

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 Hyliidae 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: *Erythronops* 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 Hyliidae and Ranidae have a dextral anus (median); the only known *Aietopus* 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 break) 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 ventrally 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 boliviensis Boulenger

1898. *Leptodactylus boliviensis* Boulenger: 45 (Holotype: Genoa Mus. 28875 A, Bolivia; Barraca and Misiones Mosetens); 1954, Taylor: 617-620 (redescription).

DIAGNOSIS. - Adult: From all *Leptodactylus* of Costa Rica except *L. melanonotus*, *L. boliviensis* is distinguished by the extensive fringing on the sides of the toes. *L. melanonotus* is a small robust frog (*L. boliviensis* 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 $\frac{3}{5}$ 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 carpal 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; internarial 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 Juleta, Finca La Ligua, 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 Nelly, 75 m; 14.5 km NW Villa Nelly 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 MINYON & 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. *Cyrtignathus labialis* Cope: 90 (Holotype: USNM 31302, Mexico?)

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

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 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 3.6-3.7, 7.3-9% standard length; head width 3.2-3.3, 6.3-5% 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 mottled 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 3.6 mm, females to 4.0 mm; femur shorter than tibia, 3.4-4.0, 3.4-4% standard length; tibia shorter than foot, 3.9-4.4, 6.4-8% standard length; foot longer than femur, 4.5-5.0, 2.5-3% standard length (Fig. 2).

Larva: Nostril slightly closer to tip of snout than to anterior edge of eye; internaral distance $\frac{1}{2}$ or slightly greater than $\frac{1}{2}$ of interorbital distance; eye large, horizontal diameter 1.2-1.3, 4.1-6% of body length; mouth subterminal; oral papillae rows 1-2 or 1-2-1; oral disk entire; oral disk width 1.7-1.9, 6.2-2% of body length; oral papilla gap 5.3-6.3, 4.6-7% 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 $\frac{2}{1-1}$ just posterior to beak, most posterior tooth row from just shorter to 2/3 length of anterior two tooth rows; more denticles in divided tooth row just posterior to beak (5.9-10.4) than in divided tooth row just anterior to beak (4.6-10.1); 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, 4.1 mm; body length 3.1-3.5, 9-40% of total length (Figs. 7, 12, 17).

LOCALITIES: ALAJUELA: Los Chiles, 70 m; GUANACASTE: Atenal, 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, 4.2 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 4 1/2 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, Highway N° 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 Barranca; Río 12 km WNW Esparta, 30 m; Esterillos Oeste, 15 km SE Jacó; Golfito, 10 m; Orofina, 213 m; 6.1 km NE mouth of Río Grande de Tarcoles; 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 Nelly, 75 m; 21.8 km NW Villa Nelly, (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 2.5-3.0 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. poecilobolus* 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 percentage 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. poecilobolus*. The number of denticles appears diagnostic (Fig. 21). I have assumed that the variation in denticle number in *L. labialis* and *L. poecilobolus* represents environmentally-induced variation within the genetic limits of the species.

Leptodactylus melanonotus (Hallowell)

1860. *Cyrtignathus melanonotus* Hallowell: 485 (Type apparently lost, Nicaragua).

1881. *Leptodactylus melanonotus*, Bocchi: 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 $1/2-2/3$ 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 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; internasal distance about $2/3$ 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: $\frac{1-1}{3}$ or $2/3$, tooth row just anterior to beak continuous or just divided, most posterior tooth 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; dorsally, greater concentration of melanophores posteriorly to nostrils and on either side of tail musculature on body or not; lighter areas lateral to eyes; spracle 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 Cortez, 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 4 1/2 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 Diriz, 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; 5 1/2 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; LIMÓN: 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 (Indices).1872. *Cystignathus pentadactylus*, Peters: 198 (synonymy).1882. *Leptodactylus pentadactylus*, Boulenger: 241-242 (records, redescription); 1932, Taylor: 649-652 (redescription).

DIAGNOSIS - Adult: The lack of prominent lateral toe fringes separates *L. pentadactylus* from *L. bolivianus* and *L. melanonotus*. The lack of a distinct light longitudinal stripe on the posterior thigh further distinguishes *L. pentadactylus* from *L. labialis* and *L. poeichobiius*. *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 posterior 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 caudal 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 foot, 42-44.4-47% standard length; foot shorter than, equal 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; internarial distance about $\frac{2}{3}$ 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: $\frac{1-1}{1-1}$, large gap in tooth row just anterior to beak, barely a gap in tooth row just posterior to beak, most posterior tooth row from $\frac{1}{3}$ to $\frac{2}{3}$ 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; Tunnel 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; LIMÓN: Alta Tamanaque, confluence of Ríos Larí and Diparí about 21 km SW Ambríz, 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 JOSÉ: 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. boliviensis* 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. *Cyrtognathus 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: 653-657 (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. boliviensis*, *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. boliviensis* 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 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 supratrempanic 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; internarcal distance about 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 $\frac{1}{2}$ just posterior to beak is divided, halves about 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;

