylus*, are widely distributed in the Atlantic and Pacific lowlands of Costa Rica. *L. bolivianus* is restricted to the Pacific lowlands.

L. labialis and *L. poecilochilus* are basically Pacific lowland forms, found on the Atlantic lowlands only in the vicinity of the Arenal pass.

HOLDRIDGE'S (11) bioclimate classification suggests factors limiting the geographic distributions of Costa Rican *Leptodactylus*. Holdridge's bioclimates, as characterized by biotemperature and approximate altitudes, are:

- Tropical Lowland — $BT^0 = >24^{\circ}C$; sea level to 500-700 m
 Subtropical — $BT^0 = 18-24^{\circ}C$; 500(700)-1500(1700) m
 Lower Montane — $BT^0 = 12-18^{\circ}C$; 1500(1700)-2500(2700) m
 Montane — $BT^0 = 6-12^{\circ}C$; 2500(2700)-3500(3700) m
 Subandean — $BT^0 = 3-6^{\circ}C$; >3500 (3700) m.

All five species are limited to the Tropical Lowland and Subtropical zones.

L. bolivianus has been collected only in the Tropical Lowland zone, and the known altitudinal range is sea level to 400 m.

L. labialis has been collected in the Tropical Lowland zone and in the drier portions of the Subtropical zone. The known altitudinal range for *L. labialis* in Costa Rica is sea level to 520 m.

L. poecilochilus has been collected from the Tropical Lowland zone and from a few localities in the Subtropical zone. The altitudinal range in Costa Rica is sea level to 1150 m.

Both *L. melanonotus* and *L. pentadactylus* are widely distributed throughout the Tropical Lowland and Subtropical zones. The altitudinal ranges for *L. melanonotus* and *L. pentadactylus* in Costa Rica are sea level to 1440 m and sea level to 1200 m, respectively.

The geographic distribution patterns appear to be the result of species-specific climatic tolerances, the five species showing a cline. *L. bolivianus*, limited to the Tropical Lowland zone, apparently has not been able to penetrate the available Tropical Lowland zone in the Atlantic lowlands due to the intervening Subtropical zone in the Arenal pass, the lowest pass (600 m) in Costa Rica. Alternatively, *L. bolivianus* may require a dry season habitat, and the annually drenched Atlantic lowlands may be ecologically unsuitable, precluding invasion from the south. At the other extreme, *L. melanonotus* and *L. pentadactylus* have greater climatic tolerances which allow broader geographic distributions. Between these extremes lie *L. labialis* and *L. poecilochilus*.

Collecting records indicate a difference in population densities of *L. melanonotus* and *L. pentadactylus* in their Costa Rican geographic ranges. More specimens of *L. melanonotus* have been collected from the drier portions of the Tropical and Subtropical zones, while more specimens of *L. pentadactylus* have been collected from the wetter portions of the same zones. Further ecologic studies are necessary to determine whether these data are artifacts of collecting techniques.

As expected, with all Costa Rican *Leptodactylus* having overlapping climatic and geographic distributions, all five species have been taken in all combinations of sympatry during the breeding period in the Pacific lowlands.

L. melanonotus and *L. pentadactylus* have often been taken in sympatry in the Atlantic lowlands.

Very little has been reported on ecologic segregation within a habitat for *Leptodactylus* species. Certain observations indicate that the larvae utilize different foods within any given pond. Holly and Andrew Starrett have observed *L. pentadactylus* tadpoles feeding on *Bufo marinus* eggs (pers. comm.), and all specimens of tadpole lot KU 104281 are engorged with frog eggs. The reduction of tooth row denticles and almost terminally placed mouthparts of this species suggest a primarily carnivorous diet, as opposed to a primarily herbivorous diet for the other species.

The total ranges observed in denticles in the tooth row just anterior to the beak suggest further differentiation in feeding habits between all the Costa Rican *Leptodactylus* larvae. The data are: *L. bolivianus*, 130-200; *L. labialis*, 46-101; *L. melanonotus*, 110-133; *L. pentadactylus* 45-67; *L. poecilochilus*, 64-142. Even with an increase in denticle number with age, a morphological segregation in this character is evident. Further, *L. labialis* larvae with pronounced, pointed, sharp beak teeth have the fewest denticles, suggesting a morphological dimorphism correlating with carnivorous and herbivorous feeding habits.

KEY TO THE ADULT *LEPTODACTYLUS* OF COSTA RICA

- 1a. Distinct light longitudinal stripe on posterior thigh; males lacking horny spines on thumb; males with paired, lateral, external vocal sacs 2
- 1b. Posterior thigh marbled, no distinct light longitudinal stripe; males with horny spine(s) on thumb; males with internal vocal sacs 3
 - 2a. Tarsus and sole of foot smooth; standard length to 49 mm in males, females to 50 mm *L. poecilochilus*
 - 2b. Tarsus and sole of foot covered with prominent white tubercles; standard length to 36 mm in males, females to 40 mm *L. labialis*
- 3a. Toes lacking prominent fringe, although sometimes with weak ridges; male with single horny spine on thumb; male with or without horny spines on chest; standard length to 142 mm in males, to 146 mm in females *L. pentadactylus*
- 3b. Toes with prominent lateral fringes; male with 2 horny spines on thumb; male never with horny spines on chest; standard length to 94 mm in males, to 88 mm in females 4
 - 4a. Vomerine teeth at least partly extending between the choanae, and in arched series; male arm may be hypertrophied; tibia long, 48-54% of standard length; standard length of males to 94 mm, females to 88 mm *L. bolivianus*
 - 4b. Vomerine teeth entirely posterior to choanae, in transverse series; male arm never noticeably hypertrophied; tibia short, 40-45% of standard length; standard length of males to 44 mm, females to 45 mm *L. melanonotus*

KEY TO THE LARVAL *LEPTODACTYLUS* OF COSTA RICA

- 1a. Tail uniform or dark with scattered, small, light flecks; tooth row formula $\frac{2}{3}$ or $\frac{1-1}{3}$, if $\frac{1-1}{3}$, a small gap in the tooth row just anterior to the beak; usually more denticles in the tooth row just anterior to the beak than in tooth row just posterior to beak 2
- 1b. Tail pattern blotched; tooth row formula $\frac{1-1}{1-1}$ or $\frac{1}{3}$, moderate to large gap in tooth row just anterior to beak; always fewer denticles in tooth row just anterior to beak than in row just posterior to beak 3
- 2a. Narrow anterior oral disk gap, 21-31% of oral disk width; tooth row formula always $\frac{2}{3}$ *L. bolivianus*
- 2b. Wide anterior oral disk gap, 40-60% of oral disk width; tooth row formula usually $\frac{1-1}{3}$, rarely $\frac{2}{3}$ *L. melanonotus*
- 3a. Oral disk almost terminal; no distinct light spot immediately behind oral disk; tadpoles large, to 83 mm total length *L. pentadactylus*
- 3b. Oral disk subterminal; light spot immediately behind oral disk; tadpoles moderate, to 41 mm total length 4
- 4a. Body lacking distinct, small, dark flecks; snout blunt; eye large, horizontal diameter 12-16% of body length; body never with mid-dorsal light stripe; beak teeth moderate, sharp; few denticles in tooth rows just anterior (46-101) and posterior (59-104) to beak. *L. labialis*
- 4b. Body with distinct, small, dark flecks; snout elongately rounded; eye moderate, horizontal diameter 9-14% of body length; body with or without a mid-dorsal light stripe; beak teeth small, usually blunt; more denticles in tooth rows just anterior (64-142) and posterior (92-152) to beak *L. poecilochilus*

CLAVE PARA LOS ADULTOS DE *LEPTODACTYLUS* DE COSTA RICA

- 1a. Parte posterior del muslo con franja clara longitudinal bien definida; el macho carece de espinas córneas en el pulgar; los sacos vocales del macho son pares, laterales y externos 2
- 1b. Parte posterior del muslo moteada, sin franja clara longitudinal; el macho tiene una o varias espinas córneas en el pulgar; los sacos vocales del macho son internos 3
- 2a. Tarso y planta del pie lisos; machos hasta 49 mm, hembras hasta 50 mm *L. poecilochilus*
- 2b. Tarso y planta del pie cubiertos por tubérculos blancos prominentes; machos hasta 36 mm, hembras hasta 40 mm. *L. labialis*
- 3a. Dedos de las patas sin rebordes cutáneos, aunque a veces con prominencias ligeras; el macho tiene una única espina córnea en el pulgar; el macho puede o no tener espinas córneas en el pecho; machos hasta 142 mm, hembras hasta 146 mm *L. pentadactylus*

- 3b. Dedos de la pata con rebordes cutáneos prominentes; el macho tiene dos espinas córneas en el pulgar; el macho nunca tiene espinas córneas en el pecho; machos hasta 94 mm, hembras hasta 88 mm 4
- 4a. Los dientes vomerianos, en series arqueadas, se extienden generalmente hasta en medio de las coanas; el brazo del macho puede ser hipertrofiado; tibia larga, 48-54% del largo total del individuo; machos hasta 94 mm, hembras hasta 88 mm *L. bolivianus*
- 4b. Los dientes vomerianos, en series transversales, totalmente posteriores a las coanas; el brazo del macho nunca es perceptiblemente hipertrofiado; tibia corta, 40-45% del largo total del individuo; machos hasta 44 mm, hembras hasta 45 mm *L. melanonotus*

CLAVE PARA LAS LARVAS DE *LEPTODACTYLUS* DE COSTA RICA

- 1a. Cola de color uniforme u oscura, con manchas claras, pequeñas, diseminadas; fórmula de dentición $\frac{2}{3}$ ó $\frac{1}{3}$, en este último caso existe una brecha pequeña en la hilera inmediatamente anterior al pico; generalmente hay más denticulos en la hilera inmediatamente anterior al pico que en la posterior 2
- 1b. Cola moteada; fórmula de dentición $\frac{1}{1-1}$ ó $\frac{1}{3}$, brecha mediana a grande en la hilera inmediatamente anterior al pico; siempre hay menos denticulos en la hilera inmediatamente anterior al pico que en la posterior 3
 - 2a. Brecha angosta en el disco oral anterior, de 21-31% del ancho del disco oral; fórmula de dentición siempre $\frac{2}{3}$ *L. bolivianus*
 - 2b. Brecha ancha en el disco oral anterior, de 40-60% del ancho del disco oral; fórmula de dentición generalmente $\frac{1}{3}$, raramente $\frac{2}{3}$ *L. melanonotus*
- 3a. Disco oral casi terminal; sin mancha clara bien definida inmediatamente posterior al disco oral; renacuajos grandes, hasta 83 mm de largo total *L. pentadactylus*
- 3b. Disco oral subterminal; mancha clara inmediatamente posterior al disco oral, renacuajos de tamaño mediano, hasta 41 mm de largo total 4
 - 4a. Cuerpo sin manchitas oscuras definidas; hocico romo; ojo grande, su diámetro horizontal es de 12-16% del largo del cuerpo; el cuerpo nunca tiene una banda clara en el dorso medio; dientes del pico de tamaño mediano y afilados; pocos denticulos en las hileras inmediatamente anteriores (46-101) y posteriores (59-104) al pico *L. labialis*
 - 4b. Cuerpo con manchitas oscuras, bien definidas; hocico alargado y redondo; ojo de tamaño mediano, en su diámetro horizontal es de 9-14% del largo del cuerpo; cuerpo con o sin banda clara en el dorso medio; dientes del pico pequeños, generalmente romos; más denticulos en las hileras inmediatamente anteriores (64-142) y posteriores (92-152) al pico *L. poecilochilus*

SUMMARY

Five species of the genus *Leptodactylus* are known from Costa Rica: *L. bolivianus*, *L. labialis*, *L. melanonotus*, *L. pentadactylus*, and *L. poecilochilus*. Diagnoses, summaries of characteristics, and keys to the adults and larvae of the five species are presented here. *L. bolivianus*, *L. labialis* and *L. poecilochilus* are Pacific lowland forms. *L. melanonotus* and *L. pentadactylus* are widely distributed in the Atlantic and Pacific lowlands. The five species are limited to the bioclimate zones of the Tropical and Subtropical lowlands.

RESUMEN

Cinco especies del género *Leptodactylus* se reconocen de Costa Rica: *L. bolivianus*, *L. labialis*, *L. melanonotus*, *L. pentadactylus*, y *L. poecilochilus*. En el presente trabajo se ofrecen diagnosis, resúmenes de las características y claves para la determinación de adultos y larvas de las cinco especies. *L. bolivianus*, *L. labialis*, y *L. poecilochilus* son formas propias de las Tierras Bajas del Pacífico. *L. melanonotus* y *L. pentadactylus* son especies ampliamente distribuidas tanto en las Tierras Bajas del Pacífico como en las del Atlántico. Las cinco especies están limitadas a las zonas bioclimáticas de las Tierras Bajas Tropicales y Subtropicales.

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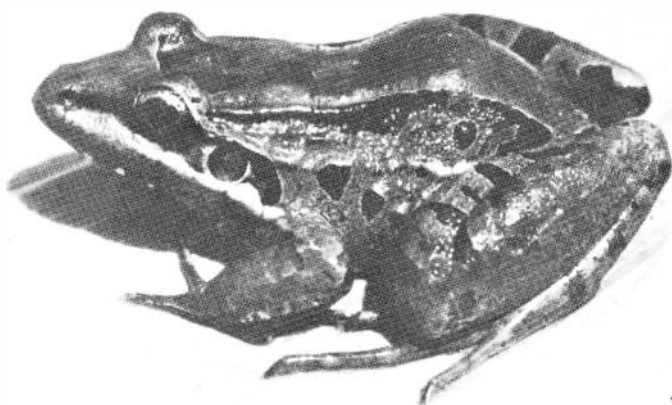
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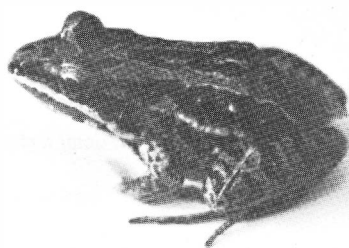
Fig. 1. Adult *L. boliviae*. Photograph by R. McDiarmid.

Fig. 2. Adult *L. labialis*. Photograph by R. McDiarmid.

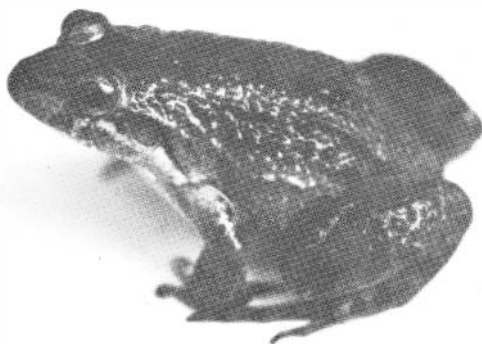
Fig. 3. Adult *L. melanonotus*. Photograph by R. McDiarmid.



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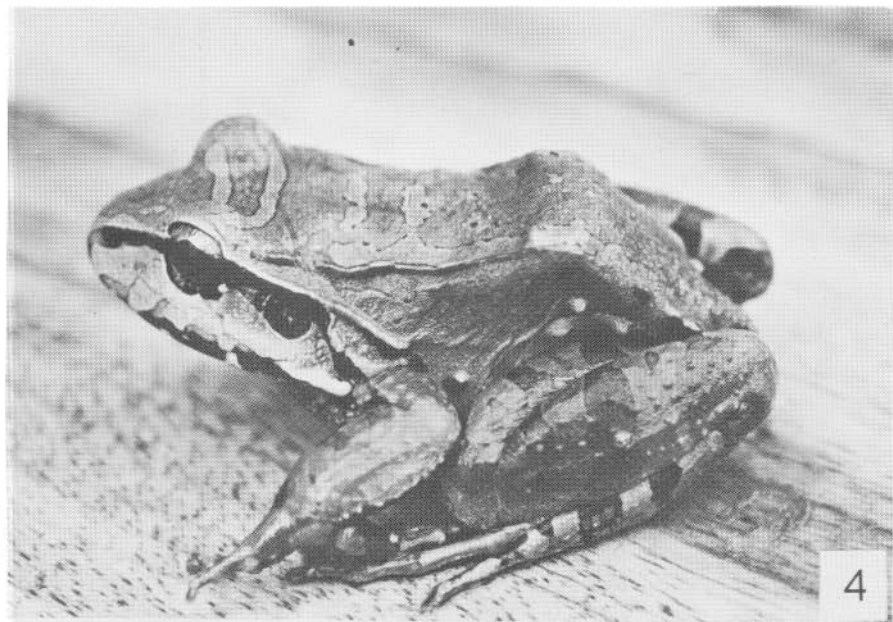


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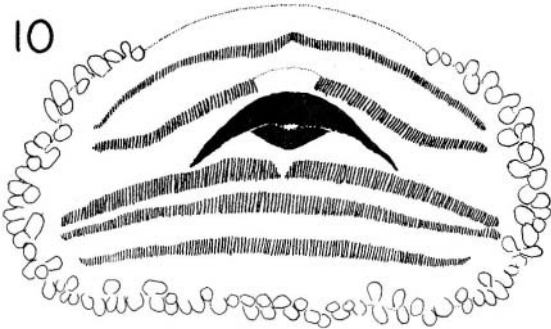
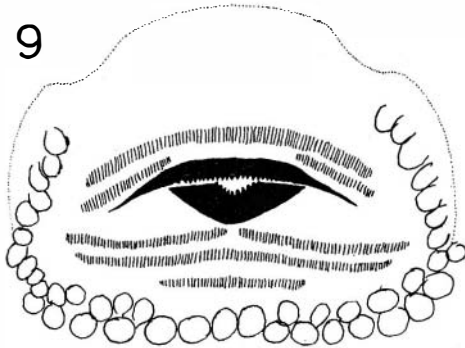
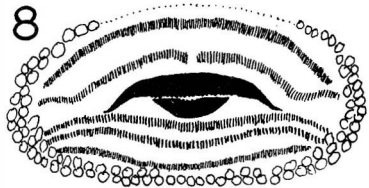
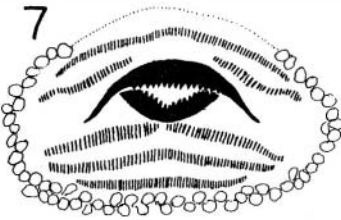
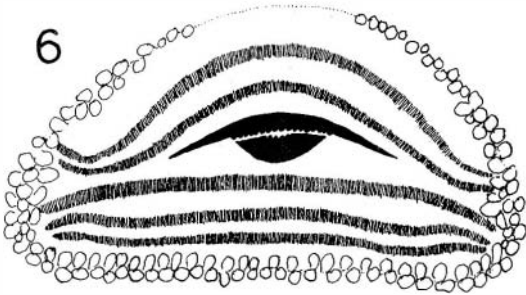
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Fig. 4. Adult *L. pentadactylus*. Photograph by R. McDiarmid.

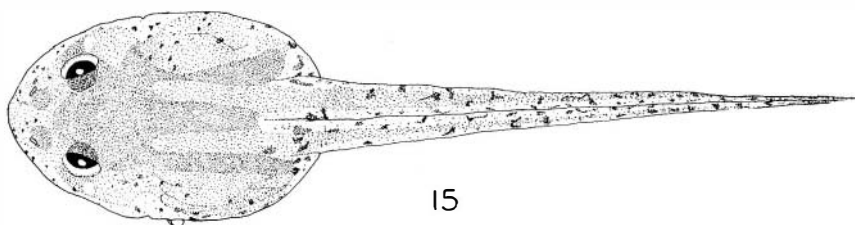
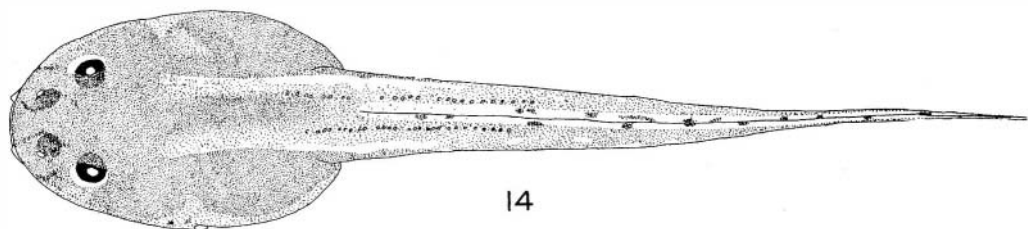
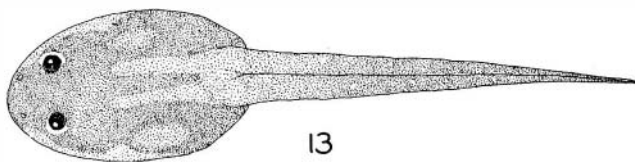
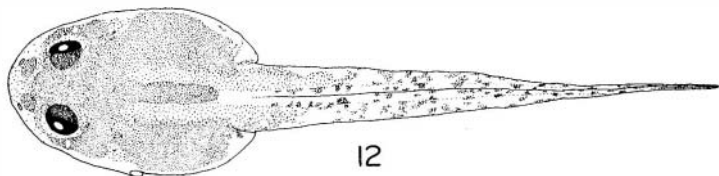
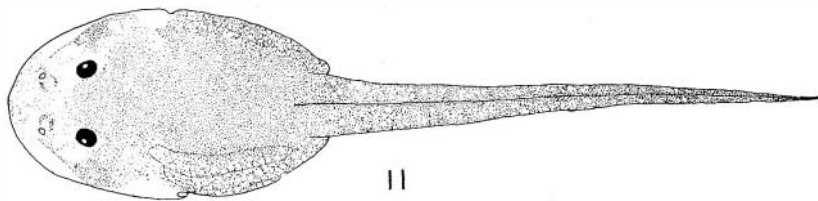
Fig. 5. Adult *L. poecilochilus*. Photograph by R. McDiarmid.



Figs. 6-10. *Leptodactylus* larval mouthparts. Line equals 1 mm.
Fig. 6 = *L. bolivianus*, stage 34; Fig. 7 = *L. labialis*, stage 37; Fig. 8 = *L. melanonotus*, stage 29; Fig. 9 = *L. pentadactylus*, stage 28; Fig. 10 = *L. poecilochilus*, stage 36.



Figs. 11-15. Dorsal views of larval *Leptodactylus*. Line equals 10 mm. Fig. 11 = *L. bolivianus*, stage 34; Fig. 12 = *L. labialis*, stage 37; Fig. 13 = *L. melanotus*, stage 29; Fig. 14 = *L. pentadactylus*, stage 28; Fig. 15 = *L. poecilochilus*, stage 36.



Figs. 16-20. Lateral views of larval *Leptodactylus*. Line equals 10 mm. Fig. 16 = *L. bolivianus*, stage 34; Fig. 17 = *L. labialis*, stage 37; Fig. 18 = *L. melanotus*, stage 29; Fig. 19 = *L. pentadactylus*, stage 28; Fig. 20 = *L. poecilochilus*, stage 36.

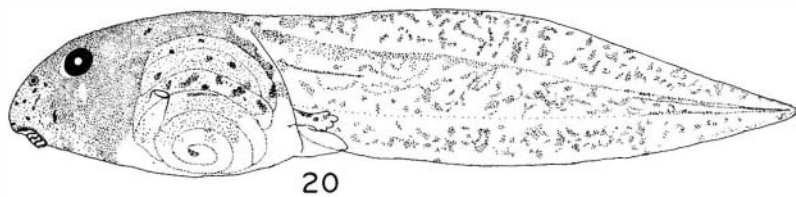
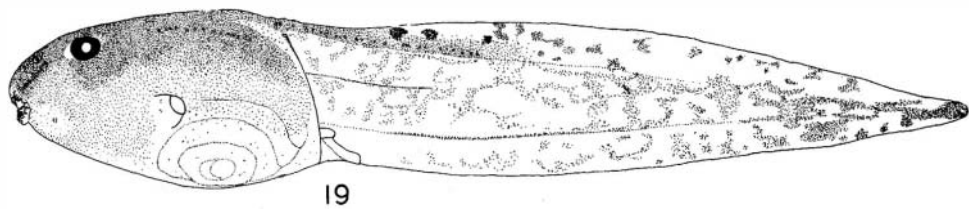
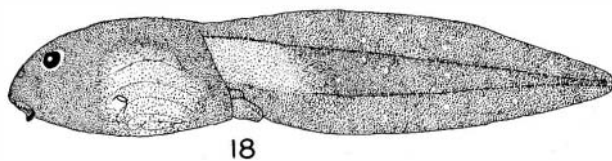
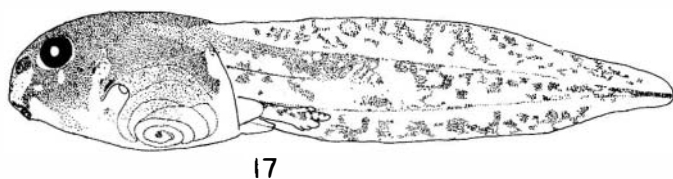
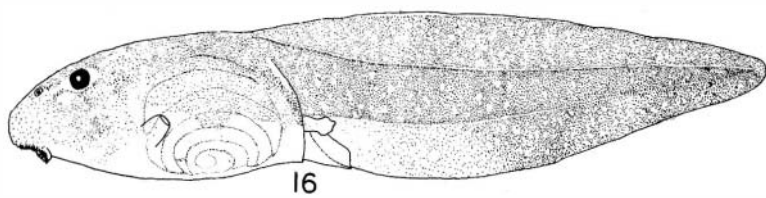
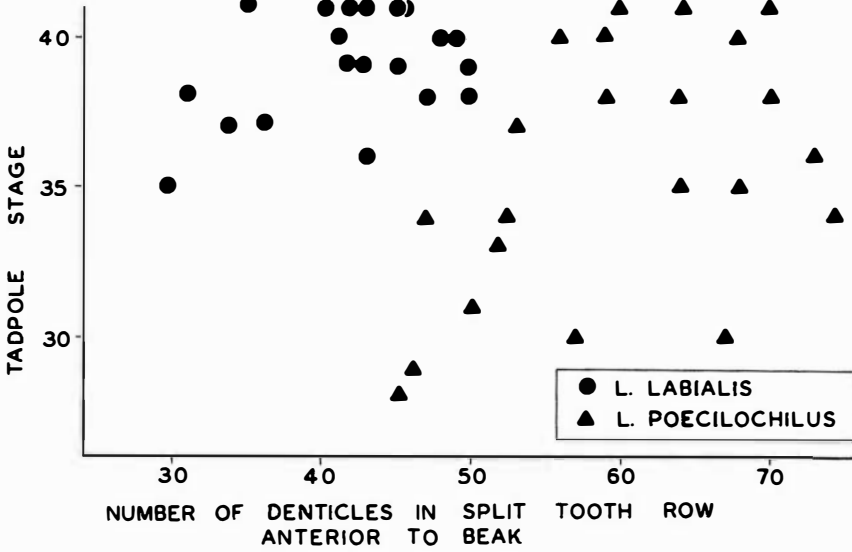
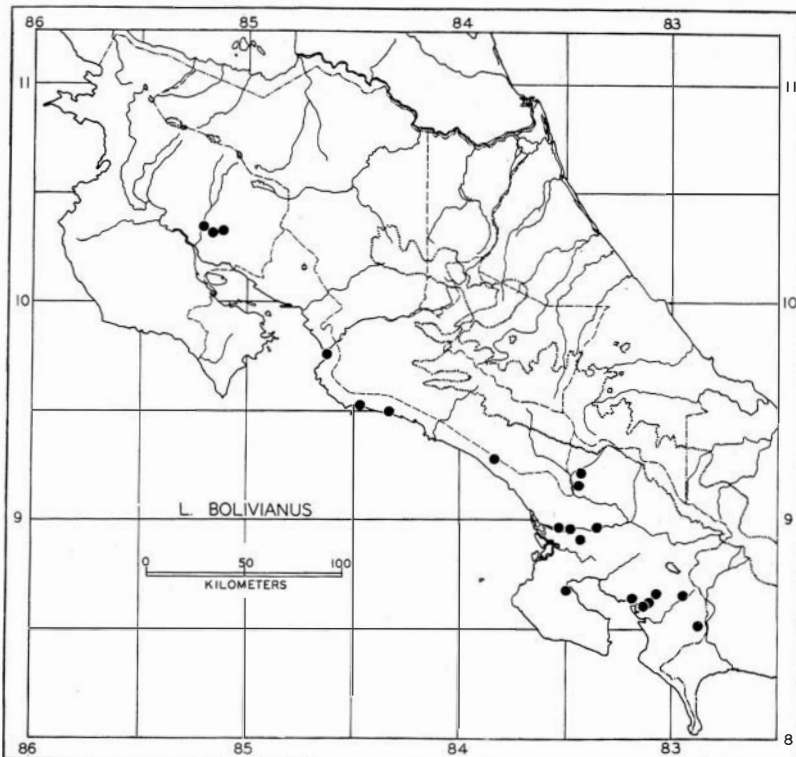


Fig. 21. Scatter diagram of number of tooth denticles in split tooth row anterior to beak of *L. labialis* and *L. poecilochilus*.

Fig. 22. Distribution of *L. bolivianus* in Costa Rica. Dotted line equals 1500 meter contour.



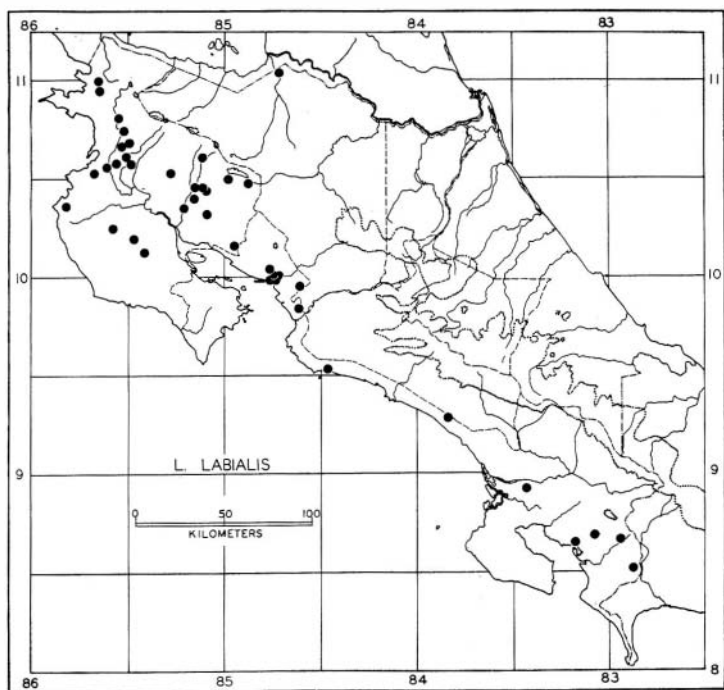
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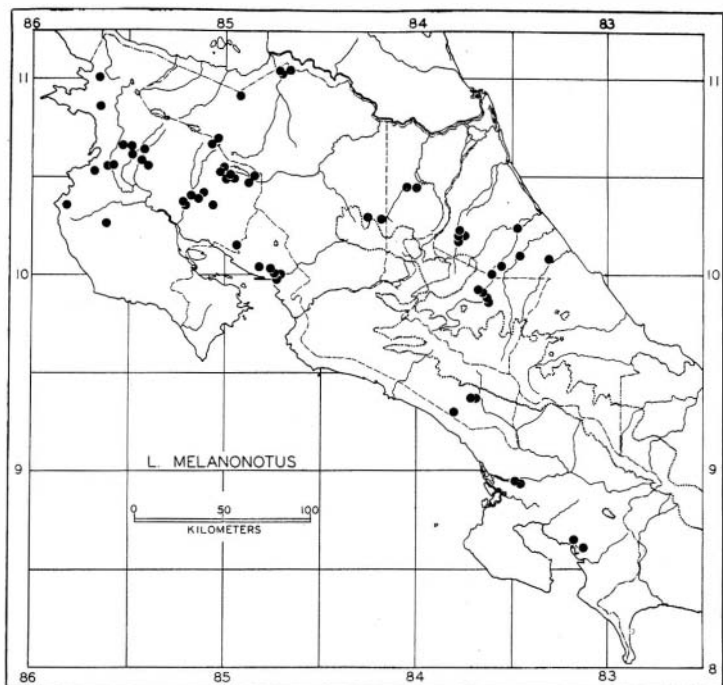
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Fig. 23. Distribution of *L. labialis* in Costa Rica. Dotted line equals 1500 meter contour.

Fig. 24. Distribution of *L. melanonotus* in Costa Rica. Dotted line equals 1500 meter contour.



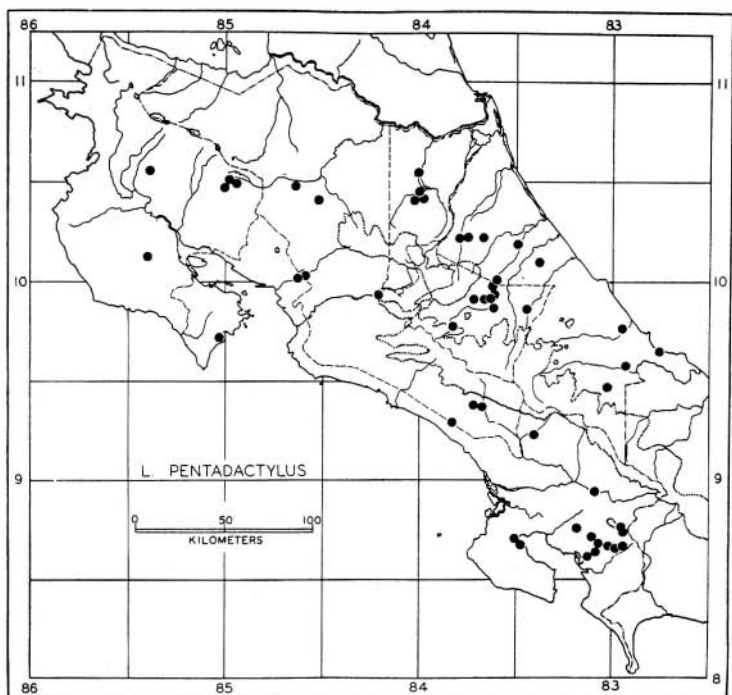
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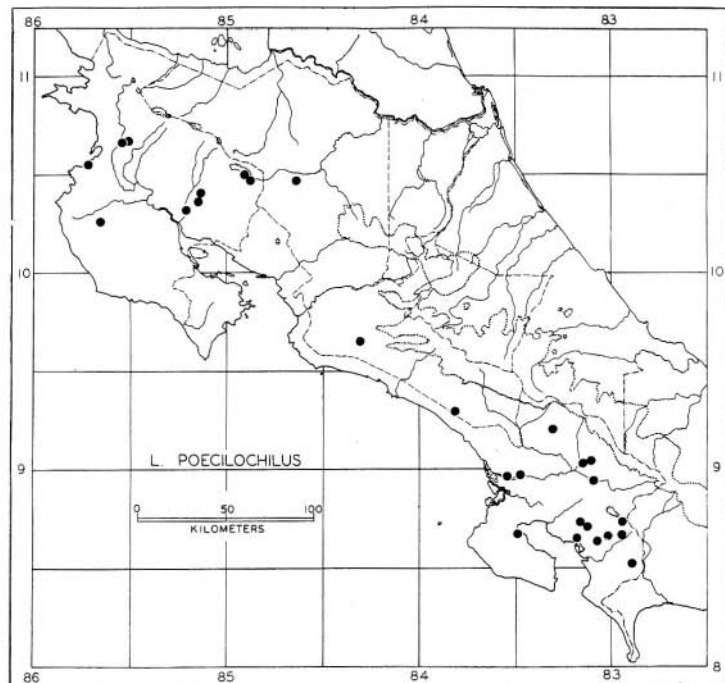
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Fig. 25. Distribution of *L. pentadactylus* in Costa Rica. Dotted line equals 1500 meter contour.

Fig. 26. Distribution of *L. poecilochilus* in Costa Rica. Dotted line equals 1500 meter contour.



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