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VARIATION AND TAXONOMIC CLARIFICATION OF THE LARGE SPECIES OF THE *LEPTODACTYLUS PENTADACTYLUS* SPECIES GROUP (AMPHIBIA: LEPTODACTYLIDAE) FROM MIDDLE AMERICA, NORTHERN SOUTH AMERICA, AND AMAZONIA

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ABSTRACT

Variation of external morphology features and advertisement calls are analyzed for species currently identified as Leptodactylus knudseni, L. labyrinthicus, L. myersi, *and* L. pentadactylus *from Middle America, the Pacific versants of Colombia and Ecuador, northern South America, greater Amazonia, and the corridor of open formations from Argentina to northeastern Brazil. Although there is noticeable geographic variation between eastern and western samples of* L. knudseni, *the variation is considered to be intraspecific in nature. Geographic variation within* L. labyrinthicus *is more pronounced and most consistent with recognizing three species:* L. labyrinthicus *(Spix, 1824),* L. turimiquensis *new species, and* L. vastus *A. Lutz, 1930. No new data are available for variation within* L. myersi, *which had previously been noted as possibly containing two species. Variation within* L. pentadactylus *is also pronounced and most consistent with recognizing four species:* L. pentadactylus *(Laurenti, 1768),* L. peritoaktites *new species,* L. rhodomerus *new species, and* L. savagei *new species. Some specimens that had been identified in collections as either* L. knudseni *or* L. labyrinthicus *from the Brazilian State of Pará are considered to represent an undescribed species, herein described as* L. paraensis *new species.*

Standard simple statistical tests of significance for sexual dimorphism in members of the study group may not indicate biological significance. Adult morphological and advertisement call differentiation patterns among the species recognized in this paper do not provide completely reliable information for identifying the species involved, suggesting a different pattern of differentiation than occurs in the Leptodactylus fuscus *species group. Larval morphological variation and habitat differentiation may be important in the evolution of species differentiation in the taxa dealt with in this paper.*

Key words: Variation, taxonomy, *Leptodactylus,* Middle America, northern South America, Amazonia.

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Introduction

Ulisses Galatti (unpublished manuscript) undertook comparative studies of the reproductive biology of *Leptodactylus pentadactylus* just north of Manaus in Brazilian Amazonia and central Panama. He found striking differences in his studies of the organisms at the two sites and convincingly concluded that the two populations studied should be recognized as distinct species. This conclusion is supported by the available genetic differentiation data (Maxson and Heyer, 1988). After receiving a draft of Galatti's unpublished manuscript for comment, I re-examined the data I had taken on specimens of *L. pentadactylus* (Heyer, 1979) to determine whether they were adequate to separate the specimens I had examined into two taxa; they were not.

At the same time, examination of certain specimens of large *Leptodactylus* from the State of Pará in Brazil indicated that they were neither *L. knudseni* nor *L. labyrinthicus.* I therefore began taking more extensive data on large species of *Leptodactylus* in an attempt to define the taxa involved and to determine their geographic distributions. The taxa included in this study involve the specimens that were or would be identified as *Leptodactylus knudseni, labyrinthicus, myersi,* or *pentadactylus* in my previous studies (Heyer, 1979, 1995). The large species of the *Leptodactylus pentadactylus* group not included in this study are *L. fallax, flavopictus,* and *laticeps,* because there is no evidence to suggest that there are taxonomic problems associated with them and they have distributions largely or entirely apart from the taxa included in this study.

Materials and Methods

Evaluating variation to discern species limits in the frogs included in this study is made difficult by two problems, both likely related to the large size of the adults. First, due to space constraints in the Division of Amphibians & Reptiles at the Smithsonian Institution, I could not borrow all of the museum specimens even if the curators of the collections involved were willing to loan the specimens to me for study. Second, over much of the geographic ranges of the taxa involved, sample sizes of adults are characteristically small, in general due to problems of storage of large specimens in museum collections.

The limited storage space available did not allow me to evaluate variation in the way I have found works most effectively. My optimum method is to borrow all available materials so that as data-taking and analysis proceed, specimens can be re-examined when questions arise. For example, during data-taking, pattern standards are continually added and specimens evaluated early in the study often should be re-inspected against the newer standards.

The generally small sample sizes of adults available for most localities do not allow a rigorous analysis of variation of specimens from single localities, a critical measuring stick for evaluating inter-population variation.

Given the nature of the above two problems, the following approach was used.

Variation in *Leptodactylus myersi* has been evaluated relatively recently (Heyer, 1995); consequently data for this species are used only to compare with data from the other taxa. As noted previously (Heyer, 1995), there is significant variation within *L. myersi* that may conform better to recognition of two species. There are no new data to address this issue.

Data were taken anew for the following characters of transformed juveniles and adults: sex; dorsal pattern; belly pattern; lip pattern; posterior thigh pattern; upper shank pattern; body folds; male arm hypertrophy; male thumb spines; male chest spines; male chin, throat, and chest tubercles; upper shank texture; outer tarsal texture; foot texture; snout-vent length (SVL); head length; head width; eye-nostril distance; maximum tympanum diameter including annulus; thigh length; shank length; foot length.

Data were accumulated during the years 1994-2003.

Museum abbreviations follow Leviton *et al.*, 1985 and Leviton and Gibbs, 1988 (for the two Swedish collections involved), with the exception of OMNH, herein used for the Sam Noble Oklahoma Museum of Natural History and the addition of CBF = Colección Boliviana de Fauna, La Paz, CV-ULA = Collection of Vertebrates, Universidad de Los Andes, Mérida, FHGO = Laboratorio de Anfibios & Reptiles, Universidad San Francisco de Quito, Fundación Herpetológica "G. Orces," Quito, MECN = Museo Ecuatoriano de Ciencias Naturales, Quito, and QCAZ = Museo de Zoología de la Pontificia Universidad Católica del Ecuador, Quito. Data on most specimens of the taxa involved were taken from the MZUSP, OMNH, and USNM collections. In addition, I took data on specimens from Colombia and Venezuela during visits to several collections in those countries. Based on my previous work on these taxa (Heyer, 1979), the data from these materials should be sufficient for the purpose of this study.

Five categories were used for sex: (1) adult females were determined by having curly oviducts or well-developed ova; (2) juvenile females were determined by having straight oviducts – only larger individuals were dissected to make this determination; (3) adult males were determined as having vocal slits; (4) juvenile males were determined as having testes or other secondary characteristics such as a small thumb spine, but lacking vocal slits – only larger individuals were dissected, if needed, to make this determination; (5) juveniles were small individuals, clearly not adults, and were not dissected.

For all the pattern characters, outline drawings of the body area involved were filled in with patterns used previously or with new sketches. Each pattern was uniquely labeled.

Body folds are unambiguous in well-preserved specimens, but may be difficult to evaluate in less well-preserved specimens. At the beginning of the data-taking phase, two folds were evaluated, namely (1) a dorsolateral fold, which (when present) extends from behind the eye towards or past where the sacrum articulates with the ilial shaft; and (2) a flank fold, extending from the supratympanic fold and curving downward on the flank, ending about mid-flank. If the dorsolateral fold is present, it is usually highlighted by a stripe of pigment which is darker than that which occurs on the area surrounding the dorsolateral fold. This dark stripe is used as a proxy for the fold itself where the state of preservation of the animal makes it unclear whether a fold is present or not. The flank fold may or may not be darkly highlighted, so its condition is much more difficult to evaluate in many less than well-preserved animals. Towards the end of the data-taking phase, I noticed that some particularly well-preserved individuals also had lateral body folds arising together from the same origin as the flank fold (from the supratympanic fold), but extending more or less in a straight line to the groin region. These lateral folds are not highlighted with darker pigment and thus much more difficult to evaluate in many of the specimens.

Information is now available that allows a better understanding of the nature of male secondary characteristics involving arm hypertrophy and thumb and chest spines. Jaslow (1985) indicated that the dark keratinized thumb and chest spines were shed by *Leptodactylus pentadactylus* from Panama during the non-breeding season. He reported that the male arm, while larger than the female arm due to humeral hypertrophy, also had additional muscle growth and diminution on a seasonal basis. Observations in captive breeding colonies support and extend Jaslow's findings. Richard Gibson (pers. comm.) observed that captive male *L. fallax* shed "… the black keratinous sheath from their thumb spines. A white hard cone is left in place." (*Leptodactylus fallax* lack chest spines.) James Ellis (pers. comm.) found that specimens identified by St. Louis zoo personnel as *L. pentadactylus* shed both thumb and chest spines on a regular annual cycle, but a marked diminution of the arm when the spines were shed was not observed in the captive colony. A smaller white core was still visible on the thumbs after the keratinized sheath was shed, but the entire chest spine was shed such that no raised protuberance was seen from where the chest spines had been shed. Under the dissecting microscope, a white basal platform from where the keratinized chest spines will be regrown can usually be seen (pers. observ.). Thus, size alone does not correlate with development of these particular secondary characteristics of male *Leptodactylus*. There also appears to be variation related to preservation. In some individuals thumb spines or chest spines are well developed but are white, presumably due to the keratin layer having fallen off. Thus, white and black spines are not different character states in the sense of character coding for phylogenetic analysis.

Measurements were taken with dial calipers recorded to the nearest 0.1 mm following Heyer *et al.* (1990) with the addition of tympanum diameter (described above) and eye-nostril distance, measured from the middle of the nares to the anterior corner of the eye. SVL of specimens that exceeded the ability of measurement with calipers was determined using a ruler. Following the recommendation and protocol of Hayek *et al.* (2001), an adult male (MZUSP 131849) and an adult female (MZUSP 64198) were each remeasured 20 times.

Advertisement calls were analyzed using Canary 1.2 (Charif *et al.*, 1995) following the terminology in Heyer *et al.* (1990) unless indicated otherwise. The calls were digitized at a sample rate of 22050 Hz, sample size of 17 bits, at an input speed of 1x. Call duration was measured from the wave form. Calls were examined using the audiospectrogram display (spectrogram in Canary terminology) to determine whether the recordings would benefit from filtering around the advertisement calls. Most calls were filtered because they had considerable signal below and/or above the advertisement call frequencies. The audiospectrogram analyses used settings of analysis resolution filter bandwidth 349.70 Hz and frame length 256 points; grid resolution of time 5.805 ms, overlap 50%, frequency 86.13 Hz, FFT size 256 points; window function hamming; amplitude logarithmic; clipping level –80 dB; display style smooth. Dominant frequency was determined using the spectrum analysis of Canary with settings of analysis resolution filter bandwidth 349.70 Hz, FFT size 256 points; window function hamming; amplitude logarithmic; clipping level –79.79 dB. For beginning and ending call frequencies, selections of the smallest value equal to or greater than 25 ms were made at the beginning and end of the call and analyzed using the same spectrum analysis settings. Frequency sweep is the difference of the ending frequency and beginning frequency. Call amplitude modulation and harmonics were evaluated from visual inspection of expanded wave form displays, audiospectrogram displays, and power spectrum displays.

Most larval samples are identified as belonging to the species included in this study by their unique facultative carnivore morphotype (Heyer *et al.*, 1975). However, few larvae are unambiguously associated with their adult parent(s). Larval characters examined are discussed in the Inter-Unit Analysis section.

Only data for juveniles and adults are (marginally) sufficient to analyze for interpopulation variation; in no cases are data sufficient for statistical comparisons. I exercised my experience with variational studies in *Leptodactylus* to form samples for analysis of geographic variation and interpreting the variation observed. In spite of the too strong an influence of experience guiding decisions rather than having adequate data for the variation to be understandable on their own, I have tried to report the process and results so that other workers could repeat the study with the same materials.

The first experience-guided decision was in choosing the basic Units for analysis of variation throughout the geographic ranges involved. Four Units were chosen to analyze individually, all based on my identifications at the outset of the study: (1) *L. knudseni;* (2) *L. pentadactylus;* (3) *L. labyrinthicus;* and (4) a previously apparently unrecognized species from the State of Pará, Brazil, called the Pará Unit. Five specimens (MZUSP 24947-8 from Jacearacanga, Pará; USNM 202518 from Barreira do Matupiri, Rio Madeira, Amazonas; MZUSP 131123, USNM 303909 from Alto Paraiso, Rondônia, all in Brazil) could not be confidently placed in these four Units. They are evaluated in the section dealing with species limits. As indicated above, *Leptodactylus myersi* was not included in this part of the study, as it has already been analyzed.

For each of the four Units, all the localities for which I had specimen data were plotted on an appropriately scaled map. Based on clustering patterns of localities and presence of at least some adult male individuals, certain near-by localities were grouped together into areas, with an attempt to have the areas cover the range of the total distribution. Data were summarized for all individuals within each area. In at least some of the taxa involved, juvenile color patterns either differ from or are more distinct than adult patterns. The pattern data were summarized for all individuals within each area separately by juvenile, male, and female categories. The pattern data were re-summarized in subsequent analyses (Inter-Unit Analysis and Species Accounts), so the word descriptions of character states differ. In addition, some of the patterns are most usefully visualized in the Inter-Unit Analysis section and the Figures involved are located there. However, as appropriate, those Figures are cited in the Intra-Unit Analyses as well.

Juveniles for the pattern analyses were defined after examination of the data for all specimens for each of the four Units and a break-off point of 90 mm SVL was established below which all specimens were considered to be juveniles. The data sheets used to record the pattern data used individual identifying symbols for the patterns (a combination of letters and numbers). For purposes of analysis, I translated the various individual patterns into more general categories described by words rather than analyzing the alphanumeric symbols which represent individual pattern standards. Pattern standards and data sheets are archived at the Smithsonian Institution.

Variation among area samples was evaluated to determine if there was geographic variation. Once the among-area variation was summarized and evaluated, the data for all other specimens from the same Unit were compared with the data for their nearest geographical area to determine whether these additional specimens demonstrated variation beyond that observed in the most approximate area samples.

The patterns of morphological variation served as one primary piece of evidence in determining the degrees of differentiation within each of the four Units. These data, in combination with available advertisement call data were used to define differentiated Units for further analysis.

The terms distinct and distinctive have different meanings as used to describe differentiation in this study. A character state is distinct when it occurs in one sample but not in one or more other samples being compared. A character state is distinctive when the relative frequency of occurrence differs markedly between or among samples being compared.

Summary and analytical procedures are described at appropriate places in the text.

Remeasurement Data

For both the male and female data, measurement variation ranges from 3.1-3.6 mm for SVL and head length, 1.4-2.2 mm for head width, 0.7-0.9 mm for eye-nostril distance and tympanum diameter, 0.5-0.8 mm for shank length, and 1.6-2.0 mm for foot length. The measurement range for female thigh length is 1.1 mm and for male 2.3 mm (Table 1).

The coefficients of variation are lower for SVL, head width, thigh length, shank length, and foot length than for head length, eye-nostril distance, and tympanum diameter for both sexes (Table 1).

Table 1. Data for one female (MZUSP 64198) and one male (MZUSP 131849), each measured 20 times.

	Minimum	Maximum	Coefficient of Variation
♀ SVL	124.7	128.2	0.006
♀ Head length	44.8	48.4	0.019
♀ Head width	47.4	49.6	0.010
♀ Eye-nostril distance	10.7	11.4	0.020
♀ Tympanum diameter	8.3	9.0	0.023
♀ Thigh length	49.6	50.7	0.007
♀ Shank length	53.4	54.2	0.004
♀ Foot length	54.7	56.7	0.010
♂ SVL	124.6	127.7	0.005
♂ Head length	42.2	45.6	0.025
♂ Head width	45.3	46.7	0.007
♂ Eye-nostril distance	11.1	12.0	0.020
♂ Tympanum diameter	8.2	8.9	0.025
♂ Thigh length	45.4	47.7	0.012
♂ Shank length	51.1	51.6	0.002
♂ Foot length	53.8	55.4	0.008

Intra-Unit Analyses

Pará Unit

Geographic Areas – Three Areas containing at least two adult males and two adult females are situated in the Belém region and on the lower and middle portion of the Rio Xingu (Figure 1).

Variation – Dorsal Pattern: There is no noticeable variation between juveniles and adults or among areas for adults. Dorsal patterns include almost uniform, dark irregularly spotted, dark regularly spotted, and dark transversely elongate bars that are distinct or slightly in contact with each other. One non-Area specimen from Tucuruí (MZUSP 62554) has alternating darker and lighter transverse bands. The other non-Area specimens do not differ from the geographic Area specimens.

Belly Pattern: Adults in Areas A, B, C have darkly vermiculated bellies (reverse of pattern of Figure 13B) or a dark- and light-spotted belly (one female) (intermediate between Figures 13B and E). The juveniles have a very distinct to less distinct labyrinthine belly pattern (Figure 13D). There is no variation among Areas. The non-Area specimen from CEMEX (OMNH 34762) has a dark belly with a few light irregular spots (intermediate between Figures 13B and E), differing in detail from geographic Area specimens. All other non-Area specimens do not differ from the geographic Area specimens.

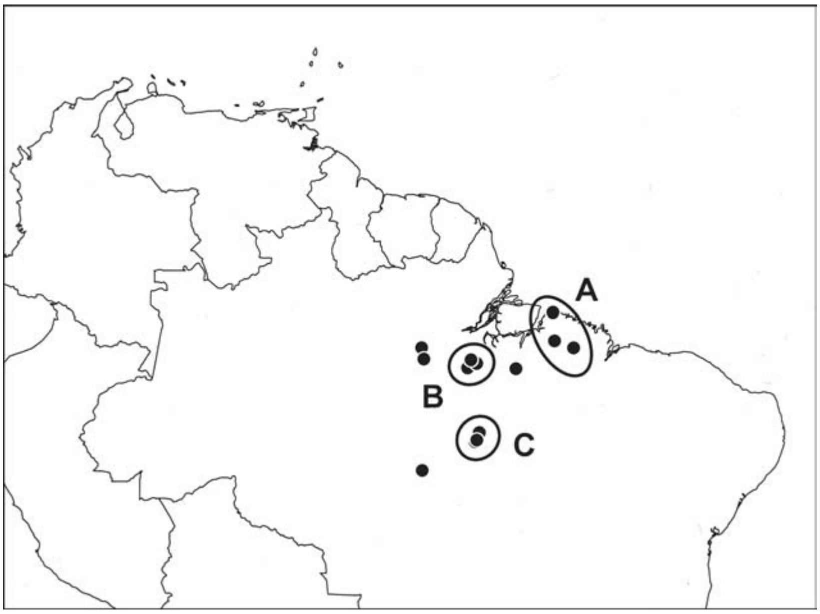

Figure 1. Geographic areas for Pará Unit. A = Belém region, B = lower, and C = middle portion of the Rio Xingu.

Lip Pattern: A pattern common to adult specimens from Areas A, B, C is one of dark triangular bars on the upper lip with apices extending to the eye/ canthal region. One of the dark bars reaches the eye in two adults from Area B (Figure 12A). The three juvenile specimens from Area C are distinct from the adults in having dark upper lips with narrow, light, angled bars from the lip to the eye/ canthal region (Figure 12B). The non-Area specimen from CEMEX (OMNH 34762) has narrow dark stripes to the eye and loreal region (Figure 12C). All other non-Area specimens do not differ from the geographic Area specimens.

Thigh Pattern: Specimens from Areas A, B, C share a pattern of dark posterior thighs with light vermiculations (Figure 14A), with or without a light extension of the light dorsal thigh bars on the upper portion of the posterior thighs. Two adults from Area A have a greater development of light markings on the thigh than the rest of the adults. One juvenile has a uniform upper posterior thigh and a darker lower posterior thigh with small, light, irregular spots. A non-Area female from Serra do Cachimbo, Pará (MNRJ 2567) has more extensive light areas on the thighs than the geographic Area specimens. All other non-Area specimens do not differ from Area A, B, C specimens.

Shank Pattern: All individuals have dark, well-defined, transverse bars on the upper shank.

The non-Area specimen from CEMEX (OMNH 34762) has interrupted transverse bars. All other non-Area specimens do not differ from Area A, B, C specimens.

Body Folds: All individuals range from having a series of warts where dorsolateral folds occur in other species extending from the eye to the sacrum to having only one or two such warts. Some individuals within each Area have lateral folds extending as far as the mid-body, with others apparently lacking lateral folds. Individuals within each Area either have no indication of a flank fold or have a series of 1-4 dark warty spots in the region where the posterior extent of the flank fold occurs in other taxa. All non-Area specimens do not differ from Area A, B, C specimens.

Male Sexual Secondary Characteristics: There is no apparent variation among Areas for any male sexual secondary characteristic. The arms range from having no hypertrophy to extreme hypertrophy. Males either have small, black tubercles on the throat, chest, anterior belly and ventral surface of the upper arms or lack them. Males have one thumb spine, ranging from small to moderate size, either black or white. All males except for one (118 mm SVL) have a pair of chest spines; the spines are black or white and of small or moderate size. There is only one adult male from a non-Area locality (OMNH 34359) and it does not differ from the Area A, B, C males.

Upper Shank Texture: Most individuals from Areas A, B, C have very few to many white or black tubercles. One individual each from Areas B and C has, in addition, a weakly developed shagreen texture. Two individuals from Area C have granular shanks in addition to the tubercles. The non-Area specimen from CEMEX (OMNH 34762) has a shagreen and scattered black tubercle texture. All other non-Area specimens do not differ from Area A, B, C specimens.

Outer Tarsal Texture: Most individuals from Areas A, B, C have few to several white or black tubercles. Two individuals from Area A and one from Area B have no or very few white tubercles on the outer tarsal region. All non-Area specimens do not differ from Area A, B, C specimens.

Foot Texture: Most individuals from Areas A, B, C have no tubercles on the sole of the foot. A few individuals from each Area have very few white or black tubercles on the sole of the foot. All non-Area specimens do not differ from Area A, B, C specimens.

Adult Size: Given the small sample sizes and ranges of sizes observed (Table 2), it would seem that the three Area samples could be drawn from the same general population. All adult non-Area specimens do not differ from Area A, B, C specimens.

Measurement Data: Sample sizes are much smaller than desired to perform discriminant function analyses. Both male and female results (Figure 2) indicate that measurement error is as great as any difference among Area samples.

Life Colors: Field notes for OMNH 34762, a 105 mm juvenile, are kindly made available by Janalee Caldwell: "Dorsum dark brown with gray crossbars. Limbs with light and dark brown stripes. Posterior surfaces of thighs black with small light orange spots. Venter gray with tiny white reticulations. Eye bicolored: upper half golden, lower copper."

Advertisement Calls: None available.

Table 2. Adult sizes (SVL in mm), Pará Unit Geographic Areas. For the definition of geographic areas, see Figure 1.

Geographic Area	Males	Females
A	104-120 (N = 2)	122-140 (N = 2)
B	112-127 (N = 5)	111-126 (N = 2)
C	99-129 (N = 4)	118-136 (N = 3)

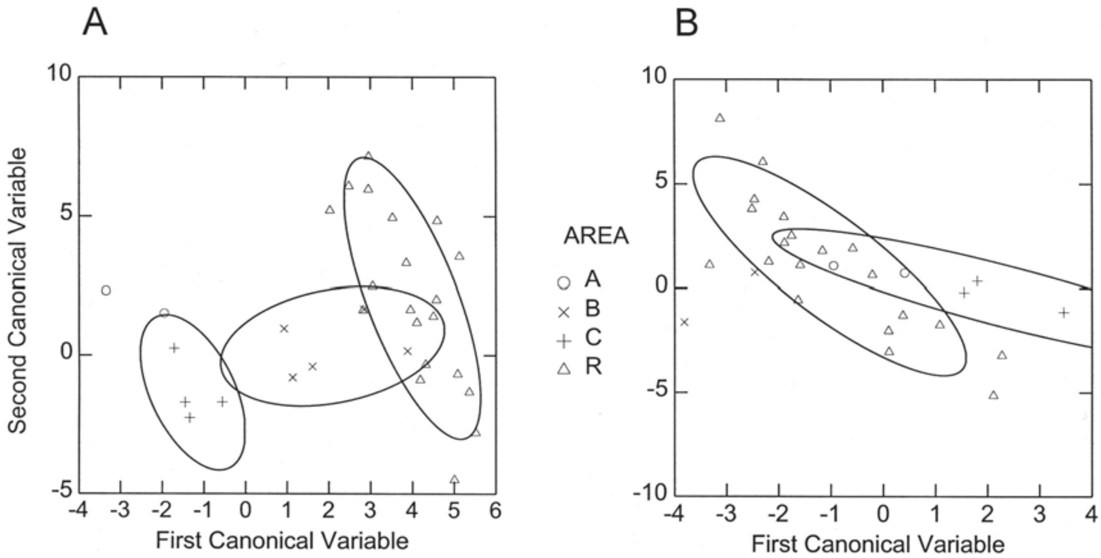

Figure 2. Discriminant function plot for male (A) and female (B) measurement data, Pará Unit geographic areas. Sample confidence ellipses *p*:0.683. A-C symbols in legend on figure represent areas A-C; the symbol for R represents remeasurement data for a single specimen (see text for further explanation).

Evaluation of Differentiation: The variation observed is consistent with being entirely intraspecific with no convincing evidence of geographic differentiation.

***Leptodactylus knudseni* Unit**

Geographic Areas – Eight geographic areas each containing at least two adult males are distributed broadly throughout the total range of the localities sampled for this study (Figure 3).

Variation – Dorsal Pattern: There are five general pattern types into which most specimens fit (Table 3). Juvenile and adult patterns are distinctive from one another (but not as distinctive as for the belly pattern). In the Area B sample, juveniles have distinctly dark outlined cross-bars and the adults are either uniformly dark or with more irregular, not as distinctly outlined transverse bars as in the juveniles. In the Area G sample, juveniles are distinct from adults in having a series of alternating dark and light sharply defined cross bars. Some adults have uniform dorsal patterns whereas all juveniles have some type of distinct pattern. All non-Area specimens do not differ from the specimens in their geographically closest Area samples.

Belly Pattern: In all Areas that have both adults and juveniles represented, the belly patterns of the juveniles are distinctive from the adult patterns. In addition, the juvenile patterns are different between Areas B and G. In Area B, a common pattern is a dark belly with distinct light spots (Figure 13E), a pattern not found in juveniles in Area G. Conversely, a common pattern in Area G is no pattern (no melanophores on belly), a pattern not found in any juveniles from Area B. The differences observed between juvenile patterns from Areas B and G could be due to relatively small sample sizes (12 juveniles from Area B, 15 for Area G), but the juvenile

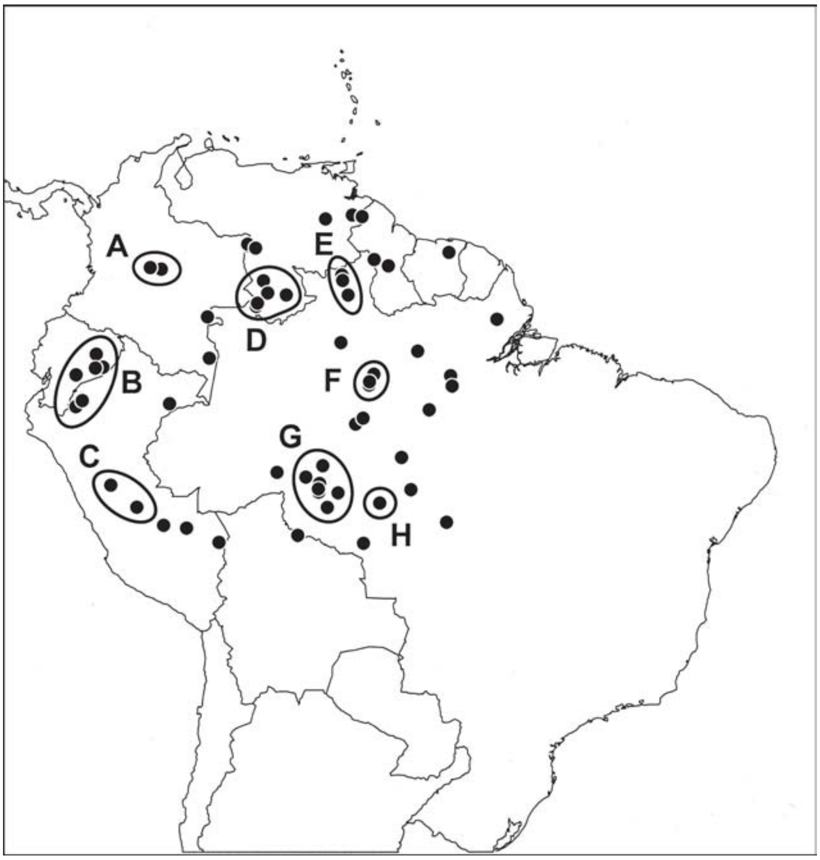

Figure 3. Geographic areas for *Leptodactylus knudseni* Unit. See text for explanation.

patterns from Areas F and G are similar to each other. Adults from areas D, E, F, G, H have uniform to indistinctly mottled bellies (Figure 13A). The only exception is a female from Area F with a light belly with distinct dark vermiculations (reverse of pattern shown in Figure 13B). Some adults from Areas B and C, in addition to having indistinctly mottled bellies, have dark bellies with distinct light spots (Figure 13E). The adult belly patterns from Area A can not be placed readily into any of the patterns described for the other Areas. The bellies are indistinctly to distinctly mottled. ZMB 6759, 8534 from Suriname have bellies with more distinct mottling than specimens from proximate Area D. All other non-Area specimens do not differ from the specimens in their geographically closest Area samples.

Lip Pattern: There are four general pattern types into which most individuals (both adult and juvenile) fall (Table 4). In the two Area samples with the most juveniles, there do appear to be differences between juvenile and adult patterns. In Area B, the juvenile lip patterns have well defined triangular marks with apices on the edge of the upper lip and with one of the triangular marks extending as far as the eye (Figure 12A) or not. The adults from Area B have either uniform dark lips or indistinct bars. In Area G, most juveniles have two dark bars that extend from the lip to under the eye (Figure 12D), whereas the adults do not have this pattern and have much more uniform lips. In addition to the patterns indicated in Table 4, one individual from Area B has an indistinctly barred lip and one individual from Area G has an unusual pattern combining elements of one versus two complete dark bars from the lip to the eye. Area G, which has the largest sample size, contains all patterns, suggesting that the variation observed among Areas may be due to inadequate sample sizes. Non-Area specimen MZUSP 15907 from Alto Rio Machado, Rondônia, Brazil lacks a lip pattern, differing from specimens from proximate Area H. All other non-Area specimens do not differ from the specimens in their geographically closest Area samples.

Thigh Pattern: There seems to be a difference between juvenile and adult thigh patterns in the Area B sample. All juveniles have a uniformly dark posterior thigh surface, while one adult male has a finely mottled thigh and two adult males have boldly mottled thighs. The thighs among specimens from Area G do not show as much contrast as for Area B. The juveniles from Area G have mottled thighs that are less boldly mottled than some of the adults, although most of the adults were scored as having the same thigh patterns as the juveniles from this Area. Other than the differences discussed above, there seems to be no variation among specimens from Areas A through H. The adult thighs are mottled, though several individuals from Area H show less distinct mottling than found in the rest of the adult specimens from Areas A through G. Non-Area specimens from Cachoerinha, Rio Madeira (MZUSP 202517) and Nova Aripuanã, Amazonas, Brazil have less distinctly patterned thighs than specimens from proximate Areas F and G. MZUSP

Table 3. Dorsal patterns, *Leptodactylus knudseni* Unit. For the definition of geographic areas, see Figure 3.

Patterns	Geographic Areas							
	A	B	C	D	E	F	G	H
Uniform	X	X				X	X	X
Distinct, narrow cross bands	X		X					
Distinct, moderately broad cross bands		X	X			X	X	
Broad cross bars	X	X	X	X	X		X	X
Irregular cross bars				X	X	X	X	X
Blotched							X	
Coalesced bars anteriorly, coalesced blotches posteriorly								X

Table 4. Lip patterns, *Leptodactylus knudseni* Unit. For the definition of geographic areas, see Figure 3.

Patterns	Geographic Areas							
	A	B	C	D	E	F	G	H
Two complete dark bars from lip to eye			X				X	X
One dark bar from lip to eye		X		X	X	X	X	
Upper lip marks only	X	X	X	X	X	X	X	X
Uniform		X	X			X	X	

25169 from Forte Príncipe da Beira, Rondônia, Brazil also has less distinctly patterned thighs than specimens from proximate Area G. OMNH 34796 from CEMEX, Pará, Brazil has light spots on the upper thigh, a pattern not found in other individuals from proximate Area F. All other non-Area specimens resemble the specimens in their geographically closest Area samples.

Shank Pattern: Area G individuals demonstrate variation found in all other specimens from the other Areas; there is no observed difference between juvenile and adult patterns.

Body Folds: There is little variation among Area samples in terms of development of the dorsolateral fold. The fold is continuous from behind the eye to the sacrum in most specimens. Variations include: the fold is interrupted; the fold extends only 3/4 distance from the eye to the sacrum; or there is a short break behind the eye before the fold begins. Specimens from Area H have less well-developed dorsolateral folds in general than specimens from the other Areas, but this could well be an artifact due to preservation differences and/or small sample sizes. The lateral fold occurs in at least some individuals from Areas A, B, C, and D. Most individuals from Areas E, F, G, H were scored as lacking lateral folds, but a few individuals from Areas E, F, H were scored as having barely recognizable lateral folds. There is no indication of a flank fold in specimens from Area B and only weak indications of a flank fold in some individuals from Areas A and C. Most individuals from Areas D, E, F, G, H have a dark elongate wart in the region where the flank fold occurs in other members of this species cluster. EBRG 2390, 2444 have complete flank folds, differing from specimens in proximate Area E. OMNH 34360-34361 from Alter do Chão, Pará, Brazil have slightly shorter dorsolateral folds (2/3 to 3/4 distance from eye to sacrum) than any specimen from proximate Area F (minimum of 7/8 distance from eye to sacrum). All other non-Area specimens do not differ from the specimens in their geographically closest Area samples.

Male Sexual Secondary Characteristics: At least some males from each Area have very extensively developed male arms, except for Area F (N = 2). At least some males from each Area have a field of black tubercles on the throat, chest, and anterior belly, except for Area F. For all Areas except G, males that have a well-developed black thumb spine also have a pair of black chest spine patches. In Area G, there are only two males that have black thumb spines, neither of which have chest spines. The other males from Area G have white thumb spines. The lack of chest spines in Area G could be due to at least two causes: (1) adult males from Area G are small (see size, below) and lack chest spines; or (2) males from Area G are as large as males from other Areas but were not sampled, and these larger, unsampled males would have both black thumb and chest spines. The present data can not distinguish between these alternatives. Non-Area specimens USNM 288740-288741 from Parque Nacional de Amazonia, Rio Tapajós, Pará, Brazil have a secondary proximal bump on the male thumb, differing from specimens from geographically proximate Area F. All other non-Area specimens do not differ from the specimens in their geographically closest Area samples.

Upper Shank Texture: The upper shanks usually have a few to several scattered black and white tubercles. A few specimens from Areas B and F also have a shagreened surface. The only Area from which a noticeable number of individuals lack any indication of shagreen or tubercles is Area C. Non-Area specimens do not differ from the characterization for Area specimens.

Outer Tarsal Texture: The outer tarsal surface usually has a few to several scattered black or white tubercles. Lack of tubercles is unusual in the samples as is presence of a shagreened surface. Area G is distinctive in having several individuals with many scattered black or white tubercles. Four non-Area specimens lack tubercles on the outer tarsal surface and differ from specimens from proximate geographic Areas (ROM 28451-28452, USNM 535773 – Area E; OMNH 34360 – Area F). All other non-Area specimens do not differ from the specimens in their geographically closest Area samples.

Foot Texture: Specimens from Areas A, B, C, D lack tubercles on the sole of the foot. Most individuals from Areas E, F, G, H also lack a shagreen or tubercles, but one to three individuals from each of these Areas have a few white tubercles scattered on the sole of the foot and one individual from Area F has a shagreened surface. All non-Area specimens do not differ from the specimens in their geographically closest Area samples.

Adult Size: The most instructive sample for understanding variation in adult size is that from Area H, where there is almost one order of magnitude of difference between the smallest and largest adult male (Table 5). When using the ranges of adult size of Area H as a standard for evaluating the other Area samples, only the sample from Area G appears unusual. It contains the largest number of males. The maximum size of these Area G males is 128 mm SVL. These Area G males may have just reached sexual maturity and if so, would be expected to grow to a larger size and develop hypertrophied arms, large thumb spines, and large chest spines. Non-Area specimen ZMB 8534 from Suriname is larger (158 mm SVL) than males from proximate Area E. The following non-Area males are larger than males in proximate Area F: MZUSP 54667, 136 mm SVL; MZUSP 54668, 146 mm SVL; OMNH 34360, 137 mm SVL; OMNH 34361, 147 mm SVL; OMNH 34796, 125 mm SVL. All other non-Area specimens do not differ from the specimens in their geographically closest Area samples.

Measurement Data: Sample sizes for most Area samples are too small for discriminant function analyses, and are minimally adequate for the male data. There is broad overlap in the plot of the first two canonical variables (Figure 4) when using the complete data option in Systat 10 (Engelman, 2000) for many of the Area samples.

Table 5. Adult sizes (SVL in mm), *Leptodactylus knudseni* Unit geographic areas. For the definition of geographic areas, see Figure 3.

Geographic Area	Males	Females
A	131-156 (N = 4)	120-129 (N = 2)
B	143-159 (N = 5)	(N = 0)
C	117-148 (N = 5)	121-133 (N = 3)
D	132-147 (N = 3)	154 (N = 1)
E	117-144 (N = 6)	134 (N = 1)
F	101-115 (N = 2)	140 (N =1)
G	94-128 (N = 13)	103-128 (N = 7)
H	96-152 (N = 7)	134 (N =1)

Using the remeasurement data as a frame of reference, Areas B, C, and G are distinct from one another. It is interesting that these three Areas are geographic neighbors among the samples (Figure 3). The Area B and G samples differ only along the first canonical axis, which is typically size related. The first axis accounts for 47% of the dispersion. The Area C sample differs on the second canonical axis, however. The second axis accounts for 29% of the dispersion and is most heavily influenced by foot length and eye-nostril distance (based on standardized by within-variance values).

Life Colors: Ecuador. In juveniles, the head is mostly yellowish green, the dorsum has greenish yellow bands enclosing brownish-green areas that are black bordered, the chin has yellow marks along the edge, the posterior thigh is jet black, the belly is gray with lighter punctations, the iris is gold yellow above and rusty gold below (Heyer, 1972:5). There is only one adult female in the study sample with color information; it had a green head in life (Coloma and Ron, 2001, fig. 50, QCAZ 16183).

Peru. Color notes by Robert P. Reynolds for 80 mm juvenile, USNM 206636: "Dorsum reddish brown with green transverse cross bands on snout, between eyes and on back. Dark brown canthal stripe from snout to behind tympanum. Side of face green with black bars on lips. Chin, throat, chest, and belly dark brown with white spots. Orange spots on flanks in front of insertion of rear legs. Arms,

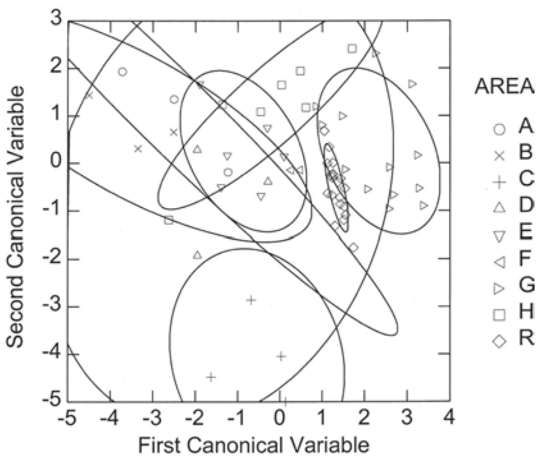

Figure 4. Discriminant function plot for male measurement data, *Leptodactylus knudseni* Unit geographic areas. Sample confidence ellipses *p*:0.683. A-H symbols in legend on figure represent Areas A-H; the symbol for R represents remeasurement data for a single specimen (see text for further explanation).

legs, and flanks dark brown." A color photo of USNM 342999, a 28 mm specimen, shows dorsal crossbands that are tan, brown, and almost black. The side of the head is tan and brown. The flanks are dark, but not as dark as the juveniles from Ecuador. There is no indication of green. A color photo of USNM 343244, a 83 mm specimen, shows the dorsum with alternating green and brown transverse bars, the side of the head is tan (not green) and the flanks are yellow-tan. An unvouchered photo of an adult from Tambopata, Madre de Dios (Roy W. McDiarmid photo) shows the dorsum indistinctly marked with different shades of dark browns, the side of the head is tan/ brown and the lower flanks are golden tan. William E. Duellman provided the following description from a manuscript on the Cuzco Amazonico, Madre de Dios herpetofauna (pers. comm.): "In life, the dorsum in adults is tan to reddish brown with dark brown markings consisting of an irregularly shaped spot on top of the head anterior to the orbits, a transverse bar between the orbits, three-to five broad transverse marks on the body to the level of the sacrum, and several small spots postsacrally. All markings on the body are between the orange-brown dorsolateral folds. The dorsal surfaces of the limbs are tan to reddish brown with narrow transverse brown bars. The flanks are dull orange, and a pale orange-brown longitudinal stripe is present on the upper surface of the forearm (Fig.). The upper lip is tan with a brown margin and brown spots, at least posteriorly, and a dark brown canthal stripe is present. The venter is cream with diffuse brown mottling, except for the throat, which is dark brown with creamy white flecks. Notable ontogenetic changes occur in the color pattern. Juveniles tend to have a greenish yellow dorsum and gray flanks, and the markings on the face and body are distinct; in the largest individuals, the pattern is barely discernible. Also, in juveniles, the posterior surfaces of the thighs are black, whereas in large adults they are black to dark brown with a few creamy white spots dorsally." The juvenile color pattern is illustrated by a W. Lamar photograph from Peru, Loreto (Rodríguez and Duellman, 1994, Plate 11, fig. D, data for photo provided by W.E. Duellman, pers. comm.). This distinctive green and black juvenile color pattern occurs in many but not all Peruvian juveniles.

Bolivia. De la Riva *et al.* (2000) have a color photo of presumably an adult individual with a brown dorsum (no evidence of green), and the posterior thigh has tan markings on a black background.

Venezuela. A color photograph from the Llanos of Venezuela (Kornacker and Dederichs, 1998:72, fig. 12, as *L. pentadactylus*) shows a brown dorsum with striking narrow chartreuse green cross stripes; the side of the face is predominantly lemon yellow and flanks are uniform orange-tan. No size is given for the animal photographed and it is not possible to tell from the photograph whether the individual is a juvenile or adult. A color photo of AMNH 131088 from Neblina shows a dorsum with alternating lighter and darker brown transverse bars, a brown side of the head, and golden tan lower flanks. A color photo of an unvouchered specimen (juvenile judging by size of frog relative to leaves on ground in photo) from Neblina (Roy W. McDiarmid photo) shows the dorsum with alternating greenish-yellow (not vivid) and brown transverse bars; the side of the head and flanks are tan. Gorzula and Señaris (1998: color photograph 49) show an adult (no locality information, in contrast to other photo captions) with a brown and tan dorsum (no evidence of green).

French Guiana. Individual specimens have reddish maroon backs with broad transverse bands of yellow chestnut bordered by black, posterior thighs black crossed by orange bars or orange red (Hoogmoed and Avila Pires, 1991; Lescure and Marty, 2000 [presumably based on French Guiana adults]); anterior part of flank red, a large orange spot on the posterior part of the flanks on a glandular area just in front of the groin, throat dark grey with white spots (Hoogmoed and Avila Pires, 1991); pale gray belly with yellow marbling, red maroon iris below, golden above (Lescure and Marty, 2000).

Brazil. Specimens have tan/brown on the dorsum and sides of head and flanks with a large central orange-tan spot (Rodríguez and Duellman, 1994, Plate 11, fig. C, W. Hödl photo of adult from Manaus, fide W.E. Duellman, pers. comm.).

Advertisement Calls: Although there are several recordings available for the *Leptodactylus knudseni* Unit throughout its distributional range, many of the calls lack associated voucher specimens (Table 6) and half of them have considerable background noise in the same broadcast channel that the frogs are using. The best quality recordings have calls that rise moderately quickly in intensity and maintain relatively high intensity until the final

Table 6. Advertisement call data for *Leptodactylus knudseni* Unit. Numbers associated with States indicate whether the data are for the same or different specific localities in the same State.

Tape & Cut, Country, State, Vouchered	N	Air temp, C	Call rate/ minute	Call duration range in s	# pulses per call	Mean pulse rate per s	Frequency modulation, Hz Entire call Mean, start	Mean, range	Mid-call pulse Mean, start	Mean, range	Mean dominant frequency, Hz
105, 1, Peru, Amazonas, +	5	–	29	0.21-0.25	8-10	36.8	343	174	146	447	342
265, 10, Peru, M. de Dios1, –	6	23	28	0.20-0.24	6-7	27.7	487	29	293	435	514
267, 3, Peru, M. de Dios1, –	2	26	20	0.31-0.34	8-9	26.0	260	82	156	798	342
21, 1, Brazil, Amazonas1, –	4	–	18	0.25-0.27	9-10	35.8	343	171	150	606	514
224, 4, Brazil, Amazonas2, –	4	–	20	0.34-0.38	11-13	36.5	346	168	198	526	517
209, 3, Brazil, Roraima1, –	3	–	16	0.32-0.34	9-10	29.7	341	175	139	498	344
213, 13, Brazil, Roraima2, +	4	–	20	0.42-0.43	13	31.0	346	174	212	461	344+515
French Guiana CD, –	4	–	25	0.36-0.38	10-11	29.0	344	177	177	499	515
227, 1, Brazil, Pará1, –	10	25	60	0.26-0.30	8-10	31.0	516	170	285	591	516-687
227, 2, Brazil, Pará1, +	7	25	66	0.16-0.20	6-7	35.6	540	319	479	432	690
228, 1, Brazil, Pará1, +	9	–	48	0.32-0.36	12-14	38.1	515	173	238	679	687

1/3 to 1/4 of the call, which diminishes in intensity (Figures 5, 6). In the noisiest recordings, the final portion of the call is apparently indistinguishable from the background noise, which would result in data that are truncated in terms of call duration and pulses per call. The noisy recordings are USNM recordings 105 cut 1, 265 cut 10, 21 cut 1, 209 cut 3, and 227 cut 1. Of the four recordings with museum vouchers, I have examined two for this study (USNM recording 105 cut 1, USNM 566002; USNM recording 213 cut 13, MZUSP 65675).

General features of all calls include: (1) each call consists of a single note which is either almost entirely or partially pulsed (Figures 5, 6); (2) most calls have modest, but noticeable increasing dominant frequencies from the beginning to the end of the call (USNM recordings 265, cut 10 and 267 cut 3 are exceptions with little or no modulation of the entire call); (3) within each call, individual pulses are frequency modulated in a complex fashion – the best recordings indicate both a sharp rise and fall of frequency within each pulse (Figure 6); and (4) the dominant frequencies are all low pitched (Table 6).

Understanding the variation among calls is not straightforward.

Given the ranges in adult sizes (Table 5), one would expect there to be a correlation between call duration and carrier frequency with size, as amply demonstrated in other studies (Duellman and Trueb, 1986). The available data are inadequate for such an evaluation, however.

Two recordings from Tambopata, Madre de Dios, Peru (USNM recordings 265 cut 10, 267 cut 3) and three recordings from Usina Kararahô, Altamira, Pará, Brazil (USNM recordings 227 cut 1, 227 cut 2*, 228 cut 1) provide data for evaluating intrapopulation call variation. Variation of calls within each of these localities encompasses the total range of all variation observed in call duration and number of pulses per call. The lowest values for these two parameters from both localities are from noisy recordings. It is likely that the actual call values for these two recordings approximate the values for cleaner recordings at each locality.

* A.J. Cardoso associated specimen ZUEC 7232, *Leptodactylus pentadactylus,* as the voucher specimen for this recording. The specimen is a 106.5 mm SVL juvenile female, however, and could not be the source of the recording.

There are some features unique to given recordings. USNM recording 213 cut 13 has two equal but distinct dominant frequencies for the entire call (Table 6). USNM recording 227 cut 1 has a dominant frequency band extending from 516 to 687 Hz.

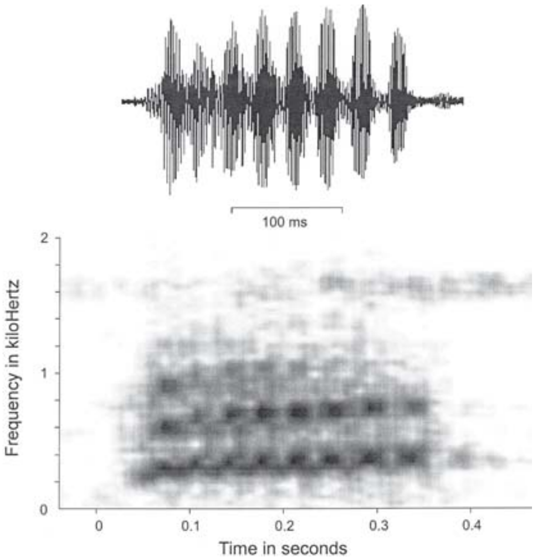

Figure 5. Wave form and audiospectrogram of advertisement call of *Leptodactylus knudseni* Unit from Peru (USNM recording 267, cut 3).

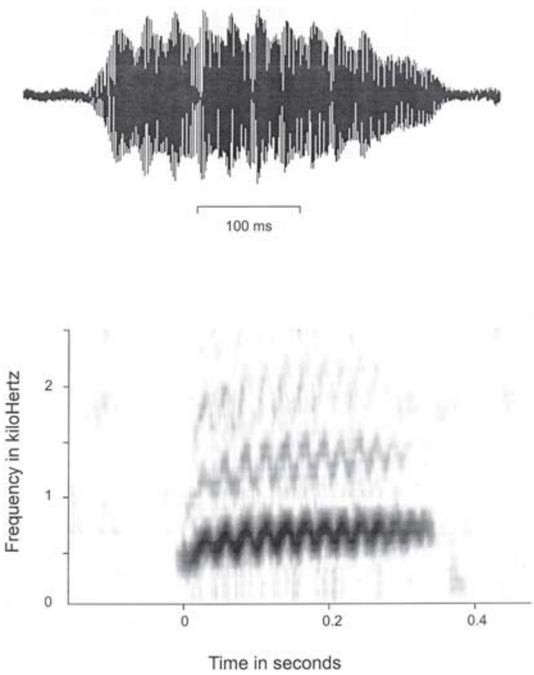

Figure 6. Wave form and audiospectrogram of advertisement call of *Leptodactylus knudseni* Unit from Pará, Brazil (USNM recording 228, cut 1).

Most of the rest of the variation is interpreted as individual variation with two exceptions.

1) Two of the three recordings from Usina Kararahô, Pará, Brazil have more pronounced pulsatile notes than observed in all other recordings (contrast Figures 5 and 6).
2) The call rate for the recordings from Usina Kararahô is much greater than for all other recordings. The voice tags on USNM recording 227 sound as though the tape was recorded at a slightly lower speed than normal, because the human voice seems somewhat high in pitch. However, the USNM recording 228 cut 1 voice tag appears normal and the call rate for this individual specimen is still much greater than for recordings from other localities. The few recordings with temperature data indicate that this call rate difference is not due to temperature differences.

Given the nature of the data, the calls from Usina Kararahô, Pará, Brazil and Tambopata, Madre de Dios, Peru are considered distinctive from each other and from all other recordings.

Evaluation of Differentiation: There is unquestionably geographic variation within the *L. knudseni* Unit, both in terms of morphology and advertisement calls.

The dorsal pattern, belly pattern and flank fold data indicate that the Ecuador and Peru samples are similar to each other and distinctive from all other samples. The measurement data indicate that the Area B and C samples are distinctive from each other. The advertisement call data indicate that the Pará, Brazil and Madre de Dios, Peru samples are distinct from each other and all other samples.

Only the call rate sharply defines the Pará sample from all other samples.

The life color patterns of juveniles from Ecuador (Area B) and southern Peru (Area C) are similar. There is an imbalance of males and females between the samples of Ecuadorian and Peruvian specimens that were included in Area B. Only one adult female and 12 juveniles from Ecuador and 5 adult males from Peru comprise the Area B sample. The data for the Peruvian Area B specimens do not closely match either the data for the Ecuadorian

Area B specimens or those for Peruvian Area C. Additional data were obtained for the Inter Unit analysis section.

The variation within the *Leptodactylus knudseni* Unit is interpreted to mean that there is one differentiated Unit for combined Area A, D-H specimens and either two or three differentiated Units for Area B and C individuals.

***Leptodactylus pentadactylus* Unit**

Geographic Areas – Nine geographic areas are distributed broadly throughout the total range of the localities sampled for this study (Figure 7). Due to small sample sizes, many of the geographic areas are relatively large and one (Area I) does not contain any adult male individuals.

Variation – Dorsal Pattern: There is no indication of differences in juvenile and adult patterns in the available data. This finding is surprising. I remember collecting juvenile *Leptodactylus pentadactylus* in Costa Rica during my first tropical field experience (1964) and thinking that they were a different species from adult *L. pentadactylus* from the same locality. The life coloration is more vivid in juveniles (see below), but the patterns that remain after preservation are similar in juveniles and adults. There is no indication of variation between adult sexes or among geographic areas. Dorsal patterns range from uniform; one narrow transverse bar in the scapular region; two narrow transverse bars with the second in the sacral region; a series of irregular dark-outlined transversely elongate rectangles alternating dark and light and the same pattern except the irregular rectangles are larger and coalesce and may be uniform in intensity rather than alternating dark and light. One non-Area specimen (La Salle 272 from Florencia, La Vega, Caquetá, Colombia) has a completely variegated dorsal pattern. All other non-Area specimens match dorsal patterns found in their closest geographic area.

Belly Pattern: There is a suggestion that juveniles from Areas B, C, E, F, I more commonly have a pattern of a dark belly with rather distinct, small, light spots than adults have. Otherwise, there is no indication of juvenile belly patterns being different from adult patterns. At least some individuals in all Areas except Area E have dark bellies with distinct, relatively small light vermiculations (Figure 13B). The majority of specimens from Areas A, B, D, F

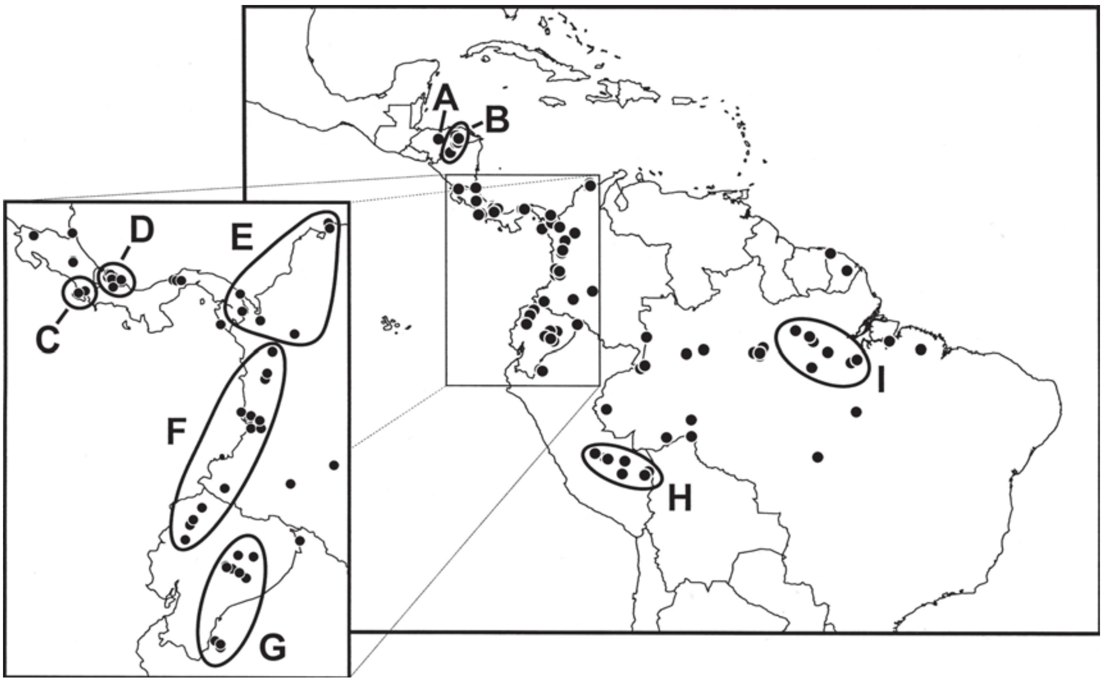

Figure 7. Geographic areas for *Leptodactylus pentadactylus* Unit. See text for explanation.

have a visually striking pattern of dark bellies with distinct, large and regular (Figure 13E) to irregular, spots on the belly. A few individuals from Areas B, C, D, E, G have much more indistinctly mottled bellies (Figure 13A) than the rest of the individuals from those Areas. All non-Area individuals match patterns with the closest geographic sample specimens.

Lip Pattern: Juveniles do not appear to have different lip patterns from adults. There is as much variation among individuals within the geographic area samples as among samples. Most individuals have dark inverted triangular markings on the upper lip, one of which often extends to the eye (Figure 12A). Two individuals from Area A and one individual from Area C were recorded as having no lip pattern. All non-Area individuals match patterns with the closest geographic sample specimens.

Thigh Pattern: Juveniles do not appear to have different thigh patterns from adults. Most individuals exhibit one of four primary kinds of thigh patterns, three of which vary among geographic area samples for the specimens analyzed (Table 7). In addition to these four patterns, (Table 7), a few individuals from Areas C and E have extended horizontal light stripes connecting light vertical markings; one individual each from Areas F and I were scored as having indistinctly mottled to uniformly patterned thighs; one individual each from Areas F and G were scored as having a boldly patterned thigh with extensive, irregular, more-or-less horizontally oriented light stripes; and several individuals from Area H were scored as demonstrating a distinct to less distinct pattern of large dark blotches outlined by a contrasting light border (Figure 14C). One non-Area specimen (UNSM 521020 from Aguas Negras, Río Lagarto Cocha, Loreto, Peru) is closest geographically to Area G but has the distinctive pattern described for Area H. All other non-Area individuals match patterns found in the closest geographic samples.

Shank Pattern: Juvenile upper shank patterns do not differ from adult patterns. There is as much variation among individuals within geographic areas as among areas. The upper shanks are either uniformly dark or with dark transverse bands on a lighter background. For patterns with dark bands, they either traverse the entire upper shank surface or fall short distally. There was no additional variation observed in the non-Area specimens.

Body Folds: Lateral folds are difficult to determine in most of the specimens. The range includes no indication of a lateral fold, an interrupted lateral fold, and a weak but distinct entire lateral fold. There is considerable variation in the extent of expression of dorsolateral and flank folds, with variation in degree of development among areas (Tables 8, 9). Two non-Area specimens that are nearest to Area C (USNM 1976 from San Juan del Norte, Río San Juan, Nicaragua; USNM 29953 from Turrialba, Cartago, Costa Rica) have dorsolateral folds that are continuous to the sacrum. Two specimens that are closest to Area G differ by either having the dorsolateral fold fall just short of the sacrum on one side but past the sacrum on the other (La Salle 272 from Florencia, La Vega, Caquetá, Colombia) or having no indication of a flank fold (La Salle 293, same locality as La Salle 272). All other non-Area specimens match conditions found in specimens from the nearest geographic area samples.

Male Sexual Secondary Characteristics: The arms are not hypertrophied in most of the males from Areas A, B, F, G, H. Three males from Area B and one male from Area F show a modest degree of hypertrophy. At least some males in Areas C, D, E have extensively hypertrophied arms. One male from Area G has very weakly hypertrophied arms.

All males from Areas A and H lack tubercles on the chin, throat, and chest. Data were not recorded for this feature from Area E individuals. One male from Area B has tubercles on the throat. Most males from Areas C and D have tubercles on the throat or on the throat and chest. One male from Area F has tubercles on the throat and chest. One individual from Area G has tiny white tubercles limited to the side of the throat.

All males from Areas A, F, G, H lack chest spines. At least some, if not most, individuals from Areas B, C, D, E have a well-developed pair of black chest spines.

All males except from Area D have one spine per thumb (medially placed). The thumb spines from

Table 7. Posterior thigh patterns, *Leptodactylus pentadactylus* Unit. For the definition of geographic areas, see Figure 7.

Major pattern types	Geographic Areas								
	A	B	C	D	E	F	G	H	I
1. Dark thighs with small to medium sized light vermiculations (Fig. 14A)	X	X	X	X	X	X	X	X	X
2. Boldly patterned thighs with large light regular or irregular spots	X	X			X	X			
3. Light dorsal transverse bars ending in light spots on posterior thigh (Fig. 14 B)	X	X	X	X					
4. Extensive light areas (Fig. 14 D)		X			X	X			

Table 8. Dorsolateral fold conditions, *Leptodactylus pentadactylus* Unit. For the definition of geographic areas, see Figure 7.

Major character states	Geographic Areas								
	A	B	C	D	E	F	G	H	I
1. Folds continuous to just short of sacrum		X							X
2. Folds continuous to sacrum	X	X		X	X	X			
3. Folds continuous to sacrum, interrupted from sacrum to groin	X	X	X	X	X	X	X	X	
4. Folds complete from eye to groin, but interrupted			X	X					X
5. Folds complete from eye to groin	X	X	X	X	X	X	X	X	X

Table 9. Flank fold conditions, *Leptodactylus pentadactylus* Unit. For the definition of geographic areas, see Figure 7.

Major character states	Geographic Areas								
	A	B	C	D	E	F	G	H	I
1. Very short, lying somewhere in flank fold field					X	X			
2. Interrupted from tympanum to posterior arm insertion area						X	X		
3. Complete from tympanum to posterior arm insertion area	X	X	X	X	X	X	X	X	X
4. Interrupted from tympanum to mid-body	X	X	X	X	X	X	X	X	X
5. Complete from tympanum to mid-body	X	X	X	X	X	X	X	X	X

Area A males range from tiny to moderate size white; Area B males have small to large white spines; all Area C males have a large black spine on each thumb; Area D male variation includes small to large white spines, large black spines, one large white and an additional small white spine at the base of the thumb, and one large black spine and one tiny white spine at the base of the thumb; Area E males have small, white to large, black spines; Area F male spines range from tiny white to large black; Area G males have tiny or small white spines; Area H males have no spines or tiny white spines.

One non-Area male (Berlin 30972) from Rio Gutaki (probably Jutahy = Jutaí), Amazonas, Brazil differs from Area G and H males in having just slightly more hypertrophied arms and having a larger white thumb spine. All other non-Area males match conditions found in specimens from the nearest geographic area samples.

Upper Shank Texture: There is as much within as among Area variation. The conditions include smooth, with or without a shagreen, and none to many white or black tubercles. There is no additional variation in non-Area specimens.

Outer Tarsal Texture: Most individuals from Area A have smooth surfaces; two individuals have shagreened surfaces. Individuals from the other geographic areas range from having smooth, shagreened, or several white or black tubercles. There is no additional variation in non-Area specimens.

Foot Texture: The within Area sample variation is as great as among Area sample variation. The foot texture is smooth in most specimens; a few individuals have no more than a few white or black tubercles. There is no additional variation in non-Area specimens.

Adult Size: The ranges of adult size within areas combined with generally small sample sizes may be masking real size differences. The most suggestive size variation is that the females from Areas G, H, I may be larger than females from the other Areas (Table 10). One non-Area female (USNM 192577 from 10 miles S Turrialba, Cartago, Costa Rica) is smaller (110.2 mm SVL) than females from its nearest Area sample (Area C). One male (MZUSP 40303 from São José (Jacaré), Rio Solimões, Amazonas, Brasil) is considerably larger than any male in the Area G

Table 10. Adult sizes (SVL in mm), *Leptodactylus pentadactylus* Unit. For the definition of geographic areas, see Figure 7.

Geographic Area	Males	Females
A	128-151 (N = 3)	134-149 (N = 12)
B	118-142 (N = 7)	119-148 (N = 5)
C	134-148 (N = 6)	122-145 (N = 4)
D	113-154 (N = 8)	118-152 (N = 10)
E	119-144 (N = 6)	121-164 (N = 6)
F	112-146 (N = 6)	115-158 (N = 7)
G	121-161 (N = 4)	142-174 (N = 5)
H	100-150 (N = 4)	146-155 (N = 4)
I	(N = 0)	135-162 (N = 5)

and H samples (195 mm SVL). This large male has very weakly hypertrophied arms and a small white spine on each thumb.

Measurement Data: Sample sizes are minimal for discriminant function analyses (note that no males are available for Area I). Results using the complete model and forward step options of discriminant function analyses of the measurement data for males and females are quite similar using Systat 10 software (Engelman, 2000). The forward step model does slightly better in terms of classification; scores for Wilks' lambda, Pillai's trace, Lawley-Hotelling trace; and cumulative proportion of total dispersion of the canonical functions. Therefore, the forward step procedure is the model used for the *L. pentadactylus* Unit measurement data.

Both the male and female discriminant function analyses perform rather poorly in separating the geographic area data. For the male data, 63% of the sample was correctly identified in the posterior classification matrix, with only 42% of the sample correctly identified using the posterior jackknifed classification procedure. Forty four percent of the total dispersion is accounted for with the first canonical function, 82% by the first and second, and 100% is accounted for with the first through fourth canonical functions. For the female data, 49% of the sample is correctly identified in the posterior classification matrix, with 38% of the sample correctly identified using the posterior jackknifed classification procedure. Sixty four percent of the total dispersion is accounted for with the first canonical function, 89% with the first and second, and 100% is accounted for with the first through fifth canonical functions.

The plot of the first against second canonical variables (Figure 8) indicates that the female data perform slightly better in discriminating among Area samples because the envelope for the

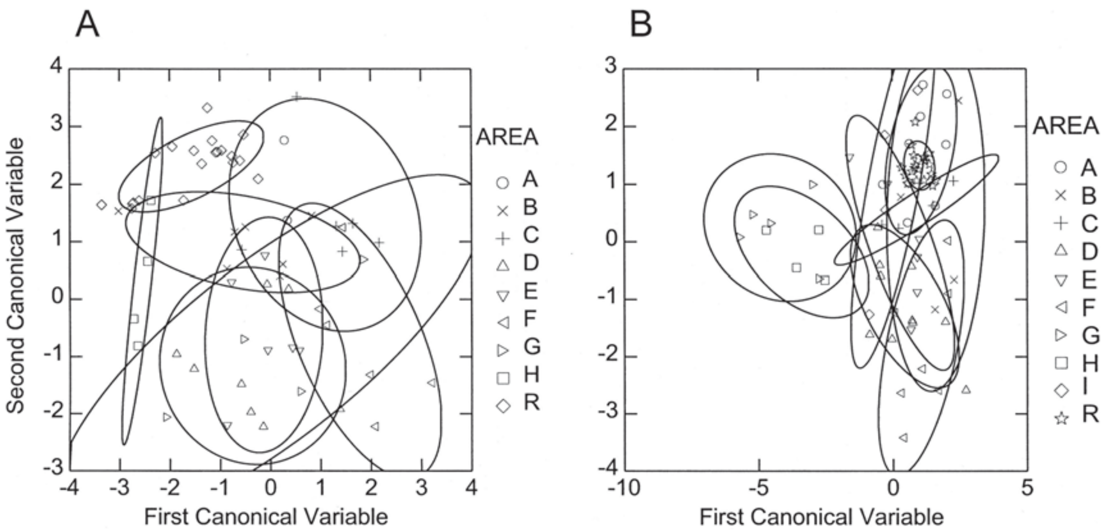

Figure 8. Discriminant function plot for measurement data, *Leptodactylus pentadactylus* Unit geographic areas. A = male data; B = female data. Sample confidence ellipses *p*:0.683. A-I symbols in legend on figure represent Areas A-I; the symbol for R represents remeasurement data for a single specimen (see text for further explanation).

remeasurement data is smaller in the female plot (Figure 8B) than for the male data (Figure 8A). There is no meaningful separation of Area groups for the male data (Figure 8A). There is modest separation of Areas G and H from the rest of the Area samples in the female data along the first axis, which is typically size-related (Figure 8B). However, the raw size data (Table 10) would indicate that Area samples G, H, I would cluster together if based only on size. Area F demonstrates some distinctiveness from Areas A and C on the second axis (Figure 8B), although the size of the remeasurement envelope suggests that this separation as well as the separation on the first axis, are not robust and the discrimination among area results would likely change considerably if new data were added to the analyses.

Life Colors: **Middle America.** Honduras. "Color in life of a female (USNM 319943): dorsum of head and body Drab (27) with slightly darker brown spots; dorsolateral ridges Drab (27) with slightly darker brown pigment along lower edges; supratympanic folds Drab (27), outlined below by dark chocolate brown; dorsal surface of forelimbs mottled Drab (27) and slightly darker brown; dorsal surface of hind limbs Drab (27) with darker brown crossbars on thighs and shanks; upper lip with dark brown bars; flanks with large Peach Red (94) ovoid blotch; flank glands Pale Horn Color (92); ventral surfaces mottled Drab (27) and Buff (124); iris pale brown with dark brown reticulations on upper half, lower half dark brown. Color in life of a juvenile (LSUMZ 33648; SVL 45.0 mm): dorsal surface of body between dorsolateral folds rust-red with dark brown markings; dorsal surface of head rust-red with dark brown-edged interorbital bar; dorsal surfaces of limbs dark grayish green with dark crossbars; side of head pale copper with dark brown markings; flanks grayish green; venter dark gray with numerous small white spots; iris dark copper with fine black reticulations (McCranie and Wilson, 2002:452)."

Nicaragua. "All of the specimens but the largest one have the ventral surface dark brown spotted with white – the characteristic coloration of the immature. In all of the specimens there was, in life, a considerable amount of red on the thighs (Noble, 1918)."

Costa Rica. Roy W. McDiarmid unvouchered photos from the Osa Peninsula show: (1) a juvenile with a mostly chocolate brown dorsum that is sharply demarcated from the gray flanks by the dorsolateral folds; the side of the head is tan and black (posterior thighs not visible); (2) an adult with a dorsum of lighter and darker brown markings, the side of the head is tan/brown, there is a light cream post-commissural stripe, the flanks are brown (ventral-most flanks and posterior thighs not visible; these same color patterns are demonstrated in two color photos in Savage (2002, Plates 86,87), which also do not show the ventral-most flanks or posterior thighs.

Panama. "Groin and anterior surfaces of thighs with red orange color; … throat grayish brown with white spots; chest and venter white to pale yellow and mottled with gray; posterior surfaces of thighs red orange with black reticulations, in the inferior part these reticulations enclose white spots (Ibáñez *et al.*, 1999)."

West Coast South America. Colombia. Dorsally, a broad cream band from tip of snout to vent, delimited on head by broad dark brown band, the line that extends to posterior extent of tympanum is without border. Large broad band-like spots dark brown, rest of dorsum reddish brown. Anterior surface of thigh brown, posterior red with continuous irregular dark brown spots. Shank and tarsus olive brown. Concealed surfaces of shank and tarsus red. Ventrally: throat and chest brown with cream spots. Flanks pink. Iris yellow bordered above with bronze, bordered below by copper color; these colors separated by a reddish brown spot. (Color notes for ICN 16663 provided and translated by John D. Lynch.)

Ecuador. A photo of MCZ A 91719 from Pichincha Province shows a dorsum of darker and lighter browns, the side of the head is tan with bold black markings, the flanks are tan and brown (posterior thighs not visible). Posterior thighs with bright red marks (Rafael de Sá color photo, QCAZ 17056).

Amazonia. Peru. There are 10 photos/color descriptions available. The variation is encompassed with the following three characterizations. USNM 538196: "Dorsum light gray brown with darker transverse brown bands. Laterally opalescent gray with red tinge. Iris gold. Black band from snout through eye to behind tympanum. Legs gray with brown cross bars. Venter brown with white spots and white mottling. Lips with black bars." Photo of USNM 317518: Dorsum olive drab and brown, lower lip tan-brown, flanks brown above and yellow-brown ventralmost, bits of exposed posterior thighs are black with white markings. USNM 346146: "Greenish brown-tan dorsum. Crossbands between eyes and along back. Arms and legs gray with black crossbars. Dorsolateral ridges edged with black. Belly mottled tan and black."

Brazil. "Dorsum reddish-brown, sides grayish red, demarcated by dark brown dorsolateral lines. Limbs gray with fine black lines. Very dark brown line from snout through eye to arm insertion. Sides of head below canthus reddish-gray. Lips with dark brown and white stripes. All undersurfaces white with gray reticulations. Eye copper." (Janalee P. Caldwell field notes for JPC 12294, a juvenile female.)

French Guiana. "Iris red-copper below, golden above. … Dorsal surface reddish-brown with 5 or 6 transverse bands, those of juveniles are white bordered on a grayer background. … Posterior face of the thighs mottled white and black. Venter marbled cream-white and black, especially posteriorly." (Crude translation of Lescure and Marty, 2000, presumably based on specimens from French Guiana.)

Advertisement Calls: None of the calls analyzed has an associated voucher specimen. Most of the recordings are both noisy (other signals in the same broadcast channel as the frog calls) and recorded from afar. Only two recordings have a good signal to noise ratio, the BCI CD recording from Panama and USNM recording 254 cut 3 from Brazil. Certain call parameters are difficult to measure accurately in most of the recordings. Only three recordings have associated temperature data (Table 11).

Interpreting the variation observed among the available recordings is difficult. For example, given the range in size of calling males (100-195 mm SVL), one would expect there to be a strong and significant correlation of carrier frequency with size. Thus, the total variation observed in carrier frequency might be accounted for by size differences in calling males.

Common features of all calls include: (1) each call consists of a single note; (2) calls have increasing carrier frequency, especially in the first half of the call; and (3) there appears to be frequency modulation within calls associated with pulse structure when pulses are distinct.

The temporal structure of the calls is variable and complex. All of the calls except one

Table 11. Advertisement call data for *Leptodactylus pentadactylus* Unit. Numbers associated with States indicate whether the data are for the same or different specific localities in the same State.

Tape & Cut, Country, State, Vouchered	N	Air temp, C	Call rate/ minute	Call duration range in s	# pulses per call	Mean pulse rate per s	Frequency modulation, Hz Entire call		Mid-call pulse		Mean dominant frequency, Hz
							Mean, start	Mean, range	Mean, start	Mean, range	
106, 1, Costa Rica, San José, –	7	–	40	0.26-0.28	8-10	36.6	342	171	162	437	346+515
89, 6, Costa Rica, Puntarenas, –	8	–	40	0.34-0.42	11-13	31.1	301	214	142	459	340
BCI CD, Panama, –	10		49	0.24-0.28	5-6	45.7	343	171	248	466	514
98, 5, Ecuador, Pichincha 1, –	5	–	37	0.20-0.24	6-7	26.8	549	312	629	415	860
103, 10, Ecuador, Pichincha 1, –	4	–	34	0.20-0.30	5-8	22.8	686	173	613	420	863
115, 5, Colombia, Meta, –	7	23.2	37	0.20-0.23	-	-	442	369	438	508	691
64, 7, Peru, M. de Dios 1, –	1	–	4	0.24	12	50	690	343	705	450	863
72, 7, Peru, M. de Dios 1, –	3	–	15	0.18-0.29	13-18	64.6	861	169	796	454	1029
104, 18, Peru, M. de Dios 1, –	2	–	12	0.38	16	43.5	860	170	787	456	1031
254, 3, Brazil, Amazonas 1, –	3	26.0	15	0.18-0.19	-	-	690	342	793	439	1030
251, 17, Brazil, Amazonas 2, –	4	26.0	23	0.24-0.28	-	49.5	342	347	460	424	686

(see next paragraph) have at least pulsatile structure. The rate of pulse or pulsatile structure among the calls spans the threshold at which human ears detect sounds as either continuous or pulsed (~ 50 pulses per s). As noted by Hero and Galatti (1990), the calls of the two large *Leptodactylus* that occur sympatrically in the central Amazon, sound completely different to the human ear. However, the frogs themselves do not necessarily make the same kind of distinctions as humans do, because frogs have much better temporal resolution than humans have (Walkowiak, 1988:279, showed that frogs can process discrete signals given at a rate of least 100 times per s, whereas Greenewalt, 1968:102, indicated that humans can differentiate a trill or vibrato if the rate does not exceed 30 times per s). Frogs could be expected to perceive the calls as different in degree, not in kind.

The calls Schneider *et al.* (1988) described and figured from Reserva Ducke and near Manaus, Amazonas, Brazil are different from all other calls analyzed in lacking pulse or pulsatile structure (Tables 11, 12, see also Schneider *et al.*, 1988 figs. 7-8, p. 84). Schneider *et al.* (1988) also indicated that the calls they analyzed started at 170 Hz, but their figure of the audiospectrogram (fig. 8) exhibits no energy below about 300 Hz. The Schneider *et al.* (1988) calls contrast with the calls of *Leptodactylus pentadactylus* reported by Zimmerman and Bogart (1984) recorded from Reserva Ducke and the INPA-WWF Reserves north of Manaus, Amazonas, Brazil. The calls and data analyzed by Zimmerman and Bogart (1984) match the variation observed in the other recording data (Tables 11, 12) and contrast with the call described by Schneider *et al.* (1988) in terms of pulse/pulsatile structure. The seemingly obvious explanation is that the Schneider *et al.* (1988) recording represents a different species from those represented by all other known recordings of the *L. pentadactylus* Unit. There is no voucher specimen for the recording published by Schneider *et al.* (1988). No specimen was collected. Walter Hödl (pers. comm.) only saw one individual calling from 2 m down in a large burrow. The identification was based on information from W. Magnusson and J.-M. Hero that calls obtained from such burrows and lacking the audibly pulsed component of *L. knudseni* were from *L. pentadactylus.* It is impossible to address this problem by comparing specimens. Therefore, the Schneider *et al.* (1988) recording is considered to be an anomalous recording, probably representing a different species than those represented by the Zimmerman and Bogart (1984) recordings.

Call temporal organization varies among the calls as follows (refer to Table 11 for call recording associations): (A) the two calls from Costa Rica are pulsatile from beginning to end; (B) the call from Panama starts weakly partially pulsed followed by two pulses followed by either (i) one long unpulsed portion or (ii) a weakly partially pulsed long pulse, followed by a terminal pulse that is itself weakly partially pulsed; (C) the two calls from Pichincha Province, Ecuador are pulsed throughout; (D) the call from Colombia has a mixture of pulsed and partially pulsed structure at the beginning and end of the calls with a middle unpulsed portion; (E) the three recordings from Peru range from calls with a mixture of pulses and partial pulses throughout to pulsed at the beginning and end with a partially pulsed central portion; (F) calls of USNM recording 254 cut 3 from Brazil are essentially unpulsed from the beginning until the very end, which is partially pulsed; (G) calls of USNM recording 215 cut 17 from Brazil are partially to not pulsed at the beginning and partially to completely pulsed for the rest of the calls.

The pulse rates for calls were determined for all pulses after the initial pulse of each call except for the pulse rate in the Panama recording

Table 12. Published advertisement call data for *Leptodactylus pentadactylus* Unit. The Brazilian data are from the same localities in part. Asterisk indicates mean value.

Publication; Country, State; Vouchered	N individuals/calls	Temperature	Call rate/minute	Call duration range in s.	# pulses per call	Beginning call frequency	Ending call frequency	Dominant frequency
Schlüter, 1980; Peru, Huanuco; ?	?	26	26	0.3-0.4	?	200-300?	700-800?	800?
Zimmerman & Bogart, 1984; Brazil, Amazonas; ?	7/59	?	4-33	0.16-0.25	?	700-830	880-1020	770-920
Schneider *et al.*, 1988; Brazil, Amazonas; –	?/many	Includes 22.8-23.8	28-34	0.16-0.19*	1	170 (~300?)	880	?

which was based only on the two distinct pulses following the initial call pulse. All calls from Amazonia sound continuous to the human ear; all the other calls sound pulsed.

Sympatric species of the *Leptodactylus fuscus* group are characterized as differing by at least an order of magnitude in either a temporal or frequency component (e.g. Heyer, 1978, Straughan and Heyer, 1976). Even though Galatti (pers. comm.) has demonstrated that the Panamanian and Amazonian populations currently identified as *L. pentadactylus* represent two distinct species, the recordings for the Middle American and Amazonian populations do not differ from each other by an order of magnitude in any feature analyzed (Tables 11, 12, with exception of the Schneider *et al.* 1988 data noted previously).

Taking the kinds of differences among calls from Middle America and Amazonia as guidelines, the recordings from Costa Rica differ somewhat from the Panamanian recording. The Middle American recordings are different from the western Ecuador recordings; the western Ecuador recordings are quite distinctive from all other recordings. The three recordings from Peru and USNM recording 254 cut 3 from Brazil appear to be similar to each other and differ somewhat from the other Amazonian calls from Colombia and Brazil (USNM recording 251 cut 17), while the latter two recordings are somewhat similar to each other.

The published data by Schlüter (1980) and Zimmerman and Bogart (1984) for Amazonian calls from Peru and Brazil respectively differ somewhat from the other recordings analyzed (compare Tables 11 and 12). The differences could be due to different analytic techniques. Given that possibility, it is best to conclude that the calls are those of the same species represented by the other Peruvian and Brazilian specimens analyzed (Table 11).

Finally, the Middle American calls of the *L. pentadactylus* Unit are extremely similar to the calls of the *L. knudseni* Unit (compare Tables 6 and 11).

Evaluation of Differentiation: There is considerable variation within the *L. pentadactylus* Unit in terms of size, patterns, male secondary sexual characteristics, and advertisement calls. The relationship between observed variation and species limits is not clear, however.

The variation among specimens from Amazonia is interpreted as intraspecific (with the possible exception of the specimens represented by the recording of Schneider *et al.*, 1988). Small sample sizes preclude a firm understanding of the nature of the geographic variation involved, but the data do indicate that a geographic component exists.

There is also variation among the Middle American samples of the *L. pentadactylus* Unit. The differences between Area A and B individuals could be due to sampling problems. For example, there is only one large male from Area A and the fourth pattern type of the posterior thigh (Table 7) is represented by only one individual from Area B. The most striking difference between the Area C and D samples is that more individuals from Area D have dark bellies with rather discrete, regular light spots than found in the Area C sample. There are no discrete differences either between Area C and D samples or among Area A, B, C, D samples, which is consistent with the hypothesis that variation in the Middle American samples represents intraspecific geographic variation and is not indicative of species level differentiation.

Thus, the Middle American samples and Amazonian samples are considered to each represent a single species distinct from one another.

The Area E and F samples are more similar to the Middle American species than the Amazonian species, especially with respect to advertisement calls (based on the few recordings analyzed). However, there is variation within Areas E and F that needs to be evaluated at a finer scale than analyzed above.

The more detailed analysis of Area E and F samples was done in three steps.

The first step was to combine the data for all specimens from Costa Rica and Panama (except for the two Panamanian samples that were included in the Area E sample) as one sample. A second sample consisted of the specimens from two localities from the Departamento de Magdalena, Colombia. The third sample comprised specimens from coastal Ecuador.

The second step was to compare the data among these three samples to determine whether any two of them were identical (when taking sample sizes into account). Each of the three samples differ from each other, but it is not clear from the data whether the differences represent sampling problems or geographic variation, particularly between the

Costa Rica/Panama and Magdalena, Colombia samples.

The third step consisted of comparing the data for all other locality samples from Area F with the three samples defined above, starting with the samples closest to the coastal Ecuador sample and proceeding northward.

The results are modestly surprising but geographically coherent. There is a morphological break between the coastal Ecuador sample and the specimens from the west coast of Colombia. Many of the West Coast Colombia specimens have extensive light areas on the posterior thighs, a pattern not found in any specimen from the Coastal Ecuador sample. All males from West Coast Colombia have either tiny or small white or tan thumb spines while the two males from Coastal Ecuador have a large white or black spine on each thumb. The data on specimens from near Valdivia, Antioquia, Colombia (ICN 9934, 9936) match the data for the Magdalena, Colombia sample. The specimen data from the two Panamanian localities previously included in Area E and the data for the specimen from near Turbo, Antioquia, Colombia bridge the differences between the Costa Rica/ Panama and Magdalena, Colombia samples. The combined data for the specimens from Costa Rica/ Panama/Antioquia, Colombia/Magdalena, Colombia in turn are distinct from data from the West Coast Colombia specimens. The thigh pattern difference described for the Coastal Ecuador and West Coast Colombia specimens exists between the more northern specimens and the West Coast Colombia specimens. The more northern specimens have well developed chest spines, throat and chest tubercles, and a large thumb spine on each thumb, differing from the conditions observed in the West Coast Colombia specimens.

Thus, there are three geographically coherent Units involved: (1) Specimens from Honduras, Nicaragua, Costa Rica, Panama, and northern Colombia in the general Isthmus of Panama region; (2) specimens from west coast Colombia; and (3) specimens from coastal Ecuador. The specimens from coastal Ecuador differ somewhat in advertisement calls from the Middle American and northern Colombia Unit as discussed previously. In addition, one male from coastal Ecuador (USNM 196745) has throat and chest tubercles but no chest spines, indicating that this Unit in fact lacks chest spines, while the Middle American and northern Colombia specimens do have chest spines. After this analysis was completed, specimens examined in Ecuadorian collections (EPN, QCAZ) in March 2002 extended the distribution of the west coast Colombia Unit into adjacent Ecuador. The additional data do not add information to the morphological analyses and are not added to the data for the Inter-Unit analysis in the next section. The measurement data are included in the Inter-Unit analysis.

The data are most consistent with recognizing four differentiated population groupings: (1) Middle America and northern Colombia; (2) West Coast Colombia; (3) West Coast Ecuador; and (4) Amazonia.

Leptodactylus labyrinthicus Unit

Geographic Areas – Eight geographic areas are distributed broadly throughout the total range of localities sampled for this study (Figure 9).

Variation – Dorsal Pattern: The available data do not demonstrate any differences between juveniles and adults or between males and females. There is considerable variation in dorsal pattern, but the entire range of variation occurs within the Area A sample. There is no obvious variation in dorsal pattern among the Area samples. Dorsal patterns include uniform light, uniform dark, a few small scattered marks, indistinctly defined dark blotches, broad dark almost coalescing bands anteriorly with large dark blotches posteriorly, and a broad dark irregular interorbital bar and two large dark spots in the shoulder and sacral regions either light outlined or not.

Belly Pattern: The only specimens lacking belly patterns from Areas F and H are juveniles and one male from Area A lacks a belly pattern. Otherwise, the available data do not demonstrate any differences between juveniles and adults or males and females. There is notable variation in belly patterns within Area samples, but there is some variation among Area samples that is not likely explained by relatively small sample sizes (Table 13). All non-Area specimens do not differ from the specimens in the most proximate geographic Area with the exception of MZUSP 24936 from Serra

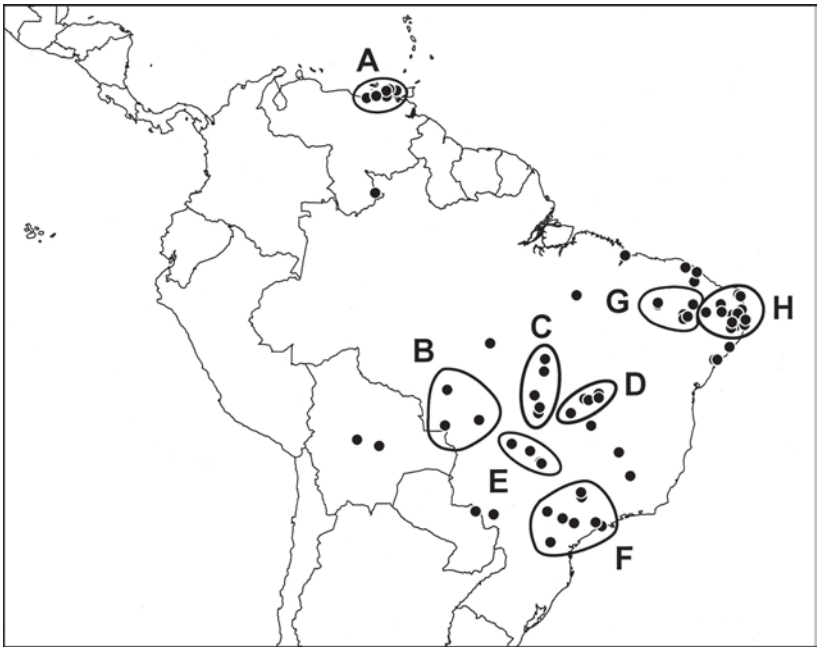

Figure 9. Geographic areas for *Leptodactylus labyrinthicus* Unit. See text for explanation.

de Parima, Roraima, Brazil, which has a distinct labyrinth pattern (Figure 13D) not found in specimens from Area A, but found in all other Areas.

Lip Pattern: The available data do not demonstrate any differences between juveniles and adults or males and females. A pattern of the upper lip with broad alternating dark and light vertical bands, distinct above the lip and fading as they reach the eye level occurs in some specimens from all Areas. Beyond that, there is variation both within and among Area samples (Table 14). Non-Area specimen USNM 146521 from near Buena Vista, Santa Cruz, Bolivia has a dark lip with two distinct, narrow light stripes from the lip to the anterior and posterior eye (Figure 12B), a pattern not found in specimens from the nearest geographic Area B. Several specimens from Cachimbo, Pará, Brazil have the same aforementioned lip pattern, which was not found in specimens from proximate Area C. Specimens from Araguatins and São Domingos, Goiás, Brazil, have an upper lip with broad alternating dark and light bands from the lip to the eye level, a pattern not found in specimens from proximate Area G.

Thigh Pattern: The only two individuals with finely mottled or indistinctly mottled thigh patterns are small juveniles (23-30 mm SVL). Late Gosner stage larvae have indistinct thigh patterns, suggesting that post-metamorphic individuals retain the larval pattern before developing the patterns found in larger juveniles and adults. Otherwise, the available data do not demonstrate any differences between juveniles and adults or males and females. Some specimens from all Areas have boldly mottled thighs. There is also variation within and among Area samples for additional thigh patterns (Table 15). Non-Area specimen MZUSP 21746 has a darkly mottled thigh with distinct large light spots extending from light dorsal bands and the thigh of MZUSP 21747 exhibits very large contrasting dark and light markings with a large central dark spot that resembles a large eye. Both of these specimens are from São Luis, Maranhão, Brazil and the patterns do not occur in proximate Area G. Specimens from Santo Amaro das Brotas, Sergipe and São Miguel dos Campos, Alagoas, Brazil have the pattern described for MZUSP 21746 (above), which pattern was not encountered in specimens from proximate Areas G and H.

Shank Pattern: The available data do not demonstrate any differences between juveniles and adults or males and females. The variation within Area samples is comparable to inter-Area variation. Patterns include uniform dark, a few small dark

Table 13. Belly patterns, *Leptodactylus labyrinthicus* Unit. For the definition of geographic areas, see Figure 9.

Major pattern types	Geographic Areas							
	A	B	C	D	E	F	G	H
1. Virtually no pattern	X					X		X
2. Mottled (Fig. 13A)	X	X	X	X			X	X
3. Light with scattered dark irregular marks		X	X		X	X	X	X
4. Dark with large light irregular marks (Fig. 13 C)	X		X				X	
5. Distinct labyrinth pattern (Fig. 13D)		X	X	X	X	X	X	X

Table 14. Lip patterns, *Leptodactylus labyrinthicus* Unit. For the definition of geographic areas, see Figure 9.

Major pattern types	Geographic Areas							
	A	B	C	D	E	F	G	H
1. No light or dark stripes/bars from upper lip to eye	X	X	X	X	X		X	
2. Upper lip dark with two distinct, narrow light stripes from lip to anterior and posterior eye (Fig. 12B)	X					X	X	X
3. Upper lip with broad alternating dark and light bands from lip to eye (Fig. 12D)		X	X	X	X			X
4. Upper lip with broad alternating dark and light bands, distinct above lip, fading as reaching eye level	X	X	X	X	X	X	X	X
5. Upper lip with narrow dark bands from lip to eye level (Fig. 12C)						X		

Table 15. Thigh patterns, *Leptodactylus labyrinthicus* Unit. For the definition of geographic areas, see Figure 9.

Major pattern types	Geographic Areas							
	A	B	C	D	E	F	G	H
1. Bold mottle	X	X	X	X	X	X	X	X
2. Dark mottle with large light spots extending from darker dorsal bands (Fig. 14 B)	X					X		
3. Mostly (and obviously) light, with or without a few dark irregular marks (Fig. 14 D)		X	X	X	X		X	
4. Distinct labyrinth pattern							X	X

dots, or (usually) dark broad transverse bands that are either sharply or roughly defined and extend the entire width of the upper shank surface or about two-thirds the distance starting from the outer edge.

Body Folds: Lateral fold conditions were recorded for relatively few specimens. The most data are available for Area G individuals (N = 7) and the conditions range from none visible, interrupted, to continuous and complete.

Most specimens have interrupted dorsolateral folds that extend from the eye to at least 1/2 the distance toward the sacrum to the full distance toward the sacrum. There is some additional variation in dorsolateral fold development that does vary among geographic areas (Table 16). Non-Area specimens do not differ from dorsolateral fold conditions found in the proximate Area sample(s).

There is considerable variation in the extent of expression of flank folds, with variation in degree of development among Areas (Table 17). All specimens (N = 4) from Alto Palmar, Cochabamba and near Buena Vista, Santa Cruz, Bolivia have no discernible flank folds, differing from proximate Area B specimens. All other non-Area specimens match flank fold conditions found in proximate Area sample(s).

Male Sexual Secondary Characteristics: Three large males from Area C have weakly hyptertrophied arms. At least some males from all other Areas have pronounced arm hypertrophy and some males from Areas A, D, E, F, and H have arms as extensively hypertrophied as can occur in *Leptodactylus.*

Data were not recorded for development of tubercles for males from Area C. At least some males in all other Area samples have a field of black or tan-tipped tubercles on the throat, chest, and anterior belly. One male from Area F (USNM 121284) has black tubercles only on the throat, as

Table 16. Dorsolateral fold conditions, *Leptodactylus labyrinthicus* Unit. Parentheses indicate interrupted folds; no parentheses indicate continuous folds. For the definition of geographic areas, see Figure 9.

Major character states	Geographic Areas							
	A	B	C	D	E	F	G	H
1. None	X				X			
2. Extend from 1/4 to less than 1/2 the distance from eye to sacrum	X, (X)							
3. Extend from 1/2 to the full distance from eye to the sacrum	(X)	(X)	(X)	(X)	(X)	X, (X)	X, (X)	(X)
4. Extend from the eye to beyond the sacrum	X				(X)			

Table 17. Flank folds, *Leptodactylus labyrinthicus* Unit. For the definition of geographic areas, see Figure 9.

Degree of development	Geographic Areas							
	A	B	C	D	E	F	G	H
1. None	X		X			X	X	X
2. Elongate wart in flank fold field	X	X	X	X	X		X	X
3. Interrupted, complete		X	X		X	X	X	
4. Continuous, complete			X		X			

does non-Area specimen USNM 146507 from Alto Palmar, Cochabamba, Bolivia.

Some adult males lack chest spines (presumably the males were collected during the non-reproductive season). Most Area males have a pair of well-developed black (usually), tan-tipped, or white chest spines.

One or two males from Areas C, D, E, F lack thumb spines, which, as with chest spines, indicates the specimens could have been collected in the non-reproductive season. Most males from all Areas have a single white or black spine on each thumb. Three males from Area A have an additional black keratin tip on an expanded prepollex, forming a smaller second spine on each thumb. Non-Area specimen USNM 146507 from Alto Palmar, Cochabamba, Bolivia has slightly larger prepollical spines in addition to the medial thumb spines found in three of the males from Area A. There are no other differences between non-Area male thumb spines and males from proximate Areas.

Shank Texture: The Area E sample (the largest sample size), has no specimens that were scored as lacking tubercles. The Area A, G, H samples each have two to four specimens scored as lacking tubercles. All Area samples have individuals with few to many black and/or white tubercles on the dorsal surface of the shank. Some individuals from Areas A, C, D, E were scored as also having a shagreened surface. Non-Area specimen USNM 146507 from Alto Palmar, Cochabamba, Bolivia was scored as lacking tubercles, differing from the proximate sample from Area B. There are no other noteworthy differences between non-Area specimens with proximate Area specimens.

Outer Tarsal Texture: Most individuals from Area A and many individuals from Area H have smooth outer tarsal textures; single individuals from Areas D, F were scored as lacking texture. All Area samples have individuals with few to several black and/or white tubercles. Some individuals from Areas B, D, E, G, H have many black and/or white tubercles. Only one individual each from Area C and E has a shagreened surface. Non-Area specimen USNM 146507 from Alto Palmar, Cochabamba, Bolivia was scored as lacking tubercles, differing from specimens from proximate Area B. USNM 96978 from Belo Horizonte, Minas Gerais, Brazil was scored as having many white tubercles, differing from specimens from proximate Area F. All other non-Area specimens do not differ from proximate Area specimens.

Foot Texture: Most individuals from all Areas lack tubercles on the sole of the foot. All Areas have a few individuals with few to scattered black or white tubercles. No individual was scored as having a shagreened surface. All non-Area specimens have conditions found in specimens from proximate Areas.

Adult Size: Small sample sizes preclude definitive statements regarding size variation (Table

18). The following two points are suggested by the available data. First, there may be some variation in size among Areas as indicated by size differences (albeit overlapping) between males from Areas A and H, although males from Area E demonstrate as much variation as occurs among all Areas (Table 18). Second, males apparently reach larger sizes than females (Table 18). Non-Area specimen USNM 21746 from São Luiz, Maranhão, Brazil is an adult female of 120 mm SVL with large ova, just smaller than any female from Areas A-H.

Measurement Data: Sample sizes are minimally adequate only for male data from all Areas. The forward step discriminant function analysis of the male data did not have any variables which meet the default F-value to enter (0.15) in SYSTAT10 (Engelman, 2000), indicating that the variation among Areas is not dramatically different than the variation within Areas. The backward step model only used two variables in the final model. There are no clear indications that the backward step model performs better than the complete data model and vice versa. The complete data model analysis is used for discussion.

The discriminant function analysis performs rather poorly in separating the geographic area data. Sixty-nine percent of the individuals are correctly identified in the posterior classification matrix with only 51% of the sample correctly identified using the posterior jackknifed classification procedure. Fifty-six percent of the total dispersion is accounted for by the first canonical function, 75% by the first and second canonical functions, 88% by the first, second, and third canonical functions. All variation is accounted for with the first through seventh canonical functions.

Two variables have much higher loading values on the first canonical function than the other variables: head width and shank length. The two variables with the highest loading values on the second canonical variable are head width and eye-nostril distance. The plot of the first against second canonical variable (Figure 10) indicates essentially no discrimination for all but one Area sample. The males from Area F are distinctive in the analysis.

Life Colors: Lutz (1926, Plate 30, figs. 1, 2) and Bokermann and Sazima (1974) have color illustrations of specimens with crimson red groins and posterior thigh marks, but there are no locality data for the illustrations. De la Riva *et al.* (2000) and Gorzula and Señaris (1998) have color photos of specimens from Bolivia and north coast Venezuela respectively, but the aspects photographed do not show any areas where flash colors occur.

USNM 207674, an adult female from Assis, São Paulo, Brazil (Area F) had the following colors in life (WRH field notes): "Throat and chest white. Belly and limb venters yellow. Thigh spots rust brown dorsally and yellow ventrally. Dorsum rust brown."

Table 18. Adult sizes (SVL in mm), *Leptodactylus labyrinthicus* Unit geographic areas. For the definition of geographic areas, see Figure 9.

Geographic Area	Males	Females
A	127-160 (N = 23)	122-128 (N = 2)
B	122-170 (N = 9)	147-149 (N = 3)
C	129-170 (N = 4)	124-155 (N = 5)
D	110-182 (N = 5)	150-163 (N = 2)
E	115-188 (N = 13)	132-166 (N = 7)
F	118-163 (N = 5)	127-139 (N = 2)
G	140-167 (N = 5)	127-167 (N = 9)
H	135-180 (N = 10)	121-162 (N = 3)

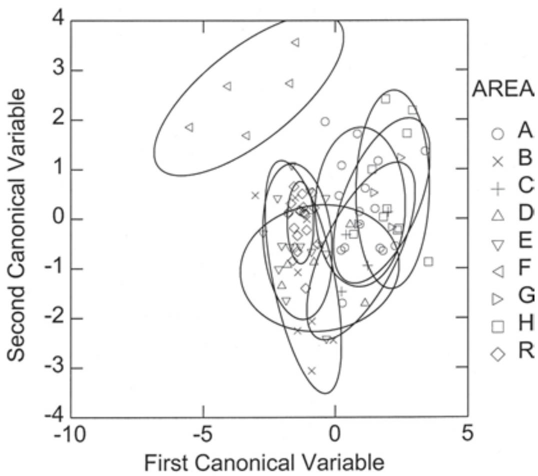

Figure 10. Discriminant function plot for male measurement data, *Leptodactylus labyrinthicus* Unit geographic areas. Sample confidence ellipses *p*:0.683. A-H symbols in legend on figure represent Areas A-H; the symbol for R represents remeasurement data for a single specimen (see text for further explanation).

Hödl (1993, fig. 3) has a color photo of a specimen from João Pessoa, Brazil (Area H) showing a pale yellow and dark gray reticulum on the hidden portions of the shanks. Lutz (1926, Plate 30, figs. 3, 4) has a color illustration of a specimen from near Independencia (now Guarabira, Paraiba fide P.E. Vanzolini, pers. comm.), Brazil (Area H) with bright yellow markings on the backs of the thighs and a faint yellow wash only on the posterior belly and hidden portions of the shanks. Lutz (1926) considered this yellow-thighed frog to represent a species (*L. gigas*) distinct from the rest of the Brazilian material with red marked thighs that he considered to be *L. labyrinthicus.*

Advertisement Calls: None of the calls analyzed has an associated voucher specimen that I have examined. Three of the recordings have photo vouchers (not found in photo collection at ZUEC) (Table 19). All recordings (for which data elements are available) are similar in terms of call rate, dominant frequency, and beginning frequency (Table 19). The recordings of three individuals from the same locality (Paraíba) demonstrate little variation among themselves (Table 19).

The most striking differences in the calls are in terms of call modulation. Six of the calls are amplitude and/or frequency modulated to such a degree that the calls sound distinctly pulsed to the human ear; two of the calls lack amplitude modulation within the call and they sound unpulsed to the human ear (Haddad *et al.*, 1988:16; Figure 11). Differences of this magnitude correlate with species limits in other *Leptodactylus* species (e.g., Heyer *et al.*, 1996). However, Marcos Gridi Papp (personal communication, 12 December 2001) informed me that individuals of *Leptodactylus ocellatus* in the State of São Paulo, Brazil, give pulsed and unpulsed calls at the same site. He did not know if an individual gives both kinds of calls, however. Clearly, this is an interesting situation that begs for detailed study. It would seem as though two alternatives are most likely: (1) two species currently called *L. ocellatus* occur at some localities in the State of São Paulo; or (2) there is individual or intra-population variation in calls including pulsed and non-pulsed calls. If the latter is correct, that might apply to the observed variation in *Leptodactylus labyrinthicus* as well. The two recordings with unpulsed calls are from

Table 19. Advertisement call data for *Leptodactylus labyrinthicus* Unit. Recordings from Paraíba are from the same locality. Bolivian data are from same recording reported on by Marquez *et al.*, 1995. Venezuelan call data are from Rivero and Esteves, 1969. NA = not applicable.

Tape & Cut, Country, State, Vouchered	N	Air temp, C	Call rate/ minute	Call duration range in s	# pulses per call	Mean pulse rate per s	Frequency modulation, Hz Entire call Mean, start	Mean, range	Mid-call pulse Mean, start	Mean, range	Mean dominant frequency, Hz
Venezuela, Sucre, ?	1	–		0.33	9?	27?	400	100			400
Bolivia, Santa Cruz, ?	4	–	54	0.15-0.24	3-5	20	386	98	310	154	386
321, 3, Brazil, Mato Grosso, –	2	21.5	41	0.14-0.18	1?		258	130	?	?	?
229, 1, Brazil, Minas Gerais, –	10	24.0	35	0.18-0.21	1	NA	258	171	NA	NA	429
229, 2, Brazil, São Paulo, –	10	23.0	50	0.19-0.21	1	NA	292	215	NA	NA	428
233, 1, Brazil, Paraíba, photo	10	21.0	56	0.14-0.17	4-6	31	257	207	320	277	429
233, 2, Brazil, Paraíba, photo	10	21.0	61	0.18-0.19	5-6	28	258	214	326	276	430
233, 3, Brazil, Paraíba, photo	10	22.0	54	0.17-0.19	4-5	23	258	180	309	273	430

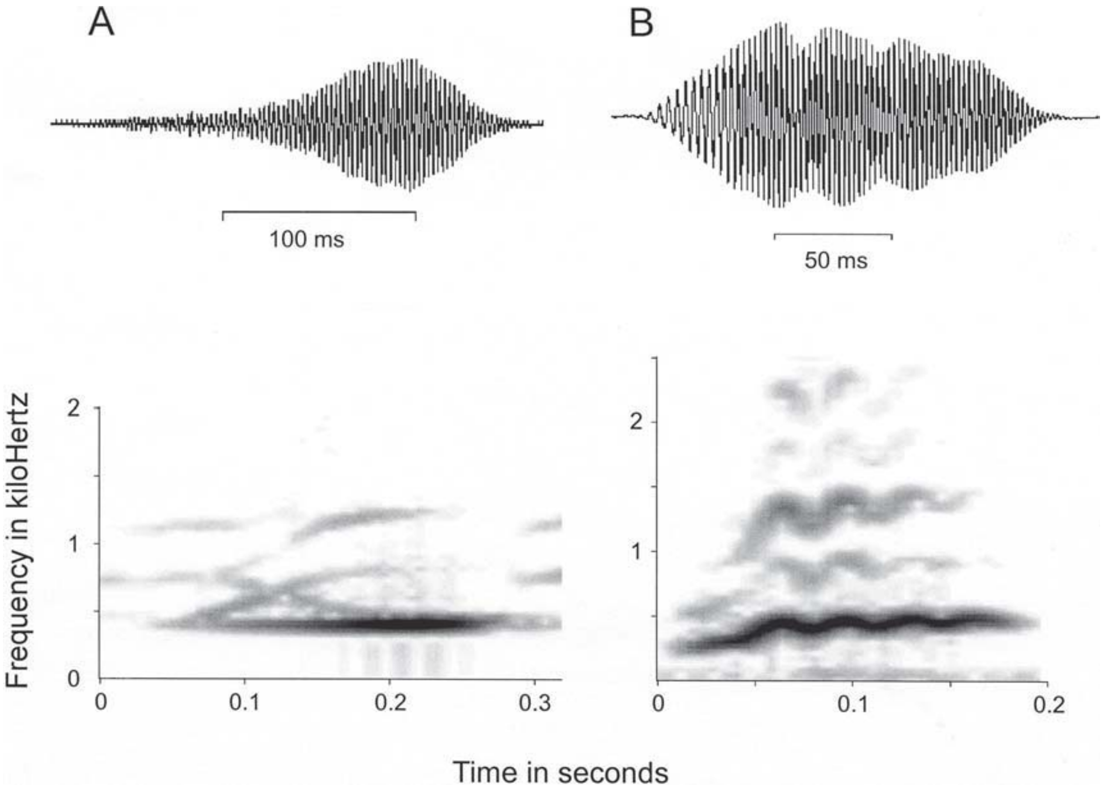

Figure 11. Advertisement calls of *Leptodactylus labyrinthicus* Unit showing wave form and audiospectrogram. A = USNM recording 229, cut 1 from Minas Gerais, Brazil; B = USNM recording 233, cut 3 from Paraíba, Brazil.

Area F. The pulsed recordings are from Areas A and H and from a locality that is closest to Area B. The recording from Area B is equivocal relative to pulse structure due to the poor quality of the recording.

In addition to the striking pulse differences among calls, there is additional variation. The call from Area A (Pico del Mango, Sucre, Venezuela, Rivero and Esteves, 1969) is notably longer (and probably has more pulses as a consequence) than all other recordings of calls except for the recording from Puerto Almacén, Santa Cruz, Bolivia. The frequency sweep of the recordings associated with Areas A and B is notably less than that seen in the other recordings (Table 19).

Evaluation of Differentiation: There is considerable variation within the *Leptodactylus labyrinthicus* Unit in terms of patterns, measurement data, and advertisement calls.

The advertisement call data are consistent with recognizing the specimens from Area F as distinct from all other specimens (although see previous section). In addition, a particular lip pattern is found only in some individuals from Area F and Area F male measurement data are distinctive from all other male measurement data in a discriminant function analysis (Figure 10).

The Area A sample demonstrates some differentiation in terms of belly pattern, male thumb spine development, and perhaps advertisement calls. The Area A sample appears to represent a geographic isolate. As indicated previously, (Heyer, 1979), the *Leptodactylus labyrinthicus* Unit occurs in open formations. However, the Area A sample occurs in humid forest or partially cleared humid forest habitats (Péfaur and Sierra, 1995). Interestingly, however, there are no *Leptodactylus labyrinthicus* Unit members known from the Venezuelan llanos (Péfaur and Sierra, 1995). The only other Area samples demonstrating regional differentiation are the Area G and H samples. These samples have individuals that share a thigh pattern unobserved elsewhere.

The available data are most consistent with recognizing four differentiated population systems: (1) *Leptodactylus labyrinthicus* Area A; (2) *L. labyrinthicus* Areas B-E; (3) *L. labyrinthicus* Area F; and (4) *L. labyrinthicus* Areas G-H.

Inter-Unit Analysis

Morphological Data

The morphological data represent the most extensive type of data available for the frogs in this study. These data are used as a first step in analyzing the nature of variation among the differentiated Units recognized in the previous section together with data for *Leptodactylus myersi*.

The intra-unit analyses resulted in most variation among differentiated Units occurring in lip pattern, belly pattern, thigh pattern, dorsolateral folds, flank folds, male thumb spines, and male chest spines. These characters were re-summarized for the differentiation Units recognized in the previous section and for *L. myersi*. Additional data were obtained for *L. knudseni* from Area B in March 2002 and are included in the Inter-Unit Analysis.

Character state distributions were summarized for each differentiated Unit. In addition, character states were summarized for specimens that are from localities between the differentiated Units. In all cases but one, the distribution of character states for specimens from localities between differentiated Units unambiguously associated with one of the differentiated Units and not the other. After additional data for Ecuadorian *L. knudseni* were taken in March 2002, the specimens from northern Amazonian Peru could not unambiguously be associated with the samples from (more geographically proximate) Ecuador or southern Amazonian Peru. The data for these north Amazonian Peru *L. knudseni* are omitted from the Inter-Unit Analysis.

Upon completion of the summaries of character state distribution, the range of variation was assessed to recognize major character states, described as:

Lip Patterns. (1) Uniform light, no pattern, (2) dark triangular marks on edge of upper lip only, (3) dark triangular marks on edge of upper lip, one or two elongate and approaching or reaching the lower eye border (Figure 12A), (4) elongate dark triangular marks on upper lip edge, fading towards eye, two dark marks under eye, (5) dark with two narrow, light chevrons from lip entering eye (Figure 12B), (6) alternating broad light bands and narrow dark vertical stripes, 1-3 dark stripes entering eye (Figure 12C), (7) broad irregular darker and lighter bands, two dark bands entering eye (Figure 12D), (8) broad light stripe, regular above, regular or irregularly defined below (Figure 12E), (9) uniform dark.

Belly Patterns. (1) Light belly, without pattern, (2) belly light with lateral and anterior mottling, (3) belly mottled or uniform dark (Figure 13A), (4) belly dark with small light vermiculations (Figure 13B), (5) belly dark with large light vermiculations (Figure 13C), (6) belly light with dark vermiculations, (7) labyrinthine pattern (Figure 13D), (8) dark with small light discrete spots, (9) belly dark with large light discrete spots (Figure 13E).

Posterior Thigh Patterns. (1) Very dark and uniform, (2) relatively uniformly dark or indistinctly mottled, (3) dark with small distinct light vermiculations (Figure 14A), (4) dark with large light vermiculations, some coalescing of vermiculations, (5) labyrinthine (same pattern as for Figure 13D) (6) dark with distinct, discrete light spots, (7) dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B), (8) very dark irregular blotches highlighted by light pin stripe on dark background (Figure 14C), (9) mostly very distinctly light with few irregular dark marks (Figure 14D).

Dorsolateral Folds. (1) None, (2) entire or interrupted fold extending from eye to 1/4 distance to sacrum, (3) interrupted fold extending from eye to more than 1/4 distance to 1/2 distance to sacrum, (4) interrupted fold extending more than 1/2 distance to sacrum or to the sacrum, (5) entire fold extending from eye to at least 1/2 distance to sacrum or to sacrum, (6) interrupted fold from eye to past sacrum, (7) entire fold extending from eye to past sacrum but not to leg, (8) entire fold extending from eye to leg.

Flank Folds. (1) None, (2) elongate dark spot in flank fold field, (3) interrupted fold to shoulder region, (4) entire fold to shoulder region, (5) interrupted complete fold, (6) entire, complete fold.

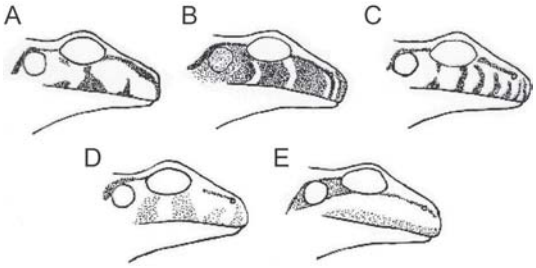

Figure 12. Lip patterns. A – Dark triangular marks, one or two elongate approaching or entering lower eye; B – Dark with two narrow light chevrons from lip entering eye; C – Alternating broad light bands and narrow dark vertical stripes, 1-3 dark stripes entering eye; D – Broad irregular darker and lighter bands, 2 dark bands entering eye; E – Broad light stripe regular above, regularly or irregularly defined below.

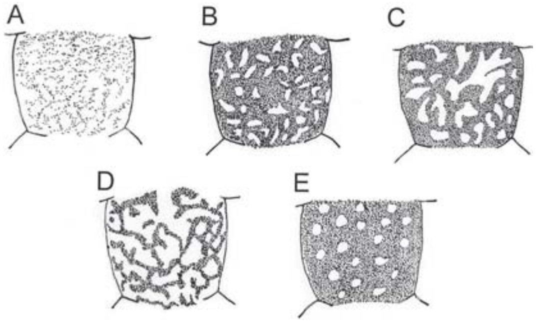

Figure 13. Belly patterns. A – Mottled; B – Dark with small light vermiculations; C – Dark with large light vermiculations; D – Labyrinthine; E – Dark with large, light, discrete spots.

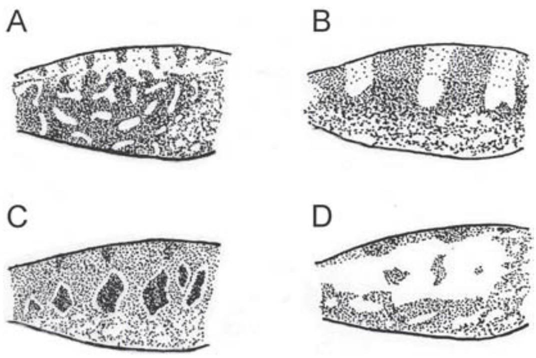

Figure 14. Posterior thigh patterns. A – Dark with small, distinct light vermiculations or vermiculations and spots; B – Dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations; C – Very dark irregular blotches highlighted by light pin stripe on dark background; D – Mostly very distinctly light with few irregular dark marks.

Male Thumb Spines. (1) Absent, (2) one tiny to small, (3) one large white or black, (4) one large black and second smaller bump.

Male Chest Spines. Male chest spines are completely deciduous seasonally and may leave no trace of their former presence in preservation, so the state deemed to be characteristic of sexually active males is defined for each differentiated Unit in terms of whether chest spines are present or absent.

The frequency distribution of states for all characters except chest spines are presented in Tables 20 and 21. Presence and absence of chest spines is presented in Table 21. There is considerable variation in relative and absolute differences in distribution of states among the differentiated Units.

The focus of the remainder of this section is to evaluate differentiation in terms of delineating species boundaries.

The first step is to evaluate the morphological data (Tables 20, 21) in terms of levels of differentiation among the differentiated Units. The data from Tables 20 and 21 were compared pairwise to determine the number of characters that completely diagnose the pair from one another and the number of characters for which some states are unique to one or the other differentiated Unit being compared. For these latter distinctive, but not completely diagnostic characters, an evaluation of whether the unique states could be due to small sample sizes was assessed by visual examination of the data. For example, if Sample A of 40 specimens has State 1 in 39 individuals and State 2 in one individual and Sample B of 3 specimens has only State 1, the differences are considered likely to be due to the small sample size of Sample B. However, if the 40 specimens of Sample A all have State 1 and Sample B contains two specimens with State 1 and one specimen with State 2, these differences are considered to be meaningful as they are probably not due to sampling problems.

Table 22 shows the results of the numbers of diagnostic and distinctive characters of pairwise comparisons for the differentiated Units. The total number of characters involved in the comparisons is seven. Two conclusions can be drawn from this analysis: (1) there is some level of distinctiveness among all differentiated pairs for the morphological data involved, and (2) no differentiated Unit is

Table 20. Lip, belly, and posterior thigh pattern character state distribution for Inter-Unit analysis. J = juvenile data, A = adult data. myersi = *Leptodactylus myersi,* para = Pará Unit, knud B = *L. knudseni* Unit from Ecuador, knud C = *L. knudseni* Unit from central and southern Peru, knud A, D-H = rest of *L. knudseni,* labyr A = *L. labyrinthicus* Unit from coastal Venezuela, labyr B-E = *L. labyrinthicus* Unit from Areas B-E, labyr F = *L. labyrinthicus* Unit from Area F, labyr G+H = *L. labyrinthicus* Unit from Areas G+H, pent 1 = *L. pentadactylus* Unit from Middle America and adjacent Colombia, pent 2 = *L. pentadactylus* Unit from Pacific coastal Colombia and adjacent Ecuador, pent 3 = *L. pentadactylus* Unit from central coastal Ecuador, pent 4 = *L. pentadactylus* Unit from Amazonia.

	myersi		para		knud B		knud C		knud A, D-H		labyr A		labry B-E		labyr F		labyr G+H		pent 1		pent 2		pent 3		pent 4	
	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A	J	A
Lip pattern																										
Patternless, uniform light		2		1		3				12				1						3						
Dark triangular marks on edge of upper lip only	9	5			2	2	4	7	2	6				9						14				1	2	16
Dark triangular marks, one or two elongate approaching or entering lower eye	11	4		7	22	3	3	4	20	60		3		1				2	13	62	4	9	3	6	36	33
Elongate triangular marks dark on lip edge, fading towards eye, two dark marks under eye	29	1	2	8						2		12	4	30		5	7	19								
Dark with two narrow light chevrons from lip entering eye	3	5	3	1			2					7	3	3	1	1	7	20								
Alternating broad light bands and narrow dark vertical stripes, 1-3 dark stripes entering eye				1					4	3					6	3	1	2								
Broad irregular darker and lighter bands, 2 dark bands entering eye	8	2	1	1				3	8	2			9	34			1	8								
Broad light stripe regular above, regularly or irregularly defined below	10	1																								
Uniform dark								1				5						1								
Belly Pattern																										
Patternless (light)	2	4							9	21					1				1	2						
Lateral and anterior mottling	8					1	1			8			1							1						
Mottled or uniform dark	5	2	2	3	4	6		4	8	52		21		7				10		8				1		6
Dark with small light vermiculations	14	7		7	4	1	4	4	1	4		1							3	30	1		1		30	29
Dark with large light vermiculations	17			9	1				8	4				10			1	1	3	8	1	7			4	12
Light with dark vermiculations			1						5	2			2	11	1	2	5	7								2
Labyrinthine			3						2				14	50	3	7	9	36								
Dark with small, light, discrete spots	24	9		1	15	1	4	6	1										5	4	1				3	
Dark with large, light, discrete spots					2			1											1	24	1	2	2	6		2
Posterior Thigh Pattern																										
Distinctly uniform dark	1				25		1																			
Relatively uniform dark or indistinctly mottled	5		1		2				2	6											3	1	1		1	
Dark with small, distinct, light vermiculations or vermiculations and spots	1	2	2	12		8	8	13	15	45		17	5	4	6	5	5	2	9	19		1		1	32	43
Dark with large, distinct, light vermiculations, some coalescing of vermiculations	4	3		3				1	10	24		2	9	49			4	15		15		1		1		2
Labyrinthine	3									2		1					4	22	1							1
Dark with distinct, discrete light spots		2							1	1						2				4			1			
Dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations	52	14	2	6				2	6	13		8		2	1	2	2	4	3	39		1	1	5	1	1
Very dark irregular blotches highlighted by light pin stripe on dark background										1															4	5
Mostly very distinctly light with few irregular dark marks	3									1			3	24			1	12		2	1	5				

Table 21. Dorsolateral fold, flank fold, male thumb spine, and male chest spine character state distributions for Inter-Unit analysis. myersi = *Leptodactylus myersi,* para = Pará Unit, knud B = *L. knudseni* Unit from Ecuador, knud C = *L. knudseni* Unit from central and southern Peru, knud A, D-H = rest of *L. knudseni,* labyr A = *L. labyrinthicus* Unit from coastal Venezuela, labyr B-E = *L. labyrinthicus* Unit from Areas B-E, labyr F = *L. labyrinthicus* Unit from Area F, labyr G+H = *L. labyrinthicus* Unit from Areas G+H, pent 1 = *L pentadactylus* Unit from Middle America and adjacent Colombia, pent 2 = *L. pentadactylus* Unit from Pacific coastal Colombia and adjacent Ecuador, pent 3 = *L. pentadactylus* Unit from central coastal Ecuador, pent 4 = *L. pentadactylus* Unit from Amazonia.

	myersi	para	knud B	knud C	knud A, D-H	labyr A	labry B-E	labyr F	labyr G+H	pent 1	pent 2	pent 3	pent 4
Dorsolateral folds													
None	9					7	1						
Interrupted or entire to 1/4 distance from eye to sacrum		2				3							
Interrupted from at least 1/4 distance to 1/2 distance from eye to sacrum	2	6				6	14	2	10				
Interrupted from at least 1/2 to full distance from eye to sacrum	40	18		5	27	8	72	12	51				
Entire from at least 1/4 to full distance from eye to sacrum	13		32	16	92		3	1	1	19		1	4
Interrupted to at least between sacrum and some distance to groin	17						2		1	7			5
Entire to at least between sacrum and some distance to groin	3		2	1						40	5	1	6
Entire from eye to groin						1				25	7	8	76
Flank folds													
None	6	7	33	22	9	5	5	12	13				1
Dark spot/wart in area where fold would be between tympanum and shoulder		5	1	1	96	13	49		33	1	1		
Interrupted from tympanum to shoulder	10	12											
Entire from tympanum to shoulder	9		1		3					28		1	15
Interrupted from tympanum to lower flank					1		5	1		20	4	2	32
Entire from tympanum to lower flank	1				4		3		3	36	7	7	43
Male thumb spines													
None												1	2
1 tiny to small	1	1	1	2	10		5	1	1	6	4		12
1	16	9	5		46	19	29	5	22	22		2	1
1 + prepollical bump				2	5	3	1			2			
Male chest spines	–	+	+	+	+	+	+	+	+	+	–	–	–

Table 22. Differentiation summary of morphological characters from Inter-Unit analysis. Value to left of slash is number of diagnostic characters (those that completely differentiate all specimens of the two Units being compared). Values to right of slash are number of characters that differentiate Units (the number of characters for which some states only occur in one of the two Units being compared); the first value is the number of characters for which sample sizes are substantial, the second value is the number of characters which might be impacted by small sample sizes. myersi = *Leptodactylus myersi,* para = Pará Unit, knud B = *L. knudseni* Unit from Ecuador, knud C = *L. knudseni* Unit from central and southern Peru, knud A, D-H = rest of *L. knudseni,* labyr A = *L. labyrinthicus* Unit from coastal Venezuela, labyr B-E = *L. labyrinthicus* Unit from Areas B-E, labyr F = *L. labyrinthicus* Unit from Area F, labyr G+H = *L. labyrinthicus* Unit from Areas G+H, pent 1 = *L. pentadactylus* Unit from Middle America and adjacent Colombia, pent 2 = *L. pentadactylus* Unit from Pacific coastal Colombia and adjacent Ecuador, pent 3 = *L. pentadactylus* Unit from central coastal Ecuador, pent 4 = *L. pentadactylus* Unit from Amazonia.

	myersi	para	knud B	knud C	knud A, D-H	labyr A	labry B-E	labyr F	labyr G+H	pent 1	pent 2	pent 3	pent 4
myersi	*	1/4+1	1/5+0	1/5+1	1/3+2	1/5+1	1/3+2	1/5+0	1/5+0	1/5+1	0/5+1	0/4+1	0/5+0
para		*	0/5+1	0/5+1	0/3+3	0/4+2	0/3+3	0/3+2	0/4+1	1/3+2	2/5+0	3/3+1	2/5+0
knud B			*	0/1+4	0/5+1	0/4+2	0/5+0	2/4+1	0/5+0	0/3+2	1/4+2	1/4+2	1/5+1
knud C				*	0/3+3	0/3+2	0/4+2	1/1+4	0/5+1	0/3+3	1/5+1	2/2+3	1/5+1
knud A, D-H					*	0/3+3	0/4+1	0/4+2	0/4+2	0/6+0	2/2+3	1/4+2	1/5+1
labyr A						*	0/5+1	1/4+1	0/4+2	0/5+1	1/6+0	2/4+1	1/6+0
labyr B-E							*	0/3+3	0/2+2	0/5+0	2/4+1	1/5+1	1/6+0
labyr F								*	0/2+2	1/4+1	3/3+0	4/3+1	2/5+0
labyr G+H									*	0/5+1	2/5+0	1/5+1	1/6+0
pent 1										*	1/5+1	1/0+5	1/4+1
pent 2											*	0/3+2	0/2+4
pent 3												*	0/3+1
pent 4													*

entirely diagnostic from all other differentiated Units.

The following combination of diagnostic and distinctive characters is conservatively considered to represent species-level differentiation: at least one diagnostic character and at least three distinctive characters not likely due to small sample sizes. Thirty-nine of the total 78 comparisons fit this conservative criterion.

The remaining 39 comparisons were ranked from most differentiated to least differentiated to serve as a template to add information from additional characters (Table 23). In cases where more than one pair had the same formula in Table 22 (e.g., -/5 + 1), ranking was based on the total number of individual differentiated states not impacted by small sample sizes for the lip, belly, and thigh patterns. The one comparison that may be misplaced in the relative ranking is that of Middle American *L. pentadactylus* – West Coast Ecuador *L. pentadactylus,* because the placement is high in the ranking order based on having a diagnostic difference (chest spines), but there are no other characters that differentiate this pair except those that could be due to small sample sizes.

Morphometric Data

Measurement data were analyzed using discriminant function analysis (SYSTAT 10, Engelman, 2000). In general, discriminant function analyses are more robust with larger data sets. As specimens examined for the previous study (Heyer, 1979) did not have tympanum diameter data, two data sets were evaluated: (1) specimens without tympanum data (this data set is larger in terms of number of individuals); and (2) specimens with tympanum data (this data set is larger in terms of number of variables). Any specimen with a missing value (other than tympanum diameter) was not included in the analyses. The conservative approach of analyzing male and female data separately as recommended by Hayek *et al.* (2001) was followed, resulting in four basic data sets.

Each of the four basic data sets was analyzed using the complete data model and the backward step model, using the default options in SYSTAT 10.

The backward step procedure results were identical for three of the four data sets (that is, the

Table 23. Ranking of morphological differentiation of pairs of differentiated Units that may or may not represent distinct species based on morphological characters. The most differentiated Units are at the top of the list. Morphometrics data: m or f indicates male or female data; lower case indicates diagnostic either in data set without tympanum diameter or data set with tympanum diameter; upper case indicates diagnostic for both data sets; parentheses indicate that N<10 for both Units. Juvenile and adult life colors: + indicates support, – indicates no support to diagnose the Unit pairs. Tadpoles: IOA indicates distinctive internal oral anatomy features; + or – indicate support or lack thereof based on larval tooth row formulae. Advertisement calls: the number of features that differ between the calls of the Units being compared (also see Table 24). See text for evaluation of characters.

Differentiated Unit Pairs	Morphometrics	Life Colors		Tadpoles	Advertisement Calls
		J	A		
knudseni C – labyrinthicus F	(F)		+	+	1
MA pentadactylus – WCE pentadactylus	–		–		2
knudseni A, D-H – MA pentadactylus	–		–	IOA, –	0
knudseni B – knudseni A, D-H	–				
knudseni C – labyrinthicus G+H	M, f		+		1
labyrinthicus G+H – MA pentadactylus	–		+		2
labyrinthicus A – MA pentadactylus	F				0
labyrinthicus A – labyrinthicus B-E	–				2
para – knudseni B	(F)	+			
para – knudseni C	M, (F)	+			
myersi – WCC pentadactylus	M, (F)		+		
myersi – Amazonian pentadactylus	M, F		–		2
knudseni B – labyrinthicus G+H	M, f				
labyrinthicus B-E – MA pentadactylus	–		–	+	2
knudseni B – labyrinthicus A	(F)				
knudseni C – labyrinthicus B-E	m, F		+	+	2
knudseni A, D-H – labyrinthicus F	m, F		+	+	1
knudseni A, D-H – labyrinthicus G+H	M, f		+		0
labyrinthicus A – labyrinthicus G+H	f				2
para – labyrinthicus A	(f)				
myersi – WCE pentadactylus	M, (F)		+		4
para – labyrinthicus G+H	–				
knudseni A, D-H – labyrinthicus B-E	f		–	+	1
knudseni C – knudseni A, D-H	f		+	–	0
knudseni C – MA pentadactylus	f	+	+	–	0
labyrinthicus B-E – labyrinthicus F	–		+	–	0
para – labyrinthicus B-E	–				
para – knudseni A, D-H	–				
knudseni A, D-H – labyrinthicus A	–				1?
knudseni B – MA pentadactylus	–	+			
knudseni C – labyrinthicus A	M, (F)				0
para – labyrinthicus F	m, (F)				
WCC pentadactylus – WCE pentadactylus	(m)		–		
WCE pentadactylus – Amazonian pentadactylus	F		+		2
WCC pentadactylus – Amazonian pentadactylus	m		+		
labyrinthicus F – labyrinthicus G+H	M, F		–		1
labyrinthicus B-E – labyrinthicus G+H	–		+		1
knudseni B – knudseni C	(m), (f)	–			

backward step analysis used all variables in the final model). The female data set including tympanum diameter data omitted SVL and head length in the final backward step model.

The results of the five different analyses were evaluated for Unit pairwise diagnostic information as follows. Both the classification matrix using all data and the jackknifed classification matrix were examined for whether any specimens were incorrectly identified in the posterior classification results. For example, for the first cell in Table 23 [value of (F) under Morphometric column], no specimens of *L. knudseni* C were posteriorly identified as *L. labyrinthicus* F in any results; 1 individual of *L. labyrinthicus* F was posteriorly identified as *L. knudseni* C in both male data sets including or excluding tympanum diameter in the posterior classification using all data; 2 individuals of *L. labyrinthicus* F were posteriorly identified as *L. knudseni* C in both male data sets including or excluding tympanum diameter in the jackknife matrix; and no *L. labyrinthicus* F individuals were posteriorly identified as *L. knudseni* C individuals in the female data sets including or excluding tympanum diameter for all results using the complete data posterior classification model and the jackknife model.

The posterior classification results are summarized as follows. All values for each posterior classification must be zero for the data set to be considered diagnostic. That is, using the first cell in Table 23 as an example, the male data without tympanum, the male data with tympanum, and the female data without tympanum measurements, no *L. knudseni* C individuals could be posteriorly classified as *L. labyrinthicus* F individuals and no *L. labyrinthicus* F individuals could be posteriorly classified as *L. knudseni* C individuals in both the complete data posterior classification matrix and the jackknife matrix for that data set to be considered diagnostic. For the female data with tympanum diameter data, in addition to the previous conditions, all values had to be zero for both the complete data discriminant function model and the backward step model for the female data set with tympanum measurements to be considered diagnostic. If only one of the two data sets for each sex was diagnostic, a lower-case letter (either m or f) is used; if both data sets for each sex are diagnostic, a capital letter is used. As discriminant function analyses can be unrealiable for cells with small sample sizes, parentheses are used to indicate that the sample sizes for both Units being compared are less than 10 individuals.

Life Colors

Many aspects of life colors are (apparently) undocumented for the Units being evaluated. There are three aspects of life colors that appear to vary markedly among the Units: juvenile dorsal colors of greenish-yellow versus brown or brownish-red, posterior thighs black or with red/orange markings; and adult posterior thighs with white, yellow, or orange/red markings. Additional information on life colors will certainly help diagnose several of the Units involved. For example, it is very likely that all *L. labyrinthicus* Units can be differentiated from *L. knudseni* B and *L. knudseni* C Units by juvenile life color patterns, but at present, I find no documented life colors for the critical features for any juveniles from any *L. labyrinthicus* Units. The available comparisons are indicated in Table 23. For juvenile colors, a + indicates a difference in either dorsal or posterior thigh colors.

Tadpoles

There is not a lot of descriptive published data available on tadpoles of the *Leptodactylus* treated herein.

Wassersug and Heyer (1988: Table 1) found several differences between the larvae of *L. knudseni* (from the Area A, D-H Unit) and *L. pentadactylus* (Middle American Unit) in terms of internal oral features. The single larvae they examined for each species were about the same size, but the *L. knudseni* was developmentally more advanced (Gosner, 1960, stage 39 versus 34 for the *L. pentadactylus* larva). Although many of the differences categorized in Table 1 of Wassersug and Heyer (1988) could possibly be related to different developmental stages, at least three of them are not (number of filter rows per plate on ceratobranchial IV, folding pattern of filter rows, number of postnarial papillae). The differences of internal oral features are diagnostic for these two Units.

Larson and de Sá (1998) found just one variable character in chondrocranial morphology among *L. knudseni, labyrinthicus,* and *pentadactylus* larvae they examined: chondrocranial width to length ratio. For purposes of this exercise, the level of variation observed is not considered diagnostic between any of the specimens of *L. knudseni, labyrinthicus,* and *pentadactylus* they studied.

External morphologies have been described for four Units being evaluated in this section. All larvae share a unique morphology within *Leptodactylus* related to being at least facultative carnivores. The tadpoles have long muscular tails, the oral disk is smaller and much more anteriorly oriented than in typical pond-dwelling surface-scraping feeder tadpoles, and the larvae grow to quite large sizes (at least 70 mm total length).

The only consistent variation found among the known larvae of the taxa in this study is in the number of tooth rows.

Hero (1990) found that larval *L. pentadactylus* (Amazonian Unit) completed their entire development within burrows where the foam nest was laid and had a tooth row formula of 1/2(1);

whereas syntopic *L. knudseni* (Area A, D-H Unit) had post-hatching free-living aquatic larvae with a tooth row formula of 2(2)/2(1). I think that all free-living aquatic larvae of the *L. pentadactylus* type that have been collected in Amazonia belong to *L. knudseni* Units. I examined Amazonian larval samples of *L. knudseni* Units (from Area C Unit and Area A, D-H Unit) and found that in most larvae there is an abbreviated entire third tooth row on the lower labium. There is variation in presence or absence of the third posterior tooth row in larvae from the Biological Dynamics of Forest Fragments sites north of Manaus, Amazonas, Brazil (USNM 313497-313499).

Middle American *L. pentadactylus* Unit larvae have been illustrated and described by several authors from different localities throughout much of its distribution (Breder, 1946; Heyer, 1970; McCranie and Wilson, 2002; Villa, 1972). The tooth row formula for the Middle American *L. pentadactylus* Unit is 2(2)/3(1).

Vizotto (1967) described the larva of *L. labyrinthicus* (Area F) as having a tooth row formula of 1/2(1). USNM specimens examined from Paraguay (USNM 253610, outside of Area B-E and F Units) and the Area B-E Unit (USNM 507875) also have the tooth row formula 1/2(1).

Karyotypes

The few specimens that pertain to this study that have been karyotyped have a diploid number of 22. I find the available data uninformative with respect to diagnosing any Units for which individuals have been reported (see individual species accounts for literature involved).

Advertisement Calls

The summary data for advertisement calls from Tables 6, 11, 12, and 19 were combined by Units with data for *Leptodactylus myersi* taken from the compact disk recording, Sound Guide to the Tailless Amphibians of French Guiana by C. Marty and P. Gaucher. The variation in call rate within the *L. knudseni* Area A, D-H Unit almost encompassed the total variation. The call rate data were not used to determine differentiation of advertisement calls among Units.

Advertisement calls between Units are considered distinctive if there is (1) no overlap of ranges of values for call duration, number of pulses per call, pulse rate in seconds; (2) at least a 300 Hz difference between ranges of values for the beginning frequency; and (3) at least a 100 Hz difference between ranges of values for call range (none of the Units differ by this criterion).

There are no experimental data on large *Leptodactylus* species to know whether the above thresholds used for assessing distinctiveness in call features are sufficient for the frogs to recognize the calls as different. Generally, frogs can discriminate amplitude/timing aspects of calls very well. If the basilar papilla is the organ used in hearing advertisement call frequencies, generally calls need to differ by at least 400 Hz, beyond which the frog essentially does not hear the sound (see experimental data in Zakon and Wilczynski, 1988 and empirical data in Blair and Littlejohn, 1960). If the amphibian papilla is the hearing organ used (for around 1000 Hz and less, Zakon and Wilczynski, 1988:147), discrimination is much better within the range of frequencies the organ can process. The frogs in this study should be using their amphibian papillae to process advertisement calls. A difference in any of the parameters included in this analysis could be sufficient for the frogs to perceive them as different. A difference in two parameters should have a high degree of likelihood that the frogs perceive the calls as different (Table 24). Of course, the frogs could be able to discriminate smaller differences than those used as threshold values in this exercise.

Species Limits

The preceding data, as summarized in Table 23, is now evaluated in terms of species-level recognition among the Units.

The level of differentiation of *Leptodactylus myersi* from all other Units is at a level consistent with recognizing it as a distinct species.

The Pará Unit is very distinct from all *L. pentadactylus* Units at a level considered to represent species-level differentiation. The Pará Unit is equivocally differentiated from all the *L. knudseni* and *L. labyrinthicus* Units. There are no data for larvae or advertisement calls for the Pará Unit. Larval data should differentiate the Pará

Table 24. Call differentiation among Units. 1 = no overlap in call duration; 2 = no overlap in number of pulses/call; 3 = no overlap in pulse rate/s; 4 = at least 300 Hz difference between beginning frequencies; 5 = at least 300 Hz difference between dominant frequencies.

	k C	k A, D-H	MA p	WCE p	Amaz p	l A	l B-E	l F	l G+H	*L. myersi*
knudseni C	–	0	0	4, 5	2, 3	0	1, 2	2	1	2, 3
knudseni A, D-H		–	0	0	3	3?	2	2	0	2, 3
MA pentadactylus			–	3, 5	5	0	1, 2	1, 2	1	2, 3
WCE pentadactylus				–	2, 3	1, 5	1, 2	2, 5	1, 5	1, 2, 3, 4
Amazonian pentadactylus					–	2, 3	2	2	2, 3	2, 3
labyrinthicus A						–	1, 2	1, 2	1, 2	2, 3
labyrinthicus B-E							–	0	2	1, 2
labyrinthicus F								–	2	1, 2
labyrinthicus G+H									–	1, 2, 3
L. myersi										–

Unit from either all *L. knudseni* Units or all *L. labyrinthicus* Units. At present, the available data (morphological) are equivocal. My subjective impression and current conclusion is that the Pará Unit is specifically distinct from all *L. knudseni* Units and all *L. labyrinthicus* Units.

The *Leptodactylus knudseni* Units are distinct from the *L. labyrinthicus* B-E and F Units at a level consistent with species level differentiation. The *L. knudseni* C Unit has the same magnitude of differentiation from the *L. labyrinthicus* G+H Unit, but the *L. knudseni* B and A, D-H Units do not have the same level of differentiation from the *L. labyrinthicus* G+H Unit. Advertisement calls do not differ at the previously defined levels associated with species limits between the *L. knudseni* C – *L. labyrinthicus* A Units and the *L. knudseni* A, D-H – *L. labyrinthicus* G+H Units; thus, currently additional call data may not aid resolution of species limits among the equivocal Units under discussion. However, life colors and larval characters will probably provide helpful data to robustly define species limits among at least some of the Unit pairs under discussion. With the available data (primarily morphological), my subjective evaluation and current conclusion is that all of the *L. knudseni* Units differ from all of the *L. labyrinthicus* Units at the species level.

All *Leptodactylus knudseni* Units are distinct from all *L. pentadactylus* Units at a level consistent with species level differentiation except when comparing the *L. knudseni* B and C Units with the Middle American *L. pentadactylus* Unit. Advertisement calls do not differ between the *L. knudseni* A, D-H and C Units with the Middle American *L. pentadactylus* Unit, therefore calls may not differ between the *L. knudseni* B Unit and the Middle American *L. pentadactylus* Unit when calls of the *L. knudseni* B Unit become available. I find the level of differentiation of larval internal oral features to be surprisingly great between the *L. knudseni* A, D-H Unit and the Middle American *L. pentadactylus* Unit tadpoles. I anticipate that when larvae of the *L. knudseni* B and C Units are examined for internal oral features, they will also demonstrate significant variation relative to the Middle American *L. pentadactylus* Unit. I think that the *L. knudseni* Units and the Middle American *L. pentadactylus* Unit are separate species, and that the Middle American *L. pentadactylus* Unit is the sister-group to the *L. knudseni* Units rather than to the Amazonian *L. pentadactylus* Unit.

All *Leptodactylus labyrinthicus* Units differ from all *L. pentadactylus* Units at a level consistent with species level differentiation except for the *L. labyrinthicus* A Unit and the Middle American *L. pentadactylus* Unit. The advertisement calls do not differ between the *L. labyrinthicus* A and Middle American *L. pentadactylus* Units at the previously defined levels for species level differentiation. Larvae are not known for the *L. labyrinthicus* A Unit. The available data are equivocal whether the *L. labyrinthicus* A Unit and the Middle American *L. pentadactylus* Unit represent distinct species. My subjective impression is that they do; thus all *L. labyrinthicus* Units are considered to be distinct at the species level from all *L. pentadactylus* Units.

The *Leptodactylus knudseni* Units either do not differ from each other at levels expected for species differentiation (*L. knudseni* B – *L. knudseni* A, D-H Units) or at equivocal levels of differentiation. The *L. knudseni* B and C Units were not combined after the intra-Unit analysis because the only available juvenile color information was for one *L. knudseni* C Unit specimen, which lacked the distinctive greenish yellow colors and black posterior thigh colors of *L. knudseni* B Unit juveniles. Subsequently, life colors were obtained for additional *L. knudseni* C specimens, and they are identical to those of the distinctively colored *L. knudseni* B Unit juveniles. There is minimal variation between the *L. knudseni* B and C Units which raises the question of whether the *L. knudseni* B+C Unit represents a different species from the *L. knudseni* A, D-H Unit. There is weak morphological and measurement differentiation; some life color differentiation; and no larval or advertisement call differentiation between the *L. knudseni* B+C and A, D-H Units. I interpret the available information to be most consistent with recognizing a single species for all *L. knudseni* Units.

Variation among the *Leptodactylus labyrinthicus* Units is consistent with species level differentiation except for the *L. labyrinthicus* B-E and F Unit comparisons. The differentiation between these two Units is primarily yellow versus red posterior thigh color in life. There is also some morphological differentiation, but the larvae and advertisement calls apparently do not differ. Call recordings from Area F consist of a single pulse, and calls of the single poor quality Area B-E recording sounds the same as recordings from Area F. The two Units may eventually prove to represent distinct species, but available data indicate that the variation is intraspecific in nature. The following are recognized as distinct species: the *L. labyrinthicus* A Unit; the *L. labyrinthicus* B-F Unit; and the *L. labyrinthicus* G+H Unit. Two geographic samples can not be assigned with certainty to the three species as recognized: (1) the recording from Santa Cruz, Bolivia is clearly pulsed, differing from the unpulsed calls of the geographically proximate *L. labyrinthicus* B-F species; (2) the locality of Serra de Parima, Roraima, Brazil (MZUSP 24936) is a geographic outlier and cannot be associated with any of the three recognized species. For present purposes, all Bolivian specimens exhibiting the general *L. labyrinthicus* morphology and the specimen from Roraima, Brazil are treated as unknown species.

Diagnostic characters among *Leptodactylus pentadactylus* Units provide clear as well as ambiguous interpretations for species level differentiation (Table 25). The level of differentiation between the pairs Middle American Unit – West Coast Colombia Unit, Middle American Unit – Amazonian Unit, and West Coast Ecuador Unit – Amazonian Unit strongly supports species level differentiation. There is moderate support for recognizing the Middle American Unit and West Coast Ecuador Unit as distinct species. Equivocal support exists for species level differentiation between the West Coast Colombia Unit – West Coast Ecuador Unit and the West Coast Colombia Unit – Amazonian Unit. The following example illustrates the difficulty in interpretation of the moderate and equivocal levels of support for species level differentiation. If the data were interpreted to mean that the West Coast Colombia Unit represented the same species as the Amazonian Unit and the West Coast Colombia Unit represented

Table 25. Diagnostic characters among *Leptodactylus pentadactylus* Units. Bold indicates characters considered to be robustly diagnostic in terms of species level differentiation.

	West Coast Colombia Unit	West Coast Ecuador Unit	Amazonian Unit
Middle American Unit	**Chest spines** **Thumb spines** Belly pattern Thigh pattern Dorsolateral folds Flank folds	**Call** **Chest spines**	**Call** **Tadpoles** **Life colors** **Chest spines** **Thumb spines** Belly pattern Lip pattern Thigh pattern
West Coast Colombia Unit	X	**Thumb spines** Belly pattern Thigh pattern	**Life colors** Thigh pattern Flank fold
West Coast Ecuador Unit	X	X	**Call** **Life colors** **Thumb spines** Female measurements Belly pattern Thigh pattern

the same species as the West Coast Ecuador Unit, then one would expect there to be much less differentiation between the West Coast Ecuador Unit and Amazonian Unit than is represented in the data summarized in Table 25. There are four alternative interpretations of the equivocal and moderate levels of differentiated Units (Table 25): (1) the West Coast Colombia Unit represents the same species as the West Coast Ecuador Unit; (2) the West Coast Colombia Unit represents the same species as the Amazonian Unit; (3) the Middle American Unit represents the same species as the West Coast Ecuador Unit; and (4) each Unit represents a distinct species. The first two alternatives would be easier to evaluate if advertisement calls and tadpole data were available for the West Coast Colombia Unit. If alternative (2) were correct, one would predict that the West Coast Colombia Unit would have a tadpole that completes development within the terrestrial burrow where the foam nest was deposited and that the larvae would have a tooth row formula of 1/2(1). My evaluation of the available data is that they best support the fourth alternative. Acceptance of the fourth alternative has the consequence of not being able to determine whether the specimen from La Tola, Esmeraldas, Ecuador (QCAZ 19859) belongs to the West Coast Colombia or West Coast Ecuador Unit, as the female does not have sufficient diagnostic characteristics. The available albumin microcomplement fixation data support recognition of the Amazonian Unit, the Middle American Unit, and the West Coast Ecuador Units as distinct species (Maxson and Heyer, 1988).

In summary, the following are recognized as distinct species:

- *Leptodactylus myersi*
- the Pará Unit
- *Leptodactylus knudseni* (B+C+A, D-H Unit)
- *Leptodactylus labyrinthicus* Unit A
- *Leptodactylus labyrinthicus* B-F Unit
- *Leptodactylus labyrinthicus* G+H Unit
- *Leptodactylus pentadactylus* Middle American Unit
- *Leptodactylus pentadactylus* Amazonian Unit
- *Leptodactylus pentadactylus* West Coast Colombia Unit (extending geographically into adjacent Ecuador)
- *Leptodactylus pentadactylus* West Coast Ecuador Unit.

Problematic Specimens. – Earlier, certain individuals were identified as exhibiting features that did not allow their assignment to any of the groupings being analyzed. These distinctive samples are discussed relative to the species as recognized herein.

Specimen OMNH 37583. The specimen is a 95 mm SVL male with a moderate-sized black spine on each thumb. It fails to match almost all *L. knudseni* males in lacking chest spines. Other small male *L. knudseni* also have a thumb spine and lack chest spines, such as MZUSP 80660, 96 mm SVL, from Aripuanã, Mato Grosso, Brazil. Larger males from Aripuanã have chest spines in addition to thumb spines. OMNH 37583 is considered to be a small male *L. knudseni.*

Specimens MZUSP 131123, USNM 303909. The two males, 129 and 110 mm SVL respectively, are from Alto Paraiso, Rondônia, Brazil. I did not associate these specimens with the OTUs (Operational Taxonomic Units) in this study because both males have a single thumb spine but lack chest spines and the larger male with extensively hypertrophied arms has black tubercles on the throat, chest, and anterior belly, indicating that the specimens from this locality do lack chest spines. After this manuscript was completed, I discovered that there were an additional three males and two small juveniles from the same locality (AMNH 124825-124829), collected at the same time as MZUSP 131123 and USNM 303909.

AMNH 124825 is a 132 mm SVL adult male with extensively hypertrophied arms that has one large black spine on each thumb, one pair of chest spines, and a field of black tubercles on the throat, chest, and anterior belly. The combined morphological data for the AMNH, MZUSP, and USNM specimens match those for either *L. knudseni* or the *L. labyrinthicus* B-F Unit. Discriminant function analyses using measurement data for males of the species recognized herein result in poor discrimination among species, with only 47-55% of the specimens being correctly assigned posteriorly in either the standard classification or jackknife classification matrices using data sets with and without the tympanum diameter variable (results not shown). The data from the Rondônia adult males were not used to develop the discriminant function models but were included to determine with which species the Rondônia adult male data were most consistent. The discriminant function model not including tympanum diameter data predicts that three of the specimens are *L. knudseni* and two specimens belong to the Pará Unit. The discriminant function model including tympanum diameter data predicts that two specimens are *L. knudseni,* two specimens belong to the Pará Unit, and one specimen belongs to the *L. pentadactylus* Middle American Unit.

Ronald I. Crombie recorded the following for MZUSP 131123: "Light brown with reddish-brown darker transverse markings. Upper thighs very reddish. Bright yellow on concealed thighs, tibiae and in groin. Venter dirty white, suffused with ivory to dull yellow reticulum, particularly on limbs and edges of jaws. Soles of feet purplish. Iris gold with median lateral reddish marks." Charles W. Myers recorded the following for the AMNH specimens: "Adults (18406-07) [= AMNH 124825-124826] light gray over head and upper arms, turning light grayish brown over back and hindquarters. Dull yellow and black mottling on rear thigh. Ventral surfaces whitish. Iris golden bronze with variable black venation and bright orange-brown butterfly mark. Juveniles (18408-09) [= AMNH 124827-124828] pale greenish brown with dark gray-brown crossbands. Rear thighs spotted with pale gray. Iris pale orange above, pale gray below (no butterfly mark)."

The combined data for these specimens is consistent only with those of *L. knudseni,* although the posterior thigh colors of the adults are not the same as those for which descriptions are available (but are variations of the same pigment cell type) and the juveniles are not as distinctively colored as those from Ecuador and Peru (see color descriptions in *L. knudseni* Unit portion of Intra-unit Analyses section). These specimens are considered to represent the same species as the *L. knudseni* Unit species. Morphological and measurement data for these specimens are not included in the Species Accounts section for *L. knudseni.*

Specimens MZUSP 24947-24948. The two male specimens, 150 and 152 mm SVL respectively, are from Jacareacanga, Pará, Brazil (Figure 17). The specimens share the most character states and have most similarity with *L. knudseni* and *L. myersi*. Both specimens have well-developed thumb spines, but lack chest spines. Both specimens have small black chest tubercles, indicating that the lack of chest spines is real and not due to seasonal shedding of the spines (but note the problem of interpretation of chest spine presence/absence in small sample sizes in immediately preceding paragraphs). When the two Jacareacanga specimens were posteriorly classified using the same models described for the preceding Rondônia specimens, MZUSP 24947 was classified as *L. knudseni* in the model that excluded tympanum diameter data and as Middle American *L. pentadactylus* in the model that included tympanum diameter data. MZUSP 24948 was posteriorly classified as *L. knudseni* in both models that included and excluded tympanum diameter data. I know of no data on life colors or habitat for these specimens. The data are equivocal whether the specimens represent *L. knudseni* or a new species. For present purposes, they are considered unidentifiable to species.

Specimen USNM 202518 (Figure 20). The adult female is most similar to *L. pentadactylus* with the exception that it does not have any bars on the lip as found in all individuals examined of *L. pentadactylus.* Pending further data, I consider this difference to be of enough significance to retain it as unidentifiable to species and not significant enough to consider it a distinct species.

Nomenclature

The information previously provided on nomenclature of this group of frogs under study (Heyer, 1979) is not repeated here.

Rana pentadactyla Laurenti, 1768. I previously designated the name bearer to be the specimen illustrated in Seba, 1734, Plate 75, Figure 1 (Heyer, 1979:13). This figure could represent any of the four species currently identified as *Leptodactylus pentadactylus*. The available evidence indicates that Seba's frog came from Suriname, South America (Bauer, 2002:9; Heyer, 1979:13).

Seba's collections have had a complicated history (Boeseman, 1970); those specimens still surviving are in a number of collections. To date, no one has identified and published that the type of *Rana pentadactyla* is extant in their collection. Boeseman (1970) indicates nine collections have Seba specimens: (1) Academy of Sciences, St.

Petersburg (ZIL), (2) Copenhagen Museum of Natural History (ZMUC), (3) Museum National d'Histoire Naturelle, Paris (MNHN), (4) Naturhistoriska Riksmuseet, Stockholm (NRM), (5) The Natural History Museum, Leiden (RMNH), (6) The Natural History Museum. London (BMNH), (7) Uberseemuseum, Bremen (UMB), (8) Universität Humboldt, Berlin (ZMB), and (9) Universitein van Amsterdam (ZMA).

Each of the nine collections Boeseman (1970) indicated as obtaining Seba specimens was contacted to determine whether any Seba specimens that Laurenti included in materials described as *Rana pentadactyla* are extant.

The following curators reported that they did not have a Seba specimen that could be a potential type of *Rana pentadactyla* (numbering from paragraph above).

2) Dr. Jens Rasmussen, ZMUC, in an e-mail message dated 14 October 2002 stated: "To the best of my knowledge we do not possess any herptiles originating from the Seba collection. All the specimens (a dozen) which we possess of the requested species seem to have been caught in nature by well known Danish collectors. Accordingly, I do not believe the type is here."

3) Dr. Annemarie Ohler, MNHN, in an e-mail message dated 5 November 2003 wrote: "I checked our files and could not find any specimen that might come from the Seba collection. All specimens have French collectors and seem to be more recent than Seba. There are no frogs from Leiden "exchange" (the usual origin of Seba specimens)."

5) Dr. Marinus Hoogmoed (e-mail message dated 24 July 2002) informed me that the RMNH, does have three Seba specimens of *L. pentadactylus* from Suriname, but none of the three match Seba's figure. Dr. Hoogmoed stated, "Thus, I can assure you we do not have the depicted Seba specimen here."

6) Dr. Mark Wilkinson, BMNH, in an e-mail message of 3 November 2003 wrote in response to my query of any *Leptodactylus* that came from Seba's second collection: "I've just searched through our catalogues and can find no specimen with any indication of a linkage to Seba … ."

7) Dr. Peter Renè Becker, UMB, responded in an e-mail message of 9 January 2004: "I am sorry to say that we hold neither *Leptodactylus pentadactylus* nor any Seba specimens in our collections."

8) Dr. Rainer Günther, ZMB, in an e-mail message dated 15 October 2002, stated: "None of our specimens of *Leptodactylus pentadactylus* could be identified as a 'Seba-type.' We also do not have indications in our catalogues that such a type should be stored here."

9) Dr. Axel Groenveld, ZMA, in an e-mail message dated 8 September 2003, stated: "I could find only five specimens of *Leptodactylus pentadactylus* in our collection … . Although three of them are from doubtful origin, none of them refer to the Seba collection. … ."

I examined the holdings of *Leptodactylus* at the NRM (4 in paragraph above) in August 2003 and did not find any specimen that could be a Seba specimen of *Rana pentadactyla.*

Dr. Natalia Ananjeva and Konstantin Milto, ZIL (1 in paragraph above) informed me that a Seba specimen identified as *Leptodactylus pentadactylus* was in their collection. I examined the specimen, ZIL 274, in August 2003. The specimen is an adult male *Leptodactylus knudseni.* Seba's illustration (1734, Plate 75, Figure 1), although somewhat stylized (it has five full fingers on each hand, which no known extant frog has), is very clear in showing a pair of complete dorsolateral folds extending from the eye to the groin. ZIL 274 has a pair of dorsolateral folds that are distinct only from the eye to the sacral region. Hence ZIL 274 could not represent the specimen illustrated in Seba and is not a potential syntype of *Rana pentadactyla* Laurenti, 1768.

Given the morphological similarities among the species to which the name *Rana pentadactyla* Laurenti, 1768 has been applied, designation of a neotype is necessary to associate the name with a specimen to achieve nomenclatural stability. As Seba's specimens came from Suriname, I hereby designate RMNH 29559 as the neotype of *Rana pentadactyla* Laurenti, 1768. RMNH 29559 is a 134 mm adult male (with vocal slits and a tiny white spine on each thumb) from Suriname, Marowijne, Lelygebergte, Suralcokamp V, collected on 15 August 1975 by Marinus S. Hoogmoed.

Rana pentadactyla Laurenti, 1768 is the oldest available name for the species analyzed herein as the Amazonian *L. pentadactylus* Unit.

Rana gigas Spix, 1824. Hoogmoed and Gruber (1983:355) did not find the type in the collections in Munich or Leiden. Peters (1873) and

Heyer (1979) provided evidence that the name applied to the Amazonian *L. pentadactylus* Unit as defined in this paper. Smith *et al.* (1977) pointed out that *Rana gigas* Spix is a preoccupied name and not available for any species of *Leptodactylus.* Since *Rana gigas* Spix is a synonym of *Leptodactylus pentadactylus* (Laurenti, 1768), there is no need to propose a replacement name for *Rana gigas* Spix.

Rana coriacea Spix, 1824. Hoogmoed and Gruber (1983:355) reported the type was lost. Peters (1873) and Heyer (1979) concluded that *Rana coriacea* Spix was a member of the Amazonian *L. pentadactylus* Unit as defined in this paper. Thus, *Rana coriacea* Spix is considered to be a synonym of *Leptodactylus pentadactylus* (Laurenti, 1768) and there is no present need to designate a neotype for *Rana coriacea* Spix.

Rana labyrinthica Spix, 1824. Heyer (1979) indicated that this name applies to the Area F *L. labyrinthicus* Unit as analyzed in this paper and is thus the oldest name for the *Leptodactylus labyrinthicus* Area B-F Unit species.

Leptodactylus goliath Jiménez de la Espada, 1875. Heyer (1979) indicated that the lectotype is a member of the Amazonian *L. pentadactylus* Unit as analyzed in this paper. Hence, *Rana goliath* Jiménez de la Espada is a synonym of *Leptodactylus pentadactylus* (Laurenti, 1768).

Leptodactylus wuchereri Jiménez de la Espada, 1875. Heyer (1969) examined the type and transferred the name from the synonymy of *L. mystacinus* to *L. pentadactylus* sensu lato. Later (Heyer, 1979:22), I placed *L. wuchereri* in the synonymy of *L. labyrinthicus.* The type specimen was collected in Argentina, somewhere between Montevideo, Uruguay and Santiago, Chile, to the south of parallel 31°S, passing through the known distribution of *L. labyrinthicus* in Misiones and northern Corrientes Provinces, Argentina (De la Riva, 2000). *Leptodactylus wuchereri* is considered to be a synonym of *L. labyrinthicus* (Spix, 1824). De la Riva (2000) suggested that *L. wuchereri* could either be a synonym of *L. labyrinthicus* or *L. mystacinus,* based on the itinerary of Sr. Amor, the collector of the type of *L. wuchereri,* and thus needed further evaluation. Based on examination of the holotype and previous discussion (Heyer, 1969), the holotype could refer only to *L. labyrinthicus* in Argentina and specifically not to *L. mystacinus.*

Leptodactylus bufo Andersson, 1911. Heyer (1979:15) indicated that the name was a synonym of *Leptodactylus labyrinthicus.* The type locality (Ponta Grossa, Paraná, Brazil) is closest geographically to the Area F *L. labyrinthicus* Unit as analyzed in this paper. *Leptodactylus bufo* Andersson is herein considered to be a synonym of *Leptodactylus labyrinthicus* (Spix, 1824).

Leptodactylus macroblepharus Miranda-Ribeiro, 1926. Heyer (1979:16) indicated that the type represented the Amazonian *L. pentadactylus* Unit as defined in this paper. Hence, *L. macroblepharus* Miranda-Ribeiro is a synonym of *L. pentadactylus* (Laurenti, 1768).

Heyer (1979:16) incorrectly stated that MZUSP 377 was the holotype of *L. macroblepharus.* Miranda-Ribeiro described the species based on three specimens, which were given the same museum catalogue number. There were actually four specimens that bore MZUSP number 377. Three of the specimens were recatalogued. I examined the specimens in January 2003. The specimen that retains MZUSP 377 is a 114 mm SVL adult male with testes in the body cavity, but the other internal organs are removed. MZUSP 56719 is a 46 mm SVL juvenile with all internal organs removed; MZUSP 56720 is a 96 mm SVL male with all internal organs removed; MZUSP 56721 is a 72 mm SVL juvenile with all internal organs removed. The specimen that retains MZUSP 377 is without doubt the specimen that Miranda-Ribeiro described. MZUSP 377 is hereby designated as the lectotype of *Leptodactylus macroblepharus* Miranda-Ribeiro.

Leptodactylus vastus A. Lutz, 1930. Heyer (1979:16) indicated that this name applies to the Area G+H *L. labyrinthicus* Unit as defined in this paper. Hence, *L. vastus* A. Lutz is the oldest available name for the Area G+H *L. labyrinthicus* Unit species.

Adolpho Lutz (1930) proposed the name *vastus* for three specimens that he had previously reported and figured (as *L. ? gigas*) from Independencia (= Guarabira), Paraíba, Brazil (A. Lutz, 1926). When the Adolpho Lutz collection was transferred from the Instituto Oswaldo Cruz to the Museu Nacional collection, there was but a single specimen labeled as the type of *L. vastus,* AL-MN 70 (Ulisses Caramaschi, pers. comm.). This specimen, a 170 mm SVL adult male, is hereby designated as the lectotype of *L. vastus* A. Lutz.

Leptodactylus pentadactylus dengleri Melin, 1941. Heyer (1979:16) indicated the type from Amazonian Peru belonged to the Amazonian *L. pentadactylus* Unit as defined in this paper. Taylor (1952:649-650) concluded that his Costa Rican materials best matched the description Melin provided for *L. pentadactylus dengleri* and used that name for the Costa Rican materials he examined. The attribution of Middle American specimens to *L. pentadactylus dengleri,* following Taylor, has been used by certain other authors, most notably Cei and collaborators in a series of papers on skin secretion biochemistry (e.g., Erspamer *et al.*, 1964). *Leptodactylus pentadactylus dengleri* Melin is herein considered to be a synonym of *L. pentadactylus* (Laurenti, 1768).

Melin based his description on two specimens. No museum numbers were given for either specimen and there is no indication in the description that Melin designated one of the specimens as the holotype. I previously (Heyer, 1979:16) designated the larger of the two specimens as the lectotype. At the time I made that designation, I had not communicated with the curatorial staff at the GNM. I recently asked Dr. Göran Nilson if he could provide the GNM number for the lectotype. Dr. Nilson responded in an e-mail message of 4 September 2003: "The two types of *Leptodactylus pentadactylus dengleri* have the museum numbers GNM Ba.ex. 496 (the smaller specimen, which is the 'type' according to the original label, and listed as holotype in our museum catalogue) and GNM Ba.ex. 497 (the bigger specimen, not listed as 'type' on the original label)." In retrospect, it would have been more appropriate to designate the smaller specimen as the lectotype, as that seemed to be Melin's intent. However, a specimen label and catalogue indication that the smaller specimen is the type does not meet the requirements of Article 74 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). Therefore, my previous designation of the larger specimen as lectotype stands.

Leptodactylus pentadactylus rubidoides Andersson, 1945. Heyer (1979:16) indicated that this name applies to the Amazonian *L. pentadactylus* Unit as defined in this paper. *Leptodactylus pentadactylus rubidoides* Andersson is thus a synonym of *L. pentadactylus* (Laurenti, 1768).

Andersson (1945:49-51) identified two individuals representing his new form *rubidoides,* the specimen he described and figured in the NRM collection and a specimen he did not personally examine described by Boulenger (1882:243) as an unusual specimen of *L. rubido* from Canelos, Ecuador. These two specimens clearly constitute the type series of *L. pentadactylus rubidoides* according to Article 72.4.1 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). I hereby designate NRM 1928 as the lectotype of *Leptodactylus pentadactylus rubidoides.*

Leptodactylus pentadactylus mattogrossensis Schmidt and Inger, 1951. Heyer (1979:16-17) indicated that this name applies to the Area B *L. labyrinthicus* Unit as analyzed in this paper. Thus, *L. pentadactylus mattogrossensis* Schmidt and Inger is a synonym of *L. labyrinthicus* (Spix, 1824).

Leptodactylus knudseni Heyer, 1972. Heyer (1979:17) indicated that this name applies to the Area B *L. knudseni* Unit as analyzed in this paper. Thus, *L. knudseni* is the oldest available name for the *L. knudseni* (Area B+C+A, D-H Units) species.

No names are available for the following Units recognized as distinct species: Pará Unit; *L. labyrinthicus* Unit A; Middle American *L. pentadactylus* Unit; West Coast Colombia (extending into adjacent Ecuador) *L. pentadactylus* Unit; and the West Coast Ecuador *L. pentadactylus* Unit. These are described as new in the following section.

Species Accounts

Dorsal patterns were not treated in the Inter-Unit analysis section. Dorsal patterns were categorized anew for inclusion in the adult characteristic sections of the species accounts. Only those character states that occur at a frequency > 5% in any species are included in the adult characteristic descriptions (Table 26).

The character states analyzed in the Inter-Unit Analysis section are included in the adult characteristic sections of the species accounts only

Table 26. Dorsal pattern characterization among species. N = number of individuals. Other values are percentages.

	L. myersi	Pará species	*L. knudseni*	*L. labyrinthicus*	*L. vastus*	Venezuela species	*L. pentadactylus*	Middle America species	West Coast Colombia + species	West Coast Ecuador species
Uniform light or dark	4	12	9	27	31	25	4	12		
Series of regularly or irregularly placed small, dark spots	2	4		32	14	11	1			
Uniform with 1 or 2 well-defined, narrow transverse bars	3		6	3	4		62	30	67	31
Well developed dark interorbital band/chevron and 2 moderate to large equally intense dark chevrons, second chevron in sacral region, chevrons confluent or not	60	24	8	1	1	11				
More than 2 dark, broad transverse bands of equal intensity in addition to interorbital band, confluent laterally or not	6	16	37			7		1		6
Two broad dark transverse bands between interorbital bar and arm insertion area, rest of dorsum with large spots		4	0	1		25				
Irregular quadrangular or rectangular markings, of equal intensity or alternating lighter/darker, confluent laterally or not	3	4	39				31	55	33	62
Broad, irregular, dark longitudinal band			0				1	1		
Series of regularly spaced, well-defined small blotches	17									
Series of irregularly spaced, fuzzy small blotches	2	8		15	17					
Single broad dark chevron posterior to interorbital bar followed by series of fairly regularly spaced large dark spots		32	0	21	31	18				
Dark with light interorbital bar and scattered, irregular light marks	4									
Variegated						4	1	1		
N	106	25	186	104	70	28	140	93	15	16

if they occur at frequencies > 5% in any species. Pattern data are based on both juveniles and adults; measurement data, unless otherwise noted, are based on adults only. Use of the word "usually" means the state involved occurs in more than 50% of the sample; "often" means an occurrence from 10-50%; and "rare" an occurrence of less than 10%.

The larval materials examined for this study were those in the USNM collection, none of which can be unambiguously associated with adults. For this reason, only published larval information is summarized in the following species accounts.

There are virtually no morphological or advertisement call character states that will consistently diagnose adults of all the taxa in this study. To attempt to diagnose a given species from all others would result in very long statements that would defeat the purpose of a diagnosis. The approach taken here is to limit the diagnoses to taxa that occur in the same geographic areas and major habitat types and/or that are most similar to each other and most likely to be confused.

Measurement data were evaluated for sexual dimorphism using the separate variance t-test in SYSTAT 10 (Anonymous, 2000). The ratio variables were arcsine transformed prior to evaluation with t-tests. A *P*-value of 0.05 or less is considered significant. Initial sample sizes pertain for all variables unless specified otherwise. Mean values are indicated by the letter "m."

Leptodactylus knudseni Heyer, 1972

Leptodactylus knudseni Heyer, 1972:3. Type locality: Limoncocha, Napo, Ecuador, 00°25'S, 76°38'W. Holotype: LACM 72117, juvenile female.

Suggested English name – Knudsen's thin-toed frog.

Suggested Portuguese name – Rã-de-dedos-delgados-de-Knudsen.

Suggested Spanish name – *Rana de dedos delgados de Knudsen.*

Diagnosis – *Leptodactylus knudseni* has a broad Amazonian distribution, occurring in the same general areas as *L. labyrinthicus, L. myersi, L. paraensis,* and *L. pentadactylus.* Juvenile *L. knudseni* often have green dorsal coloration in life and solid black posterior thighs; juvenile *L. labyrinthicus, L. myersi, L. paraensis,* and *L. pentadactylus* are not green in life nor do they have solid black posterior thigh patterns. The advertisement calls of *L. knudseni* are pulsed, the advertisement calls of *L. labyrinthicus* are not pulsed. The dorsolateral folds of *L. knudseni* are usually entire, the dorsolateral folds in *L. paraensis* are interrupted and are often interrupted in *L. labyrinthicus.* Large, sexually active male *L. knudseni* have a pair of chest spines; chest spines are lacking in *L. myersi* and *L. pentadactylus.*

Adult Characteristics – Lip pattern usually with dark triangular marks, 1 or 2 elongate, approaching or entering lower eye (Figure 12A). Lip pattern often of dark triangular marks on edge of upper lip only. Lip pattern rarely uniform light; or dark elongate triangular marks on lip edge, fading towards eye, 2 dark marks under eye; or dark with 2 narrow light chevrons from lip entering eye (Figure 12B); or alternating broad light bands and narrow dark vertical stripes, 1-3 dark stripes entering eye (Figure 12C); or broad irregular darker and lighter bands, 2 dark bands entering eye (Figure 12D); or uniform dark.

Dorsal pattern often with more than 2 dark, broad transverse bands of equal intensity in addition to interorbital band, confluent laterally or not; or irregular quadrangular or rectangular markings, of equal or alternating lighter/darker intensity, confluent laterally or not. Dorsal pattern rarely uniform light; or uniform with 1 or 2 well-defined, narrow transverse bands; or well developed dark interorbital band/chevron and 2 moderate to large equally intense dark chevrons, second chevron in sacral region, chevrons confluent or not; or 2 broad dark transverse bands between interorbital bar and arm insertion area, rest of dorsum with large spots; or dorsum with single broad dark chevron posterior to interorbital bar followed by a series of fairly regularly spaced large dark spots.

Belly pattern often light (no pattern); or mottled (Figure 13A) or uniform dark; or dark with small light vermiculations (Figure 13B); or dark with small light discrete spots. Belly pattern rarely with lateral and anterior mottling only; or dark with large light vermiculations (Figure 13C); or light with dark vermiculations; or labyrinthine (Figure 13D); or dark with large light discrete spots (Figure 13E).

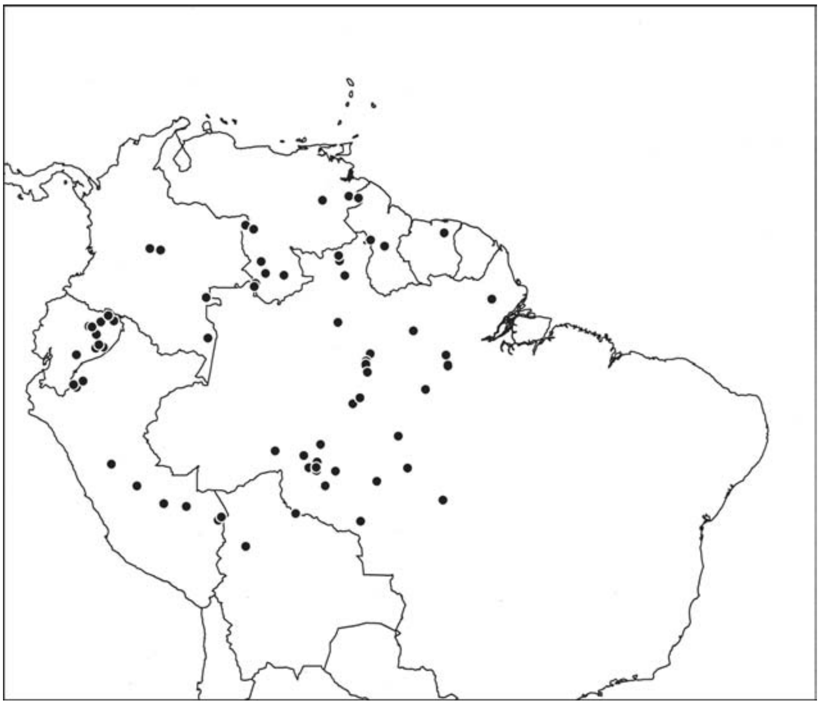

Figure 15. Distribution map for *Leptodactylus knudseni.*

Posterior thigh pattern often distinctly uniform dark; or dark with small distinct light vermiculations or spots (Figure 14A); or dark with large distinct light vermiculations, some coalescing of vermiculations; or dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B). Thigh rarely relatively uniform dark or indistinctly mottled; or labyrinthine; or dark with distinct, discrete light spots; or very dark, irregular blotches highlighted by light pin-stripe on dark background (Figure 14C); or mostly very distinctly light with few irregular dark marks (Figure 14D).

Dorsolateral folds usually entire from at least 1/4 to full distance from eye to sacrum. Dorsolateral folds often interrupted from at least 1/2 to full distance from eye to sacrum. Dorsolateral folds rarely entire to at least between sacrum and some distance to groin.

Flank folds usually a dark spot/wart in area where fold would be between tympanum and shoulder. Flank folds often absent. Flank folds rarely entire from tympanum to shoulder; or interrupted from tympanum to lower flank; or entire from tympanum to lower flank.

Male thumb usually with 1 large spine. Male thumb often with 1 tiny to small spine; or 1 large spine and a prepollical bump.

Large breeding males with chest spines.

Female (N = 37) SVL 102.7-154.0 mm (m = 132.0), male (N = 78) SVL 94.0-170.0 mm (m = 131.4), not sexually dimorphic (t = 0.253, df = 104.4, P = 0.801). Female head length/SVL ratio 0.32-0.46 (m = 0.354), male head length/SVL ratio 0.32-0.40 (m = 0.357), not sexually dimorphic (t = -0.724, df = 55.3, P = 0.472). Female head width/SVL ratio 0.34-0.42 (m = 0.371), male head width/SVL ratio 0.34-0.44 (m = 0.380), sexually dimorphic (t = -2.832, df = 90.6, P = 0.006). Female eye-nostril distance/SVL ratio 0.08-0.11 (m = 0.093), male eye-nostril distance/SVL ratio 0.08-0.10 (m = 0.094), not sexually dimorphic (t = -0.832, df = 63.2, P = 0.409). Female (N = 32) tympanum diameter/SVL ratio 0.06-0.09 (m = 0.072), male (N = 77) tympanum diameter/SVL ratio 0.05-0.08 (m = 0.071), not sexually dimorphic (t = 0.890, df = 57.7, P = 0.377). Female thigh/SVL ratio 0.35-0.45 (m = 0.405), male thigh/SVL ratio 0.35-0.46 (m = 0.414), not sexually dimorphic (t = -1.780, df = 67.3, P = 0.080). Female shank/SVL ratio 0.38-0.46 (m = 0.419), male shank/SVL ratio 0.38-0.48 (m = 0.424), not sexually dimorphic (t = -1.368, df = 80.9, P = 0.175). Female foot/SVL ratio 0.40-0.50 (m = 0.444), male (N = 76) foot/SVL ratio 0.38-0.51 (m = 0.444), not sexually dimorphic (t = -0.050, df = 73.8, P = 0.960).

Larvae – At least the later stage larvae live and feed in streamside and isolated forest ponds in the central Amazon (Hero, 1990). Larvae elongate; spiracle sinistral; vent median; oral disk entire, almost terminal, with single row of marginal papillae with broad anterior gap; tooth row formula 2(2)/2-3(1); maximum total length, stage 40, 69 mm (Hero, 1990).

Advertisement Call – Calls of single notes, given at rates of 16-66 calls/min; call duration 0.16-0.43 s; calls pulsed, 6-14 pulses/call, mean pulse rates among individuals 26-38 pulses/s; call frequency modulated, rising whoop, mean initial frequency among individuals 260-540 Hz; dominant frequency 340-690 Hz (Table 6, Figures 5, 6).

Karyotype – Diploid number 22, fundamental number 44, commonly with 3 pairs of metacentrics, 4 pairs of submetacentrics, and 4 pairs of subtelocentrics (Heyer, 1972).

Habitat and Distribution – *Leptodactylus knudseni* occurs in primary rain forest, secondary forests, and open habitats throughout the Amazonian Morphoclimatic Domain as defined by Ab'Sáber (1977) (Appendix, Figure 15).

Leptodactylus labyrinthicus (Spix, 1824)

Rana labyrinthica Spix, 1824:31. Type locality: Rio de Janeiro (State), Brazil. Holotype: ZSM 2501/0, lost (Hoogmoed and Gruber, 1983).

Leptodactylus wuchereri Jiménez de la Espada, 1875:68. Type locality: "Republica Argentina," somewhere between Montevideo, Uruguay and Santiago, Chile. Holotype: MNCN 1694, juvenile.

Leptodactylus bufo Andersson, 1911:1. Type locality: "Ponta Grossa, Paraná, Brazil," 25°06'S, 50°10'W. Holotype: NRM 1495, male.

Leptodactylus pentadactylus mattogrossensis Schmidt and Inger, 1951:444. Type locality: "Urucum de Corumba, Matto Grosso, Brazil," (locality now in Mato Grosso do Sul) 19°10'S, 57°39'W. Holotype: FMNH 9240, adult female.

English name – Pepper frog.

Portuguese name – Rã-pimenta.

Spanish name – Rana pimienta.

Diagnosis – *Leptodactylus labyrinthicus* occurs in open formation habitats, including cerrado enclaves in Amazonia. The species most likely to be confused with *L. labyrinthicus* are *L. knudseni, L. paraensis,* and *L. vastus*. Most adult *L. labyrinthicus* have a distinctive labyrinthine belly pattern; adult *L. knudseni* lack this pattern. The advertisement call of *L. labyrinthicus* is unpulsed; the advertisement call of *L. knudseni* is pulsed. *Leptodactylus paraensis* is documented only from closed canopy rain forest. There is no consistent morphological feature that completely diagnoses *L. labyrinthicus* from *L. paraensis*. *Leptodactylus labyrinthicus* is somewhat larger (males 117-188 mm SVL, females 124-166 mm SVL) than *L. paraensis* (males 94-170 mm SVL, females 102-154 mm SVL).

Adult Characteristics – Lip pattern often dark elongate triangular marks on lip edge, fading towards eye, 2 dark marks under eye; or broad irregular darker and lighter bands, 2 dark bands entering eye (Figure 12D). Lip pattern rarely uniform light; or dark triangular marks on edge of upper lip only; or dark triangular marks, 1 or 2 elongate approaching or entering lower eye (Figure 12A); or dark with two narrow light chevrons from lip entering eye (Figure 12B); or alternating broad light bands and narrow dark vertical stripes, 1-3 dark stripes entering eye (Figure 12C).

Dorsal pattern often uniform light or dark; or with a series of regularly or irregularly placed small, dark spots; or with series of irregularly spaced, ill-defined small blotches; or with single broad dark chevron posterior to interorbital bar followed by a series of fairly regularly spaced large dark spots. Dorsal pattern rarely uniform light with 1-2 well-defined, narrow transverse bands; or well developed dark interorbital band/chevron and 2 moderate to large equally intense dark chevrons, second chevron in sacral region, chevrons confluent or not; or two broad dark transverse bands between interorbital bar and arm insertion area, rest of dorsum with large spots.

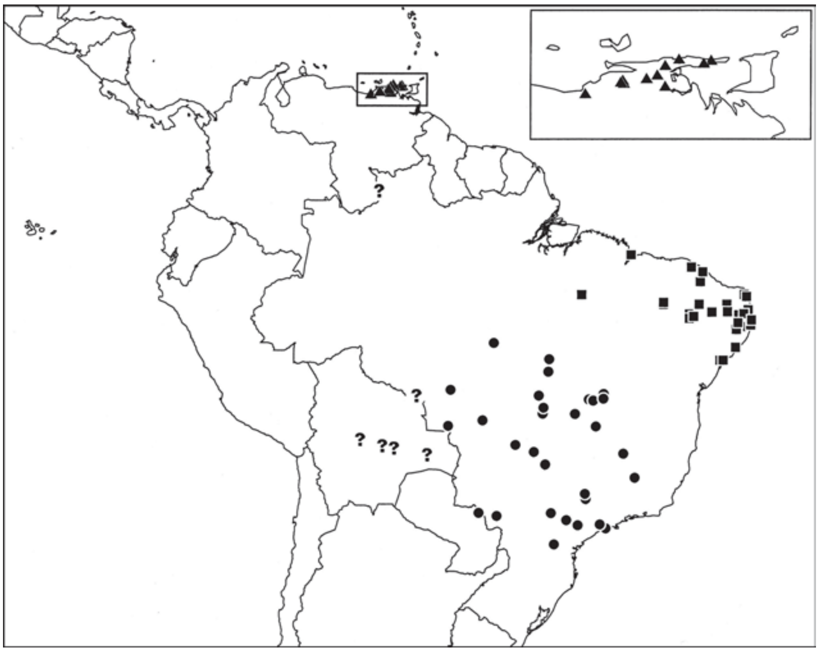

Figure 16. Distribution map for *Leptodactylus labyrinthicus* (dots), *L. turimiquensis* (triangles), and *L. vastus* (squares). Question marks indicate specimen localities from which individuals are currently unidentifiable to species.

Belly usually labyrinthine (Figure 13D). Belly often light with dark vermiculations. Belly rarely light (no pattern); or with lateral and anterior mottling only; or mottled (Figure 13A) or uniform dark; or dark with large light vermiculations (Figure 13C).

Posterior thigh pattern usually dark with large light vermiculations, some coalescing of vermiculations. Thigh often dark with small distinct light vermiculations or spots (Figure 14A); or mostly very distinctly light with few irregular dark marks (Figure 14D). Thigh rarely dark with distinct, discrete light spots; or dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B).

Dorsolateral folds usually interrupted from at least 1/2 to full distance from eye to sacrum. Dorsolateral folds often interrupted from at least 1/4 distance to 1/2 distance from eye to sacrum. Dorsolateral folds rarely absent; or entire from at least 1/4 to full distance from eye to sacrum; or interrupted to at least between sacrum and some distance to groin.

Flank folds usually with dark spot/wart in area where fold would be between tympanum and shoulder. Flank folds often absent. Flank folds rarely interrupted from tympanum to lower flank; or entire from tympanum to lower flank.

Male thumb usually with one large spine. Male thumb often with one tiny to small spine. Male thumb rarely with one large spine and a prepollical bump.

Large breeding males with chest spines.

Female (N = 16) SVL 124.0-166.0 mm (m = 141.6), male (N = 40) SVL 117.1-188.0 mm (m = 149.6), not sexually dimorphic (t = -1.892, df = 42.6, P = 0.065). Female head length/SVL ratio 0.34-0.39 (m = 0.364), male head length/SVL ratio 0.33-0.40 (m = 0.369), not sexually dimorphic (t = -1.062, df = 25.9, P = 0.298. Female head width/SVL ratio 0.36-0.45 (m = 0.389), male head width/SVL ratio 0.35-0.45 (m = 0.392), not sexually dimorphic (t = -0.480, df = 24.8, P = 0.635). Female eye-nostril distance/SVL ratio 0.08-0.10 (m = 0.90), male eye-nostril distance/SVL ratio 0.08-0.10 (m = 0.091), not sexually dimorphic (t = -0.828, df = 40.0, P = 0.412). Female tympanum diameter/SVL ratio 0.06-0.08 (m = 0.069), male tympanum diameter/SVL ratio

0.06-0.08 (m = 0.070), not sexually dimorphic (t = -0.328, df = 30.8, P = 0.745). Female thigh/SVL ratio 0.40-0.47 (m = 0.435), male thigh/SVL ratio 0.33-0.48 (m = 0.425), not sexually dimorphic (t = 1.395, df = 44.5, P = 0.170). Female shank/SVL ratio 0.40-0.47 (m = 0.438), male shank/SVL ratio 0.39-0.48 (m = 0.436), not sexually dimorphic (t = 0.292, df = 32.9, P = 0.772). Female foot/SVL ratio 0.39-0.47 (m = 0.434), male (N = 39) foot/SVL ratio 0.39-0.50 (m = 0.439), not sexually dimorphic (t = -0.636, df = 34.1, P = 0.529).

Larvae – Larvae occur in temporary ponds. Larvae elongate; spiracle sinistral; vent median; oral disk almost terminal, entire, with single row of marginal papillae with broad anterior gap; tooth row formula 1/2(1); maximum total length stage 40, 80 mm (Vizotto, 1967).

Advertisement Call – Calls of single notes, given at rates of 35-50 calls/min; call duration 0.14-0.21 s; calls unpulsed; call frequency modulated, rising whoop, mean initial frequency among individuals 258-292 Hz; dominant frequency about 430 Hz (Table 19, Figure 11A).

Karyotype – Diploid number 22, 3 pairs of metacentrics, 4 pairs of submetacentrics, and 4 pairs of small metacentrics or submetacentrics; nucleolus organizer region on short arms of chromosome pair 8 (Denaro, 1972; Silva *et al.*, 2000).

Habitat and Distribution – *Leptodactylus labyrinthicus* occurs in subtropical and tropical open formations, including much of the Cerrado Morphoclimatic Domain as defined by Ab'Sáber (1977) and cerrado-like enclaves in tropical rain forests. The species occurrence suggests that it is a good colonizer of man-made open habitats in formerly closed-forest habitats (Appendix, Figure 16).

Leptodactylus myersi Heyer, 1995

Leptodactylus myersi Heyer, 1995:712. Type locality: Mucajaí, Roraima, Brazil, 2°25'N, 60°55'W. Holotype: MZUSP 66089, male.

Suggested English name – Myers' thin-toed frog.

Suggested Portuguese name – Rã-de-dedos-delgados-de-Myers.

Suggested Spanish name – Rana de dedos delgados de Myers.

Diagnosis – *Leptodactylus myersi* is most likely to be confused with *L. knudseni. Leptodactylus myersi* occurs in the same geographic region as *L. knudseni,* but *L. myersi* is typically limited to rocky outcrops and *L. knudseni* is not. Large reproductively active males of *L. myersi* lack chest spines; such males of *L. knudseni* have chest spines. Juvenile *L. myersi* have brilliant red on their venters and posterior thigh surfaces; juvenile *L. knudseni* do not have such red coloration, but often have obvious dorsal green coloration not found in *L. myersi.*

Adult Characteristics – Lip pattern often with dark triangular marks on edge of upper lip only; or dark triangular marks, 1 or 2 elongate approaching or entering lower eye (Figure 12A); or dark elongate triangular marks on lip edge, fading towards eye, 2 dark marks under eye; or broad irregular darker and lighter bands, 2 dark bands entering eye (Figure 12D); or broad light stripe, regular above, regularly or irregularly defined below (Figure 12E). Lip pattern rarely uniform light; or dark with two narrow light chevrons from lip entering eye (Figure 12B).

Dorsal pattern usually with well developed dark interorbital band/chevron and 2 moderate to large equally intense dark chevrons, second chevron in sacral region, chevrons confluent or not. Dorsal pattern often with series of regularly spaced, well-defined small blotches. Dorsal pattern rarely uniform light or dark; or with a series of regularly or irregularly placed small, dark spots; or uniform light with 1 or 2 well-defined, narrow transverse bands; or more than 2 dark, broad transverse bands of equal intensity in addition to interorbital band, confluent laterally or not; or with irregular quadrangular or rectangular markings, of equal or alternating lighter/darker intensity, confluent laterally or not; or with series of irregularly spaced, ill-defined small blotches.

Belly pattern often dark with small light vermiculations (Figure 13B); or dark with large light vermiculations (Figure 13C); or dark with small light discrete spots. Belly pattern rarely light (no pattern); or with lateral and anterior mottling only; or mottled (Figure 13A) or uniformly dark.

Posterior thigh pattern usually dark with contrasting large, light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with

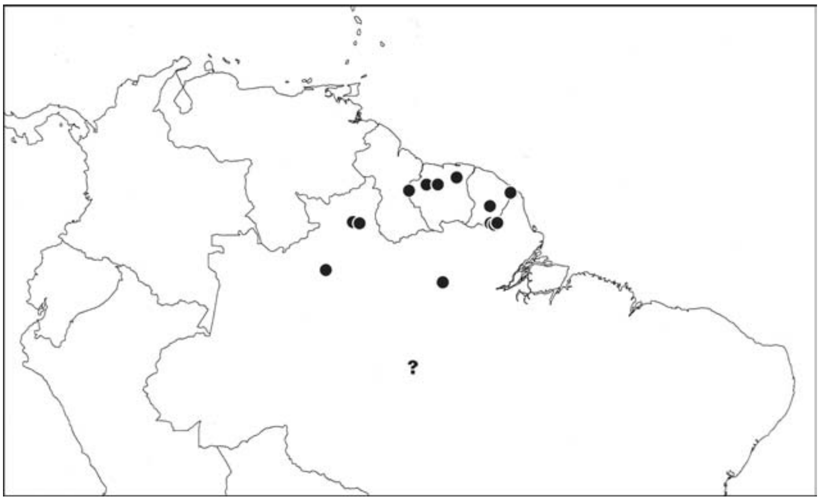

Figure 17. Distribution map for *Leptodactylus myersi* (dots) and MZUSP 24947-24948 (question mark), currently unidentifiable to species.

light vermiculations (Figure 14B). Thigh rarely distinctly uniform dark; or relatively uniform dark or indistinctly mottled; or dark with small distinct light vermiculations or spots (Figure 14A); or dark with large distinct light vermiculations, some coalescing of vermiculations; or labyrinthine; or dark with distinct, discrete light spots; or mostly very distinctly light with few irregular dark marks (Figure 14D).

Dorsolateral folds often absent; or interrupted from at least 1/2 to full distance from eye to sacrum; or entire from at least 1/4 to full distance from eye to sacrum; or interrupted to at least between sacrum and some distance to groin. Dorsolateral folds rarely interrupted from at least 1/4 distance to 1/2 distance from eye to sacrum; or entire to at least between sacrum and some distance to groin.

Flank folds often absent; or interrupted from tympanum to shoulder; or entire from tympanum to shoulder. Flank folds rarely entire from tympanum to lower flank.

Male thumb usually with one large spine. Male thumb rarely with one tiny to small spine.

Large breeding males without chest spines.

Female (N = 5) SVL 78.9-112.9 mm (m = 103.2), male (N = 20) SVL 74.2-123.4 mm (m = 101.0), not sexually dimorphic (t = 0.298, df = 6.9, P = 0.774). Female head length/SVL ratio 0.37-0.38 (m = 0.378), male head length/SVL ratio 0.33-0.40 (m = 0.376), not sexually dimorphic (t = 0.431, df = 20.0, P = 0.671). Female head width/SVL ratio 0.39-0.42 (m = 0.401), male head width/SVL ratio 0.36-0.44 (m = 0.399), not sexually dimorphic (t = 0.181, df = 12.8, P = 0.859). Female eye-nostril distance/SVL ratio 0.07-0.09 (m = 0.087), male eye-nostril distance/SVL ratio 0.07-0.10 (m = 0.091), not sexually dimorphic (t = -1.049, df = 5.5, P = 0.338). Female (N = 4) tympanum diameter/SVL ratio 0.07-0.08 (m = 0.077), male (N = 14) tympanum diameter/SVL ratio 0.07-0.09 (m = 0.077), not sexually dimorphic (t = -0.168, df = 4.8, P = 0.874). Female thigh/SVL ratio 0.43-0.46 (m = 0.441), male (N = 16) thigh/SVL ratio 0.40-0.45 (m = 0.431), not sexually dimorphic (t = 1.864, df = 9.2, P = 0.095). Female shank/SVL ratio 0.41-0.44 (m = 0.424), male (N = 16) shank/SVL ratio 0.38-0.44 (m = 0.413), not sexually dimorphic (t = 1.502, df = 6.8, P = 0.178). Female foot/SVL ratio 0.42-0.47 (m = 0.444), male (N = 16) foot/SVL ratio 0.40-0.48 (m = 0.438), not sexually dimorphic (t = 0.621, df = 6.8, P = 0.555).

Larvae – Unknown.

Advertisement Call – Calls of single notes, given at a rate of 36 calls/min; call duration 0.33-0.36 s; calls pulsed, 2-3 pulses/call, pulse rates 5-9 pulses/s; call frequency modulated, rising whoop, initial frequency about 190 Hz, dominant frequency 600-690 Hz (data from compact disk recording, Guide Sonore des Amphibiens Anoures de Guyane by C. Marty and P. Gaucher).

Karyotype – Unknown.

Habitat and Distribution – *Leptodactylus myersi* is restricted to rocky outcrop habitats in French Guiana, Suriname, and northern Brazil (Acre, Pará, Roraima) (Appendix, Figure 17).

Leptodactylus paraensis sp. nov.

Figure 18

Holotype. – MZUSP 69321, an adult male from Brazil; Pará, Serra de Kukoinhokren, 07°46'S, 51°57'W. Collected by Miguel T. Rodrigues and Barbara Zimmerman on 17 November 1992.

Paratopotypes. – MZUSP 69318, 69320, 69322, USNM 559809 (one female and three males respectively), collected by Miguel T. Rodrigues and Barbara Zimmerman on 17 November 1992; 70365 (juvenile), collected by Andrew A. Chek on 1 December 1993; MZUSP 70549 (female), collected by Miguel T. Rodrigues on 2 November 1994; MZUSP 70918 (juvenile), collected by Andrew A. Chek, 22 February – 12 March 1995.

Suggested English name – Pará thin-toed frog.

Suggested Portuguese name – Rã-de-dedos-delgados-do-Pará.

Suggested Spanish name – Rana de dedos delgados de Pará.

Diagnosis – *Leptodactylus paraensis* has an eastern Amazonian distribution, occurring in the same general region with *L. knudseni, L. myersi,* and *L. pentadactylus. Leptodactylus paraensis* is morphologically most similar to *L. labyrinthicus, L. turimiquensis,* and *L. vastus,* of which only *L. labyrinthicus* has a possibly overlapping distribution. The only habitat data for *L. paraensis* indicate that the species is limited to primary rain forests as is *L. pentadactylus,* whereas *L. labyrinthicus* is only found in open formations and *L. myersi* is restricted to rocky outcrops. The dorsolateral folds in *L. paraensis* are interrupted and extend no further from the eye than to the sacrum; the dorsolateral folds of *L. pentadactylus* are either continuous or, if interrupted, extend beyond the sacrum. Large, sexually active male *L. paraensis* have a pair of black chest spines; *L. myersi* lacks chest spines. *Leptodactylus paraensis* is smaller (males 99-129 mm SVL,

Figure 18. Holotype of *Leptodactylus paraensis* sp. nov.

females 110-140 mm SVL) than both *L. knudseni* (males 94-170 mm SVL, females 102-154 mm SVL) and *L. labyrinthicus* (males 117-188 mm SVL, females 124-166 mm SVL). Most *L. knudseni* have continuous dorsolateral folds. Juvenile *L. paraensis* do not have any green color in life; juvenile *L. knudseni* often have green color in life on the dorsum.

Description of Holotype – Snout nearly rounded in dorsal and profile views. Canthus rostralis indistinct. Loreal obtusely weakly concave. Tympanum distinct, greatest diameter about 7/8 eye diameter. Vomerine teeth in 2 strongly arched series, between and extending posterior to choanae, narrowly separated medially. Vocal slits elongate, parallel to lower jaw. Vocal sac not visible externally. Finger lengths in increasing order II < IV < I < III. Inner surfaces of fingers II and III strongly ridged, otherwise fingers smooth. Metacarpal tubercles large; inner triangular-rounded, almost as large as cordiform outer tubercle. Arms hypertrophied. Each thumb with 1 large sharp black spine. One pair of well-developed black chest spines, each with 3-4 cusps. Throat, chest, ventral arm surfaces, and anterior belly with many small black tubercles. Dorsum with scattered pustules, often capped with a small tubercle. Tympanic fold well-developed from eye to posterior 1/2 of vertical diameter of tympanum, then weakly developed to above arm insertion area. Two very short ridges, 1 behind eye, 1 above arm insertion area in dorsolateral fold field. Lateral fold weak, interrupted. No flank fold. Flanks glandular appearing. Venter smooth except for small tubercles described above and ventral-posterior thigh surfaces granular. Belly disk fold only weakly defined posteriorly. Toe tips rounded or very slightly swollen. Toes with very weak ridges on inner sides of toes I and II, otherwise smooth. Subarticular tubercles moderately pungent, ovoid. Outer metatarsal tubercle ovoid, about 2/3 size of ovoid inner metatarsal tubercle. Tarsal fold well-developed, straight, extending about 3/4 length of tarsus. No metatarsal fold. Upper shank with a few scattered pustules. Outer tarsus with a few scattered light spots, but spots not raised into distinct tubercles. Sole of foot with 3 low, rounded whitish tubercles.

Upper lip with 3 dark triangular marks, fading dorsally, middle mark extending to anterior portion of lower eye. Dorsum with light tan interorbital bar followed by darker, broader brownish-gray interorbital band; elongate transverse dark brownish-gray spot above arm insertion area followed by series of large irregular brownish-gray spots on a lighter background, pattern most distinct past sacrum. Flanks coarsely marbled. Upper arms with indistinct cross-bands, upper legs with well-defined, regular dark cross bands. Throat dark with indistinct lighter marks. Chest finely mottled. Anterior belly with large light vermiculations on a slightly darker background, posterior belly with faint but distinct labyrinthine pattern. Ventral limb surfaces with indistinct bold mottling, most distinct on distal portions of thighs. Posterior thigh surfaces dark with scattered light vermiculations, some light vermiculations extending from dark dorsal transverse bands.

Measurements (mm): SVL 128.7, head length 48.1, head width 49.9, eye-nostril distance 11.6, greatest tympanum diameter 9.6, thigh length 56.8, shank length 54.0, foot length 55.2.

Adult Characteristics – Lip pattern often with 1 or 2 dark elongate triangular marks approaching or entering the lower eye (Figure 12A); or dark elongate triangular marks on lip edge, fading towards eye, 2 dark marks under eye; or dark with two narrow light chevrons from lip entering eye (Figure 12B). Lip pattern rarely patternless; or alternating broad light bands and narrow dark vertical stripes, 1-3 dark stripes entering eye (Figure 12C); or broad light stripe, regular above, regularly or irregularly defined below (Figure 12E).

Dorsal pattern often uniform light or dark; or well developed dark interorbital band/chevron and 2 moderate to large equally intense dark chevrons, second chevron in sacral region, chevrons confluent or not; or more than 2 dark, broad transverse bands of equal intensity in addition to interorbital band, confluent laterally or not; or single broad dark chevron posterior to interorbital bar followed by a series of fairly regularly spaced large dark spots. Dorsal pattern rarely with series of regularly or irregularly placed small, dark spots; or 2 broad dark transverse bands between interorbital bar and arm insertion area, rest of dorsum with large spots; or irregular quadrangular or rectangular markings, of equal or alternating lighter/darker intensity, confluent laterally or not; or series of irregularly spaced, ill-defined small blotches.

Belly pattern often mottled (Figure 13A) or uniform dark; or dark with small light vermiculations (Figure

13B); or dark with large light vermiculations (Figure 13C); or labyrinthine (Figure 13D). Belly pattern rarely light with dark vermiculations; or dark with small light discrete spots.

Posterior thigh pattern usually dark with small distinct light vermiculations or spots (Figure 14A). Thigh pattern often dark with large distinct light vermiculations, some coalescing of vermiculations; or dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B). Thigh rarely relatively uniform dark or indistinctly mottled.

Dorsolateral folds usually interrupted from at least 1/2 to full distance from eye to sacrum. Dorsolateral folds often interrupted from at least 1/4 to 1/2 distance from eye to sacrum. Dorsolateral folds rarely interrupted or entire to 1/4 distance from eye to sacrum.

Flank folds often absent; or dark spot/wart in area where fold would be between tympanum and shoulder; or interrupted from tympanum to shoulder.

Male thumb usually with 1 large spine. Male thumb rarely with 1 tiny to small spine.

Large breeding males with chest spines.

Female (N = 7) SVL 110.8-139.8 mm (m = 126.6), male (N = 12) SVL 99.1-128.7 (m = 117.3), not sexually dimorphic (t = 1.986, df = 10.9, P = 0.073). Female head length/SVL ratio 0.36-0.39 (m = 0.373), male head length/SVL ratio 0.35-0.40 (m = 0.379), not sexually dimorphic (t = -0.925, df = 16.8, P = 0.368). Female head width/SVL ratio 0.36-0.40 (m = 0.378), male head width/SVL ratio 0.37-0.47 (m = 0.398), sexually dimorphic (t = -2.213, df = 16.7, P = 0.041). Female eye-nostril distance/SVL ratio 0.08-0.09 (m = 0.088), male eye-nostril distance/SVL ratio 0.08-0.10 (m = 0.91), not sexually dimorphic (t = -0.895, df = 10.6, P = 0.391). Female tympanum diameter/SVL ratio 0.07-0.08 (m = 0.072), male tympanum diameter/SVL ratio 0.06-0.08 (m = 0.074), not sexually dimorphic (t = -1.042, df = 16.9, P = 0.312). Female thigh/SVL ratio 0.39-0.46 (m = 0.414), male thigh/SVL ratio 0.37-0.46 (m = 0.418), not sexually dimorphic (t = -0.376, df = 13.7, P = 0.713). Female shank/SVL ratio 0.40-0.45 (m = 0.418), male shank/SVL ratio 0.39-0.45 (m = 0.424), not sexually dimorphic (t = -0.755, df = 13.0, P = 0.463). Female foot/SVL ratio 0.40-0.47 (m = 0.432), male foot/SVL ratio 0.42-0.49 (m = 0.445), not sexually dimorphic (t = -1.108, df = 10.3, P = 0.293).

Etymology – The species is named after the Brazilian State of Pará, from which all known specimens occur.

Larvae – Unknown.

Advertisement Call – Unknown.

Karyotype – Unknown.

Habitat and Distribution – *Leptodactylus paraensis* is known only from rain forest habitats in eastern Amazonia in the Brazilian State of Pará (Appendix, Figure 1).

Leptodactylus pentadactylus (Laurenti, 1768)

Rana pentadactyla Laurenti, 1768:32. Type locality: "Indiis," corrected to Suriname by Müller (1927:276). Neotype: RMNH 29559, adult male.

Rana gigas Spix, 1824:25. Type locality: "in locis paludosis fluminis Amazonum," Brazil. Type: ZSM 89/1921, now destroyed (Frost, 2002).

Rana coriacea Spix, 1824:29. Type locality: "aquis lacustribus fluvii Amazonum," Brazil. Type: ZSM 2502/0, now destroyed (Frost, 2002).

Leptodactylus goliath Jiménez de la Espada, 1875:57. Type locality: "Archidona (Oriente del Ecuador)," 00°55'S, 77°48'W. Lectotype: MNCN 1691, adult female.

Leptodactylus macroblepharus Miranda Ribeiro, 1926:144. Type locality: "Manáos – Amazonas," Brazil, 03°04'S, 60°00'W. Lectotype: MZUSP 377, adult male.

Leptodactylus pentadactylus dengleri Melin, 1941:51. Type locality: "Roque, Peru," 06°24'S, 76°48'W. Lectotype: GNM 497.

Leptodactylus pentadactylus rubidoides Andersson, 1945:47. Type locality: "Rio Pastaza," Ecuador. Holotype: NRM 1928, juvenile female.

English name – Smoky jungle frog.

Portuguese name – Rã-defumada-da-selva.

Spanish name – Rana ahumado de la selva.

Diagnosis – *Leptodactylus pentadactylus* has an Amazonian distribution, overlapping distributions with *L. knudseni, L. labyrinthicus, L. myersi,* and *L. paraensis*. *Leptodactylus pentadactylus* occurs in the tropical wet forests themselves; *L. labyrinthicus* occurs only in open formations (the forest canopy is not closed) within Amazonia, *L. myersi* is limited to rocky outcrops, *L. knudseni* occurs in primary rain forest, secondary forest, and open habitats, the few data for *L. paraensis* indicate that it is also limited to primary rain forest habitat. Most *L. pentadactylus* have a well-developed continuous pair of dorsolateral folds from the eye to at least the sacrum; almost no *L. labyrinthicus* and no *L. paraensis* have such extensively developed folds. Large, sexually active male *L. pentadactylus* usually do not have a large black spine on each thumb; large, sexually active male *L. knudseni, L. labyrinthicus, L. myersi,* and *L. paraensis* have a large black spine on each thumb. Large, sexually active male *L. pentadactylus* lack chest spines; large, sexually active *L. knudseni, L. labyrinthicus,* and *L. paraensis* have a pair of black chest spines.

Adult Characteristics – Lip pattern usually dark triangular marks, 1 or 2 elongate approaching or entering lower eye (Figure 12A). Lip pattern often dark triangular marks on edge of upper lip only.

Dorsal pattern usually uniform light with 1 or 2 well-defined, narrow transverse bands. Dorsal pattern often with irregular quadrangular or rectangular markings, or equal or alternating lighter/darker intensity, confluent laterally or not. Dorsal pattern rarely uniform light or dark; or with a series of regularly or irregularly placed small, dark spots.

Belly usually dark with small light vermiculations (Figure 13B). Belly often dark with large light vermiculations (Figure 13C). Belly rarely mottled (Figure 13A) or uniform dark; or light with dark reticulations; or dark with small light discrete spots; or dark with large light discrete spots (Figure 13E).

Posterior thigh pattern usually dark with small distinct light vermiculations or spots (Figure 14A). Thigh pattern often with very dark irregular blotches highlighted by light pin-stripe on dark background (Figure 14C). Thigh pattern rarely uniform dark or indistinctly mottled; or dark with large distinct light vermiculations, some coalescing of vermiculations; or labyrinthine; or dark with contrasting large, light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B).

Dorsolateral folds usually entire from eye to groin. Dorsolateral folds rarely entire from at least 1/4 to full distance from eye to sacrum; or interrupted to at least between sacrum and some distance to groin; or entire to at least between sacrum and some distance to groin.

Flank folds often entire from tympanum to shoulder; or interrupted from tympanum to lower flank; or entire from tympanum to lower flank. Flank folds rarely absent.

Male thumb usually with one tiny to small spine. Male thumb often lacking spines. Male thumb rarely with one spine.

Males lacking chest spines.

Female (N = 26) SVL 135.0-174.2 mm (m = 154.5), male (N = 26) SVL 100.2-195.0 (m = 140.8), sexually dimorphic (t = 3.081, df = 41.2, P = 0.004). Female head length/SVL ratio 0.33-0.40 (m = 0.363), male head length/SVL ratio 0.34-0.42 (m = 0.370), not sexually dimorphic (t = -1.270, df = 49.8, P = 0.210). Female head width/SVL ratio 0.36-0.42 (m = 0.394), male head width/SVL ratio 0.36-0.46 (m = 0.402), not sexually dimorphic (t = -1.421, df = 47.1, P = 0.162). Female eye-nostril distance/SVL ratio 0.08-0.10 (m = 0.090), male eye-nostril distance/SVL ratio 0.08-0.11 (m = 0.093), sexually dimorphic (t = -2.161, df = 50.0, P = 0.036). Female tympanum diameter/SVL ratio 0.06-0.07 (m = 0.064), male tympanum diameter/SVL ratio 0.06-0.08 (m = 0.067), not sexually dimorphic (t = -1.565, df = 44.3, P = 0.125). Female thigh/SVL ratio 0.38-0.48 (m = 0.435), male thigh/SVL ratio 0.37-0.50 (m = 0.436), not sexually dimorphic (t = -0.192, df = 48.1, P = 0.849). Female shank/SVL ratio 0.41-0.50 (m = 0.449), male shank/SVL ratio 0.39-0.54 (m = 0.455), not sexually dimorphic (t = -0.804, df = 46.6, P = 0.426). Female foot/SVL ratio 0.42-0.50 (m = 0.454), male foot/SVL ratio 0.42-0.55 (m = 0.459), not sexually dimorphic (t = 0.684, df = 46.4, P = 0.497).

Larvae – Tadpoles complete their development through metamorphosis in terrestrial burrows (Hero, 1990). Larvae elongate; spiracle sinistral; vent median; oral disk terminal, entire, with single row of marginal papillae with broad anterior gap; tooth row formula 1/2(1); maximum total length, stage 39, 81 mm (Hero, 1990).

Advertisement Call – Calls of single notes, given at rates of 4-37 calls/min; call duration 0.18-0.40 s; calls pulsed, 12-18 pulses/call, mean pulse rate among individuals 44-65 pulses/s; call frequency modulated, rising whoop, mean initial frequency among individuals about 340-860 Hz; mean dominant frequency among individuals about 680-1030 Hz (Tables 11, 12, Figure 19).

Karyotype – Diploid number 22, 2 pairs of metacentrics, 6 pairs of submetacentrics, 3 pairs of subtelocentrics (Heyer and Diment, 1974). The karyotype data reported for *L. pentadactylus* by Bogart (1974) are based on specimens of *L. flavopictus* from Boracéia, São Paulo, Brazil and specimens, presumably of *L. pentadactylus,* from Peru (James P. Bogart, pers. comm.).

Habitat and Distribution – *Leptodactylus pentadactylus* occurs in closed canopied rain forest habitat throughout the Amazonian Morphoclimatic Domain as defined by Ab'Sáber (1977) (Appendix, Figure 20).

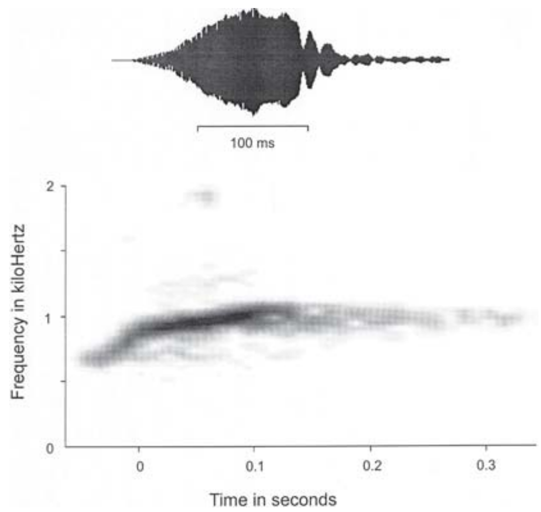

Figure 19. Wave form and audiospectrogram of advertisement call of *Leptodactylus pentadactylus,* USNM recording 254, cut 3 from the Rio Juruá, Amazonas, Brazil.

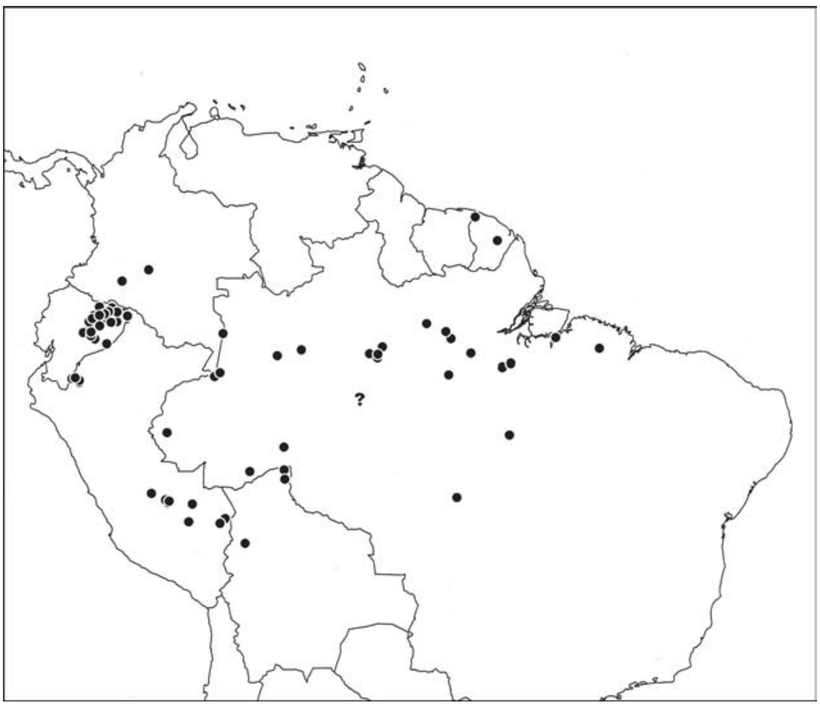

Figure 20. Distribution map for *Leptodactylus pentadactylus.* Question mark indicates specimen from this locality questionably identifiable to *L. pentadactylus.*

Leptodactylus peritoaktites sp. nov.
Figure 21

Holotype – USNM 196739, an adult male from Hacienda Equinox, 38 km NNW of Santo Domingo de los Colorados, Esmeraldas, Ecuador, 1000’, 00°03’S, 79°20’W. Collected by James A. Peters on 22 June 1954.

Suggested English name – Coastal Ecuador smoky jungle frog.

Suggested Portuguese name – Rã-defumada-de-selva-costeira-de-Ecuador.

Suggested Spanish name – Rana ahumada de la selva costera de Ecuador.

Diagnosis – *Leptodactylus peritoaktites* has a parapatric distribution with *L. rhodomerus; L. peritoaktites* occurs in the more southern wet tropical forest region of Pacific coastal South America than *L. rhodomerus.* Large sexually active male *L. peritoaktites* have a single large spine on each thumb; large sexually active male *L. rhodomerus* either lack thumb spines or have only a small spine on each thumb. Most *L. rhodomerus* have dark with large light vermiculation belly patterns; no *L. peritoaktites* have this pattern.

Description of Holotype – Snout nearly rounded from above, rounded-obtuse in profile. Canthus rostralis indistinct. Loreal region weakly concave-obtuse. Tympanum distinct, greatest diameter about 3/4 eye diameter. Vomerine teeth in two strongly arched series, between and extending posteriorly to choanae, narrowly separated medially. Vocal slits elongate, parallel to lower jaw. Vocal sac single, median. Finger lengths in increasing order II ~ IV < I ~ III. Inner sides of fingers II and III ridged, other lateral surfaces smooth. Metacarpal tubercles large, triangular-rounded inner more distinct and just larger than ovoid bifid outer tubercle. Arms not hypertrophied. Each thumb with 1 medium large white spine. No other secondary sexual characters. Dorsal texture smooth. Tympanic fold distinct from eye to shoulder. Dorsolateral fold entire from eye to groin. Lateral fold not indicated. Flank fold extending from tympanic fold to above posterior arm insertion region, then interrupted to lower flank. Commissural glands

Figure 21. Holotype of *Leptodactylus peritoaktites* sp. nov.

distinct. Flanks and posterior thighs with extensive dark brown glands, gland in groin squarish-oblong, about 20 x 40 mm. Ventral texture smooth, posterior portion of ventral surfaces of thighs weakly granular. Belly disk fold weakly indicated posteriorly. Toe tips rounded, not expanded. Sides of toes weakly ridged. Subarticular tubercles weakly pungent, ovoid. Outer metatarsal tubercle weakly developed, rounded, about 1/4 size of distinct, elongate-ovate inner metatarsal tubercle. No metatarsal fold. Upper shank with several keratinized tubercles. Outer tarsal surface smooth. Sole of foot smooth.

Upper lip with dark brown marks, 1 elongate, extending almost to eye. Dorsum brown with 2 faintly outlined irregular transverse bands in addition to faintly outlined interorbital bar. Dorsolateral, tympanic, flank folds dark brown highlighted. Upper arms with faint darker brown cross bands, upper shanks almost uniform dark brown, rest of upper legs with indistinct to distinct darker brown transverse bands. Throat uniform brown, rest of venter brown with moderate sized, distinct dirty cream spots. Dark brown glands on posterior surfaces of thighs in a wide swath from vent sweeping down and laterally across thighs, rest of posterior thighs with bold dirty cream mottle on brown background.

Measurements (mm): SVL 146.3, head length 52.7, head width 55.4, eye-nostril distance 13.1, greatest tympanum diameter 8.7, thigh length 60.0, shank length 62.6, foot length 64.4.

Adult Characteristics – Lip pattern usually with dark triangular marks, 1 or 2 elongate approaching or entering lower eye (Figure 12A). Lip pattern often with dark triangular marks on edge of upper lip only.

Dorsal pattern usually with irregular quadrangular or rectangular markings, of equal or alternating intensity, confluent laterally or not. Dorsal pattern often uniform light with 1 or 2 well-defined, narrow transverse bands. Dorsal pattern rarely with more than 2 dark, broad transverse bands of equal intensity in addition to interorbital band, confluent laterally or not.

Belly usually dark with large light discrete spots (Figure 13E). Belly often mottled (Figure 13A) or uniform dark; or dark with small light vermiculations (Figure 13B).

Posterior thigh pattern usually dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B). Thigh pattern often relatively uniform dark or indistinctly mottled; or dark with small distinct light vermiculations or spots (Figure 14A); or dark with large distinct light vermiculations, some coalescing or vermiculations; or dark with distinct, discrete light spots.

Dorsolateral folds usually entire from eye to groin. Dorsolateral folds often entire from at least 1/4 to full distance from eye to sacrum; or entire to at least between sacrum and some distance to groin.

Flank folds usually entire from tympanum to lower flank. Flank folds often entire from tympanum to shoulder; or interrupted from tympanum to lower flank.

Male thumb usually with 1 moderate to large spine; male thumb often lacking spines.

Males without chest spines.

Female (N = 5) SVL 115.3-133.1 mm (m = 121.0), male (N = 3) SVL 124.0-146.3 (m = 132.4), not sexually dimorphic (t = -1.488, df = 2.8, P = 0.238). Female head length/SVL ratio 0.34-0.38 (m = 0.364), male head length/SVL ratio 0.36-0.39 (0 = 0.379), not sexually dirmorphic (t = -1.297, df = 4.0, P = 0.265). Female head width/SVL ratio 0.36-0.38 (m = 0.372), male head width/SVL ratio 0.38-0.40 (m = 0.389), not sexually dimorphic (t = -3.024, df = 3.0, P = 0.057). Female eye-nostril distance/SVL ratio 0.10 (m = 0.098), male eye-nostril distance/SVL ratio 0.09-0.10 (m = 0.098), not sexually dimorphic (t = -0.067, df = 2.5, P = 0.952). Female tympanum diameter/SVL ratio 0.06-0.07 (m = 0.066), male tympanum diameter/SVL ratio 0.06-0.07 (m = 0.066), not sexually dimorphic (t = 0.084, df = 4.1, P = 0.937). Female thigh/SVL ratio 0.40-0.44 (m = 0.426), male thigh/SVL ratio 0.41-0.47 (m = 0.440), not sexually dimorphic (t = -0.701, df = 3.1, P = 0.532). Female shank/SVL ratio 0.46-0.47 (m = 0.462), male shank/SVL ratio 0.43-0.47 (m = 0.455). Female foot/SVL ratio 0.46-0.49 (m = 0.474), male foot/SVL ratio 0.44-0.48 (m = 0.462), not sexually dimorphic (t = 0.944, df = 3.3, P = 0.409).

Etymology – From the Greek *peritos* – west, and *aktites* – coast dweller, in allusion to the geographic distribution of the species.

Larvae – Unknown.

Advertisement Call – Calls of single notes, given at rates of 34-37 calls/min; call duration 0.20-0.30 s; calls pulsed, 5-8 pulses/call, mean pulse rate among individuals 23-27 pulses/s; call frequency modulated, rising whoop, mean initial frequency among individuals about 550-690 Hz; mean dominant frequency about 860 Hz (Table 11).

Habitat and Distribution – *Leptodactylus peritoaktites* occurs inside rain forests and in previously rainforested habitats in the middle and southern rain forests of coastal Ecuador (Appendix, Figure 22).

***Leptodactylus rhodomerus* sp. nov.**
Figure 23

Holotype – ICN 13322, an adult male from campamento Chancos, Vereda Campo Alegre, Municipio de Restrepo, Valle de Cauca, Colombia, 460 m, 3°58'N, 76°44'W. Collected by John D. Lynch on 3 June 1983.

Paratopotypes – ICN 13320-13321 (juveniles), exact same locality as for holotype, collected by John D. Lynch on 23 and 27 May 1983 respectively; 13323 (female), taken slightly up road from locality as for holotype at Quebrada La Mula, collected by Juan Manuel Renjifo from 4-15 February 1984.

Suggested English name – Red-thighed thin-toed frog.

Suggested Portuguese name – Rã-de-dedos-delgados-de-coxas-vermelhas.

Suggested Spanish name – Rana de dedos delgados de muslos rojos.

Diagnosis – *Leptodactylus rhodomerus* is most similar morphologically to *L. pentadactylus,* which has an allopatric distribution with *L. rhodomerus; L. rhodomerus* occurs in the wet tropical forest regions of western Colombia and adjacent Ecuador, *L. pentadactylus* occurs in the Amazonian wet tropical forests. *Leptodactylus rhodomerus* has bright red markings on the posterior thigh surfaces in life; *L. pentadactylus* does not have red on the thighs in life.

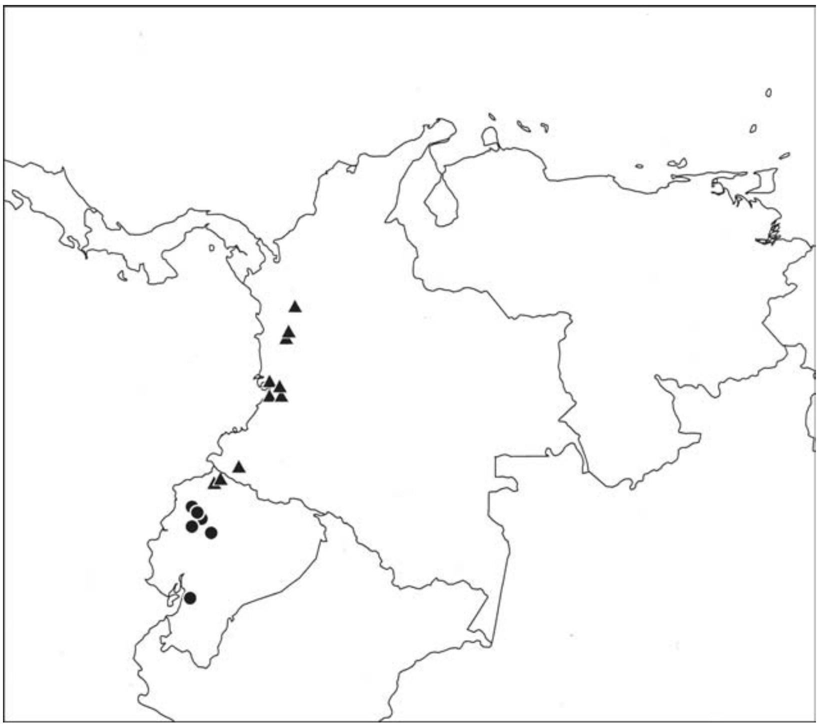

Figure 22. Distribution map for *Leptodactylus peritoaktites* (dots) and *L. rhodomerus* (triangles).

Figure 23. Holotype of *Leptodactylus rhodomerus* sp. nov.

Leptodactylus rhodomerus has a parapatric distribution with *L. savagei* to the north and *L. peritoaktites* to the south along Pacific coastal South America. Large sexually active male *L. rhodomerus* have either no thumb spines or a single small spine on each thumb and lack chest spines; large sexually active male *L. savagei* have a single large black spine on each thumb and have a pair of black chest spines. *Leptodactylus rhodomerus* specimens often have very extensive distinctly light areas (bright red in life) on the posterior thigh surfaces; *L. savagei* individuals only rarely have this pattern. Large sexually active male *L. peritoaktites* have a single large black spine on each thumb, contrasting with the condition that occurs in *L. rhodomerus* described above. Most *L. rhodomerus* have dark with large light vermiculated belly patterns; no *L. peritoaktites* have this pattern.

Description of Holotype – Snout nearly rounded from above, rounded in profile. Canthus rostralis indistinct. Loreal region obtuse-concave. Tympanum distinct, greatest diameter about 2/3 eye diameter. Vomerine teeth in strongly arched series, between and extending posterior to choanae, separated medially by about 1/4 length of single vomerine tooth row. Vocal slits elongate, parallel to lower jaw. Single vocal sac not expressed externally. Finger lengths in increasing order II ~ IV < I < III. Fingers with strong ridges medially, weak ridges laterally. Inner metacarpal tubercle protuberant, triangular-rounded in shape, just smaller than weakly developed, rounded, heart-shaped outer metacarpal tubercle. Arms not hypertrophied. Thumb with a single tiny tan-tipped spine; no other male secondary sexual characteristics. Dorsal texture weakly shagreened with small, scattered keratinized-tipped tubercles in the post-sacral region. Tympanic fold well-developed from eye to above arm insertion. Dorsolateral fold weak, but outlined with light and dark striping from just behind eye complete to above mid-thigh insertion. No lateral fold. Flank fold distinct from supratympanic fold to lower flanks about 3/5 distance posteriorly between limb insertions; folds very glandular; right fold entire, left fold with very short interruption above upper arm insertion. Commissural glands distinct; very extensive irregular-shaped glands in groin extending anteriorly about 3/4 distance on flanks. Ventral texture smooth except for areolate ventral-posterior thighs. Belly fold weakly defined anteriorly, well-defined posteriorly. Toe tips rounded, just broader than toes immediately behind tips. Toes with strong ridges medially, weak ridges laterally; very vestigial webbing best developed between toes II-III-IV. Subarticular tubercles moderately pungent, ovate. Low relief outer metatarsal tubercle rounded, diameter about 2/3 length of ovate, well-developed, inner metatarsal tubercle. Tarsal fold well-developed, slightly curved, extending from medial surface of inner metatarsal tubercle to about 3/4 length of tarsus. No metatarsal fold. Upper shank scattered with tan-tipped tubercles. Outer tarsus profused with very small white tubercles, among which, many large, white, tan-tipped tubercles. Sole of foot with 3-6 moderate-sized white, tan-tipped tubercles.

Upper lip with 3 well-developed dark triangular-shaped bars, middle triangle extending to just short of lower eye. Dorsum generally almost uniform brown with a well-defined dark-outlined transverse interocular band and a moderately defined narrow transverse band mid-dorsally above arm insertion area; dorsolateral folds with well-defined lighter medial stripes and dark-outlined stripes laterally. Upper limbs dark brown with narrow darker brown incomplete or complete transverse bands. Ventral surfaces dark with small, well-defined light spots and vermiculations. Posterior thigh with extensive light area with dark brown irregular markings encroaching the light area dorsally and ventrally.

Measurements (mm): SVL 134.1, head length 50.4, head width 50.7, eye-nostril distance 13.1, greatest tympanum diameter 8.9, femur length 64.0, shank length 66.4, foot length 71.9.

Adult Characteristics – Lip pattern with dark triangular marks, 1 or 2 elongate approaching or entering lower eye (Figure 12A).

Dorsal pattern usually uniform light with one or two well-defined, narrow transverse bands. Dorsal pattern often with irregular quadrangular or rectangular markings, of equal or alternating lighter/darker intensity, confluent laterally or not.

Belly usually dark with large light vermiculations (Figure 13C). Belly often dark with large light discrete spots (Figure 13E). Belly rarely dark with small light vermiculations (Figure 13B); or dark with small light discrete spots.

Posterior thigh pattern often relatively uniform dark or indistinctly mottled; or mostly very distinctly light with few irregular dark marks (Figure 14D). Thigh pattern rarely dark with small distinct light vermiculations or spots (Figure 14A); or dark with large distinct light vermiculations, some coalescing of vermiculations; or dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B).

Dorsolateral folds usually entire from eye to groin. Dorsolateral folds often entire to at least between sacrum and some distance to groin.

Flank folds usually entire from tympanum to lower flank. Flank folds often interrupted from tympanum to lower flank. Flank fold rarely with dark spot/wart in area where fold occurring in other specimens.

Male thumb with one tiny to small spine.

Males without chest spines.

Female (N = 5) SVL 133.5-157.8 mm (m = 140.4), male (N = 6) SVL 112.2-143.8 (m = 132.0), not sexually dimorphic ($t = 1.317$, df = 8.9, $P = 0.221$). Female head length/SVL ratio 0.36-0.40 (m = 0.381), male head length/SVL ratio 0.36-0.41 (m = 0.378), not sexually dimorphic ($t = 0.317$, df = 8.8, $P = 0.759$). Female head width/SVL ratio 0.38-0.40 (m = 0.384), male head width/SVL ratio 0.35-0.39 (m = 0.378), not sexually dimorphic ($t = 0.737$, df = 8.5, $P = 0.481$). Female eye-nostril distance/SVL ratio 0.09-0.11 (m = 0.100), male eye-nostril distance/SVL ratio 0.10-0.11 (m = 0.101), not sexually dimorphic ($t = -0.252$, df = 8.5, $P = 0.807$). Female tympanum diameter/SVL ratio 0.06-0.07 (m = 0.064), male tympanum diameter/SVL ratio 0.06-0.07 (m = 0.065), not sexually dimorphic ($t = -0.680$, df = 7.9, $P = 0.516$). Female thigh/SVL ratio 0.46-0.50 (m = 0.478), male thigh/SVL ratio 0.39-0.48 (m = 0.455), not sexually dimorphic ($t = 1.454$, df = 8.0, $P = 0.184$). Female shank/SVL ratio 0.48-0.52 (m = 0.487), male shank/SVL ratio 0.36-0.50 (m = 0.460, not sexually dimorphic ($t = 1.236$, df = 6.4, $P = 0.260$). Female foot/SVL ratio 0.48-0.53 (m = 0.497), male foot/SVL ratio 0.44-0.54 (m = 0.496), not sexually dimorphic ($t = 0.096$, df = 8.4, $P = 0.926$).

Etymology – From the Greek *rhodon* – rose, and *meros* – thigh, in reference to the bright red coloration on the posterior thighs in life in most individuals.

Larvae – Unknown.

Advertisement Call – Unknown.

Karyotype – Unknown.

Habitat and Distribution – *Leptodactylus rhodomerus* occurs in the Colombian Choco and adjacent rain forests of Ecuador (Appendix, Figure 22).

Leptodactylus savagei sp. nov.

Figure 24

Holotype – USNM 227652, an adult male from Rincon de Osa, Puntarenas, Costa Rica, 08°42'N, 83°29'W. Collected by Miriam H. and W. Ronald Heyer on 11 June 1973.

Paratopotypes – USNM 219538, juvenile, collected by Roy W. McDiarmid, 13 July 1973, USNM 227645-227646, 227649, females, collected by Heyers on 9 June 1973, USNM 227647-227648, 227650-227651, males, collected by Heyers on 9 June 1973, USNM 227653-227654, juveniles, collected by Heyers on 13 June 1973, USNM 227655, juvenile, collected by Heyers on 15 June 1973, USNM 227656, female, collected by Heyers on 19 June 1973.

Suggested English name – Savage's thin-toed frog.

Suggested Portuguese name – Rã-de-dedos-delgados-de-Savage.

Suggested Spanish name – Rana de dedos delgados de Savage.

Diagnosis – *Leptodactylus savagei* is morphologically very similar to *L. knudseni*. The two species are allopatric in their distributions, with *L. savagei* occurring only in northern Colombia adjacent to Panama in South America, whereas *L. knudseni* has an Amazonian distribution. There are no adult morphological or advertisement call characters that consistently diagnose these two species from each other. Larval *L. savagei* have nine filter rows per plate on ceratobranchial IV; *L. knudseni* larvae have seven rows. *Leptodactylus savagei* and *L. rhodomerus* are the only two species of the *L. pentadactylus* group that occur in coastal Pacific and northern Colombia. The known locality data indicate parapatric distributions of these two species, with *L. savagei* occurring from Colombia adjacent to Panama to Honduras and *L. rhodomerus* occurring in the Colombian Choco and just extending into neighboring Ecuador. Large sexually

Figure 24. Holotype of *Leptodactylus savagei* sp. nov.

active male *L. savagei* have a single large black thumb spine and a pair of black chest spines; large sexually active male *L. rhodomerus* have either no thumb spines or a single small spine on each thumb and lack chest spines. *Leptodactylus rhodomerus* specimens often have very extensive distinctly light areas (bright red in life) on the posterior thighs with a few irregular dark markings; *L. savagei* specimens rarely have this pattern.

Description of Holotype – Snout nearly rounded from above, rounded-obtuse in profile. Canthus rostralis indistinct. Loreal region obtusely flared. Tympanum distinct, greatest diameter about 4/5 eye diameter. Vomerine teeth in two strongly arched series, between and extending posteriorly to choanae, narrowly separated medially. Vocal slits elongate, parallel to lower jaw. Vocal sac not visible externally. Finger lengths in increasing order II ~ IV < I < III. Inner lateral surfaces of fingers I, II, III strongly ridged, other lateral surfaces very weakly ridged or smooth. Metacarpal tubercles low and large, about equal in size; inner triangular-rounded, outer strongly bifid. Arms moderately hypertrophied. Each thumb with one large black spine. Chest with pair of small black spines of a single cusp. Throat, chest, under arms, and flanks profused with small black tubercles. Dorsal texture smooth. Tympanic fold well developed from eye to shoulder. Dorsolateral folds well-developed, continuous from eye to groin. Lateral fold glandular, complete from supratympanic fold to groin. Flank fold glandular, diverging from lateral fold extending to lower flank. Flanks glandular with pronounced glands, especially in groin region. Ventral texture smooth except for small black tubercles described above and posterior ventral thighs granular. Belly disk fold weakly indicated posteriorly. Toe tips just larger than toe widths immediately behind tips, rounded. Toes ridged laterally, strongest on toes I-IV. Subarticular tubercles weakly pungent, ovoid. Outer metatarsal tubercle low, rounded-ovoid, about 1/4 size of elongate ovoid inner metatarsal tubercle. Tarsal fold distinct, straight, extending about 5/6 length of tarsus. No metatarsal fold. Upper shank with weak shagreen and scattered white tubercles. Outer tarsus scattered with low, white tubercles. Sole of foot smooth.

Upper lip with series of dark brown marks next to jaw, bordered above by tan then becoming darker brown. Commissural gland cream-tan. Dorsum with a faint pattern of complex, coalescing transverse bars/rectangles beginning with interorbital chevron. Dorsolateral folds weakly highlighted by light and dark pin-striping, darker highlights most pronounced posteriorly. Upper arm with one transverse darker brown band. Upper legs with series of distinct dark brown transverse bands on a lighter brown background. Throat almost uniform gray, rest of venter mottled gray/brown and dirty cream. Posterior thigh surfaces almost black with a few sinuous light marks, some extending from light dorsal transverse bands and a few irregular light spots, especially ventrally.

Measurements (mm): SVL 144.4, head length 56.3, head width 60.3, eye-nostril distance 13.8, greatest tympanum diameter 10.8, thigh length 63.5, shank length 62.8, foot length 64.6.

Adult Characteristics – Lip pattern usually dark triangular marks, one or two elongate approaching or entering lower eye (Figure 12A). Lip pattern often dark triangular marks on edge of upper lip only. Lip pattern rarely uniform light.

Dorsal pattern usually with irregular quadrangular or rectangular markings, of equal or alternating lighter/darker intensity, confluent laterally or not. Dorsal pattern often uniform light or dark; or uniform light with one or two well-defined, narrow transverse bands. Dorsal pattern rarely with more than two dark broad transverse bands of equal intensity in addition to interorbital band, confluent laterally or not.

Belly often dark with small light vermiculations (Figure 13B); or dark with large light vermiculations (Figure 13C); or dark with small light discrete spots; or dark with large light discrete spots (Figure 13E).

Posterior thigh pattern often dark with small distinct light vermiculations or spots (Figure 14A); or dark with large distinct light vermiculations, some coalescing of vermiculations; or dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B). Thigh pattern rarely labyrinthine; or dark with distinct, discrete light spots; or mostly very distinctly light with few irregular dark marks (Figure 14D).

Dorsolateral folds often entire from at least 1/4 to full distance from eye to sacrum; or entire to at least between sacrum and some distance to groin; or entire from eye to groin. Dorsolateral folds rarely interrupted to at least between sacrum and some distance to groin.

Flank folds often entire from tympanum to shoulder; or interrupted from tympanum to lower flanks; or entire from tympanum to lower flank. Flank folds rarely with dark spot/wart in area where fold would be between tympanum and shoulder.

Male thumb usually with one large spine. Male thumb often with one tiny to small spine. Male thumb rarely with one large spine and a prepollical bump.

Large breeding males with chest spines.

Female (N = 74) SVL 110.2-164.1 mm (m = 137.1), male (N = 75) SVL 106.0-156.3 mm (m = 133.2), sexually dimorphic (t = 2.165, df = 146.1, P = 0.032). Female head length/SVL ratio 0.34-0.40 (m = 0.371), male head length/SVL ratio 0.33-0.40 (m = 0.377), sexually dimorphic (t = -3.049, df = 146.8, P = 0.003). Female head width/SVL ratio 0.33-0.42 (m = 0.383), male head width/SVL ratio 0.36-0.44 (m = 0.392), sexually dimorphic (t = -3.880, df = 145.3, P = 0.000). Female eye-nostril distance/SVL ratio 0.08-0.11 (m = 0.094), male eye-nostril distance/SVL ratio 0.08-0.10 (m = 0.094), not sexually dimorphic (t = -0.269, df = 143.9, P = 0.789). Female (N = 44) tympanum diameter/SVL ratio 0.06-0.08 (m = 0.069), male (N = 30) tympanum diameter/SVL ratio 0.06-0.08 (m = 0.069), not sexually dimorphic (t = -0.052, df = 50.1, P = 0.959). Female thigh/SVL ratio 0.37-0.46 (m = 0.420), male thigh/SVL ratio 0.37-0.47 (m = 0.425), not sexually dimorphic (t = -1.129, df = 145.0, P = 0.261). Female shank/SVL ratio 0.39-0.48 (m = 0.441), male shank/SVL ratio 0.40-0.49 (m = 0.444), not sexually dimorphic (t = -0.850, df = 136.3, P = 0.397). Female (N = 71) foot/SVL ratio 0.40-0.51 (m = 0.457), male (N = 74) foot/SVL ratio 0.38-0.51 (m = 0.458), not sexually dimorphic (t = -0.139), df = 139.8, P = 0.890).

Etymology – The species is named in honor of Jay M. Savage for his substantial contributions to furthering biological research in the Neotropics in general and those of the Middle American herpetofauna in particular.

Larvae – Larvae either live in temporary ponds or complete development in burrows that the foam nest was laid in and are facultative carnivores (Heyer *et al.*, 1975; Muedeking and Heyer, 1976). Larvae elongate; spiracle sinistral; vent median; oral disk almost terminal, entire; broad anterior gap in oral disk lacking marginal papillae, followed by single row of papillae laterally, double row ventrolaterally, and single row ventrally; tooth row formula 2(2)/3(1); maximum total length, stage 40, 83 mm (Heyer, 1970).

Advertisement Call – Calls of single notes, given at rates of 40-49 calls/min; call duration 0.24-0.42 s, calls pulsed, 5-13 pulses/call, mean pulse rate among individuals 31-46 pulses/s; call frequency modulated, rising whoop, mean initial frequency among individuals about 300-345 Hz; mean dominant frequency among individuals about 350-520 Hz (Table 11, Figure 25).

Karyotype – Unknown.

Habitat and Distribution – *Leptodactylus savagei* occurs in primary and secondary forests, forest edges, and deforested areas from Honduras (McCranie and Wilson, 2002:453) to northern Colombia adjacent to Panama (Appendix, Figure 26).

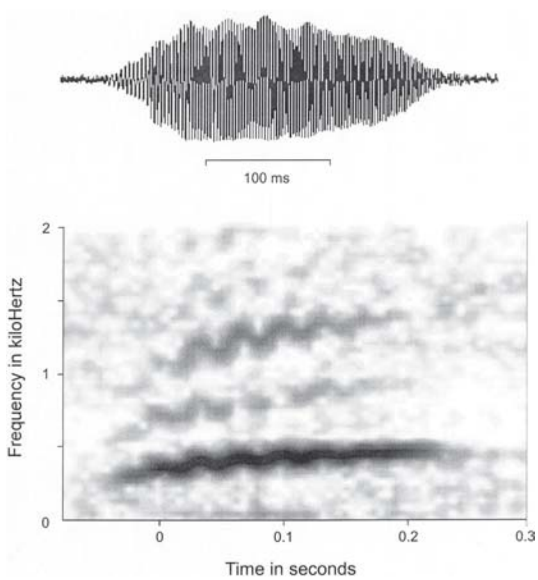

Figure 25. Wave form and audiospectrogram of advertisement call of holotype of *Leptodactylus savagei,* USNM recording 106, cut 1.

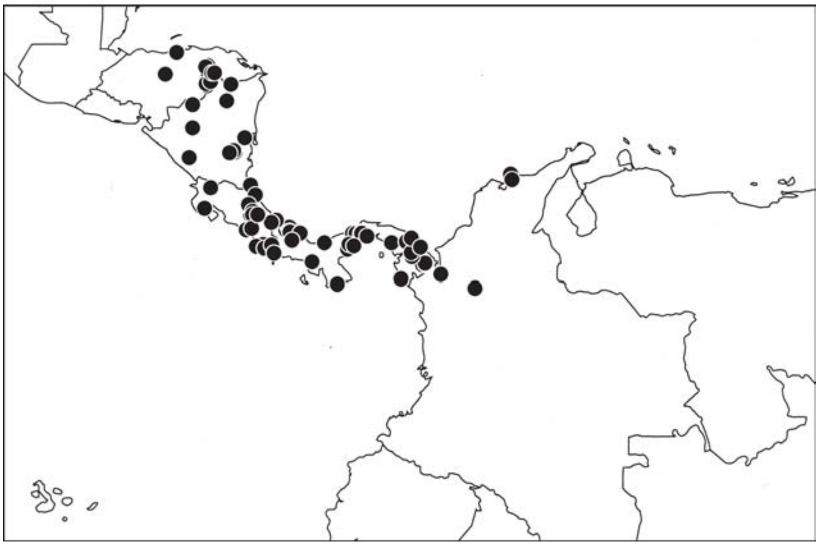

Figure 26. Distribution map for *Leptodactylus savagei.*

Leptodactylus turimiquensis sp. nov.
Figure 27

Holotype – AMNH 70667, an adult male from Caripito, Monagas, Venezuela, ~ 100 m, 10°08'N, 63°06'W. Collected by William Beebe in 1942.

Paratopotype – AMNH 70668, adult male, same data as for holotype.

Suggested English name – Calf frog.

Suggested Portuguese name – Rã-vitelo.

Suggested Spanish name – Rana ternero.

Diagnosis – *Leptodactylus turimiquensis* is known from and proximate to the State of Sucre in Venezuela and is the only large species of the *L. pentadactylus* group that occurs in the region. *Leptodactylus turimiquensis* is most similar to *L. labyrinthicus* and *L. vastus.* The available data indicate a substantial distributional hiatus between *L. turimiquensis* and *L. labyrinthicus* and an extensive hiatus between *L. turimiquensis* and *L. vastus. Leptodactylus turimiquensis* occurs in forested or previously forested habitats; *L. labyrinthicus* and *L. vastus* occur exclusively in open formation habitats. *Leptodactylus turimiquensis* has a pulsed advertisement call; the call of *L. labyrinthicus* is unpulsed. *Leptodactylus turimiquensis* specimens rarely have a labyrinthine belly pattern; most *L. vastus* have this pattern.

Description of Holotype – Snout rounded from above, rounded-obtuse in profile. Canthus rostralis indistinct. Loreal region concave-obtuse. Tympanum distinct, greatest diameter about 2/3 eye diameter. Vomerine teeth in strongly arched series, between and extending posterior to choanae, narrowly separated medially. Vocal slits elongate, at obtuse angle to lower jaw. Vocal sac not expressed externally. Finger lengths in increasing order II ~ IV < I < III. Strong ridges on outer side of finger I and inner sides of fingers II and III, other sides smooth. Inner metacarpal tubercle pronounced, triangular-rounded, about same size as flat, ovoid, bifid outer metacarpal tubercle. Arms greatly hypertrophied. Thumb with one large black spine and a bump on the prepollex. Chest with one large dark four-cusped spine (right) and one large white three-cusped spine (left). Small dark tubercles on finger ridges and inner dorsal surfaces of fingers II and III, chest, anterior flanks and belly; throat with many small white tubercles and a few brown tubercles. Dorsum with scattered warts and short ridges, more pronounced posteriorly. Tympanic fold well developed from eye to above arm insertion. No dorsolateral fold; a few small warts in dorsal fold area. Lateral fold weak from tympanic fold to posterior arm insertion area then a disconnected series of warty glands to groin. No flank fold. Commissural gland moderately developed, flanks glandular. Ventral texture smooth except for small tubercles described above and granular ventral-posterior thighs. Belly disk fold moderately defined posteriorly only. Toe tips rounded, just broader than

Figure 27. Holotype of *Leptodactylus turimiquensis* sp. nov.

toes immediately behind tips. Toes smooth laterally except for barely discernible ridge on inner side of toe II; barest trace of vestigial web between toes II and III. Subarticular tubercles weakly pungent, ovoid. Outer metatarsal tubercle low, round, about 1/3 size of elongate ovoid inner metatarsal tubercle. Tarsal fold distinct, straight, about 2/3 length of tarsus. No metatarsal fold. Upper shank with several scattered white tubercles. Outer tarsus with a few scattered white tubercles. Sole of foot smooth.

Upper lip with a series of ill-defined vertical bars, just darker than background, 2 bars extending to lower eye. Dorsum brown with scattered small dark spots associated with warts/short ridges. Upper arm with irregular, just darker brown than background, transverse bands. Upper legs with well defined broad darker brown transverse bands on a lighter brown background. Throat uniform dark brown. Chest light brown with faint pattern of bold mottling. Belly and ventral limb surfaces brown with large dirty cream vermiculations. Posterior thigh with light narrow elongate extensions from light dorsal bands, rest of thigh dark brown with scattered large light dirty cream vermiculations.

Measurements (mm): SVL 142.6, head length 51.0, head width 59.2, eye-nostril distance 12.3, greatest tympanum diameter 9.3, thigh length 57.9, shank length 59.9, foot length 60.7.

Adult Characteristics – Lip pattern often with dark triangular marks, one or two elongate approaching or entering lower eye (Figure 12A); or dark elongate triangular marks on lip edge, fading towards eye, two dark marks under eye; or dark with two narrow light chevrons from lip entering eye (Figure 12B); or uniform dark.

Dorsal pattern often uniform light or dark; or with series of regularly or irregularly placed small, dark spots; or well-developed dark interorbital band/chevron and two moderate to large equally intense dark chevrons, second chevron in sacral region, chevrons confluent or not; or two broad dark transverse bands between interorbital bar and arm insertion area, rest of dorsum with large spots; or with single broad dark chevron posterior to interorbital bar followed by a series of fairly regularly spaced large dark spots. Dorsal pattern rarely with more than two dark, broad transverse bands of equal intensity in addition to interorbital band, confluent laterally or not.

Belly usually mottled (Figure 13A) or uniform dark. Belly rarely dark with small light vermiculations (Figure 13B).

Posterior thigh pattern usually dark with small distinct light vermiculations or spots (Figure 14A). Thigh pattern often dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B). Thigh pattern rarely dark with large distinct light vermiculations, some coalescing of vermiculations; or labyrinthine.

Dorsolateral folds often absent; or interrupted or entire to 1/4 distance from eye to sacrum; or interrupted from at least 1/4 distance to 1/2 distance from eye to sacrum; or interrupted from at least 1/2 to full distance from eye to sacrum. Dorsolateral folds rarely entire from eye to groin.

Flank folds usually with a dark spot/wart in area where fold would be between tympanum and shoulder. Flank folds often absent.

Male thumb usually with one spine. Male thumb often with one spine and a prepollical bump.

Large breeding males with chest spines.

Female (N = 2) SVL 122.4-128.0 mm, male (N = 23) SVL 127.2-160.0 mm (m = 144.0), sexually dimorphic (t= -5.492, df = 2.2, P = 0.025). Female head length/SVL ratio 0.35-0.36, male head length/SVL ratio 0.34-0.39 (m = 0.370), not sexually dimorphic (t = -1.860, df = 1.6, P = 0.231). Female head width/SVL ratio 0.39-0.40, male head width/SVL ratio 0.39-0.46 (m = 0.418), not sexually dimorphic (t = -2.344, df = 1.4, P = 0.198). Female eye-nostril distance/SVL ratio 0.09-0.10, male eye-nostril distance/SVL ratio 0.09-0.10 (m = 0.093), not sexually dimorphic (t = -0.197, df = 1.5, P = 0.867). Female tympanum diameter/SVL ratio 0.07, male (N = 17) tympanum diameter/SVL ratio 0.06-0.08 (m = 0.070), not sexually dimorphic (t = -0.183, df = 5.2, P = 0.862). Female thigh/SVL ratio 0.42-0.43, male thigh/SVL ratio 0.38-0.47 (m = 0.421), not sexually dimorphic (t = 0.698, df = 22.7, P = 0.492). Female shank/SVL ratio 0.40-0.42, male shank/SVL ratio 0.39-0.47 (m = 0.430), not sexually dimorphic (t = -1.409, df = 1.3, P = 0.352). Female foot/SVL ratio 0.42-0.44, male foot/SVL ratio 0.38-0.47 (m = 0.433), not sexually dimorphic (t = -0.458, df = 1.5, P = 0.704).

Etymology – Jaime E. Péfaur, at my request, kindly suggested naming this species *L. turimiquensis* after the Serranía de Turimiquire, which encompasses the known distribution of the species (see Péfaur and Sierra, 1995: fig.2). Spanish and English authors have transliterated the indigenous name for the mountain range involved as Turimiquire and Turumiquire. Although some of the botanical and ornithological literature uses Turumiquire, the name used in official papers of the Republic of Venezuela is Turimiquire (J.E. Péfaur, e-mail message of 5 August 2003).

Larvae – Unknown.

Advertisement Call – Calls of single notes; call duration 0.33 s; calls pulsed, about 9 pulses/call, mean pulse rate about 27 pulses/s; call weakly frequency modulated; initial frequency about 400 Hz; dominant frequency about 400 Hz (Table 19, data extrapolated from Rivero and Esteves, 1969).

Karyotype – Unknown.

Habitat and Distribution – *Leptodactylus turimiquensis* occurs in and proximate to the State of Sucre, Venezuela and is found in relatively undisturbed rain forests, second growth, and agricultural clearings of previously forested habitats (Péfaur and Sierra, 1995) (Appendix, Figure 17).

Leptodactylus vastus A. Lutz, 1930

Leptodactylus vastus A. Lutz, 1930:14. Type locality: “Independencia,” now Guarabira, Paraiba, Brazil, 06°51’S, 35°29’W. Lectotype: AL-MN 70, adult male.

Suggested English name – Northeastern pepper frog.

Suggested Portuguese name – Rã-pimenta-do-Nordeste.

Suggested Spanish name – Rana pimienta del nordeste.

Diagnosis – *Leptodactylus vastus* is known from northeast Brazil and is the only large species of the *L. pentadactylus* group that occurs in the region it occupies. The available data indicate a modest hiatus in the distributions of *L. vastus* and *L. labyrinthicus* and an extensive hiatus between *L. vastus* and *L. turimiquensis*. *Leptodactylus vastus* and *L. labyrinthicus* occur in open formations; *L. turimiquensis* occurs in wet forest or former wet forest habitats. *Leptodactylus vastus* has a pulsed advertisement call; *L. labyrinthicus* has an unpulsed advertisement call.

Adult Characteristics – Lip pattern often dark elongate triangular marks on lip edge, fading towards eye, two dark marks under eye (Figure 12B); or dark with two narrow light chevrons from lip entering eye; or broad irregular darker and lighter bands, two dark bands entering eye (Figure 12D). Lip pattern rarely dark triangular marks, one or two elongate approaching or entering eye (Figure 12A); or alternating broad light bands and narrow dark vertical stripes, one to three dark stripes entering eye (Figure 12C); or uniform dark.

Dorsal pattern often uniform light or dark; or with a series of regularly or irregularly placed small, dark spots; or with series of irregularly spaced, ill-defined small blotches; or with single broad dark chevron posterior to interorbital bar followed by a series of fairly regularly spaced large dark spots. Dorsal pattern rarely uniform light with one or two well-defined, narrow transverse bands; or well developed dark interorbital band/chevron and two moderate to large equally intense dark chevrons, second chevron in sacral region, chevrons confluent or not.

Belly usually labyrinthine (Figure 13D). Belly often mottled (Figure 13A) or uniform dark; or light with dark vermiculations. Belly rarely dark with light vermiculations (Figure 13B, C).

Posterior thigh pattern often dark with small distinct light vermiculations or spots (Figure 14A); or dark with large distinct light vermiculations, some coalescing of vermiculations; or labyrinthine; or mostly very distinctly light with few irregular dark marks (Figure 14D). Thigh pattern rarely dark with contrasting large light irregular blotches/spots extending from light dorsal transverse bars, rest of thigh dark with light vermiculations (Figure 14B).

Dorsolateral folds usually interrupted from at least 1/2 to full distance from eye to sacrum. Dorsolateral folds often interrupted from at least 1/4 distance to 1/2 distance from eye to sacrum. Dorsolateral folds rarely entire from at least 1/4 to full distance from eye to sacrum; or interrupted to at least between sacrum and some distance to groin.

Flank folds usually a dark spot/wart in area where fold would be between tympanum and shoulder. Flank folds often absent. Flank folds rarely entire from tympanum to lower flank.

Male thumb usually with one large spine. Male thumb rarely with one tiny to small spine.

Large breeding males with chest spines.

Female (N = 27) SVL 120.4-167.0 (m = 151.1), male (N = 28) SVL 110.6-180.3 (m = 156.0), not sexually dimorphic (t = -1.293, df = 50.2, P = 0.202). Female head length/SVL ratio 0.35-0.40 (m = 0.374), male head length/SVL ratio 0.34-0.41 (m = 0.378), not sexually dimorphic (t = -1.047, df = 52.9, P = 0.300). Female head width/SVL ratio 0.36-0.42 (m = 0.398), male head width/SVL ratio 0.38-0.45 (m = 0.410), sexually dimorphic (t = -2.857, df = 52.9, P = 0.006). Female eye-nostril distance/SVL ratio 0.08-0.10 (m = 0.089), male eye-nostril distance/SVL ratio 0.08-0.10 (m = 0.089), not sexually dimorphic (t = -0.586, df = 51.9, P = 0.560). Female tympanum diameter/SVL ratio 0.06-0.08 (m = 0.068), male tympanum diameter/SVL ratio 0.06-0.08 (m = 0.070), not sexually dimorphic (t = -0.843, df = 46.2, P = 0.404). Female thigh/SVL ratio 0.34-0.46 (m = 0.416), male thigh/SVL ratio 0.39-0.48 (m = 0.435), sexually dimorphic (t = -3.182, df = 50.7, P = 0.003). Female shank/SVL ratio 0.37-0.46 (m = 0.413), male shank/SVL ratio 0.40-0.46 (m = 0.423), not sexually dimorphic (t = -1.853, df = 49.8, P = 0.070). Female foot/SVL ratio 0.38-0.47 (m = 0.423), male foot/SVL ratio 0.37-0.47 (m = 0.432), not sexually dimorphic (t = -1.538, df = 52.7, P = 0.130).

Larvae – Unknown.

Advertisement Call – Calls of single notes, given at rates of 54-61 calls/min; call duration 0.14-0.19 s; calls pulsed, 4-6 pulses/call, mean pulse rate among individuals 23-31 pulses/s; call frequency modulated, rising whoop, initial frequency about 260 Hz; dominant frequency about 430 Hz (Table 19, Figure 11B).

Karyotype – Unknown.

Habitat and Distribution – *Leptodactylus vastus* occurs in tropical open formations, including the Caatinga Morphoclimatic Domain and adjacent northern portion of the Cerrado Morphoclimatic Domain as defined by Ab'Sáber (1977) (Figure 17).

Discussion

Relationships and zoogeography are being treated separately (de Sá and Heyer, in preparation).

Sexual Dimorphism

Standard statistical tests with standard significance levels indicate that there are several sexually dimorphic features in size and shape in the species included in this study. However, determining whether the statistically significant sexually dimorphic features are biologically significant is not straightforward. The examples in the following two paragraphs describe the problems involved.

Males and females are sexually dimorphic in size, with females being larger in most species of frogs (Duellman and Trueb, 1986:54). Some feature of reproductive biology is typically associated with situations in which there is no sexual dimorphism or the male is larger, such as vigorous male territorial defense or male parental care (Shine, 1974). Thus, the statistical results of no dimorphism in *L. knudseni* and *L. vastus* and larger males in *L. labyrinthicus,* for which sample sizes are quite reasonable, are unusual and suggest that some interesting aspect of their reproductive biology is involved. The *L. pentadactylus t*- test results for SVL indicate that females are statistically larger than males. However, there is one male that is much larger than any female measured (195 mm SVL, 174 mm SVL, respectively). This finding suggests two interrelated possibilities: (1) males are biologically significantly larger than females; and/or (2) there might be a strong sampling bias in terms of field collecting of adult *L. pentadactylus.* For example, suitable burrows for foam nest placement and larval development may be very limited and only the largest males can defend these sites. Younger and smaller males may be prevented from having access to burrows and spend much more of their time on the forest floor where they are more available to collecting than large males residing in burrows. There is often a collecting bias against large individuals of frogs, as well. Typically, field storage specimen containers limit the total volume of material that can be collected and preserved. I usually collected no more than one or two large specimens of *L. pentadactylus* cluster species from any locality, while I was much more unbiased in collecting and preserving juvenile specimens. Parenthetically, it is worth pointing out that the MZUSP collections are unique in being much more unbiased relative to specimen size than other collections with which I have familiarity. Sampling is often biased, posing problems for standard statistics, which assume unbiased sampling.

Head width in frogs determines the upper size limit of their prey. Thus, sexual dimorphism in head width should indicate that males and females are differentially capable of capturing and swallowing the largest size prey. Typically, one large prey item of equal weight to two smaller prey items provides the frog more nutrition than the two smaller-sized prey because of the surface to volume relationships of the digestible portions of the prey. For head width, the typical statistical significance convention of 0.05 may be too strict in biological terms. Why wouldn't a 0.20 level be biologically meaningful in this case? If the 0.20 level were accepted for head width significance, then 7 species differ significantly in head width ratio and in all cases, the male has the wider head. The biological implications are actually different for the different species depending on whether there is variation in sexual dimorphism in size as well. For example, in *L. savagei* the females are larger than males, and male head widths are wider, suggesting that adults are actually eating the same-sized prey. Conversely, available data indicate that male *L. turimiquensis* are larger than females and have proportionally broader heads, suggesting that males and females are not eating the same largest sized prey.

The problems of sampling bias, biological versus statistical significance, and appropriate statistical models for evaluating sexual dimorphism in *Leptodactylus* are being explored elsewhere (Hayek and Heyer, 2005).

Fuzzy Morphological and Bioacoustic Species Differentiation

Biologists in the field have no problems in recognizing the minimum number of species of the taxa in this study at any given site. Biologists may err in recognizing too many species at a site in thinking that juveniles of some species represent a species different from the adults.

Determining whether samples collected from different sites represent the same species is not at all straightforward, however. In many instances, there are neither features of external adult form morphology nor advertisement call that completely and consistently diagnose the species recognized herein (the reason that no artificial key to the species is attempted in this paper). The limited data suggest that habitat and larval morphology differentiation have been at least as important historically for the species of this study as adult form morphology and advertisement call differentiation. For example, there are three known distinct larval morphology and larval habitat associations involved: (1) tooth row formula of 1/2(1) pond-dwellers; (2) tooth row 2(2)/2-3[1][2] pond or terrestrial burrow dwellers; and (3) tooth row formula 1/2(1) obligate terrestrial burrow dwellers. *Leptodactylus myersi* is restricted to rocky outcrops, a habitat not used by the other species. The available data indicate that *L. turimiquensis* occurs only in closed canopy rainforests and human-modified rainforest habitats, whereas the morphologically similar *L. labyrinthicus* and *L. vastus* are restricted to open formation habitats. This topic is explored further in Heyer *et al.* (2005).

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Appendix. Specimens examined.

Unassignable Specimens

BOLIVIA. COCHABAMBA. Chapare: lake at Alto Palmar, on road from Cochabamba to Villa Tunari, 2500', USNM 146507. SANTA CRUZ. Chiquitos: El Pailón, 350 m, CM 36170; El Portón, 550 m, MCZ 30135. German Busch: El Carmen, CM 336166. Ichilo: Buenavista, 400 m, CM 3808; 5 km W Buenavista, 400 m, USNM 146519-146521. Sara: Río Colorado, CM 4296. Velasco: Flor de Oro, Parque Nacional Noel Kempff Mercado, CBF 2305. All of these specimens are most similar to *Leptodactylus labyrinthicus, turimiquensis,* and *vastus.*

BRAZIL. AMAZONAS. Barreira do Matupirí, USNM 202518. This specimen is most similar to *L. pentadactylus.* BAHIA. Fazenda Cana Brava, mun. Maracás, MNRJ 30947; Ilhéus, MNRJ 703. The Bahia specimens are either *L. labyrinthicus* or *vastus.* PARÁ. Jacareacanga, MZUSP 24947-24948. These specimens are most similar to *L. knudseni.* RORAIMA. Serra do Parima, MZUSP 24936. This specimen is most similar to *L. labyrinthicus, turimiquensis,* and *vastus.*

ECUADOR. ESMERALDAS. La Tola, QCAZ 19859; San Miguel and environs, EPN 7861-7868. These specimens are either *L. peritoaktites* or *L. rhodomerus.*

Leptodactylus knudseni

BOLIVIA. BENI. Moxos: Areruta, CBF 01491. LA PAZ. Iturralde: Rurrenabaque, CBF 3673-3674, UMMZ 108594-108596. Sud Yungas: Canton Cotapata, CBF 3086.

BRAZIL. STATE NOT KNOWN. Lower Amazonia, USNM 28966. AMAPÁ. Serra do Navio, Rio Amapari, MZUSP 10140. AMAZONAS. Cachoeirinha, Rio Madeira, MZUSP 56592, USNM 202517; Biological Dynamics of Forest Fragments Project sites, north of Manaus, MZUSP 60077, 60132, 60134; Manaus, MZUSP 53743-53744; 40 km S Manaus at km 12 on road to Autazes, OMNH 37583; Novo Aripuanã, MZUSP 56593-56594; Reserva Ducke, MZUSP 53745-53747; Rio Ituixi, Scheffer Madeireira, OMNH 36854; Tefé, MCZ 1294. MATO GROSSO. Apiacás, MZUSP 80865-80869; Aripuanã, MZUSP 80655-80662; Claudia (Fazenda Iracema), MZUSP 83175-83176; Rio Teles Pires, MZUSP 71187. PARÁ. Alter do Chão, OMNH 34360-34361; CEMEX, 101 km S, 15 km E Santarém, OMNH 34796; Parque Nacional da Amazônia, Rio Tapajós, MZUSP 54667-54668, 58218, USNM 288734-288741; Reserva Biológica Rio Trombetas, MZUSP 56624-56639, USNM 289039-289047; Rio Mapuera, at equator, AMNH 49484. RONDÔNIA. Alto Paraiso, AMNH 124825-124829, MZUSP 131123, USNM 303909; Cachoeira de Nazaré, Rio Machado, MZUSP 63826; Calama, Rio Madeira, USNM 202516; Forte Príncipe da Beira, MZUSP 25169; Porto Novo, MZUSP 62179; Porto Velho, MZUSP 16658-16664, 16667, 16670, 16672-16674, 16676-16680, 16684; Rio Maçangana, fl. Jamari, prx. Alto Paraiso, MZUSP 60404; alto Rio Machado, MZUSP 15907; RO-399, km 21, MZUSP 62210; Santa Barbara, MZUSP 62033-62034, 62036-62038; Santa Cruz da Serra, MZUSP 61556. RORAIMA. Colonia Apiaú, MZUSP 65890, 65963, 66087-66088; Igarapé Cocal, MZUSP 67086-67087, USNM 302415; Ilha de Maracá, MZUSP 63294, 65675; Santa Maria do Boiaçu, MZUSP 67331, 67354, 68293, 68295.

COLOMBIA. AMAZONAS. Río Apaporis, USNM 144847. META. Menegua, E of Puerto López, upper Río Meta, USNM 147272; Villavicencio, ICN 2359, 14094, MLS 482; Villavicencio, Pozo Azul, ICN 13941-13943. VAUPÉS. Mitú, ICN 03283.

ECUADOR. FRANCISCO ORELLANA. Parque Nacional Yasuní, QCAZ 6670, 8182, 8314, 9676, 13077, 13079, 13094, 13244, 16183, QCAZ 24323-24324, 24326. MORONA-SANTIAGO. San José, USNM 283829-283831; Sucúa, 2 miles E of on trail from Sucúa to Río Upano, 2700', USNM 196722. NAPO. Archidona, QCAZ 429, 670; Estrellayacu, QCAZ 4502; Yampuna, QCAZ 2257. PASTAZA. Cachiyacu, 138.5 km S of Coca (= Francisco de Orellana), 288 m, USNM 320985; Río Conambo, USNM 196723; Río Danta, 500 m, EPN 3103; Río Pucayacu, Río Bobonaza, USNM 196726; alto Río Pucayacu, Río Bobonaza, USNM 196724, 527975-527977; Río Shyona, mouth of, in Conambo River, USNM 196725. SUCUMBÍOS. Cuyabeno, EPN 7209; Reserva Faunistica Cuyabeno, QCAZ 5862; Lago Agrio, EPN 4064; La Selva Hostría, QCAZ 8496; Pozo Sacha, QCAZ 6319; Comunidad Quichua Singüe, QCAZ 16324.

GUYANA. DISTRICT UNKNOWN. Marudi, AMNH 49264. EAST BERBICE. Shudi-kar-wau (River), AMNH 70117; EAST DEMERARA. Georgetown, AMNH 39636. MAZARUNI-POTARO. Kamakusa, AMNH 21406. NORTH WEST. Arakaka, UMMZ 66782; Baramita, USNM 535773. POTARO-SIPIRUNI. Paramakatoi, ROM 28451-28452. RUPUNUNI. Iwokrama Forest Reserve, USNM 531512-531520, IWK 282, 392, 602.

PERU. AMAZONAS. Huampami, on Río Cenepa, USNM 317514-317516; La Poza, USNM 566002; Shaim, Río Cenepa, USNM 560371. CUZCO. San Martín, ca 5 km N Camisea River, 474 m, USNM 538184. HUANUCO. Tingo María, USNM 193875-193883. MADRE DE DIOS. Lago Sandoval, 200 m, KU 215130-215131; Pakitza, USNM 298922, 345285; Tambopata Reserve, Explorer's Inn, 280 m, USNM 247356-247357, 268968-268969, 342999, 343244. PASCO. Tsioventeni, 4200', USNM 205553.

SURINAME. BROKOPONDO. Bergen Tal (= Bergendaal), ZMB 7321. NO OTHER DATA. ZMB 6759, 8534.

VENEZUELA. AMAZONAS. Apepada, alto Río Ventuari, EBRG 1907; Atabapo, Río Puruname, EBRG 1155; Brazo Casiquiare, Capibara, 106 km SW of Esmeralda, USNM 216784-216785; Esmeralda, 108 km SSE of, Río Mavaca, 140 m, USNM 216786, 216794; Maraquita, alto Río Orinoco, EBRG 2915; Mavaca, alto Río Orinoco, EBRG 2934; Misión Coromoto-Atures, FLSM 1193; Paso del Diablo, AMNH 23164; Puerto Ayacucho, Rincones de Chacorro, Atures, EBRG 775; carretera Puerto Ayacucho-Gavilán, 18 km de Planta Inos, Atures, EBRG 1274; Río Negro, frente a Isla Cigarrón, EBRG 76; Río Negro, Solano, upstream from Cano Manu, tributary of Río Casiquiare, 250 m, USNM 248008; Stanford Zent, alto Río Cuao, EBRG 1869. BOLÍVAR. Puente Cuyuni, 13 km S and 1 km E, KU 166495-166497; Reserva Forestal de Imataca, 40 km ENE de Tumeremo, 180 m, EBRG 2271, 2390, 2442-2444; Vaso de Guri, quebrada de San Luis, FLSM 11114.

Leptodactylus labyrinthicus

BRAZIL. BAHIA. Barreiras, MNRJ 1087-1088. GOIÁS. Aruanã, MZUSP 4989-4990, 25306-25308; Cachoeira Alta, MZUSP 10429-10433; Cavalcante (Fazenda Santo Antonio), MZUSP 66565; Jataí (Fazenda Nova Orlandia), MZUSP 25298-25301, (Fazenda Santa Adelia), MZUSP 20988-20990, 25298-25301; Lagoa Formosa, Cabeceiras, MZUSP 25296; Minaçu, Serra da Mesa, MNRJ 30941-30942; Monte Alegre de Goiás (Córrego Riacho Dagua), MZUSP 66388; Rio Verde (Fazenda Transvaal), MZUSP 12506-12507, 24538-24540, 25329-25339; Santa Rita do Araguaia (Fazenda Babilonia), MZUSP 66681; complexo das cavernas São Mateus – São Domingos, MZUSP 58676; UHE Serra da Mesa, MNRJ 20292, 20296, MZUSP 71532-71534, 71792-71796, 72153-72154, 72578. MATO GROSSO. Barra do Tapirapés, MZUSP 24541-24542, 25250-25253; Chapada dos Guimarães, Burití, MZUSP 37333-37343; Chapada dos Guimarães, Salgadeira, USNM 507904; Dumbá, MZUSP 4311; Porto Esperidião, MZUSP 59732, 56595; São Domingos, Rio das Mortes, MZUSP 1777, 1779, 4301-4306; São Felix, MZUSP 25327-25328; Utiariti, MZUSP 24543, 25203. MATO GROSSO DO SUL. Santa Luzia, MZUSP 28548-28549. MINAS GERAIS. Belo Horizonte, USNM 96978-96980; Lassance, Santa Rita, USNM 98786-98787. PARÁ.

Cachimbo, MZUSP 21734, 21862-21864, 21870, 21872, 25950-25951. PARANÁ. Ponta Grossa, USNM 125504. RIO DE JANEIRO. No other data, USNM 70593. SÃO PAULO. Assis, km 433, USNM 207674; Bertioga, USNM 123393; Jurumirim, USNM 121286; Luis Antonio, ca 5 km S of, Fazenda Jataí, USNM 303175-303178; Rechã, USNM 121284; near Ribeirão Preto, farm Schmidt, railway Mogyana, USNM 100970; São Paulo, USNM 100971, 121285.

PARAGUAY. AMAMBAY. Parque Nacional Cerro Cora, ca 32 km WSW of Pedro Juan Caballero, ca 500 m, USNM 253115.

Leptodactylus myersi

BRAZIL. AMAZONAS. Rio Aracá (Serrinha), MZUSP 59016, 59018, 59026-59028. PARÁ. Igarapé Jaramacaru, Campos do Ariramba, MZUSP 28405, 54110-54114. RORAIMA. Colonia Apiaú, MZUSP 65949, USNM 302267; Mucajaí, AMNH 128021-128031, MZUSP 66089 (Holotype), 70976-70986, USNM 302190-302206.

FRENCH GUIANA. No further data, MNHN 1982•81; Massif des Emerillons, MNHN 1982•82; Montagne des Trois Pitons, MNHN 1982•153; Montagne St. Marcel, MNHN 1982•73-1982•80; Peolaue (Ht. Oyapock), MNHN 1982•83; Trois Saut, MNHN 1982•84.

SURINAME. BROKOPONDO. Tafelberg, MCZ 97259-97261, 97303, 97306, 97308, RMNH 23912, 23919-23930, 23951-23961. NICKERIE. Amotopo, RMNH 23964-23968; Blanche Marie-Vall, RMNH 23910-23911. SARAMACCA. Voltzberg, RMNH 23974-23976; Raleighvallen-Voltzberg Nature Preserve, MCZ 92363.

Leptodactylus paraensis

BRAZIL. PARÁ. Aldeia Aukre, MZUSP 70023; Alegre, MZUSP 24997, 25949; Altamira, MZUSP 63337; Alter do Chão, OMNH 34359; BR 010, km 93, Belém-Brasilia, MZUSP 24945; Canindé, MZUSP 25009; CEMEX, 101 km S, 15 km E Santarém, OMNH 34762; Juruá, Rio Xingu, MZUSP 64198; Rio Vermelho, MZUSP 70075; Serra do Cachimbo, MNRJ 2567, 11721; Serra de Kukoinhokren, MZUSP 69318, 69320-69322 (69321 = Holotype), 70365, 70549, 70918, USNM 559809; Tucuruí, MZUSP 62554, 75618, 85170, USNM 523765; Xingó dam site, MZUSP 131849-131853.

Leptodactylus pentadactylus

BOLIVIA. LA PAZ. Iturralde: Serranía de Eslabon, CBF 3876, 23925. PANDO. General Federico Roman: Río Negro, ca 150 m, USNM 336179. Manuripi: 8 km SO Santa Rosa, CBF 1303.

BRAZIL. NO STATE. Pará to Manaus, lower Amazonia, USNM 28929. ACRE. Recordação, Rio Moa, MZUSP 51552; Rio Branco, MZUSP 70974. AMAZONAS. Igarapé Belém, Rio Solimões, MZUSP 24897; Lago Amanã, MZUSP 58527; Manaus, MZUSP 377, 56719-56721; Reserva Ducke, MZUSP 53748; Reservas BDFF, north of Manaus, MZUSP 57359, 60087, 68200-68201; Rio Cuieiras, MZUSP 65406; Rio Gutaki (probably Jutahi = Jutaí), ZMB 30972; Rio Ituxí, Scheffer Madeireira, OMNH 36851; São José (Jacaré), Rio Solimões, MZUSP 40303; Serrinha, Rio Japurá, MZUSP 56777-56779. MATO GROSSO. Claudia (Fazenda Iracema), MZUSP 83181-83183. PARÁ. Altamira, ca 50 km (airline) S of, near Cachoeira do Espelho, rocky island in Rio Xingu, USNM 303466; Altamira, Usina Kararahô, km 10 do acesso do acampamento Juruá, ZUEC 7232; Altamira, Usina Kararahô, km 27 do acesso do acampamento Juruá, ZUEC 7233; Canindé, Rio Gurupi, MZUSP 25010-25011; Curuá-Una, MZUSP 58437; Furo do Panaquara, MZUSP 35677; Juruá, Rio Xingu, MZUSP 64195-64197, 64199-64201, 64253-64254; Monte Cristo, Rio Tapajós, MZUSP 38956; Óbidos, MZUSP 22126; Reserva Biologica Rio Trombetas, at junction of Igarapé Jacaré and Rio Trombetas, USNM 289058; Serra de Kukoinhokren, MZUSP 69331, 70364, 70917; Vai-Quem-Quer, MZUSP 69625.

COLOMBIA. AMAZONAS. Leticia, USNM 147053; Leticia, vereda Caña Brava, 200 m, ICN 35884. CAQUETÁ. Florencia, vereda Santa Elena, 25.9-27.5 km, 980 m, ICN 24174-24176; Florencia, La Vega, MLS 272, 293. META. Río Guayabero, Angostura No. 1, USNM 150490.

ECUADOR. FRANCISCO DE ORELLANA. No other data, QCAZ 15953; Estación Científica Yasuní, 240 m, QCAZ 5236, 16659; Llinta, Aguarico, EPN 6637-6638; Nuevo Rocafuerte, Aguarico, PCSA-2, 212 m, EPN 6572; Parque Nacional Yasuní, Aguarico, EPN 2541, 2678, 2812, 6511, QCAZ 24321-24322; Pozo Yampuna, Orellana, EPN 2813-2814. NAPO. Parque Nacional Sumaco Napo Galeras, QCAZ 16134; San José de Payamino, Loreto, EPN 1723; San Pablo de Kontesya, 300 m, MECN 275, 367-371. PASTAZA. Arajuno, Curaray, Villano, EPN 6861, 7409; Canelos, USNM 196742; Pozo Misión, 240 m, EPN 1036-1042; Puyo, Pastaza, EPN 1848; Puyo, 2 km E of on trail to Veracruz, USNM 196741, 226350; Río Arajuno, cabaceras del, tributary of Río Napo, USNM 196744; Río Pindo, USNM 196747; Río Rutuno, tributary of Río Bobonaza, USNM 196746; Sarayacu, MZUSP 12652; Tiguino, 130 km S of Coca (now Francisco de Orellana), 300 m, USNM 320986-320987. SUCUMBÍOS. Cuyabeno, MECN 344; La Selva Hostría, QCAZ 8495; Reserva de Producción Faunistica Cuyabeno, QCAZ 312, 2121, 2052, 5861-5863, 8013; Santa Cecilia, QCAZ 290. ZAMORA-CHINCHIPE. Destacamento Militar Miasi, EPN 4132-4135.

FRENCH GUIANA. CAYENNE. Arataye River, south bank of, ca 5 km below Saut Parare, 20-50 m, USNM 287753-287754.

PERU. AMAZONAS. San Antonio, vicinity of, on the Río Cenepa, USNM 317519; Shaim, vicinity of, on the Río Alto Comaina (tributary of the Río Cenepa), USNM 317517; Shaim, Río Cenepa, USNM 560372; Tseasim, on the upper Río Huampami (tributary of the Río Cenepa), USNM 317518. CUZCO. Cashiriari-2 (Armihuari), ca 4 km S of the Camisea River, 579 m, USNM 538202; Pagoreni on the Camisea River, 465 m, USNM 538203-538204; Paucartambo, 84 km (by road) NE of, puente Quita Calzon (= km 164 on Paucartambo-Atalaya road), 1180 m, USNM 346146; San Martín, ca 5 km N of the Camisea River, 474 m, USNM 538196-538201. JUNÍN. Chonkareni, near Otica, Río Tambo, USNM 234000. LORETO. Río Lagarto Cocha, Aguas Negras, USNM 521020. MADRE DE DIOS. Pakitza, Reserve Zone, ca 57 km (airline) NW mouth of Río Manu on Río Manu, 350 m, USNM 298902, 334139-334140, 342641-342642, 342856, 345286; Tambopata Reserve, Explorer's Inn, 30 km (airline) SSW Puerto Maldonado, 280 m, USNM 222283-222284, 247368-247369, 268971-268972; Zona Reservada Tambopata-Candamo, Colpa de Guacamayo, W bank of Río Tambopata, USNM 332460.

SURINAME. Albina, ZMB 5806.

Leptodactylus peritoaktites

ECUADOR. AZUAY. Tamarindo, FHGO 069. COTOPAXI. Sigchos, USNM 196743. ESMERALDAS. Hacienda Equinox, 38 km NW of Santo Domingo de Los Colorados, 1000', USNM 196739 (Holotype). PICHINCHA. Bosque Protector la Perla, QCAZ 4530; Centro Científico Río Palenque, 47 km S of Santo Domingo de Los Colorados, 150-220 m, USNM 285391-285392; Ramsey Farm, 18 km W Santo Domingo de Los Colorados, km 19 Chone road, USNM 196740, 196745, 527992.

Leptodactylus rhodomerus

COLOMBIA. ANTIOQUIA. Parque Regional Natural Los Orquideas, vereda Venados, Municipio de Frontino, 850-950 m, ICN 35540. CHOCÓ. km 39 from Carmen de Atrato to Quibdó, 700 m, ICN 17035; corrego Guayabal, ca 8 km de Quibdó, ICN 10070; Lloró, Granja Experimental “CEMA”, ICN 16663. NARIÑO. Vereda Gualcalá, Municipio de Barbacoas, 360 m, ICN 13936. VALLE DE CAUCA. Near Buenaventura, Virology Field Station, Río Raposo, USNM 151460-151461; Daqua, Queremal, 1100 m, ICN 32700; Río Calima, USNM 145094, 150756; vereda Campo Alegre, Municipio de Restrepo, 460 m, ICN 13320-13323 (13322 = Holotype).

ECUADOR. ESMERALDAS. Alto Tambo, 253 m, QCAZ 17056; Luis Vargas Torres, 8.5 km SE de la población de Selva Alegre, EPN 7869.

Leptodactylus savagei

COLOMBIA. ANTIOQUIA. Chicorodó, near Turbo, USNM 153914; 5 km S Valdivia, ICN 9934, 9936. MAGDALENA. Parque Nacional Tayrona, trail between Cañaveral and El Pueblito, USNM 200376; Parque Nacional Tayrona, Santa Marta, 360-400 m, ICN 13655-13658, 13668, 21995, 23255; Parque Nacional Tayrona, Santa Marta, localidad El Cedro, ICN 20674-20675; Santa Marta, road to Altamira, Sierra Nevada de Santa Marta, ca 680 m, ICN 20335.

COSTA RICA. NO OTHER DATA. USNM 19600. CARTAGO. La Suiza, KU 25713, 28188; Moravia de Turrialba, KU 30407, 65709, UTA 1395; near Peralta, Tunnel Camp, KU 33165, 33167; 2.7 miles NE Río Reventazon bridge, Peralta road, UMMZ 117274-117276; Turrialba, AMNH 62251, FMNH 57532, 101800, 101802, KU 30408-30411, 65707-65708, USNM 29953-29954; 10 miles S Turrialba, USNM 192577. GUANACASTE. Estación Experimental Enrique Jiménez Nuñez, 13.6 km SW of Cañas, 20 m, USNM 219777. HEREDIA. 7 km NE Puerto Viejo, 300 m, KU 33135-33139, 33144-33152, 65710-65712. LIMÓN. La Lola, KU 34967, UMMZ 117277; Los Diamantes, FMNH 101797, 101799, KU 25716-25718, 30405-30406, 65706; Puerto Viejo, KU 35924; Suretka, UMMZ 129019, 135387, 135392, KU 35927; Tortuguero, AMNH 75098, MCZ 29134. PUNTARENAS. Agua Buena, KU 35928-35929, 34965; 33 miles N Canoas, Río Barrow pit, 150’, USNM 148524; Golfito, KU 33153, 34968-34969, 65715-65717, TCWC 19305-19306; Osa Tropical Science Center, ca 2.5 km SW Rincon de Osa, 30 m, LACM 116317, USNM 219538, 227645-227656 (227652 = Holotype); Villa Neily, 75 m, KU 65713-65714, 100338-100339, 100354. SAN JOSÉ. El General, KU 25715; 3 miles SSE San Isidro del General, FMNH 101801; 13 miles SSW San Isidro del General on Dominical road, 710 m, KU 34966, 35925-35926, LACM 114334.

HONDURAS. COLÓN. Belfate, AMNH 45704; Quebrada Machín, 540 m, USNM 534216-534220; Salamá, USNM 242000-242014. EL PARAÍSO. Ca 1 km E Arenales, 390 m, USNM 524346. OLANCHO. El Torno, 180 m, USNM 514579; Quebrada de Las Marías, ca 12 km NNE La Colonia, 660 m, USNM 523764, 524347; Nueva Esperanza, 710 m, USNM 534215; Quebrada El Guásimo, 140 m, USNM 535865; near Quebrada El Mono, 100 m, USNM 538627; Río Kosmako, 130 m, USNM 538626; confluence Río Wampú and Quebrada Siksatara, 95 m, USNM 319944; confluence of Río Yanguay and Río Wampú, 100 m, USNM 319943.

NICARAGUA. BLUEFIELDS. 6 km W Rama, 50’, TCWC 19307. GRENADA. Grenada, LACM 37870. MATAGALPA. Finca Tepeyac, 10.5 km N, 9 km E Matagalpa, 960 m, KU 85146; Greytown (= San Juan del Norte), USNM 19765. ZELAYA. Bonanza, KU 85147-85148, 101168; Camp Corozo, Río Huahuashan (= Río Wawashan), AMNH 54980-54981; Camp Santa Ana, Río Huahuashan (= Río Wawashan), AMNH 54999; Cara de Mono, 50 m, KU 112703-112704; El Recreo, 25 km W Rama, KU 112666-112672, LACM 13945, 20475; Masawas, Waspuk River, AMNH 58435; Recreo, 10 miles above Río Mico, UMMZ 79751-79752.

PANAMA. BOCAS DEL TORO. Almirante, KU 79992, USNM 142334; Boca del Drago, USNM 142318; Cayo Nancy, USNM 338479-338480; Isla Colón, La Gruta, USNM 338121-338124; Isla Cristobal, Bocatorito camp, USNM 348134-348135; Isla Popa, 1 km SE Deer Island channel, USNM 298079-298080; S end of Isla Popa, 1 km E of Sumaco channel, USNM 347152-347156; Laguna de Tierra Oscura, 3.7 km S of Tiger Key, USNM 348432-348436; Peninsula Valiente, Punta Alegre, USNM 338606; Punta de Peña, USNM 38714. CHIRIQUÍ. Progreso, UMMZ 58221. COCLÉ. El Valle, AMNH 59590, KU 76573, 107229, 116825. COLÓN. Frijoles, USNM 196303. DARIÉN. Camp Creek, Camp Townsend, AMNH 40786-40788, 41061; Casita (Tacarcuna Casita), USNM 141783; near Jaqué, at jct of Río Jaqué and Río Imamado, USNM 161215; Laguna, 820 m, KU 76570-76572; Río Canglón, UMMZ 123158-123161; Río Chucunaque, ca 7 km above Río Mortí, 150 m, KU 107230; Río Silugandí, UMMZ 124018; Río Tuira at Río Mono, KU 115308; Río Ucurgantí, ca 7 km above mouth, KU 97014-97017, 107231-107232; Tacarcuna, 550 m, KU 76513-76514. LOS SANTOS. Guánico Arriba, 60 m, KU 107228. PANAMÁ. Altos de Maje, AMNH 88743; Barro Colorado Island, AMNH 69728, FMNH 175986, KU 76568, MCZ 15266, UMMZ 63594, USNM 161151; Cerro Campana, KU 76569; Chili Brillo, Cave A, AMNH 62338; Juan Mina, Chagres River, USNM 129908; near Madden Dam, AMNH 87143, KU 115306, UMMZ 78481; Tapia, AMNH 18922-18923. SAN BLAS. Armila, USNM 150090; Armila, Quebrada Venado, USNM 150089; Camp Sasardí, 12 m, KU 108688-108689. VERAGUAS. Mojara, AMNH 123320; mouth of Río Concepción, KU 115307.

Leptodactylus turimiquensis

VENEZUELA. ANZOÁTEGUI. Cueva del Agua, near Puerto La Cruz, CV-ULA iv•1180, USNM 559810; Pekin abajo, Río Neveri, SCN 2294-2295; Puerto La Cruz, SCN 12359. MONAGAS. Camp. MARNR, Río Guarapiche, EBRG 2360; Caripito, AMNH 70667-70668 (70667 = Holotype); El Caliche, Juasjuillar, Dtto. Caripe, EBRG 2085. SUCRE. Casa Inparques, Los Mangos, Paria, SCN 12323-12326; Cumanacoa, CM 9065; Guaraúnos, EBRG 422, KU 166492-166493; carretera via Hacienda Buena Vista, Península de Paria, SCN 12327-12328; La Fragua, Sierra del Turimiquire, CV-ULA iv•5541, iv•5620-5622; near Latal, Hacienda Mirasol, CM 9098; La Yaguara, 4 km E Río Salado, Paria, EBRG 423; Parare, ZMFK 36063; Parque Nacional Península de Paria, Hacienda Solís, 150 m, EBRG 2561-2562; bajada a San Juan de los Galdonas, SCN 10705.

Leptodactylus vastus

BRAZIL. ALAGOAS. Fazenda do Prata, Mun. São Miguel dos Campos, MNRJ 9925; Murici, MNRJ 9767; São Miguel dos Campos, MZUSP 9244. CEARÁ. Açude Atalhos, Mun. Brejo Santo, MNRJ 30957; estrada para o Açude Atalhos, Mun. Brejo Santo, MNRJ 30958-30959; Açude dos Prazeres, MNRJ 30951, 30955-30956; tanques de piscicultura abaixo do Açude Quixabinha, MNRJ 30933, 30962; Arajara, MZUSP 56603-56604; Aurora, MNRJ 30960; Baturité (Açudinho), MZUSP 25151-25152; Crato, MNRJ 431, 1085; Fortaleza, Macuripe, MNRJ 2589, 12035; Itapipoca, MZUSP 25110-25113; Lima Campos, MZUSP 24534; Maranguape, USNM 109148-109151; Santana do Cariri, MZUSP 54753-54754, USNM 216072-216079. GOIÁS. Araguatins, MZUSP 25309; São Domingos, MZUSP 66620, 66622. MARANHÃO. São Luiz, MZUSP 21746-21747. PARAÍBA. Campina Grande, USNM 109144; Coremas, MZUSP 22907-22908; Elembuzeiro (= Umbuzeiro), USNM 109143; Gurinhém (Fazenda Salgado), MZUSP 65367; Junco do Seridó, MZUSP 52286-52287, 60352; Mamanguape, MZUSP 22865-22867. PERNAMBUCO. No further locality data, USNM 57719; near Caruaru, on way to Serra dos Cavalos, USNM 284552; Exu and vicinity, MZUSP 54526, 56596-56598, 56605-56606; Igarassu, MZUSP 25030;

Ponta de Pedras, MZUSP 34317-34320; Recife (Dois Irmãos), MZUSP 4461; Serra dos Cavalos, 13 km ESE São Caetano, MZUSP 63167. PIAUÍ. Valença, MZUSP 50186-50187; 25 km N Valença, MZUSP 50199. RIO GRANDE DO NORTE. Ceará Mirim, MZUSP 10812; Cruzeta, USNM 109145-109147; Natal, USNM 81131. SERGIPE. Areia Branca, MZUSP 37815-37820; Fazenda Capivara, Brejo Grande, MNRJ 30944; Fazenda Cruzeiro, Cristianópolis, MNRJ 30726; Santo Amaro das Brotas, MZUSP 56599-56602.