Systematics of the *pentadactylus* Species Group of the Frog Genus *Leptodactylus* (Amphibia: Leptodactylidae)

W. RONALD HEYER

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 301

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Systematics of the *pentadactylus* Species Group of the Frog Genus *Leptodactylus* (Amphibia: Leptodactylidae)

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ABSTRACT

Heyer, W. Ronald. Systematics of the *pentadactylus* Species Group of the Frog Genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology,* number 301, 43 pages, 23 figures, 12 tables, 1979.—Sixteen mensural and pattern characters are analyzed for the adult members of the *Leptodactylus pentadactylus* species group. Available data on tadpoles, mating calls, and karyotypes are incorporated in the analyses. Results of the analyses lead to the recognition of 11 species comprising the group. For each species, the following are provided: synonymy, description of adult characteristics, a distribution map and list of localities, and specimens examined. The following are included if known: distinctive adult colors in life, larval characteristics, mating call description, and karyotype. A key is provided for the adult members of the complex.

Larval adaptations appear to be most important in interpreting the evolutionary history within this species group. Adult morphology appears to be evolutionarily rather conservative, contrasting with the patterns found in other species groups so far studied within this genus.

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Contents

Systematics of the *pentadactylus* Species Group of the Frog Genus *Leptodactylus* (Amphibia: Leptodactylidae)

W. Ronald Heyer

Introduction

This study is the fourth in a series (Heyer, 1970, 1973, 1978) treating the systematics of the species groups of the *Leptodactylus* complex.

Many names have been proposed for members of this group. These names have been used in various specific and subspecific combinations with the result that the taxonomy of this group has been confusing and unstable. The purpose of this report is to clarify the specific status of the members of this group based on examination of specimens throughout the geographic range of the group.

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Charles D. Roberts (Information Systems Division, Smithsonian Institution) aided with the statistical and multivariate analyses. Ronald I. Cromble (NMNH) discussed the work with me while it was in progress and provided a translation from German of an original description. Frances I. McCullough (NMNH) prepared Figures 1–4. James F. Lynch and George R. Zug (NMNH) and Paulo E. Vanzolini (MZUSP) read and criticized the manuscript.

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Museum abbreviations as used in the text are:

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
CM	Carnegie Museum, Pittsburgh
FML	Fundación Miguel Lillo, Tucumán
FMNH	Field Museum of Natural History, Chicago
KU	University of Kansas Museum of Natural History, Lawrence

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LACM	Natural History Museum of Los Angeles County, Los Angeles
LES	J. Lescure private collection, Paris
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNRio	Museo Nacional, Rio de Janeiro
MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo
NMNH	National Museum of Natural History, Smithsonian Institution
TCWC	Texas Cooperative Wildlife Collection, Texas A and M University, College Station
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	former United States National Museum collection in NMNH
UTA	University of Texas at Arlington, Arlington
WCAB	W.C.A. Bokermann private collection, São Paulo

METHODS AND MATERIALS.—Morphological data were recorded for a series of characters for as many members of the group as could be examined. These data form the bases of the analyses. Supplementary data are included for tadpoles, mating calls, and karyotypes.

As the data were recorded, I segregated the specimens into intuitive taxonomic units for analysis. For purposes of analysis, the number of taxonomic units was maximized in order that no species would be overlooked. Fourteen units are recognized as follows: (1) *fallax;* (2) *flavopictus;* (3) *labyrinthicus,* Brazil and south; (4) *labyrinthicus,* Venezuela; (5) *laticeps;* (6) *pentadactylus,* Middle America; (7) *pentadactylus,* Coastal Colombia and Ecuador; (8) *pentadactylus* 1, South American east of the Andes; (9) *pentadactylus* 2, South America east of the Andes; (10) *rhodomystax;* (11) *rhodonotus;* (12) *rugosus;* (13) *stenodema;* and (14) *syphax.*

These units are referred to as OTUs (Operational Taxonomic Units) for purposes of analysis. Although I do not care for the term OTU, its meaning is well established and unambiguous. Each of the characters is discussed in terms of these 14 species groupings. The particular methods of analyses are discussed when first used.

Taxonomic judgment was used to recognize the 14 OTUs thought meaningful to subject to detailed analysis. The purpose of the following section is to analyze the distribution of states among the 14 OTUs to determine the robustness of the OTUs so that taxonomic decisions can be made regarding them. For a geographically widespread group for which no large samples are available from a number of localities, I think this procedure is adequate and efficient.

Character Analysis

DORSAL PATTERN.—As data on dorsal patterns were recorded, standards were selected to approximate the various patterns encountered. The pattern from each frog was matched against these standards. If the specimen had a pattern similar to one of the standards, it was coded as that standard. If the specimen's pattern differed, a new standard was established for that pattern. A total of 31 standards were used in the original data gathering. The frequency of pattern standard occurrences for each OTU was determined. Patterns encountered in less than 15 percent of any OTU were combined with the pattern categories that they most closely resembled within that OTU. At the same time, major kinds of patterns were combined. In these cases, the standards differed in detail, although they could not be descriptively differentiated from each other. The remaining pattern standards show the major pattern types encountered in the *pentadactylus* group (Figure 1). The frequency of occurrence of the major pattern types among the OTUs is presented in Table 1.

Two OTUs, *laticeps and syphax,* have dorsal patterns that are distinctive from all other OTUs. The other OTUs share at least one pattern type. Within most OTUs some individual patterns are distinctive; however, many patterns are not unique to a single OTU. As rare, but distinctive, patterns are omitted from Figure 1 and Table 1, commonness of pattern types among OTUs is overemphasized, but not critically. The redundancy of dorsal pattern types among the OTUs is real.

LIP PATTERN.—The methodology for analyzing lip pattern is the same as that used for dorsal pattern. Of the 18 patterns originally used, four occurred at a frequency less than 15 percent in any OTU and were combined. The 14 common lip patterns encountered in the *pentadactylus* group are presented in Figure 2, and the frequency of occurrences of these patterns among the OTUs is presented in Table 2.

A distinct lip pattern occurs in only one OTU, *laticeps.* Two OTUs, *flavopictus* and *rugosus,* have

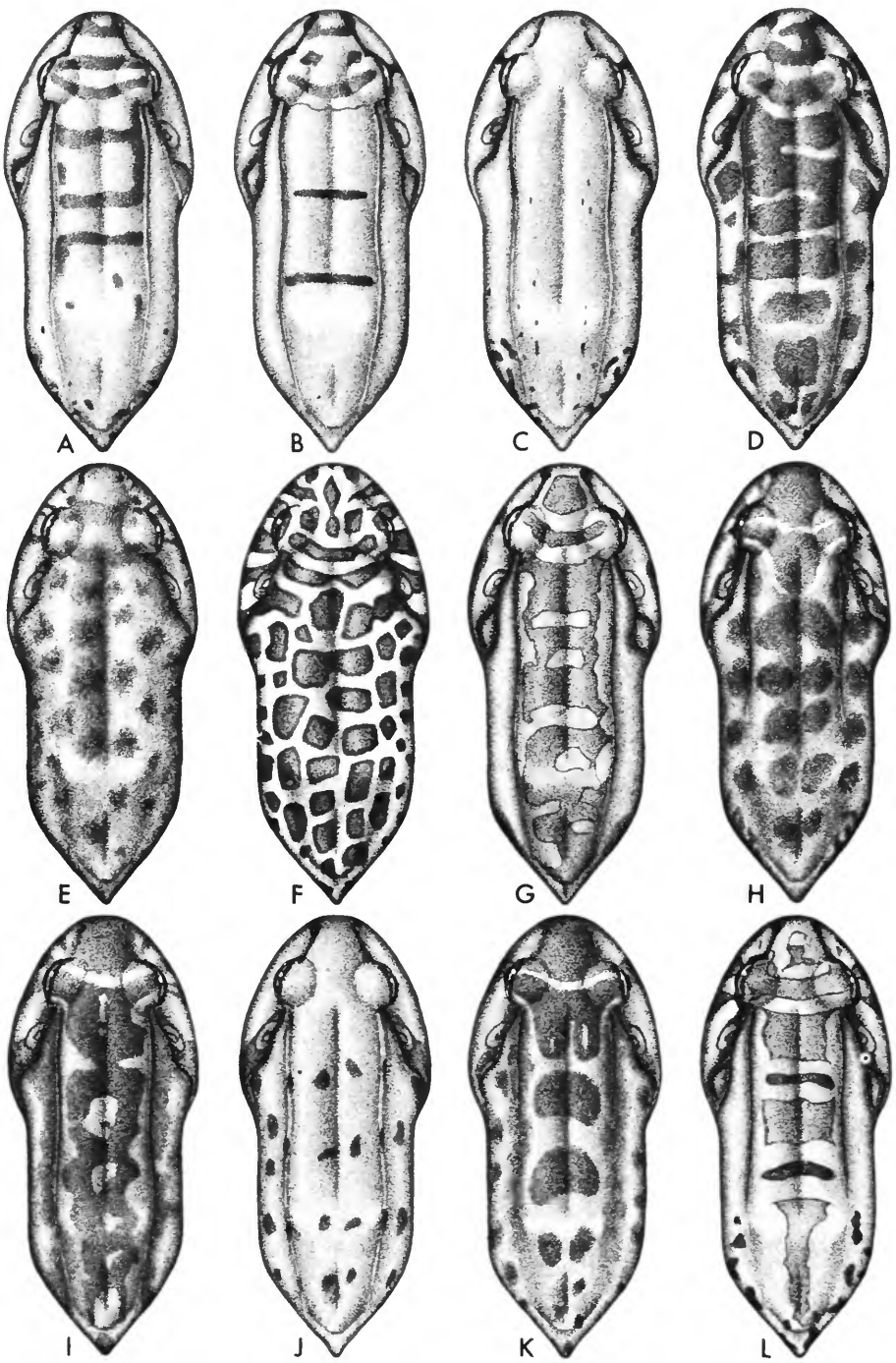

FIGURE 1.—Dorsal pattern standards used in character analysis. (Order of standards is that of convenience.)

TABLE 1.—Dorsal pattern frequencies among OTUs (OTU numbers as used in text; names associated with numbers same as Figure 5; letters of dorsal pattern standards same as Figure 1; *N* = number of individuals; TP = number of OTUs having each pattern; TO = number of pattern states shown by each OTU)

Patterns	1	2	3	4	5	6	7	8	9	10	11	12	13	14	TP
A.....	12		5			42	47	45	19	21	1				8
B.....						2		7		68					3
C.....	12	100	89	55		20	12	7	9	11	88	8	100		12
D.....	20					2			11			5			4
E.....														100	1
F.....					100										1
G.....						34	34	31	9						4
H.....	8		1						1			44			4
I.....											11	23			2
J.....	48					1						8			3
K.....			4	44								10			3
L.....							7	10	51						3
N.....	25	17	238	9	19	120	15	111	99	39	105	59	19	18	
TO....	5	1	4	2	1	6	4	5	6	3	3	6	1	1	

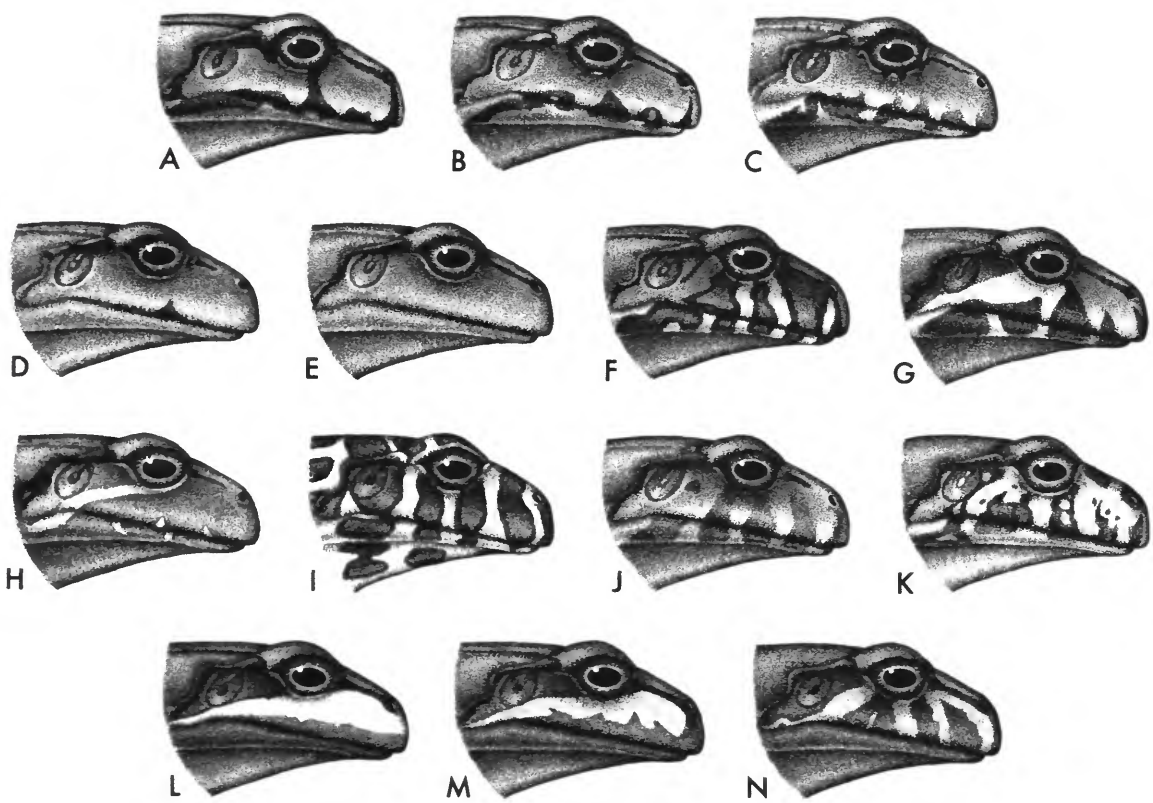

FIGURE 2.—Lip pattern standards used in character analysis. (Order of standards is that of convenience.)

TABLE 2.—Lip pattern frequencies among OTUs (OTU numbers as used in text; names associated with numbers same as Figure 5; letters of lip pattern standards same as Figure 2; *N* = number of individuals; TP = number of OTUs having each pattern; TO = number of pattern states shown by each OTU)

Patterns	1	2	3	4	5	6	7	8	9	10	11	12	13	14	TP
A.....			3			32	60	61	40		1	5	79	78	9
B.....			5			40	27	22	16		9		11		7
C.....			22			25	7	14	29		3	2			7
D.....	42								3				11		3
E.....	58		10	12		2		2	13		48	2		6	9
F.....			49	12								2			3
G.....		71													1
H.....		29								8					2
I.....					100										1
J.....			10	75		1	7					40			5
K.....												2		17	2
L.....										92	13				2
M.....											27	8			2
N.....												40			1
N.....	26	17	238	8	18	121	15	114	101	40	105	60	13	18	
TO....	2	2	6	3	1	5	4	4	5	2	6	8	3	3	

individuals with distinct lip patterns. Lip patterns are better discriminators of the OTUs than dorsal patterns. For example, the most commonly shared lip pattern occurs in nine OTUs, whereas 12 OTUs share a single dorsal pattern.

THIGH PATTERN.—The methodology for analyzing the thigh patterns is the same as that used for dorsal patterns. The 29 patterns initially recognized were combined into 19 (Figure 3). The frequency of occurrences of these patterns is presented in Table 3.

Thigh patterns are virtually distinctive for two OTUs, *laticeps and rhodomystax*. Two OTUs, *fallax* and *stenodema*, have individuals with distinctive thigh patterns. As with dorsal pattern and lip pattern, several of the thigh patterns occur in several OTUs.

TIBIA PATTERN.—The methodology for analyzing the tibia patterns is the same as that used for dorsal patterns. The nine patterns originally scored were combined into five (Figure 4). The frequency of pattern occurrences appears in Table 4.

Tibia patterns are not as diagnostic as the other patterns analyzed. Only one OTU, *flavopictus*, has individuals with a unique pattern.

DORSOLATERAL FOLDS.—For analytical purposes, the position of the fold relative to the eye and the sacrum is coded as: (A) fold long, continuous, from eye to sacrum or groin; (B) fold short, from eye to midbody, not reaching sacrum, may or may not be interrupted; (C) fold absent. The state of preservation tends to obscure the development of the dorsolateral fold in poorly preserved specimens. The fold is almost always accompanied by a dark stripe; in preserved material the presence of stripes has been interpreted as indicating the presence and extent of the dorsolateral fold.

The distribution of states among the OTUs is presented in Table 5. No OTU has a unique state, but the dorsolateral fold states do discriminate among the OTUs.

MALE THUMB SPINES.—Three states are recognized: (A) each thumb with two cornified spines; (B) each thumb with one spine; (C) no spines on thumb. State B includes individuals with some cornification of the metacarpal tubercle producing a weak second spine, but only one spine is clearly developed.

The distribution of states is presented in Table 6. One OTU, *stenodema*, has a unique state. Only one OTU, *rugosus*, possesses two states. All other OTUs have a single state.

MALE CHEST SPINES.—Males of the *L. pentadactylus* group either possess or lack cornified chest spines (Table 7). In several OTUs, some males have chest spines and some lack them; in all these cases, the largest males have chest spines. Apparently, the development of thumb spines denotes sexual ma-

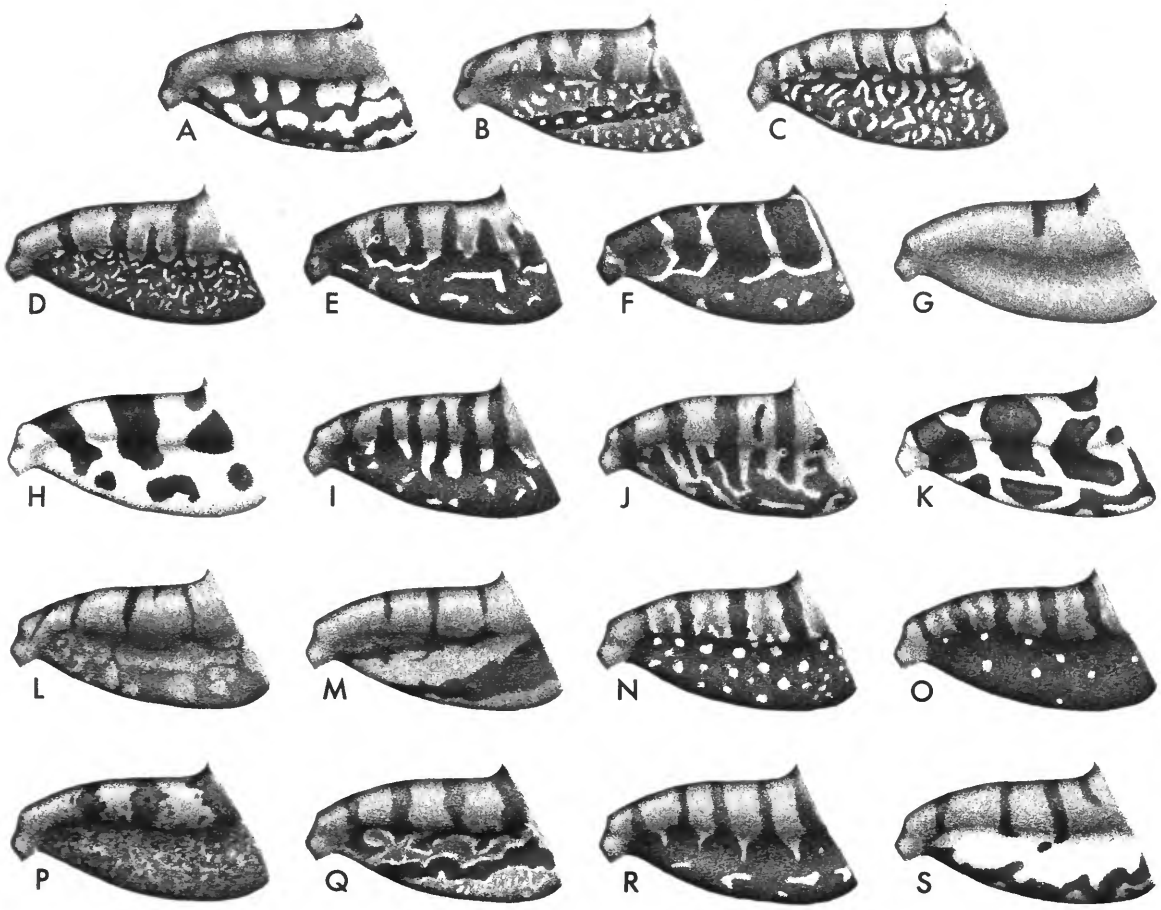

FIGURE 3.—Posterior surface of thigh pattern standards used in character analysis. (Order of standards is that of convenience.)

turity, but chest spine development can occur after the onset of sexual maturity. Neither the chest nor thumb spines are deciduous.

TIBIAL AND TARSAL TEXTURE.—Individuals either have or lack brown or white tubercles on the dorsal surface of the tibia and posterior surface of the tarsus (Table 8). The state of preservation doubtless is important in the interpretation of this character duet, but there are clearly some OTUs that uniformly have tubercles or lack them.

FOOT TEXTURE.—The presence or absence of white or brown tubercles on the sole of the foot is quite variable among the OTUs (Table 9).

MEASUREMENTS.—The following measurements were taken on each adult specimen: Snout-vent length (SVL), head length, head width, interorbital distance, distance from anterior corner of eye to midnostril (eye-nostril), femur, tibia, and foot.

The data were prepared for stepwise discriminant function analysis. The values as recorded from the specimens were used as the variables for analysis. The program used was the BMDP7M (Dixon, 1977). Because of sexual dimorphism, the data for males and females were analyzed separately. For comments on the meaning and interpretation of the results, see Heyer (1977, 1978).

Female Data: No adult females were available for OTU 4, Venezuelan *labyrinthicus*. Data for the remaining 13 OTUs were used as the preformed groups for analysis. The variables entered the stepwise discriminant analysis in the following order (the F values indicate the successive contribution

TABLE 3.—Posterior surface of thigh-pattern frequencies among OTUs (OTU numbers as used in text; names associated with numbers same as Figure 5; letters of thigh pattern standards same as Figure 3; *N* = number of individuals; TP = number of OTUs having each pattern; TO = number of pattern states shown by each OTU)

Patterns	1	2	3	4	5	6	7	8	9	10	11	12	13	14	TP
A.....	15		76	22		22		20	34		1	18		95	9
B.....	4		2			3	20		3						5
C.....	8		2	33		12	7	17	11		47	12	1		10
D.....	8			11		1		4	9		32	2		5	8
E.....			6					32	3						3
F.....		100				2		1	4						4
G.....							13	2	17				42		4
H.....					68										1
I.....			1	33		49	20	7	9						6
J.....	12		3			4		2	9			24			6
K.....					32	1									2
L.....													26		1
M.....													27		1
N.....						1				83					2
O.....										18					1
P.....							7				20	32			3
Q.....	54														1
R.....								16	3			13			3
S.....			10				33								2
N.....	26	17	239	9	19	121	15	113	102	40	105	60	19	19	
TO....	6	1	7	4	2	9	6	9	10	2	4	6	4	2	

TABLE 4.—Dorsal surface of tibia pattern frequencies among OTUs (OTU numbers as used in text; names associated with numbers same as Figure 5; letters of tibia pattern standards same as Figure 4; *N* = number of individuals; TP = number of OTUs having each pattern; TO = number of pattern states shown by each OTU)

Patterns	1	2	3	4	5	6	7	8	9	10	11	12	13	14	TP
A.....	92	29	92	89	100	85	43	98	94	90	66	90	37	94	14
B.....		71													1
C.....			8			13	57	3	5		1	3		6	8
D.....	8									9	1		62		4
E.....				11		2			1		33	7			5
N.....	25	17	238	9	19	121	14	113	100	31	102	59	16	18	
TO....	2	2	2	2	1	3	2	2	3	2	4	3	2	2	

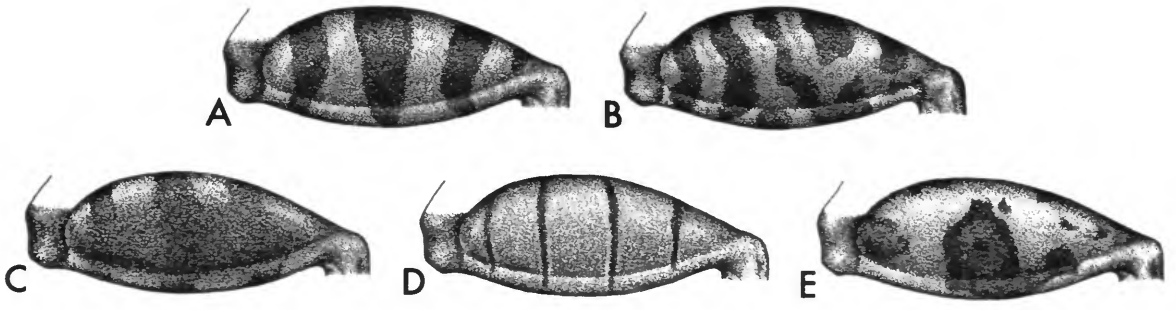

FIGURE 4.—Dorsal surface of tibia pattern standards used in character analysis (Order of standards is that of convenience.)

TABLE 5.—Dorsolateral fold condition among OTUs (OTU numbers as used in text; names associated with numbers same as Figure 5)

Condition	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Long, eye to sacrum or groin..	X	X				X	X	X		X	X		X	
Short, eye to midbody, ... not to sacrum		X	X	X					X					
Absent			X	X	X							X		X

TABLE 6.—Numbers of spines per male thumb among OTUs (OTU numbers as used in text; names associated with numbers same as Figure 5)

Numbers of spines	1	2	3	4	5	6	7	8	9	10	11	12	13	14
2.....		X			X						X	X		X
1.....	X		X	X		X	X	X	X	X		X		
0.....													X	

TABLE 7.—Presence or absence of chest spines in males among OTUs (OTU numbers as used in text; names associated with numbers same as Figure 5)

Chest spines	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Present...		X	X	X	X	X			X	X	X	X		X
Absent....	X		X		X	X	X	X	X		X	X	X	X

of each variable to the discriminant function): head length (F=179.2), tibia (F=21.7), interorbital distance (F=16.2), eye-nostril distance (F=11.0), SVL (F=6.2) head width (F=5.5), foot (F=3.5), femur (F=1.4, this is the only F value for which P>.05; the femur data do not add any information to the analysis).

The scatter of data points about the group centroid for each OTU is used to determine the a posteriori probability that each specimen-case actually belongs to the OTU to which it was assigned a priori. A high degree of morphological overlap among OTUs results in a high probability of misclassifying individual specimens. The results thus indicate how discrete the OTUs are in terms of the characters analyzed. The results for females are presented in Table 10.

The plot of the first two discriminant axes gives a visual picture of the phenetic similarities of the OTUs (Figure 5). For females, the first two axes account for 88 percent of the total among-group dispersion. The first axis probably reflects a size component, the second axis primarily reflects differences in head shapes. As can be seen (Figure 5), there are two major clusters: larger and smaller OTUs.

Male Data: Data for the 14 OTUs were used as the preformed groups for analysis. The variables entered the program in the following order: eye-nostril distance (F=304.5), tibia (F=20.7), head

TABLE 8.—Tibial and tarsal textures among OTUs (OTU numbers as used in text; names associated with numbers same as Figure 5)

Texture	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Tubercles present.....	X		X	X		X	X	X	X	X	X	X	X	X
Tubercles absent.....	X	X	X	X	X	X	X	X	X	X		X		

TABLE 9.—Foot texture among OTUs (OTU numbers as used in text; names associated with numbers same as Figure 5; parentheses = condition rarely found)

Foot tubercles	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Present.....			X	(X)	(X)	(X)			(X)	(X)	X	(X)		X
Absent.....	X	X	X	X	X	X	X	X	X	X	X	X	X	(X)

TABLE 10.—Posterior classification of females of the *Leptodactylus pentadactylus* group (numbers heading rows and columns refer to OTUs as used in text; names associated with numbers same as Figure 5; no adult females of OTU 4 available for analysis)

Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	% correct
1...	11														100
2...		3							1						75
3...		4	73			5		3	7						79
4...															
5...					11										100
6...		5	5			27	9	2	3						53
7...							3								100
8...		1	1			1	4	28							80
9...					1	1			13						87
10...										5					100
11...										3	18	3			75
12...											1	9		1	82
13...													4		100
14...														2	100

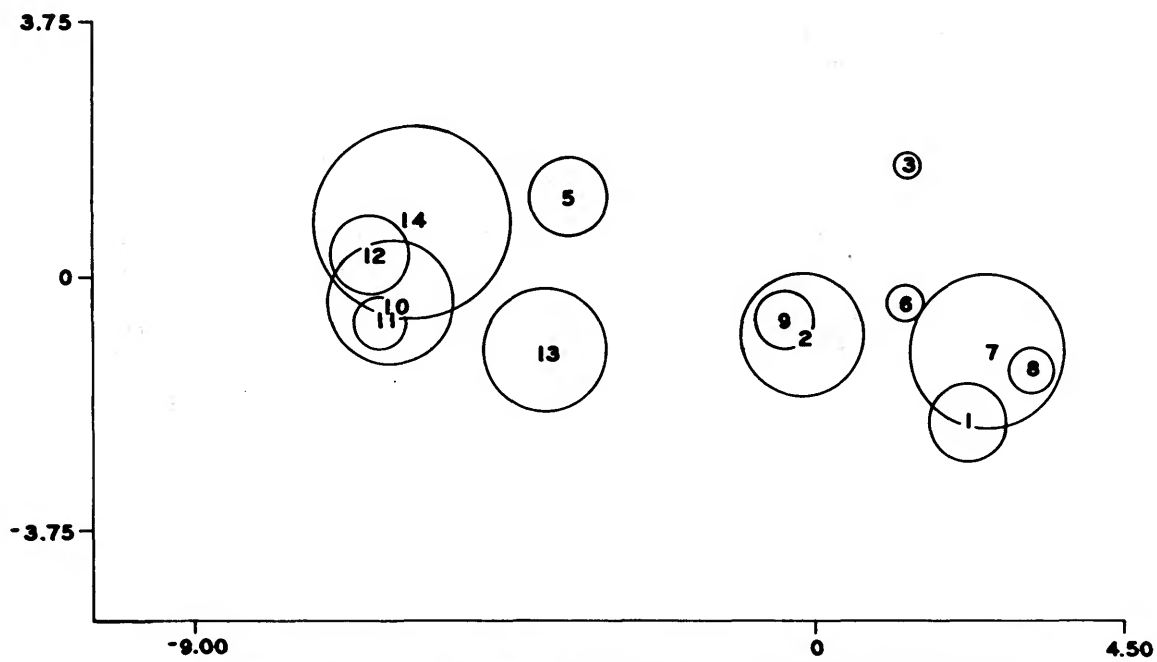

FIGURE 5.—Discriminant axis plot of females of the *Leptodactylus pentadactylus* group. (Numbers refer to OTUs: 1 = *fallax;* 2 = *flavopictus;* 3 = *labyrinthicus,* Brazil and south; 5 = *laticeps;* 6 = *pentadactylus,* Middle America; 7 = *pentadactylus,* Coastal Colombia and Ecuador; 8 = *pentadactylus* 1, South America east of the Andes; 9 = *pentadactylus* 2, South America east of the Andes; 10 = *rhodomystax;* 11 = *rhodonotus;* 12 = *rugosus;* 13 = *stenodema;* 14 = *syphax.* No adult females were available for analysis for OTU 4, *labyrinthicus,* Venezuela. Circles = 95% confidence interval for group centroids..)

TABLE 11.—Posterior classification of males of the *Leptodactylus pentadactylus* group (numbers heading rows and columns refer to OTUs as used in text; names associated with numbers same as Figure 5)

Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	% correct
1...	9														100
2...		11				1									92
3...		8	66	12		12	5	11	4						56
4...				6											100
5...					4										100
6...		10	7	2		33	5	5	4						50
7...							4	1							80
8...						2	1	9	1						69
9...		7	1	3	1	3			28				3		61
10...										9	2				82
11...										9	48	6			76
12...												31			100
13...													9		100
14...												1		15	94

length (F=23.4), interorbital distance (F=11.6), head width (F=12.1), SVL (F=7.7), foot (F=6.1), femur (F=1.4, the only variable for which P>.05).

The classification matrix (Table 11) indicates that most individuals can be sorted into the predetermined OTUs on phenetic grounds.

The plot of the first two discriminant axes (Figure 6) is very similar to the female plot (Figure 5). The first two axes account for 88 percent of the total dispersion.

Combined Results: The results for the females and males are very similar. For the female data, the original F values at step 0 to determine which variable to enter first, for the highest two variables are 179.2, head length, and 171.0, eye-nostril. For comparable male values, the highest two F values are 304.5, eye-nostril, and 274.8, head length. Thus, the differences in order of entering are not substantially different for the female and male data sets.

The classification matrices are very similar, with most OTUs being distinguishable by this analytic technique. All specimens of *fallax, laticeps,* and *stenodema* can consistently be distinguished on the basis of the morphological measurements.

The discriminant axis plots for females and males are very similar. In both sexes the first axis, which is a size-related axis, is the best discriminator. It appears as though the second axis, involving primarily head shape, is a slightly better discriminator among males than females.

TADPOLES.—The tadpoles of five OTUs are known: *flavopictus,* Brazilian *labyrinthicus,* Middle American *pentadactylus, rhodonotus,* and *rugosus.* The tadpole of *rhodonotus* has a generalized pond tadpole morphology. The tadpole of *rugosus* is a stream tadpole with an enlarged oral disk and streamlined tail. Both of these are distinctive from the tadpoles of *flavopictus,* Brasilian *labyrinthicus,* and Middle American *pentadactylus.* The tadpoles of these latter three OTUs are similar in having an anterior oral disk rather than the usual ventroanterior one. The description of *flavopictus* larvae (Bokermann, 1957) indicates that they are indistinguishable from Middle American *pentadactylus* larvae, both of which have a tooth row formula of $\frac{2}{3}$. The larvae of Brasilian *labyrinthicus* have a tooth row of $\frac{1}{2}$ (Vizotto, 1967).

MATING CALL.—The mating calls of six OTUs are available for analysis: Middle American *pentadactylus, pentadactylus* 1, *pentadactylus* 2, *rugosus, stenodema,* and *syphax.* In addition, Dr. Jean Lescure has recorded and will publish a description of the call of *fallax.* Dr. Lescure sent a picture of a sonagram of *fallax;* the call is distinctive from members of the *L. pentadactylus* species group. The calls of *rugosus, stenodema,* and *syphax* are distinctive (see appropriate species account descriptions and figures). The calls of the *pentadactylus* 1 and *pentadactylus* 2 OTUs look similar on the sona-

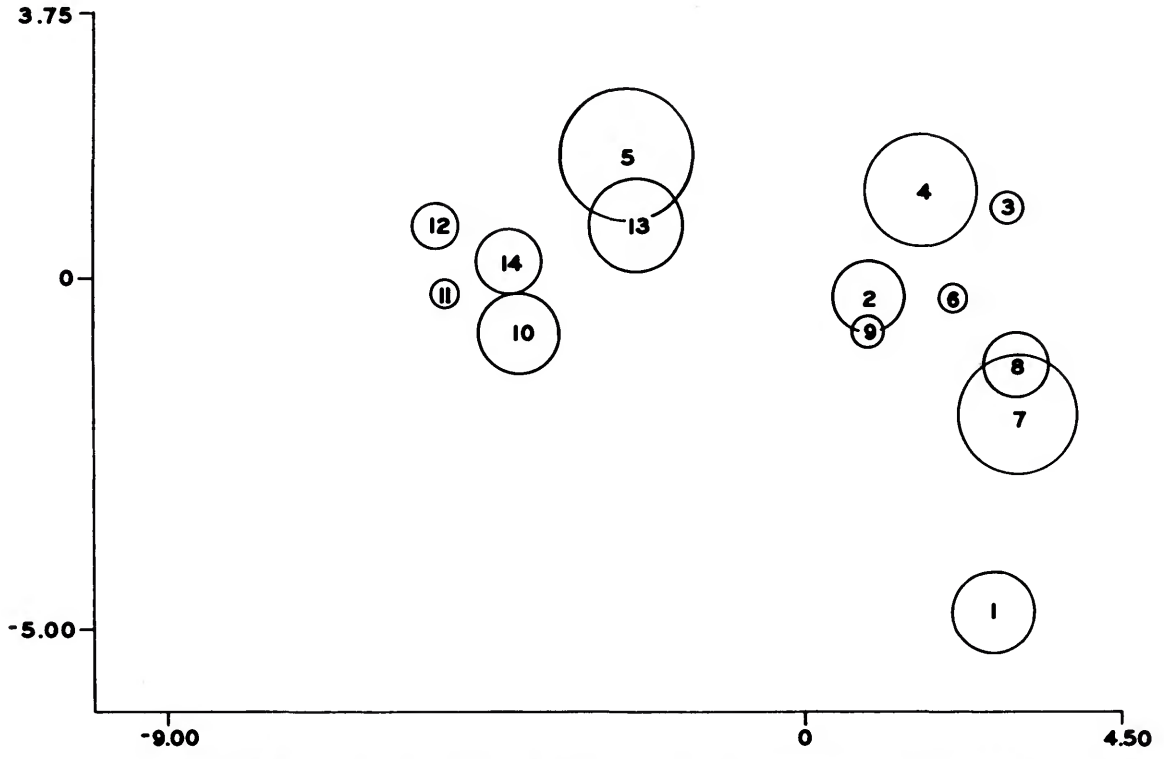

FIGURE 6.—Discriminant axis plot of males of the *Leptodactylus pentadactylus* group. (Numbers = OTUs; see Figure 5 for identifications; circles indicate 95% confidence interval for group centroids.)

grams (Figures 8, 12), but the internal pulsatile structures are radically different (Figures 9, 13). The magnitude of the differences denotes species specificity coding (Straughan, 1975). Although few data are available, the calls of the Middle American *pentadactylus* OTU and those of the *pentadactylus* 1 OTU of South America appear to form a cline of pulsatile structure (Figure 13). The calls of the Middle American *pentadactylus* and *pentadactylus* 1 OTUs are here considered to represent a single biological species.

KARYOTYPE.—Karyotypes are known for five OTUs: Brazilian *labyrinthicus,* Middle American *pentadactylus, pentadactylus* 1, *pentadactylus* 2, and *rhodonotus.* The karyotype of *rhodonotus* has a pattern of secondary constrictions unique to the species of *Leptodactylus* for which karyotypes have been described (Bogart, 1974). Allowing for differences of technique and interpretation, the described karyotypes of the other four OTUs are indistinguishable.

Taxonomic Conclusions

The single best indicator of species level differentiation in *Leptodactylus* is the mating call. Usually, those frogs with distinct mating calls also possess one or more distinctive morphological features (e.g., Heyer, 1978). In this study, mating calls are known for about half of the OTUs analyzed. Thus, the best species level indicator cannot be used for all cases, and patterns of morphological variation must be used in conjunction with the available call data in reaching taxonomic conclusions. Any OTU that consistently differs from another OTU in one or more morphological features is here considered to represent a distinct species. The available mating call data are consistent with this interpretation.

There are two clusters of OTUs that do not differ by at least one character. The first is composed of OTU 6, *pentadactylus,* Middle America; OTU 7, *pentadactylus,* coastal Colombia and Ecuador; and OTU 8, *pentadactylus* 1, east of the Andes. The second is composed of OTU 3, *labyrinthicus,* Brazil and south; OTU 4, *labyrinthicus,* Venezuela; and OTU 9, *pentadactylus* 2, east of the Andes. Within each of these two clusters, pairwise comparisons are made, listing the characters that distinguish certain individuals and the percentages involved where known. These comparisons are the only ones for which there is question concerning the species level of differentiation in my opinion.

OTU 6–OTU 7
Thigh pattern 33%
Tibia pattern 2%
Chest spines
Foot texture
Measurements

These two OTUs were separated on the basis of geography at the initiation of the study. Although the sample size for OTU 7 is small, there does appear to be a slight level of differentiation between these two OTUs. No calls are available for OTU 7. I find no other differences between these OTUs in addition to those already analyzed. The differences between these OTUs are therefore regarded as representing geographic variation in a single species.

OTU 6–OTU 8
Thigh pattern 19%
Tibia pattern 1%
Chest spines
Foot texture
Measurements

As for the previous comparison, these two OTUs were separated first on the basis of geography. Calls are available from individuals representing both OTUs. The limited call data, discussed previously, is best interpreted as representing geographic variation, complementing the morphological variation. I find no other differences between these OTUs in addition to those already analyzed. The differences between the two OTUs are interpreted here as representing geographic variation in a single species.

OTU 7–OTU 8
Thigh pattern 73%

This is the only difference I find between these OTUs. In the absence of call information for OTU 7, I consider the two OTUs to represent the same species.

OTU 3–OTU 4
Dorsal pattern 6%
Lip stripes 29%
Thigh pattern 21%
Tibia pattern 8%
Male chest spines
Measurements

These OTUs were initially separated on the basis of geography because of the hiatus in distribution between members of these two OTUs. Calls are not available for either OTU. I find no other differences between members of these OTUs other than those already analyzed. The differences are here interpreted to reflect geographic variation in a single species.

OTU 3–OTU 9
Dorsal pattern 24%
Lip stripes 42%
Thigh pattern 17%
Tibia pattern 0.3%
Dorsolateral folds
Measurements

A mating call is not presently available for OTU 3, although Bokermann (1957) described *flavopictus,* which he says was similar to *labyrinthicus* (OTU 3), as having a "gluk, gluk, gluk" call like the sound that is produced when a bottle of water is upended and the water gurgles out. This description is quite different from the low-rising whistle call of OTU 9. In contrast to the previous comparisons, I do find differences in addition to those as analyzed between these OTUs. The general aspect of individuals of the two OTUs is different, i.e., I had no difficulty assigning individuals to one OTU or the other at the beginning of the study. In particular, the nature of the dorsolateral folds differs in individuals from these two OTUs, although they were scored the same in the analysis section (the dorsolateral folds are short in both OTUs, hence they were coded the same in the previous analysis). The folds in OTU 3 are very short, extending from in back of the eye only to the scapular region. The dark pigment associated with the fold is often interrupted. The folds in OTU 9 individuals extend from behind the eye to the sacral region and the dark pigment associated with the folds is continuous. I believe these two OTUs represent two different species.

OTU 4–OTU 9
Dorsal pattern 85%
Lip stripes 88%
Thigh pattern 12%
Tibia pattern 5%
Dorsolateral folds
Chest spines
Measurements

No call is available for OTU 4, but in all other respects the situation is the same as for the previous comparison. I believe these two OTUs represent two different species.

In summary, the 14 original OTUs are reduced to 11 distinct species: *fallax, flavopictus, labyrinthicus* (including Brazil and south and Venezuela), *laticeps, pentadactylus* 1 (including Middle American and coastal Colombia and Ecuador), *pentadactylus* 2, *rhodomystax, rhodonotus, rugosus, stenodema,* and *syphax.*

Nomenclature

The nomenclature of members of the *pentadactylus* species group is complex. To my knowledge, 27 names are available (Table 12). Each name is discussed in the order the taxa were described.

Rana pentadactyla Laurenti, 1768: Laurenti based the species upon at least two specimens. The first was the specimen figured in Seba (1734 pl. 75: fig. 1). Seba lists Virginia as the locality for the specimen, as he did for what are now recognized as *Phrynohyas venulosa* and *Ceratophrys cornutus.* Neither genus occurs in eastern North America. Laurenti gives the localities for all three of these species figured in Seba as "Indiis." His designation of "Indiis" is consistent with shipping routes of the day. But the origin of at least the *Ceratophrys* had to be South American rather than from either the West Indies or Middle America. Laurenti mentions a second specimen without locality data housed in the Museo Illustrissimi Comitis Turriani. The body of this second specimen is described in different terms than that of the specimen figured by Seba. As Laurenti described the specimen figured by Seba first, the name bearer of *pentadactyla* is here considered to be Seba's figure rather than the second specimen mentioned by Laurenti. Seba's figure is somewhat stylized (the hand has 5 fingers), but the figure is recognizable as representing a member of the *pentadactylus* group by virtue of the lack of webbing and general shape and pattern. The figure clearly shows a pair of dorsolateral folds extending from behind the eye to the groin, transverse bars between the dorsolateral folds, and dark spots on the sides of the body.

The species corresponding closest to the figure is *pentadactylus* 1. The species with the dorsolateral fold condition figured in Seba are *fallax, flavopictus, pentadactylus* 1, *rhodomystax, rhodonotus,* and *stenodema.* Seba's figure shows the lip area to be blotched, as in *pentadactylus* 1, and not striped, as in either *flavopictus* or *rhodomystax.* The dorsal transverse bars in Seba's figure are characteristic of many individuals of *pentadactylus* 1 and are usually absent in *fallax, rhodonotus,* or *stenodema.* Seba's figure is here considered to represent the species *pentadactylus* 1 and Laurenti's name is applied to this species.

I do not believe restriction of the type-locality or designation of a neotype for *Rana pentadactyla* is warranted at present, as either action would involve arbitrary decisions. If it should later be shown that *pentadactylus* 1 is actually a composite, then restrictive nomenclatural action will be necessary.

Rana gigas Spix, 1824: Dr. Hoogmoed told me that certain of Spix's types were still extant in the Zoologische Staatssammlung München. I wrote to Dr. Ulrich Grüber, who responded in part: ". . . I am very sorry that the Spix types (*Rana gigas, R. pachypus, R. mystacea, R. coriacea, R. labyrinthica*) you asked for have been lost during the last world war. . . . The Spix types for Mr. Hoogmoed belonged to the genus *Bufo*; they are still available." Thus, the information available for allocating Spix's names consists of Spix's descriptions and figures and Peters' (1873) discussion of the type specimens. *Rana gigas* Spix was described from a specimen from the Amazon River. The figure shows a pair of dorsolateral folds, the upper one extending posteriorly to the groin. The dorsal pattern is blotched and is not reminiscent of any *pentadactylus* group members in the Amazon region. The dorsolateral fold condition leads me to assign the frog figured by Spix to *pentadactylus* 1. Thus, *gigas* is considered a synonym of *pentadactylus.* As Smith et al. (1977) point out, *Rana gigas* Spix is a preoccupied name and not available for any *Leptodactylus* species. Since *gigas* is a synonym of *pentadactylus,* there is no need to propose a replacement name for *gigas.*

TABLE 12.—Names described for members of the *Leptodactylus pentadactylus* species group and the current taxonomic status of each

Described name	Current status
Leptodactylus bufo Anderson, 1911	L. labyrinthicus
Rana coriacea Spix, 1824	L. pentadactylus
Leptodactylus dominicensis Müller, 1923	L. fallax
Leptodactylus fallax Müller, 1926	L. fallax
Leptodactylus flavopictus Lutz, 1926	L. flavopictus
Rana gigas Spix, 1824	L. pentadactylus
Leptodactylus goliath Jimenez de la Espada, 1875	L. pentadactylus
Cystignathus hylodes Reinhardt and Lutken, 1862	L. wagneri
Leptodactylus knudseni Heyer, 1972	L. knudseni
Rana labyrinthica Spix, 1824	L. labyrinthicus
Leptodactylus laticeps Boulenger, 1918	L. laticeps
Leptodactylus macroblepharus Miranda-Ribeiro, 1926	L. pentadactylus
Leptodactylus pachyderma Miranda-Ribeiro, 1926	L. flavopictus
Rana pentadactyla Laurenti, 1768	L. pentadactylus
Leptodactylus pentadactylus dengleri Melin, 1941	L. pentadactylus
Leptodactylus pentadactylus mattogrossensis Schmidt and Inger, 1951	L. labyrinthicus
Leptodactylus pentadactylus rubidoides Anderson, 1945	L. pentadactylus
Leptodactylus rhodomystax Boulenger, 1883	L. rhodomystax
Cystignathus rhodonotus Gunther, 1868	L. rhodonotus
Gnathophysa rubido Cope, 1874	L. rhodonotus
Leptodactylus rugosus Nobel, 1923	L. rugosus
Leptodactylus stenodema Jimenez de la Espada, 1875	L. stenodema
Leptodactylus stictigularis Nobel, 1923	L. rhodomystax
Leptodactylus syphax Bokermann, 1969	L. syphax
Leptodactylus vastus Lutz, 1930	L. labyrinthicus
Leptodactylus vilarsi Melin, 1941	L. stenodema
Leptodactylus wuchereri Jimenez de la Espada, 1875	L. labyrinthicus

Rana pachypus Spix, 1824: I previously (1974) listed *pachypus* as a synonym of *pentadactylus*. Reexamination of Spix's figures now leads me to follow Peter's allocation of *pachypus* to the synonymy of *ocellatus*.

Rana coriacea Spix, 1824: Spix figured a uniform brown frog from the Amazon River as *coriacea*. The specimen illustrated is clearly a member of the *pentadactylus* group. A single dorsolateral fold is shown from behind the eye to the sacral region. It is unclear from the picture whether the fold terminates at the sacral region or extends to the groin. Peters (1873) stated that the specimen was illustrated in natural size but that the color pattern was incorrect, actually being faded and rubbed with crossbanding and marbling on the extremities. The figure is of an 80 mm specimen. Peters said it was an adult male with vocal slits. The figured specimen does not closely resemble any Amazonian *pentadactylus* group member known to me. The

closest resemblance is to *stenodema,* having the correct size and approximately similar color pattern for the Amazonian species. A further similarity is that *stenodema* is the only member of the *pentadactylus* group in which the males lack thumb spines as adults. Thumb spines are not mentioned by either Spix or Peters and were presumably absent. In spite of these points of similarity between the descriptions and figures of *coriacea* and *stenodema,* no feature unequivocally associates the two and excludes all other species. I propose acceptance of Peters' (1873) conclusion that *Rana coriacea* Spix is the same as *Rana gigas* Spix, making *coriacea* a synonym of *Rana pentadactyla* Laurenti.

Rana labyrinthica Spix, 1824: The specimen figured by Spix is a juvenile from the state of Rio de Janeiro. The lip pattern of alternating dark and light vertical bars (Figure 2, F) is clearly represented in the figure and is characteristic of members of *labyrinthicus* as used in the preceding analysis.

Cystignathus hylodes Reinhardt and Lutken, 1862: One of the two specimens is still extant and matches the description well except for the presence of toe fringing, which the description stated was absent. The extant specimen is a member of the species currently referred to as *Leptodactylus wagneri* Peters, 1862, a member of the *L. melanonotus* group.

Dr. F. W. Braestrup has kindly clarified certain matters regarding the type of *C. hylodes.* First, Peters' *wagneri* has precedence over *hylodes,* as Reinhardt and Lutken state in the text that Prof. Peters had a short time ago described *Pl. wagneri.* The type-locality for *C. hylodes* is Cotinguiba, but Reinhardt and Lutken used the nearby locality of Maruim as it could be found on maps. I hereby designate the extant specimen, Zoologisk Museum København R 11105, as the lectotype of *Cystignathus hylodes.*

Cystignathus rhodonotus Günther, 1868: Günther described and figured a specimen from Chyavetas (= Chayavitas), eastern Peru. Previously (Heyer, 1969), I considered the holotype to represent *rhodonotus* as used in the analysis section. My subsequent examination of the holotype has confirmed my earlier conclusion.

Gnathophysa rubido Cope, 1874: Placement of *rubido* in the synonymy of *rhodonotus* has been discussed previously (Heyer, 1969).

Leptodactylus goliath Jimenez de la Espada, 1875: Heyer and Peters (1971) designated the eastern Ecuadorian specimen as the lectotype. The lectotype clearly shows the dorsolateral fold extends from behind the eye to the groin and a second fold extends to the shoulder. These states associate *goliath* with *pentadactylus* 1. The oldest available name for *pentadactylus* 1 is *Rana pentadactyla* Laurenti.

Leptodactylus stenodema Jimenez de la Espada, 1875: Pyburn and Heyer (1975) discussed the association of this name with recent specimens. The name applies to the OTU analyzed as *stenodema.*

Leptodactylus wuchereri Jimenez de la Espada, 1875: As commented upon previously (Heyer, 1969), there are discrepancies between the description and the specimen in jar 163 in the Madrid Museum. This specimen, which was chosen as the name bearer, is a member of the *pentadactylus* group. The specimen is a faded juvenile. The dorsum is warty but does not have clearly differentiated dorsolateral folds (in contrast to the description). There is only one member of the *pentadactylus* group in Argentina, the type-locality of *wuchereri: labyrinthicus.* The holotype of *wuchereri* has no character states different from individuals of *labyrinthicus. Leptodactylus wuchereri* is herein considered a synonym of *labyrinthicus.*

Leptodactylus rhodomystax Boulenger, 1883: Boulenger based *rhodomystax* on two juvenile specimens. The light lip stripe and white spotted thighs are distinctive features of the sample analyzed herein as *rhodomystax.* I hereby designate BMNH 1947.12.17.81, the larger of the two syntypes, which matches Boulenger's description, as the lectotype of *Leptodactylus rhodomystax.*

Leptodactylus bufo Andersson, 1911: The type specimen is from Ponta Grossa, Paraná, Brazil. The figure clearly shows the alternating light and dark vertical lip bars and short dorsolateral fold of *labyrinthicus. Leptodactylus bufo* is herein considered a synonym of *labyrinthicus.*

Leptodactylus laticeps Boulenger, 1918: This is the most distinctive member of the genus; consequently, there has been no confusion regarding this name since Boulenger proposed it.

Leptodactylus dominicensis Müller, 1923: This name is preoccupied by *L. dominicensis* Cochran, 1923, of the *fuscus* species group. Müller (1926)

proposed the substitute name *fallax* for his *domincensis.*

Leptodactylus stictigularis Noble, 1923: Noble recognized that his *stictigularis* was most closely related to *rhodomystax* Boulenger. The differences he used to differentiate the two could well be differences of age, since he had an adult specimen to compare with Boulenger's description based on juveniles. The light lip stripe and white spotted posterior surface of the thighs described by Noble are only found in members of *rhodomystax.* Parker's (1935) synonymy of *stictigularis* with *rhodomystax* is maintained.

Leptodactylus rugosus Noble, 1923: Paratypes of *rugosus* were included in the OTU *rugosus.* Noble incorrectly stated that the males of this species lack nuptial spines.

Leptodactylus fallax Müller, 1926: This is the substitute name Müller proposed for the West Indian member of the *pentadactylus* group. As the West Indian population is considered specifically distinct, the name *fallax* applies.

Leptodactylus flavopictus Lutz, 1926: Lutz (1926a) described *flavopictus* in March 1926 in a preliminary note, referring to a figure published later that year (1926b). A light lip stripe and light lateral stripes on the sides of the body are clearly shown in the figure: these are diagnostic features of specimens analyzed as *flavopictus.*

Leptodactylus macroblepharus Miranda-Ribeiro, 1926: The holotype from Manaus, Amazonas, Brazil, has a complete dorsolateral fold from behind the eye to the groin and another fold from the eye to the shoulder. The fold condition associates the name with the species *pentadactylus* 1. The holotype in the MZUSP is a young male with no thumb spines developed as yet.

Leptodactylus pachyderma Miranda-Ribeiro, 1926: Miranda-Ribeiro described *pachyderma* in September 1926, six months after Lutz's description of *flavopictus* appeared. The holotype still shows the light lip stripe and tibia pattern figured by Miranda-Ribeiro. *Leptodactylus pachyderma* is a synonym of *flavopictus* as indicated first by Cochran (1955).

Leptodactylus vastus Lutz, 1930: In 1930, Lutz proposed the name *vastus* for specimens he had previously figured (1926b) from Independencia (= Guarabira), Paraiba. The figures show the incomplete dorsolatoral fold and can only pertain to *labyrinthicus.*

Leptodactylus pentadactylus dengleri Melin, 1941: Melin described this subspecies from two specimens collected in eastern Peru. Dr. Doris Cochran had photographs and a description of the larger specimen, which are at hand. The dorsolateral fold is complete, extending from behind the eye to the groin. This aspect associates the name with *pentadactylus* 1. I hereby designate the larger of the two specimens, the 160 mm male, as the lectotype of *Leptodactylus pentadactylus dengleri* Melin.

Leptodactylus vilarsi Melin, 1941: The female holotype has distinct dorsolateral folds, only a few small dark spots on the dorsum, and measures 100.3 mm SVL. The combination of these characteristics is diagnostic of *L. stenodema.* Cei (1972), unaware that *stenodema* had priority, discussed this species as *vilarsi.*

Leptodactylus pentadactylus rubidoides Andersson, 1945: Andersson recognized two kinds of *pentadactylus* in a collection from east Ecuador. He designated the two types as subspecies. The figure of his nominate subspecies appears to be the same as *pentadactylus* 2. The figure of his new subspecies, *L. pentadactylus rubidoides,* clearly is the same as *pentadactylus* 1. The dorsolateral fold is complete, extending from behind the eye to the groin. A second fold extends from the eye over the tympanum to the shoulder.

Leptodactylus pentadactylus mattogrossensis Schmidt and Inger, 1951: Schmidt and Inger differentiated *mattogrossensis* from the Amazonian and Guianan form of *pentadactylus.* They state (1951: 446): "The relations with *p. labyrinthicus* Spix, of the southeast Brazilian forest region (Pernambuco to Rio Grande do Sul) are by no means clear, but apparently that form has a narrower head and smoother dorsum." This assessment is complicated by the fact that Schmidt and Inger considered *flavopictus* as a synonym of *labyrinthicus.* Thus they recognized only one form from southeastern Brazil, another from the Amazonian region, and described a third form (*L. p. mattogrossensis*) from the diagonal of open formations from Mato Grosso to northeastern Brazil. As understood here, *labyrinthicus* has a broad distribution, which includes the diagonal mentioned above as well as the southeast area of Brazil. The species is found in open forma-

tions throughout its range. In contrast, L. *flavopictus* is found only in the Atlantic forests proper. In the state of São Paulo, for example, *L. flavopictus* occurs both in the deforested areas and the more open vegetation formations of the western part of the state. Thus, *L. labyrinthicus* is found in similar habitats in northeastern and southeastern Brazil. This local ecological distribution pattern is not obvious from regional vegetation maps. Schmidt and Inger's material is here assigned to *labyrinthicus*.

Leptodactylus syphax Bokermann, 1969: Very few specimens of this taxon are represented in collections other than the type series. There has been no confusion regarding this name.

Leptodactylus knudseni Heyer, 1972: The juveniles comprising the type series have the short dorsolateral fold condition of *L. pentadactylus* 2. The color pattern, which is distinctive in juveniles from Ecuador, changes ontogenetically. The black, brown, and green dorsum of the juvenile changes into a brown and tan adult pattern. The posterior face of the thigh, which is uniform in juveniles, becomes patterned in the adults. Apparently, there is geographic variation in juvenile pattern, because Dr. Hoogmoed informs me (pers. comm.) that the Surinam juveniles are not as distinctively marked as the Ecuadorian juveniles. *Leptodactylus knudseni* represents the OTU *L. pentadactylus* 2.

Species Accounts

Members of the *pentadactylus* group are moderate to large-sized frogs. Adults lack fringes on the toes. The head is relatively broad and, in all but one species, the males have thumb spines. All members of the *melanonotus* and *ocellatus* groups have fringes on the toes. Members of the *fuscus* group are small- to moderate-sized frogs; the head is of normal width proportions and the males lack thumb spines.

In the subsequent descriptions, only those characteristics are described that differentiate the species within the *pentadactylus* group.

In the adult characteristics sections, N refers to the number of adult individuals used for statistical analyses. Numerical summaries are means plus or minus one standard deviation.

All known tadpoles have an anterior papillary gap, a median anus, and a sinistral spiracle. These features are not repeated in the species accounts. Tadpole stages are those of Gosner (1960).

The general distribution statement is based on all juvenile and adult specimens examined in this study, together with literature records where no doubt exists about the species identifications. The range maps and locality descriptions are, however, based solely on specimens examined in the present study. The locality data are recorded as nearly as possible to the original catalog data and are not standardized in terms of distances or altitudes. Numbers in parentheses after museum numbers indicate the number of specimens with the same museum number. The computer-generated maps are based only on localities for which longitudes and latitudes could be found.

Leptodactylus fallax Müller, 1926

Leptodactylus dominicensis Müller, 1923:49–52. [Preoccupied by *Leptodactylus dominicensis* (Cochran, 1923). Type-locality: Dominica. Holotype: Zoologisches Sammlung des Bayrischen Staates Herp. nr. 258/1909, female.]

Leptodactylus fallax Müller, 1926:200. [Substitute name for *Leptodactylus dominicensis* Müller.]

DIAGNOSIS.—Specimens of *L. fallax* have distinct dorsolateral folds. This condition is shared with at least some individuals of the following species: *flavopictus, labyrinthicus, pentadactylus, knudseni, rhodomystax, rhodonotus, rugosus,* and *stenodema.* Most individuals of *rugosus* lack dorsolateral folds, but if present, they are interrupted, contrasting with the continuous folds in *fallax*. All individuals of *flavopictus* and *rhodomystax* have light lip stripes; no *fallax* have distinct light stripes on the upper lip. *Leptodactylus fallax* is a large species, the minimum adult size being 121 mm SVL; *rhodonotus* and *stenodema* are moderate-sized species, not exceeding 90 mm SVL and 100 mm SVL respectively. *Leptodactylus fallax* most closely resembles *labyrinthicus, pentadactylus,* and *knudseni* among all species of the *pentadactylus* group. The dorsolateral folds of *labyrinthicus* are short, not extending to midbody and often interrupted; the folds of *fallax* are long and continuous, usually extending to the groin region. Specimens of *pentadactylus* have a fold from the upper tympanum to the side of the body, almost always dark outlined for the entire length of the fold; *fallax* specimens lack this fold. The hind limb of *fallax* is longer

(tibia of male 50 ±2 percent SVL, female 51 ±2 percent SVL, foot of male 51 ±4 percent SVL, female 53 ±1 percent SVL) than that of *knudseni* (tibia of male 43 ±2 percent SVL, female 41 ±2 percent SVL, foot of male 45 ±3 percent SVL, female 43 ±2 percent SVL). *Leptodactylus fallax* is the only member of the *pentadactylus* group in the Lesser Antilles.

ADULT CHARACTERISTICS (N=20). Dorsum spotted, barred, or rarely almost uniform (Figure 1, B–D, H, J); lip uniform or with single dark triangular mark under eye (Figure 2, D, E); posterior surface of thigh with simple or complex light and dark spotting patterns (Figure 3, A–D, J, Q); upper tibia usually broadly or rarely narrowly banded (Figure 4, A, D); usually two complete, dark outlined dorsolateral folds from eye to groin, rarely dorsolateral folds not extending completely to groin; dark outlined fold from eye over tympanum to shoulder; no distinct fold from above tympanum to side of body; male with 1 thumb spine per hand; male lacking chest spines; upper tibia and distal tarsal surfaces smooth, covered or scattered with white or black tipped tubercles, sole of foot smooth; female SVL 147.0±12.3 mm, maximum 167.2, male SVL 141.9±11.0 mm, maximum 158.7 mm; female interorbital distance/head length ratio 0.17±0.02, male 0.18±0.02; female eye-nostril distance/head length ratio 0.26±0.01; male 0.26±0.01; female head length/SVL ratio 0.36±0.02, male 0.35±0.02; female head width/SVL ratio 0.38±0.02, male 0.37±0.02; female femur/SVL ratio 0.45±0.03, male 0.48±0.03; female tibia/SVL ratio 0.50±0.02, male 0.51±0.02; female foot/SVL ratio 0.51±0.04, male 0.53±0.01.

DISTINCTIVE COLORS IN LIFE.—Iris bronze/yellow, sides of body with orange wash (from color slides of Robert Gatten).

LARVAL CHARACTERISTICS.—Unknown.

MATING CALL.—The mating call is being described by Dr. Jean Lescure (pers. comm.).

KARYOTYPE.—Unknown.

DISTRIBUTION (Figure 7).—Schwartz and Thomas (1975:44) list the distribution as "St. Christoper, Montserrat, Guadeloupe, Dominica, and St. Lucia; now extant only on Montserrat and Dominica."

WEST INDIES. DOMINICA (AMNH 3793, 76218–21); (MCZ 81150–54); (USNM 84058, 84534–37, 154530, 158907, 160541, 162244–45); (UMMZ 73524).

ST. KITTS (= ST. CHRISTOPHER) (MCZ 1971, 2182, 81147–49).

Leptodactylus flavopictus Lutz, 1926

Leptodactylus flavopictus Lutz, 1926a:144. [Type-locality: Mont Serrat, Itatiaia, Rio de Janeiro, Brazil. Holotype: Adolfo Lutz Collection 890, MNRio].

Leptodactylus pachyderma Miranda-Ribeiro, 1926:150–151. [Type-locality: Victoria Isle, São Paulo, Brazil. Holotype: MZUSP 351, adult female.]

DIAGNOSIS.—Specimens of *flavopictus* have distinct dorsolateral folds and a distinct light stripe on the upper lip. The other species in which some or all individuals share this combination of characteristics are *rhodomystax* and *rhodonotus*. Most individuals of *rhodonotus* lack a distinct light lip stripe. Individuals of *flavopictus* lack tubercles on the surfaces of the upper tibia and distal tarsus; individuals of *rhodonotus* have tuberculate upper tibial and distal tarsal surfaces. The posterior surface of the thigh of *rhodomystax* has a pattern of discrete, distinct light spots; the thigh patterns of *flavopictus* is contrasting light spots and lines on a dark background, but the spots are irregular, not discrete.

ADULT CHARACTERISTICS (N=16).—Dorsum lacking distinctive pattern (Figure 1, C); lip with broad or narrow light stripe from under eye to angle of jaw (Figure 2, G, H); posterior surface of thigh with contrasting pattern of light spots and lines on a dark background (Figure 3, F); upper tibia with broad continuous or broken bands (Figure 4, A, B); two weakly differentiated dorsolateral folds from eye to sacrum partly dark outlined; dark outlined fold from eye over tympanum to shoulder; no fold from above tympanum to side of body; male with two thumb spines per hand; male with chest spines; upper tibia and distal tarsus smooth; sole of foot smooth; female SVL 130.0±9.2 mm, maximum 139.4 mm, male SVL 123.2±6.1 mm, maximum 133.3 mm; female interorbital distance/head length ratio 0.19±0.02, male 0.18±0.02; female eye-nostril distance/head length ratio 0.25±0.01, male 0.24±0.01; female head length/SVL ratio 0.37±0.02, male 0.38±0.01; female head width/SVL ratio 0.40±0.01, male 0.39±0.02; female femur/SVL ratio 0.43±0.02, male 0.43±0.01; female tibia/SVL ratio 0.44±0.02, male 0.45±0.01; female foot/SVL ratio 0.47±0.02, male 0.48±0.02.

DISTINCTIVE COLORS IN LIFE.—Sides and belly with bright yellow wash and spotting (Lutz, 1926b, pl. 31).

LARVAL CHARACTERISTICS.—Oral disk anterior;

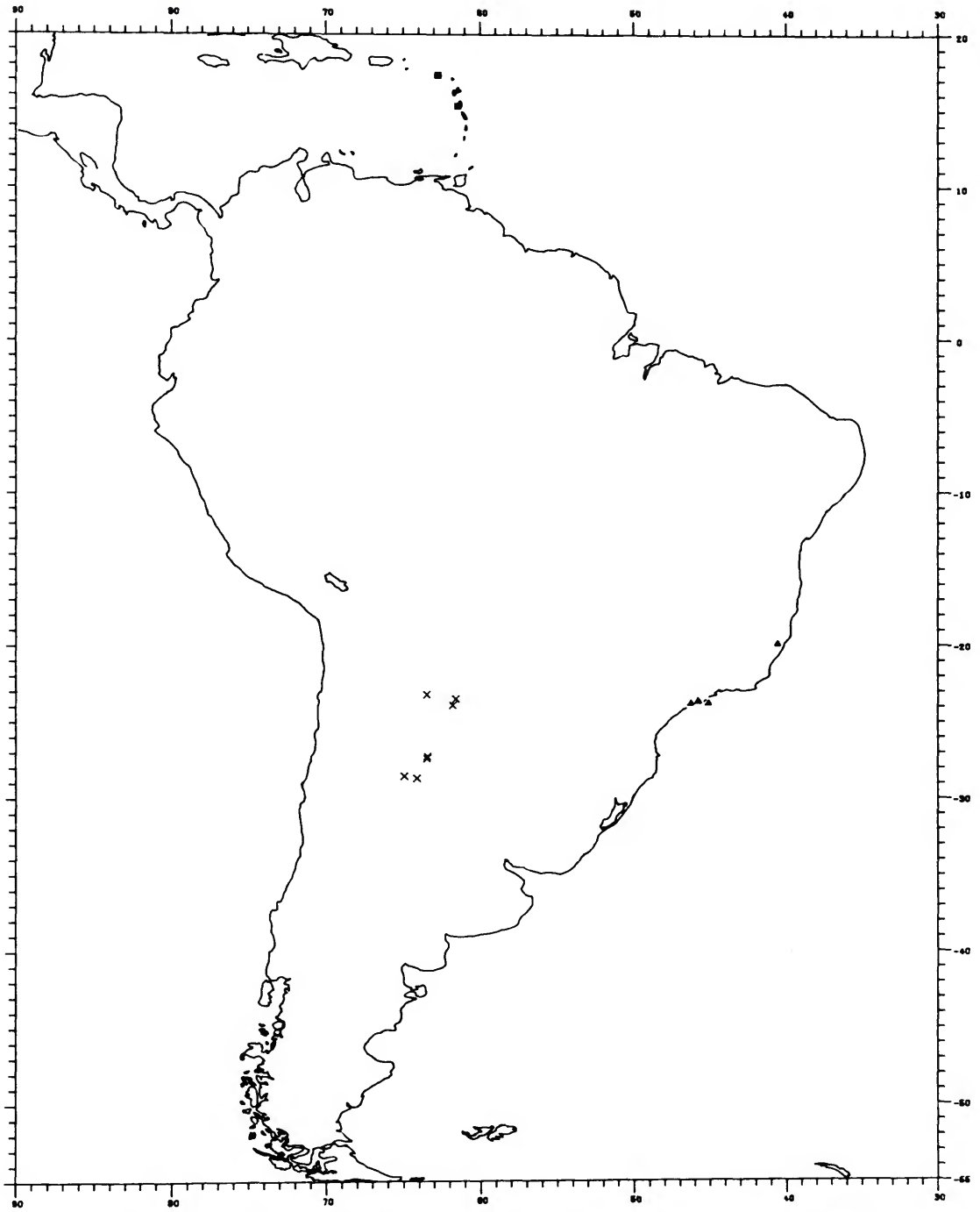

FIGURE 7.—Distribution map of *Leptodactylus fallax* (squares), *L. flavopictus* (triangles), and *L. laticeps* (x's).

oral disk entire; anterior split tooth row no more than 1/3 length of anterior entire tooth row, tooth row formula $\frac{1}{\frac{1-1}{2}}$ (from figs. 6 and 7 in Bokerman, 1957).

MATING CALL.—Bokermann (1957) described the call as a "Gluk, Gluk, Gluk," sounding like the noise when a bottle of water is turned upside down.

KARYOTYPE.—Unknown.

DISTRIBUTION (Figure 7).—Found in the Atlantic forest system of Brazil. Apparently the species is more abundant in the forests on some of the offshore islands than on the mainland.

BRAZIL. ESPÍRITO SANTO: Santa Tereza, Reserva Nova Lombardia (USNM 200454).

SÃO PAULO: Boracéia (MZUSP 21240): (USNM 209215); Ilha dos Búzios (MZUSP 21020, 24099–128); Paranapiacaba (MZUSP 10602, 11018).

Leptodactylus knudseni Heyer, 1972

Leptodactylus knudseni, Heyer, 1972:3. [Type-locality: Limoncocha, Napo, Ecuador. Holotype: LACM 72117, juvenile female.]

DIAGNOSIS.—Specimens of *L. knudseni* have a distinctive pair of dorsolateral folds. Dorsolateral folds are also found in some or all individuals of *fallax, flavopictus, labyrinthicus, pentadactylus, rhodomystax, rhodonotus, rugosus,* and *stenodema.* No individual *knudseni* has a distinct light lip stripe; all *flavopictus* and *rhodomystax* individuals do have distinct upper lip stripes. Most *rugosus* lack dorsolateral folds; when the folds are present, they are interrupted, contrasting with the continuous folds of *knudseni. Leptodactylus knudseni* is a large species (minimum adult SVL 97 mm) with a single thumb spine in the male; *rhodonotus* is a moderate-sized species (maximum adult SVL 90 mm) with two thumb spines per hand in males; *stenodema* is a moderate-sized species (maximum adult SVL 100 mm) in which the males lack thumb spines. The dorsolateral folds of *knudseni* do not extend past the sacrum, those of *stenodema* extend to the groin. *Leptodactylus knudseni* most closely resembles *fallax, pentadactylus,* and *labyrinthicus* within the *pentadactylus* group. No fold is present in *knudseni* from above the tympanum to the side of the body; such a fold occurs in *pentadactylus,* its entire length usually darkly outlined. The dorsolateral folds of *pentadactylus* extend to the groin. The hind limbs of *knudseni* are shorter (tibia of male 43±2 percent SVL, female 41±2 percent SVL, foot of male 45±3 percent SVL, female 43±2 percent SVL) than those of *fallax* (tibia of male 50±2 percent SVL, female 51±2 percent SVL, foot of male 51±4 percent SVL, female 53±1 percent SVL). Many *labyrinthicus* have light vertical bars on the upper lip; *knudseni* lack light vertical lip bars. The dorsolateral folds of *labyrinthicus* are often interrupted; those of *knudseni* are continuous. *Leptodactylus knudseni* is a smaller species (maximum SVL 170 mm) than *labyrinthicus* (maximum SVL almost 200 mm).

ADULT CHARACTERISTICS (N=61).—Dorsum usually barred, sometimes spotted or uniform (Figure 1, A–D, G, H. L); lip uniform or with dark triangular bars (Figure 2, A–E); posterior surface of thigh variously mottled, spotted, or uniform (Figure 3, A–G, I, J, R); upper tibia distinctly or indistinctly barred (Figure 4, A, C, E) or rarely lacking distinct pattern; a pair of usually dark outlined dorsolateral folds from eye to no more than sacrum, usually continuous, sometimes interrupted; dark outlined fold from eye over tympanum to shoulder; no distinct fold from above tympanum to side of body; male thumb with one spine per hand, a rudimentary second spine rarely developed; male chest spines present or absent, present in all specimens 140 mm SVL or larger; upper tibial and distal tarsal surfaces smooth or with scattered to many white or black-tipped tubercles; soles of foot usually smooth, rarely with scattered white-or black-tipped tubercles; female SVL 132.0±8.9 mm, maximum 147.8 mm, male 127.4±2.1 mm, maximum 165.5 mm, female interorbital distance/head length ratio 0.18±0.02, male 0.18±0.01; female eye-nostril distance/head length ratio 0.25±0.01, male 0.26±0.01; female head length/SVL ratio 0.35±0.01, male 0.36±0.02; female head width/SVL ratio 0.37±0.01, male 0.38±0.02; female femur/SVL ratio 0.39±0.03, male 0.41±0.03; female tibia/SVL ratio 0.41±0.02, male 0.43±0.02; female foot/SVL ratio 0.43±0.02, male 0.45±0.03.

DISTINCTIVE COLORS IN LIFE.—Juveniles from Ecuador with a yellowish green head; the dorsum with greenish yellow bands enclosing black-edged brownish green areas. Adult posterior surface of thigh dark with light orange markings; belly sometimes yellow spotted (R. W. McDiarmid color slide).

LARVAL CHARACTERISTICS.—Unknown.

MATING CALL.—Dominant frequency modulated between 350–750 Hz (Figure 8); no harmonic structure in call; 0.02 s pulse of lower frequency (below 500 Hz) immediately followed by 0.1 s complexly pulsed call of higher frequency (above 500 Hz) (Figure 9).

KARYOTYPE.—Diploid number 22, 3 pair median, 4 pair submedian, 4 pair subterminal; no secondary constrictions (Heyer, 1972).

DISTRIBUTION (Figure 10)—The species occurs through the greater Amazon Basin.

BOLIVIA. BENI: Rurrenabaque (UMMZ 108594–96).

BRAZIL. AMAZONAS: Barreira do Matupiri (USNM 202518); Cachoeirinha (MZUSP field 752040), (USNM 202517); Novo Aripuanã (MZUSP field 752046–47); Tefé (MCZ 1294–95). PARÁ: Alegre, 15 km NE Marapanim (MZUSP 24997, 25949); Rio Mapuera, at Equator (AMNH 46180(2), 49484). RONDÔNIA: Alto Rio Machado (MZUSP 15907); Calama (USNM 202516); Forte Príncipe da Beira (MZUSP 25169); Pôrto Velho (MZUSP 16658–68, 16670–84).

COLOMBIA. AMAZONAS: Río Apaporis (USNM 144847). META: Menegua, E. Puerto López (USNM 147272). VAUPÉS: Timbó (UTA 3836, 5230–31).

ECUADOR. MORONA-SANTIAGO: Sucúa, 2 mi E of, on trail from Sucúa to Río Upano, 2700′ (USNM 196722). NAPO: Limoncocha (KU 99041, 122578, LACM 72117–49); Santa Cecilia (KU 104716, 104719, 111406–07, 122576, MCZ 57947, 57953, 57957–58). PASTAZA: Río Conambo (USNM 196723); Río Pucayacu (USNM 196726); Alto Río Pucayacu, Río Bobonaza (USNM 196724 (4); mouth of Río Shyona in Conambo R (USNM 196725).

FRENCH GUIANA. Maripasoula (MCZ 44560.)

GUYANA. Arakaka (UMMZ 66782); Demerara (AMNH 39636); Issano (UMMZ 83586–88); Kamakusa (AMNH 21406); Kartabo (AMNH 10424, 13488, 70881, CM 4064 5442); Kurupung, Upper Mazaruni Dist. (UMMZ 83589–92); Marudi (AMNH 49264); Rupununi, N of Acarahy Mts, W of New R (KU 69681–84); Shudi-kar-wau (AMNH 70117).

PERU. AYACUCHO: La Mar, Sivia on Apurimac R (FMNH 39719). CUZCO: Río Apurimac, Luisiana (AMNH 70389).

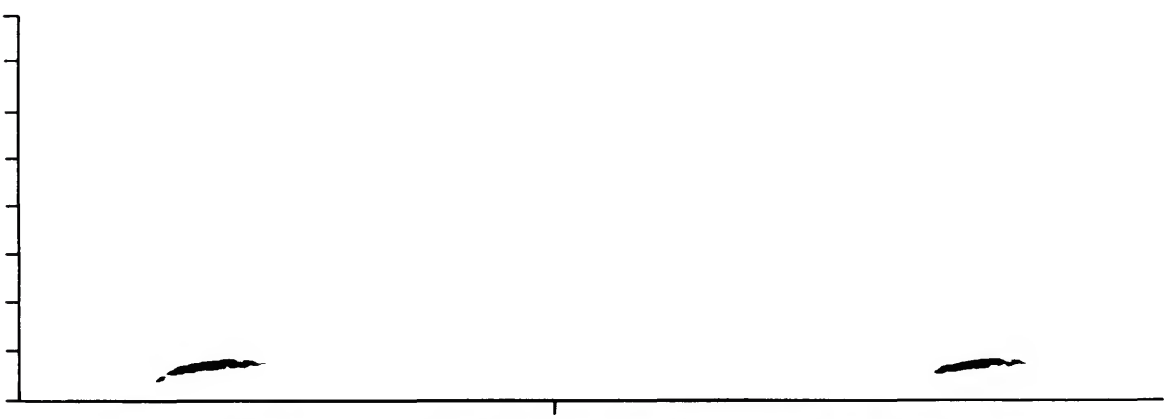

FIGURE 8.—Sonagram of the mating call of *Leptodactylus knudseni*, narrow band filter. (Vertical scale marks at 1000 Hz intervals; horizontal scale mark at 1 s; specimen UTA-5234; air temperature 23.2°C.)

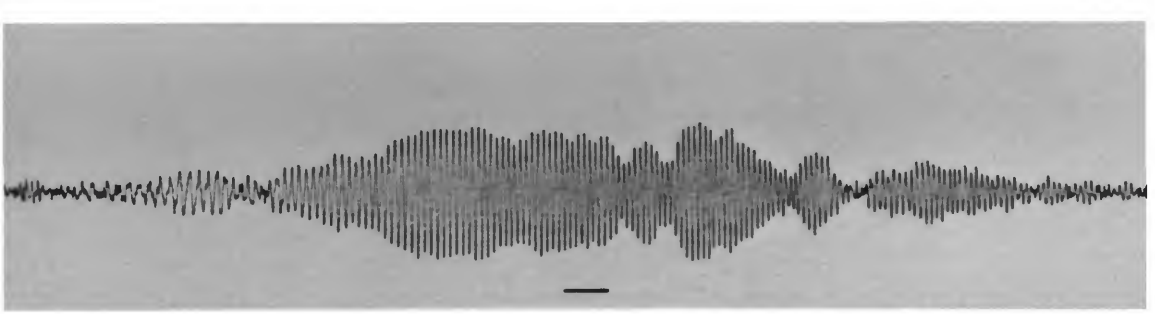

FIGURE 9.—Strip chart record of the mating call of *Leptodactylus knudseni*. (Line = 0.01 s; specimen data same as Figure 8.)

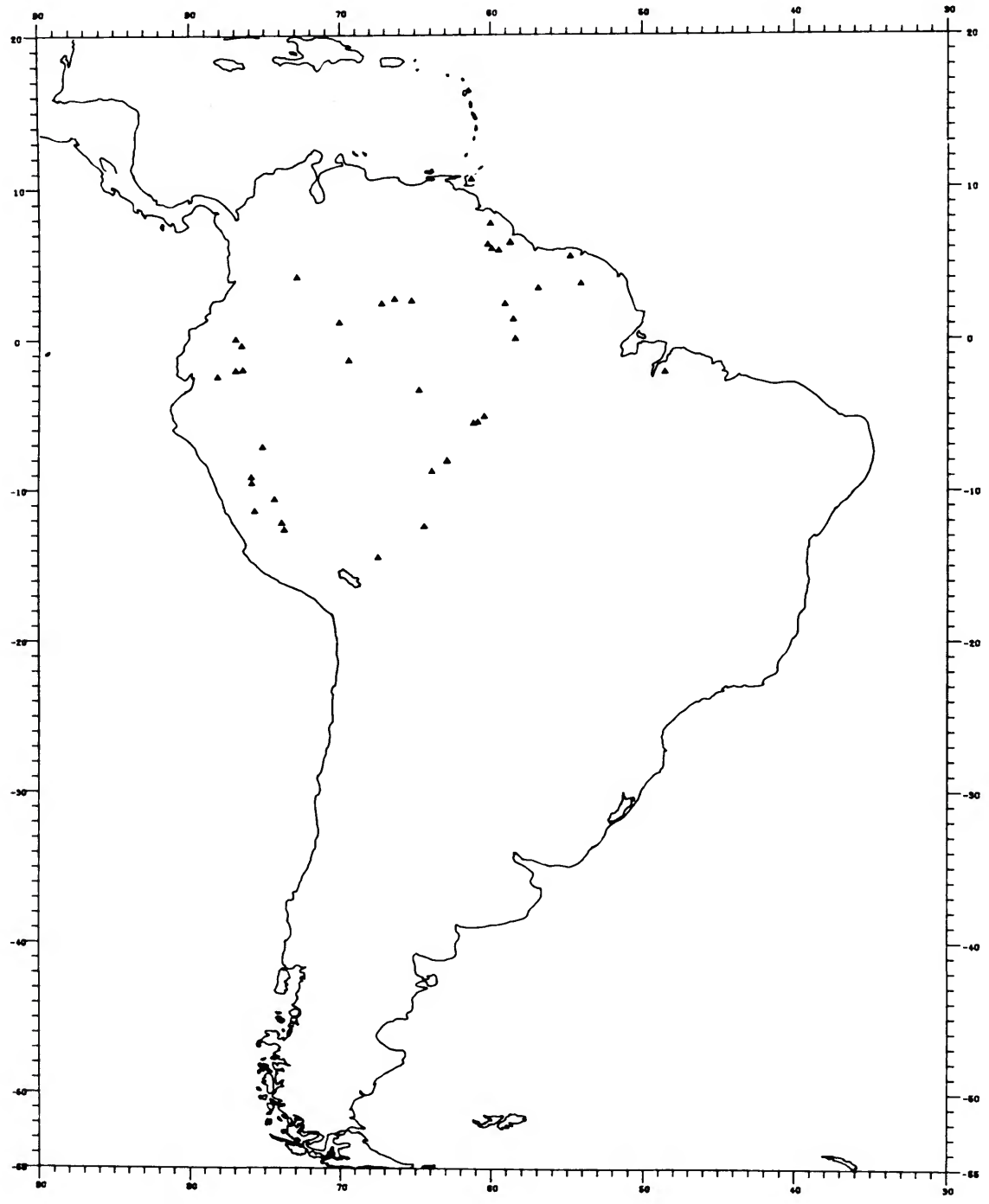

FIGURE 10.—Distribution map of *Leptodactylus knudseni*.

HUANUCO: Hacienda Pampayacu (MCZ 22821–22); Tingo Maria (USNM 193879–84). JUNIN: Tarma, valley of Vitoc R 900 m (FMNH 36831). LORETO: Pampa Hermosa (AMNH 42752). PASCO: Tsioventeni, Prov. Oxapampa (USNM 205553).

SURINAM. Godo Drai, TCWC 23563; Kaiserberg Airstrip, Zuid R (FMNH 128786–89).

TRINIDAD. No specific locality (MCZ 8663).

VENEZUELA. AMAZONAS: Capibara, 106 km SW Esmeralda, Brazo Casiquiare, 130 m (USNM field 19504–05); Paso del Diablo (AMNH 23164); Río Mavaca, 108 km SSE Esmeralda, 140 m (USNM field 17739). BOLIVAR: 13 km S and 1 km E Puente Cuyuni, 140 m (KU 166495–97).

Leptodactylus labyrinthicus (Spix), 1824

Rana labyrinthica Spix, 1824:31. [Type-locality: Rio de Janeiro (state), Brazil. Holotype: destroyed.]

Leptodactylus wuchereri Jimenez de la Espada, 1875:68. [Type-locality: Argentina. Holotype: Museu Nacional, Madrid, 163, juvenile.]

Leptodactylus bufo Andersson, 1911:1. [Type-locality: Ponta Grosso, Paraná, Brazil. Holotype: Royal Museum of Natural History, Stockholm, male.]

Leptodactylus vastus Lutz, 1930:32. [Type-locality: Independencia, Paraíba, Brazil. Holotype: Adolfo Lutz Collection 70, MNRio.]

Leptodactylus pentadactylus mattogrossensis Schmidt and Inger, 1951:444. [Type-locality: Urucum de Corumba, Mato Grosso, Brazil. Holotype: FMNH 9240, adult female.]

DIAGNOSIS.—*Leptodactylus labyrinthicus* has no single feature that immediately distinguishes every individual from all individuals of the other species. *Leptodactylus labyrinthicus* lacks distinct light lip stripes; all *flavopictus* and *rhodomystax* individuals have light upper lip stripes. *Leptodactylus laticeps* has dark squares and rectangles on a light background in a pattern resembling a tile floor; *labyrinthicus* has darker spots and bars on a lighter background but never in a tile floorlike pattern. *Leptodactylus labyrinthicus* is a large species (minimum adult SVL 117 mm), the male has one well-developed thumb spine; *rhodonotus, rugosus,* and *syphax* are moderate-sized species (maximum adult SVLs, 90, 86, 78 mm, respectively) in which almost all males have two spines per thumb (a few *rugosus* have a single thumb spine); *stenodema* is a moderate-sized species (maximum SVL 100 mm) in which the males lack thumb spines. *Leptodactylus labyrinthicus* most closely resembles *fallax, knudseni,* and *pentadactylus* within the group. Many adult *labyrinthicus* and all juveniles are distinct from *fallax, knudseni,* and *pentadactylus* in having distinct light vertical bars on the upper lip. The dorsolateral folds of *labyrinthicus* are short, not extending past midbody, and often interrupted. The dorsolateral folds are continuous in *fallax, knudseni,* and *pentadactylus,* usually reaching the groin region in *fallax* and *pentadactylus. Leptodactylus labyrinthicus* is a larger species (maximum SVL almost 200 mm) than *knudseni* (maximum SVL 170 mm).

ADULT CHARACTERISTICS (N=216).—Dorsum more or less uniform, spotted, or barred (Figure 1, B–D, H, K); lip barred or rarely uniform, usually with light vertical bars (Figure 2, A–C, E, F, J); posterior surface of thigh rarely uniform, usually with contrasting light marks on a dark background (Figure 3, A–E, I, J, S); upper tibia distinctly or indistinctly barred (Figure 3, A, C) or rarely lacking pattern; two continuous or broken dorsolateral folds extending from ¼ to ½ distance from eye to groin, dark outlined or not; dark outlined fold from eye to above tympanum, dark outline continuing or not to shoulder; broken dark outlined fold from top of tympanum to side of body present or absent; usually one thumb spine per hand in males, rarely a second rudimentary spine; male with or without chest spines, all males 170 mm SVL or larger with chest spines; upper tibial and distal tarsal surfaces smooth or with scattered to many white- or black-tipped tubercles; sole of foot smooth or with scattered white- or black-tipped tubercles; female SVL 141.8±12.3 mm, maximum 178.9 mm, male SVL 148.9±16.3 mm, maximum 195.0 mm; female interorbital distance/head length ratio 0.17±0.02, male 0.17±0.02; female eye-nostril distance/head length ratio 0.23±0.01, male 0.24±0.01; female head length/SVL ratio 0.38±0.02, male 0.38±0.02; female head width/SVL ratio 0.40±0.02, male 0.41±0.02; female femur/SVL ratio 0.43±0.03, male 0.43±0.03; female tibia/SVL ratio 0.44±0.03, male 0.44±0.02; female foot/SVL ratio 0.45±0.04, male 0.45±0.03.

DISTINCTIVE COLOR IN LIFE.—Posterior surface of thigh, groin, and belly with yellow or red (Lutz, 1926b, pl. 30).

LARVAL CHARACTERISTICS.—Oral disk anterior; oral disk entire; tooth row formula $\frac{1}{1-1}$; maximum total length, stage 40, 80 mm (from Vizotto, 1967).

MATING CALL.—Tape recording unknown.

KARYOTYPE.—Diploid number 22, 4 pair median,

3 pair submedian, 4 pair subterminal; no secondary constrictions (Denaro, 1972).

DISTRIBUTION (Figure 11).—The species is found throughout the cerrados and caatingas of central and northeastern Brazil, coastal Venezuela, and in more mesic vegetation types in southeastern Brazil to Misiones, Argentina.

ARGENTINA. MISIONES: Cerro Azul (MACN 1690); Oberá, Picada Vieja (FML 2201); Refugio Piñalto, Dept. Fronteira (MACN 2977); San Ignacio (FML 742, 825, 829); Entre San Pedro y Bernardo Irigoyen (MACN 2963).

BOLIVIA. COCHABAMBA: Lake out Alto Palmar on road from Cocabamba to Villa Tunari (USNM 146507). SANTA CRUZ: Buenavista (CM 3808, UMMZ 63963, 66473(2), 66538, USNM 146519–21); El Carmen (CM 36166); El Pailón (CM 36170); El Portón (MCZ 30135); Prov Sara, Rio Colorado (CM 4296).

BRAZIL. ALAGOAS: Usina Sinimbu, São Miguel (MZUSP 9238–44). BAHIA: Barreiras (MNRio 1087–88, 1133, UMMZ 108619–21); Cruz das Almas (MZUSP 4545, 4988, 10529); Japua, Rio São Francisco (MNRio 1086); Copec. Ilhéus (MNRio 703(2)); Itiúba (MZUSP 38517); Salvador (FMNH 71844–47, MACN 4104–05, MZUSP 8281–8306, 9155–9226, 9566–69, 9571–83). CEARÁ: Açudinho, Baturité (FMNH 5640, MZUSP 25151–52); Crato (MNRio 431, 1084–85); Fortaleza, Mucuripe (MNRio 2589(9); Itapipoca (MZUSP 25110–13); Lima Campos (MZUSP 24534); Maranguape (USNM 109148–51); Miranda (MNRio 2550(10)). DISTRITO FEDERAL: Brasilia (MNRio 2710(2)). GOIÁS: Amaro Leite (MNRio 2967); Annapolis (AMNH 43842–44); Araguatins (MZUSP 25309); Aruanã (MZUSP 4989–90 25306–08); Cachoeíra Alta, Rio Verde (MZUSP 10429–33); Cana Brava (MZUSP 24535–37); Fazenda Transvaal, Rio Verde (MZUSP 12506–07, 23059–61, 24538–40, 25329–39), Jataí (MZUSP 20988–90, 25298–301); Lagôa Formosa, Cabeceiras (MZUSP 25296); Rio São Miguel (MNRio 430). MARANHÃO: São Luis (MZUSP 21746–47). MATO GROSSO: Barra do Tapirapés (AMNH 73689–691, MZUSP 24541–42, 25250–53); Burití, Chapada dos Guimarães (MZUSP 37333–43); Dumbá (MZUSP 4311); Salobra (UMMZ 104304); Santa Luzia (ex. Juti) (MZUSP 28548–49); São Domingos, Rio das Mortes (MZUSP 1777–79, 4301–06, 14734); São Felix, Rio Araguaia (MZUSP 25327–28); São Luiz de Cáceres (MNRio 2529); Urucum, S. of Corumbá (FMNH 9206–08, 9239–41, UMMZ 120393); Utiariti (MZUSP 24543, 25203). MINAS GERAIS: Arinos (MZUSP 25052); Belo Horizonte (MZUSP 10973–75, UMMZ 108563(18), 108614–15, USNM 96978–980); Fazenda Bolivia, Unaí (MZUSP 25094); Jaguara (MZUSP 843); Lagoa Santa (MZUSP 25072, UMMZ 108564–65, 108616–18); Peirópolis (MCZ 56273–77); Poços de Caldas, Brejo na Estrada indo de Poços para Andradas (MNRio 3807); Santana, Mun. Itaobim (MZUSP 20519–20); Uberlândia (MZUSP 12043–44); Vespasiano (MZUSP 12714). PARÁ: Alegre,, 15 km NE Marapanim (MZUSP 24997, 25949); Cachimbo (MNRio 2567, MZUSP 21734, 21861–64, 25951); km 93 Belem-Brasilia (MZUSP 24945); Jacareacanga (MZUSP 24947–48). PARAÍBA: Campina Grande (USNM 109144); Coremas (MACN 4166, MZUSP 22907–08); Mamanguape (MZUSP 22865–67). PARANÁ: Parque Nacional de Iguaçu (MNRio 1786). PERNAMBUCO: Igarassú (MNRio 1127); Ponta de Pedra (MZUSP 34317–20); Recife (MNRio 3209, MZUSP 4461, 25030). PIAUÍ: Valença (MZUSP field 750208–09). RORAIMA: Serra do Parima (MZUSP 24936). RIO GRANDE DO NORTE: Ceará-Mirim (CAS 49620, 49629, 49704, 49722, FMNH 64216–19, MZUSP 10812); Cruzeta (USNM 109145–47); Lake Papery (= Lagoa Paparí) (CAS 49486); Natal (MCZ 15848); Papery (= Nísia Floresta) (CAS 49707). RIO GRANDE DO SUL: Sta Maria (MCZ 22975–76). SÃO PAULO: Assis, km 433 (USNM 207674); Avaí (MZUSP 24544–45); Boituva (MZUSP 25353); Borborema (MZUSP 25354–55); Campinas (MZUSP 24546); Colômbia (MZUSP 24547); Fazenda São José de Cachoeira, Rincão (MZUSP 25310); Franca (MZUSP 385); Guarantã (MZUSP 24548); Ipanema (MZUSP 908, 3047); Itapetinginga (MZUSP 2896); Jaboticabal (MZUSP 25549); Lusitânia (MZUSP 24557–58); M'Boi-Guaçu (MZUSP 24550–51); Nova Louzã (MZUSP 25432); Piquete (MZUSP 660, 776, 909); Piracicaba (MZUSP 6420–21); Piraçununga, Cachoeira de Emas (FMNH 71848, MNRio 2082, MZUSP 2004, 4930–37, 11159–63, 11166–69, 25356); Rechã (USNM 121284); Rio Pardo, Botucatu (FMNH 71849–50,MZUSP 2002–03, 7023, 7077–79, 7295–96, 7397–99, 10379, 14501–02, 14504–06); Salgado (= Juquiratiba) (MZUSP 25454); São Bento do Sapucaí (MZUSP 24552–54); São Paulo (MZUSP 1402, 24555); Tatu, Mun. Limeira (MZUSP 25468); Tietê (MZUSP 24218, 24556); Zeinas (MNRio 1965). SERGIPE: Areia Branca (MZUSP 37815–20).

PARAGUAY. CAAGUAZU: Pastoreo, NE of Caaguazu (MCZ 17917).

VENEZUELA. MONAGAS: Caripito (AMNH 70667–68); Escuela Granja Porcela, 8 km WSW Caripito (KU 117123). SUCRE: 25 km (by Puerto La Cruz Rd.) W Cumaná (KU 117124); Cumanacoa (CM 9065); Guaraúnos (KU 166492–94); near Latal, Hacienda "Mirasol" (CM 9098).

Leptodactylus laticeps Boulenger, 1918

Leptodactylus laticeps Boulenger, 1918:431. [Type-locality: Santa Fe, Argentina. Holotype: BMNH 98.11.24.7]

DIAGNOSIS.—*Leptodactylus laticeps* is the most distinctive member of the *pentadactylus* group. The dorsum color is apparently a warning color, with black squares and rectangles enclosing red on a yellow background. In preservative, the black squares and triangles have white areas within and are separated by white areas. The black markings are in a tile-like pattern (Figure 1, F). No other member of the group has a pattern approaching a tile floor.

ADULT CHARACTERISTICS (N=15).—Dorsum with distinct pattern of dark square and rectangular spots enclosing light areas (Figure 1, F); lip with light narrow vertical bars (Figure 2, I); posterior surface of thigh with bold light marks on a darker background (Figure 3, J, K); upper tibia with broad bands (Figure 4, A); no dorsolateral folds; fold

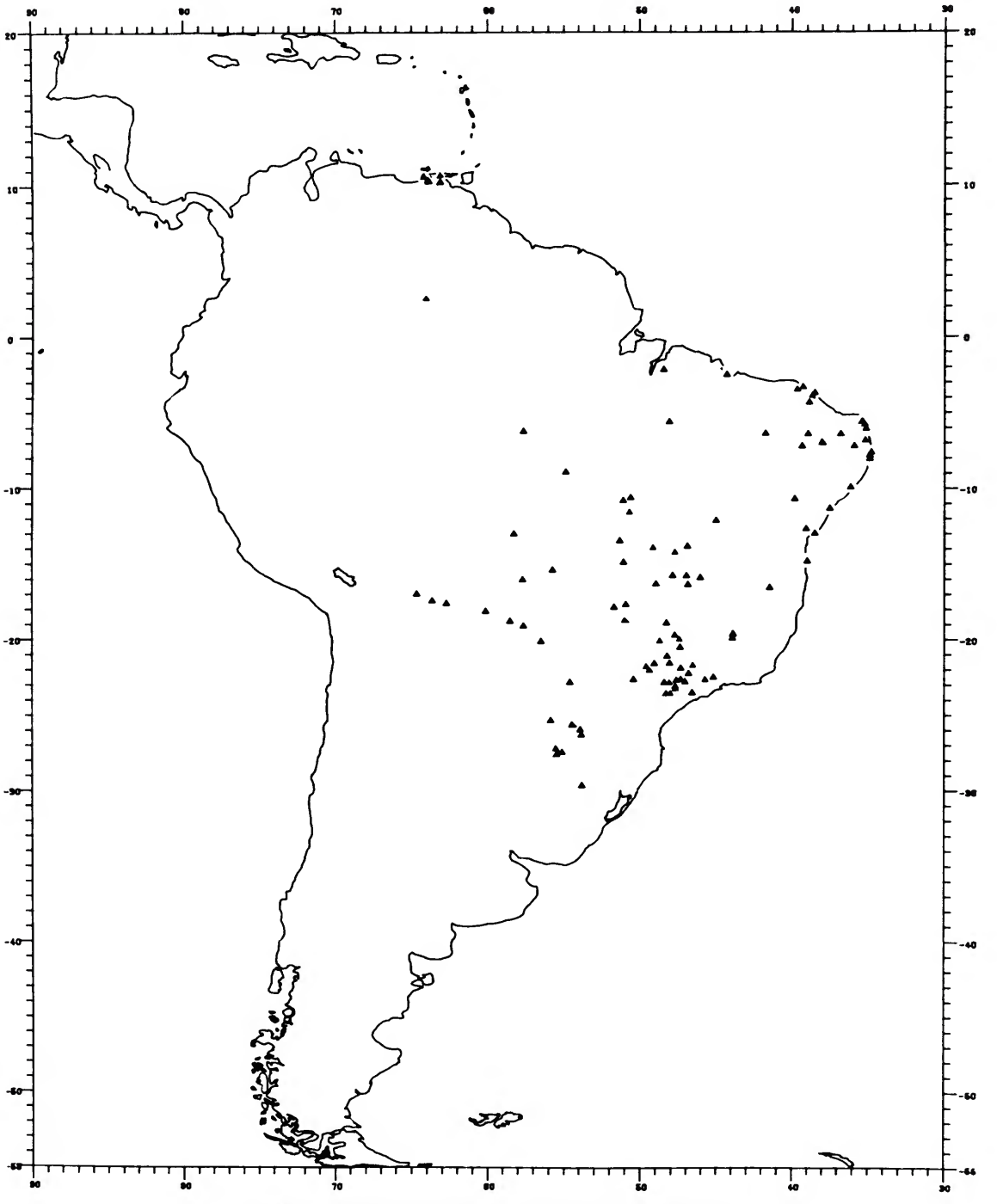

FIGURE 11.—Distribution map of *Leptodactylus labyrinthicus*.

from eye over tympanum to shoulder not distinctively marked; no fold from above tympanum to side of body; male with two thumb spines per hand; male chest spines usually present; upper tibial and distal surfaces smooth; sole of foot smooth or very scatterted with white tubercles; female SVL 106.1±6.5 mm, maximum 113.4 mm, males SVL 97.7±2.7 mm, maximum 110.0 mm; female interorbital distance/head length ratio 0.16±0.01, male 0.15±0.02; female eye-nostril distance/head length ratio 0.24±0.01, male 0.24±0.01; female head length/SVL ratio 0.36±0.01; male 0.36±0; female head width/SVL ratio 0.38±0.01, male 0.39±0.01; female femur/SVL ratio 0.39±0.03, male 0.40±0.01; female tibia/SVL ratio 0.39±0.02, male 0.40±0.01; female foot/SVL ratio 0.36±0.02, male 0.38±0.01.

Distinctive Colors in Life.—This species is quite bright, having irregular black squares and rectangles enclosing bright red, separated by bright yellow.

Larval Characteristics.—Unknown.

Mating Call.—Unknown.

Karyotype.—Unknown.

Distribution (Figure 7).—This is the southernmost member of the *pentadactylus* group, found in the Gran Chaco and Santiago del Estero region of Argentina.

ARGENTINA. Formosa: Bañados del Río Teuco, Bermejo (FML 1049); Ingeniero Juárez (FML 591, 693, 885, UMMZ 109755(3)); Lag. Vaca Perdida, 50 km Río Pilcomayo (FML 612). Salta: Hickmann (FML 159–61, 269, 280, 389–90, 415–16, 427, 436–37, 459, 862). Santiago del Estero: Bandera Bajada, 15 km from between km 30 and La Invernada (Dept Figueroa) (FML 2181, USNM 195960(2)); Caspi Corral, 96 km from Santiago del Estero (FML 2183–84, USNM 195961(2)); Loreto, 46 km S (MCZ 33943); Paraje Monte Redondo, Dept Loreto (FML 2434).

Leptodactylus pentadactylus (Laurenti), 1768

Rana pentadactyla Laurenti, 1768:32. [Type-locality: "Indiis." Type: based on pl. 75: fig. 1 in Seba, 1734.]

Rana gigas Spix, 1824:25. [Type-locality: Amazon River, Brazil. Type: lost.]

Rana coriacea Spix, 1824:29. [Type-locality: Amazon River, Brazil. Type: lost.]

Leptodactylus goliath Jiménez de la Espada, 1875:57. [Type-locality: Archidona and Chinitambo, Sierra de Guacamayos, Oriente, Ecuador. Lectotype: Museo Nacional, Madrid, 328, adult female.]

Leptodactylus macroblepharus Miranda-Ribeiro, 1926:144. [Type-locality: Manaos, Amazonas, Brazil. Holotype: MZUSP 377, adult male.]

Leptodactylus pentadactylus dengleri Melin, 1941:51. [Type-locality: Roque, San Martín, Peru. Holotype: Naturhistoriska Muséet, Göteborg.]

Leptodactylus pentadactylus rubidoides Andersson, 1945:47. [Type-locality: Rio Pastaza, Santiago-Zamora and Napo-Pastaza border, Ecuador. Holotype: Stockholm Royal Museum.]

Diagnosis.—Individuals of *L. pentadactylus* have a distinctive pair of dorsolateral folds. Dorsolateral folds are also found in some or all individuals of *fallax, flavopictus, labyrinthicus, kundseni, rhodomystax, rhodonotus, rugosus,* and *stenodema. Leptodactylus pentadactylus* lack distinct light lip stripes; all *flavopictus* and *rhodomystax* individuals have distinct light upper lip stripes. Most *rugosus* lack dorsolateral folds; when present, the folds are interrupted, contrasting with the continuous folds found in *pentadactylus. Leptodactylus pentadactylus* is a large species (minimum adult SVL 106 mm) with a single thumb spine in males; *rhodonotus* is a moderate-sized species (maximum adult SVL 90 mm) with two thumb spines per hand in males; *stenodema* is a moderate-sized species (maximum adult SVL 100 mm) in which the males lack thumb spines. *Leptodactylus pentadactylus* most closely resembles *fallax, labyrinthicus,* and *knudseni* in the *pentadactylus* group. A fold from above the tympanum to the side of the body, usually dark outlined for the extent, is found in *pentadactylus;* this fold is absent in *fallax, labyrinthicus,* and *knudseni.*

Adult Characteristics (N=173).—Dorsum uniform, spotted, or barred (Figure 1, A–D, G, J); lip uniform or usually with dark triangular bars (Figure 2, A–C, E, J); posterior surface of thigh uniform or variously spotted and mottled (Figure 3, A–G, I–K, P, R, S); upper tibia distinctly or indistinctly broadly barred (Figure 4, A, C, E); 2 distinct, dark outlined dorsolateral folds from eye to sacrum; dark outlined fold from eye to over tympanum, dark outline continuing or not on continuation of fold to shoulder; dark outlined fold from above tympanum to side of body usually continuous, rarely interrupted in Middle American specimens; males with one thumb spine per hand, rarely a weakly developed second; upper tibia and distal tarsal surfaces smooth or with scattered to many white- or black-tipped tubercles; sole of foot smooth, rarely with scattered white tubercles; female SVL 148.1±14.7 mm, maximum 176.2 mm, male SVL 137.2±14.0

mm, 185.0 mm maximum; female interorbital distance/head length ratio 0.19±0.02, male 0.19±0.02; female eye-nostril distance/head length ratio 0.25±0.01, male 0.25±0.01; female head length/SVL ratio 0.37±0.01, male 0.38±0.01; female head width/SVL ratio 0.39±0.02, male 0.39±0.02; female femur/SVL ratio 0.42±0.03, male 0.42±0.02; female tibia/SVL ratio 0.45±0.02, male 0.44±0.02; female foot/SVL ratio 0.46±0.02, male 0.45±0.02.

DISTINCTIVE COLORS IN LIFE.—Posterior surfaces of thigh mottled black and white or black and gray, most distinctive in juveniles (Villa, 1972, from Nicaragua; R. W. McDiarmid color notes from Peruvian specimen).

LARVAL CHARACTERISTICS.—Eye diameter 7–13 percent head-body length; oral disk position anterior; oral disk entire; oral disk width 15–22 percent head-body length; anterior oral papilla gap 50–74 percent oral disk width; anterior split tooth row about ⅓ length of entire anterior tooth row; 45–67 denticles in split tooth row anterior to beak; tooth row formula $\frac{1\text{–}1}{1\text{–}\frac{1}{2}}$; head body length 28–39 percent total length; maximum total length, stage 40, 83 mm.

MATING CALL.—Dominant frequency modulated between 250–500 Hz (Figure 12); no harmonic structure in call; call barely pulsed (Costa Rica), partially pulsed (Panama, Barro Colorado Island), or pulsed (Ecuador) (Figure 13); call duration 0.22–0.33 s (Figure 13).

KARYOTYPE.—Diploid number 22, 2 pair median, 6 pair submedian, 3 pair subterminal (Heyer and Diment, 1974).

DISTRIBUTION (Figure 14).—Middle America from

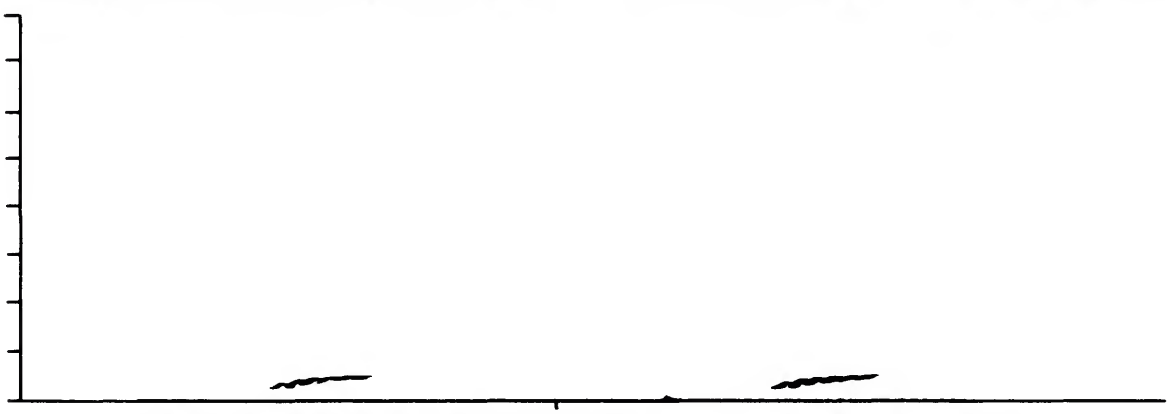

FIGURE 12.—Sonagram of mating call of *Leptodactylus pentadactylus*, narrow band filter. (Vertical scale marks at 1000 Hz intervals; horizontal scale mark at 1 s; A. S. Rand recording from Barro Colorado Island, Canal Zone, Panama.)

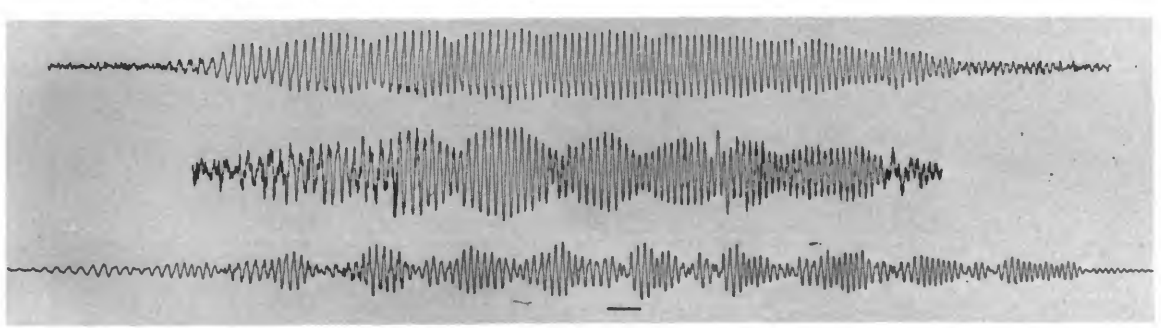

FIGURE 13.—Strip chart records of mating calls of *Leptodactylus pentadactylus*. (Line = 0.01 s; top record = R. W. McDiarmid recording from San Isidro de General, Costa Rica; middle record = A. S. Rand recording from Barro Colorado Island, Canal Zone, Panama; bottom record = KU tape 628 from Santa Cecilia, Napo, Ecuador; air temperaure 74°F.)

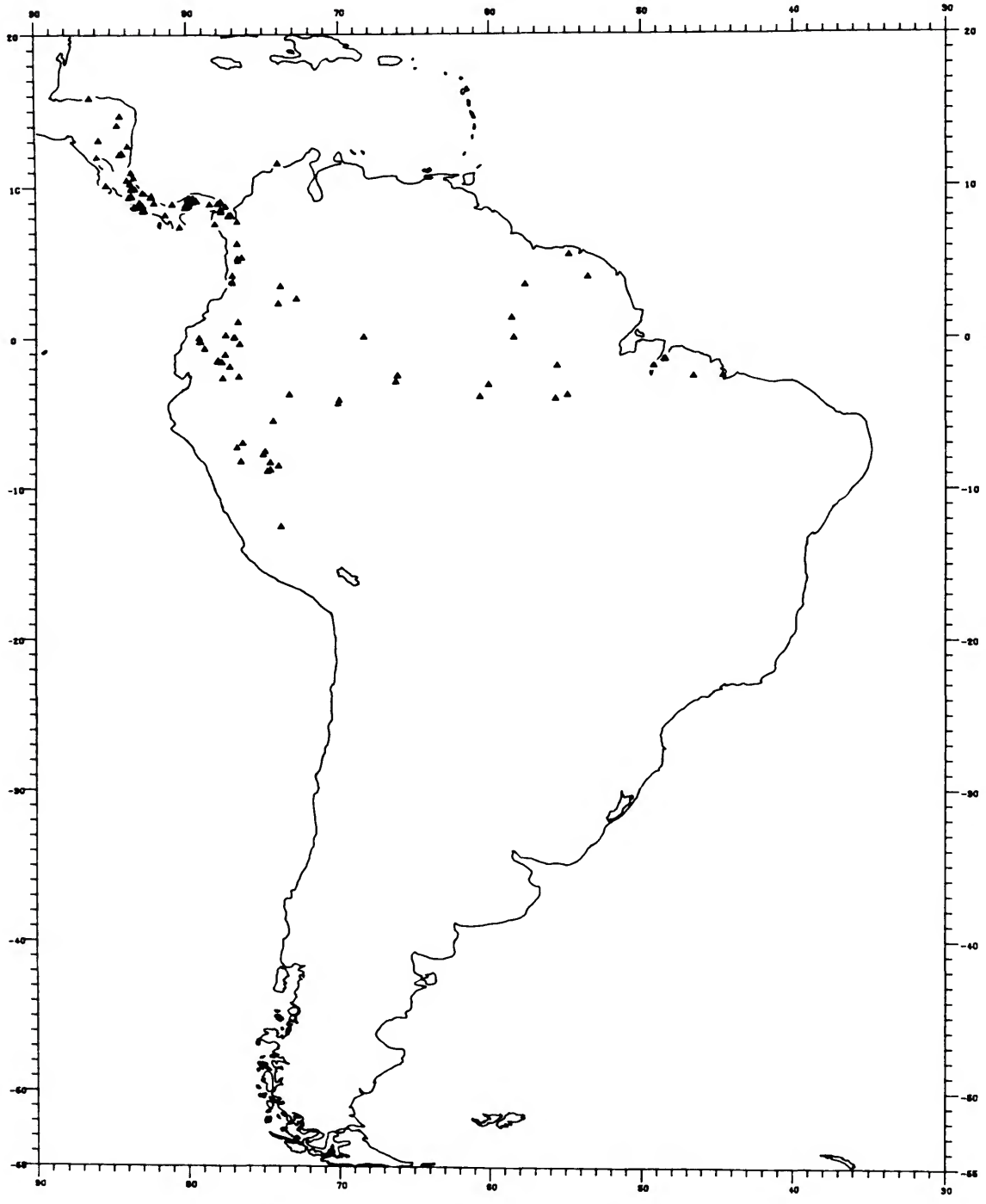

FIGURE 14.—Distribution map for *Leptodactylus pentadactylus*.

Honduras south into South America; in South America, the species occurs in coastal Colombia and Ecuador and the Amazon Basin.

BRAZIL. AMAZONAS: Benjamin Constant (MNRio 1743, 1751(2), 2559); Ducke Reserve (KU 129945); Fonte Boa, Alto Solimões (MNRio 796); Igarapé Belém, Rio Solimões (MZUSP 24897); São José (Jacaré), Rio Solimões (MZUSP 40303). MARANHÃO: Rio Aurá (CAS-SU 11830). PARÁ: Canindé, Rio Gurupi (MZUSP 25010–11); Furo do Panaquera (MZUSP 35677); IPEAN (KU 127400, 128336); Marambaia (KU 140094); Monte Cristo, Rio Tapajóz (MZUSP 38956); Óbidos (MZUSP 22126); Rio Mapuera, at Equator (AMNH 49482); Sudam Floral Reserve, 74 km SE Santarem (KU 129944).

COLOMBIA. AMAZONAS: Leticia (USNM 147053). ANTIOQUIA: Chigorodó, near Turbo (USNM 153914); Finca Chibiquí, 5 km W, Río Arquia (LACM 51211). CHOCÓ: Boca de Raspadura (AMNH 39792); Condoto (UMMZ 121418); Playa de Oro, 2 km above, upper Río San Juan (FMNH 54707). MAGDALENA: Parque Nacional Tayruna, trail between Canaveral and El Pueblito (USNM 200376). META: Río Guayabero, Angostura (USNM 150490); San Juan de Arama, Los Micos (FMNH 81329); about 30 mi WNW Vista Hermosa Caño Sardinata (UTA 5233–34). PUTUMAYO: About 15 km airline SW Mocoa, 1180 m (AMNH 84865). VALLE: Río Anchicaya, 8 km W Danubio, 300 m (KU 169090); Río Calima (USNM 150756); lower Río Calima (USNM 145094); Río Raposo, Virology Field Sta. (USNM 151460–61). VAUPÉS: Río Ariari and Río Guaviari (UTA 2719, 5232).

COSTA RICA. CARTAGO: La Suiza (KU 25713–14, 28188); Moravia de Turrialba (KU 30407, 65709, UTA 1395); 2.7 mi NE Río Reventazon Bridge, Peralta Rd, 3100′ (UMMZ 117274–76); Tunnel Camp, near Peralta (KU 33165, 33167); Turrialba (AMNH 54485, 62251, FMNH 57532, 101800, 101802, KU 30408–11, 65707–08, USNM 29953–54); 10 mi S Turrialba (USNM 192577). HEREDIA: Puerto Viejo and vicinity (KU 33135–39, 33144–52, 65710–12). LIMÓN: Guapiles (MCZ 7981–84); La Lola (KU 34967, UMMZ 117277); Los Diamantes (FMNH 101797, 101799, KU 25716–18, 30405–06(3), 65706); Puerto Viejo (KU 35924); Suretka (KU 35927, UMMZ 124019, 135387, 135392); Tortuguero (AMNH 75098–5100, MCZ 29134). PUNTARENAS: Agua Buena (KU 34965, 35928–29); Esterillos Oeste, 15 km SE Jacó (KU 33153, 34968–69, 65715–17, TCWC 19305–06); Gromaco (UMMZ 123320); Rincón de Osa and vicinity (LACM 116317, USNM field 1628, 1630–31, 1634, 1641, 1663, 1666–68, 1682); Villa Neily and vicinity, 75 m (KU 65713–14, 100338–39, 100354). SAN JOSÉ: El General (KU 25715); San Isidro del General 2½ mi E (FMNH 101801); 13 mi WSW San Isidro del General on Dominical Rd, 710 m (KU 34966, 35925–26, LACM 114334).

ECUADOR. COTOPAXI: Region of Sigchos (USNM 196743). ESMERALDAS: Hacienda Equinox, 30 km NNW Santo Domingo de los Colorados, 1000′; (USNM 196739). MORONA-SANTIAGO: Cusuime, 320 m (AMNH 93705–06). NAPO: Dureno, 320 m (KU 104714); Lago Agrio, 340 m (KU 126258–59, UMMZ 129062); Limoncocha (KU 99040, LACM 92128–31); Puerto Libre, Río Aguarico, 570 m (KU 122579); Santa Cecilia (KU 104713, 104715, 104717–18, 109152–53, 111405, 111408–09, 122574–75, 122577, 122580, 126257, 146176–80, 149354–58; MCZ 57944–46, 57948–52, 57954–56, 57959–60, UMMZ 129280–81). PASTAZA: Andoas (AMNH 71025); Canelos (USNM 196742); 2 km E Puyo (USNM 196741(2)); headwaters of Río Arajuno, tributary of Río Napo (USNM 196744); Río Pindo (USNM 196747); Río Rutuno, tributary of Río Bobonaza (USNM 196746). PICHINCHA: Espinosa, 9 km W Santo Domingo de los Colorados, road to Chone (CAS-SU 10453–54); 18 km W Santo Domingo de los Colorados, Ramsey Farm, km 19 Chone Rd. (USNM 196740(2), 196745).

FRENCH GUIANA. Sophie (MCZ 44562).

GUYANA. Rupununi, N of Acarahy Mts (KU 69685); Shudi-kar-wau (AMNH 70118–20).

HONDURAS. COLON: Belfate (AMNH 45704, 45722).

NICARAGUA. BLUEFIELDS: 6 mi W Rama, 50′ (TCWC 19307). GRANADA: N Granada (LACM 37870). MATAGALPA: 10.5 km N Finca Tepeyac, 9 km E Matagalpa, 960 m (KU 85146). Río SAN JUAN: San Juan del Norte (Greytown) (USNM 19765). ZELAYA: Bonanza (KU 85147–48, 101168); Camp Corozo, Río Huahuashan (AMNH 54980–81); Camp Santa Ana, Río Huahuashan (AMNH 54999); Cara de Mono, 50 m (KU 112673–75); Masawas, Waspuk R (AMNH 58435); El Recreo, 25 km W Rama (KU 112666–72, LACM 13945, 20475); 10 mi above Recreo, Río Mico (UMMZ 79751–52).

PANAMA. BOCAS DEL TORO: Almirante (KU 79992, USNM 142334); Boca del Drago (USNM 142318); Punta de Peña (USNM 38714). CANAL ZONE: Barro Colorado Island (AMNH 52878–79, 69728, FMNH 175986, KU 76568, MCZ 15266, UMMZ 64594, 124019, 135387, 135392, USNM 161151); Candelaria and Peluca Stas, near Boqueron (AMNH 53747); Cave A, Chili Brillo (AMNH 62338); Frijoles (USNM 196303); Las Cruces trail near Corozal (AMNH 38977); near Madden Dam (AMNH 87143, KU 155306, UMMZ 78481). CHIRIQUÍ: Progreso (UMMZ 58221). COCLÉ: El Valle, 560 m (AMNH 59590, KU 76575, 107229, 116825.) DARIÉN: Camp Creek, Camp Townsend (AMNH 40785–88, 40793, 41061, 41765); Casita (USNM 141783); Jaqué (USNM 161215); Laguna, 820 m (KU 76570–72); along Río Canglón, near mouth (UMMZ 123160–61); across from mouth of Río Canglón, along Río Chucunaque (UMMZ 123158–59); Río Chucunaque, about 7 km above Río Mortí, 150 m (KU 107230); Río Silugandí (UMMZ 124018); Río Tuira at Río Mono (KU 115308); Río Ucurgantí, about 7 km above mouth, 30 m (KU 97014–17), 107231–32); Tacarcuna, 550 m (KU 76573–74). LOS SANTOS: Guánico Arriba, 60 m (KU 107228). PANAMÁ: Altos de Maje (AMNH 88743); Cerro Campana (KU 76569); Ciricito (CAS 71514–16); Juan Mina, Chagres R (USNM 129908); Tapia (AMNH 18920, 18922–23). SAN BLAS: Armila (USNM 150090); Camp Sasardí, 12 m (KU 108688–89); Quebrada Venado (USNM 150089). VERAGUAS: Mojara (UMMZ 123320); mouth of Río Concepción, 1 m (KU 11537).

PERU. AYACUCHO: La Mar, Candalosa (FMNH 39720). HUANUCO: Ganzo Azul (FMNH 45145); Río Llullapichis, 4–5 km upstream from Río Pachitea (KU 171901). LORETO: Cashiboya (AMNH 42404); Iquitos (AMNH 42002, 42560); Peru-Brazil border, upper Utoquinea (AMNH 42751, 43371); 61 mi SE Pucallpa, 500′ (TCWC 4967); Río Pisqui (AMNH 43539); Río Ucayali, Yarinacocha (FMNH 56293, 56300). SAN MARTÍN: Upper Biabo Valley (AMNH 42656); Pachisa (AMNH 42001); Tocache Nuevo, Río Huallaga (AMNH 42562).

SURINAM. Godo Drai (TCWC 23561–63); King Frederick William IV Falls (FMNH 30912–13).

Leptodactylus rhodomystax Boulenger, 1883

Leptodactylus rhodomystax Boulenger, 1883:637. [Type-locality: Yurimaguas, Huallaga River, Peru. Lectotype: BMNH 1947.12.17.81, juvenile.]

Leptodactylus stictigularis Noble, 1923:293. [Type-locality: Kartabo, British Guiana. Holotype: AMNH A–10398, adult male.]

DIAGNOSIS.—Specimens of *rhodomystax* have distinct dorsolateral folds and a distinct light stripe on the upper lip. The other species in which some or all individuals share this combination of characteristics are *flavopictus* and *rhodonotus* (most *rhodonotus* lack a distinct lip stripe). The posterior surface of the thigh has discrete, distinct light spots on a dark field (Figure 3, N, O) in *rhodomystax*. The thighs of *flavopictus* and *rhodonotus* are variously irregularly spotted and mottled, but never have a pattern of discrete light spots.

ADULT CHARACTERISTICS (N=16).—Dorsum relatively uniform or with narrow transverse bands (Figure 1, B, C); lip with distinct light stripe (Figure 2, H, L); posterior surface of thigh with distinct light spots on a dark background (Figure 3, N, O): upper tibia broadly or narrowly banded (Figure 4, A, D) or patternless; a pair of dark outlined dorsolateral folds from eye to groin; dark outlined fold from eye over tympanum to shoulder; no fold from above tympanum to side of body; male thumb with one spine per hand; male chest spines present; upper tibia and distal tarsus smooth or covered with few to many white tubercles; sole of foot usually smooth, sometimes with a few scattered white tubercles; female SVL 76.5±6.7 mm, maximum 83.8 mm, male 80.2±7.3, maximum 89.6 mm; female interorbital distance/head length ratio 0.21±0.02, male 0.21±0.02; female eye-nostril distance/head length ratio 0.22±0.01, male 0.22±0.01; female head length/SVL ratio 0.36±0.01, male 0.36±0.01; female head width/SVL ratio 0.38±0.01, male 0.38±0.01; female femur/SVL ratio 0.43±0.01, male 0.42±0.02; female tibia/SVL ratio 0.44±0.01, male 0.45±0.02; female foot/SVL ratio 0.46±0.02, male 0.46±0.02.

DISTINCTIVE COLORS IN LIFE.—Lip stripes range from white to rosy gray, the light thigh spots range from white to yellow; the dorsum ranges from brown to bright orange(W. E. Duellman field notes).

LARVAL CHARACTERISTICS.—Unknown.

MATING CALL.—Unknown.

KAROTYPE.—Unknown.

DISTRIBUTION (Figure 15).—The species is known from scattered localities throughout the greater Amazon Basin.

BRAZIL. AMAPÁ: Serra do Navio (KU 92948–49). AMAZONAS: Ducke Reserve (KU 129946); Manjura R (AMNH 73546, 76181–82). MARANHÃO: Aldeia Araçu, Igarapé Gurupi-Una (MZUSP 23489–90). MATO GROSSO: Xingu, Parque Indígena, Posto Diauarum (MZUSP 49523). PARÁ: IPEAN (KU 127401–08).

COLOMBIA. AMAZONAS: Río Apaporis (USNM 144889–91).

ECUADOR. MORONA-SANTIAGO: Cusuime, 320 m (AMNH 93707–28). NAPO: Lago Agrio, 340 m (KU 126260); Puerto Libre, Río Aguarico, 570 m (KU 122581); Santa Cecilia (KU 109165–67). PASTAZA: Andoas (AMNH 71026–27); Río Ollaguanga, mouth of, tributary of Río Conambo (USNM 196748); Río Pindo (USNM 196751(3)); Río Pucuyacu, Río Bobonaza (USNM 196749); Río Shyona, mouth of, in Conambo R (USNM 196750); Sarayacu, 400 m (KU 120297).

GUYANA. Dunoon, Demerara R (UMMZ 48292–93); Kamakusa (AMNH 18960); Kartabo (AMNH 13489, 70902–03); between Mackreba Falls and Membaro Creek (UMMZ 85150); Rupununi, N of Acarahy Mts, W of New R (KU 69691); Shudi-kar-wau (AMNH 49246, 51942); Tukeit Hill, below Kaiteur Falls, Tumong Dist (UMMZ 63034).

PERU. LORETO: Centro Union (TCWC 41698); Estiron, Río Ampiacu (CAS 93353); Orellana, Domo Sta Clara (USNM 127925–27); Peru-Brazil border, upper Utoquinea (AMNH 42154). PASCO: Iscozazin Valley, Pan de Azucar (LACM 40650).

SURINAM. Kaiserberg Airstrip, Zuid R (FMNH 128819, 128833–40); Lely Mts (MCZ 89647).

Leptodactylus rhodonotus (Günther), 1868

Cystignathus rhodonotus Günther, 1868:481. [Type-locality: Chyavetas, Peru. Holotype: BMNH 1947.2.17.39, juvenile.]

Gnathophysa rubido Cope, 1874:128. [Type-locality: Moyabamba, San Martin, Peru. Lectotype: MCZ 4780, adult male.]

DIAGNOSIS.—Specimens of *rhodonotus* have a distinct dark outlined dorsolateral fold from the eye to the sacrum or groin. This condition occurs in some or all individuals of *fallax, flavopictus, labyrinthicus, pentadactylus, knudseni, rhodomystax, rugosus,* and *stenodema.* Most *rugosus* lack dorsolateral folds; when folds are present in *rugosus,* they are interrupted, contrasting with the continuous folds of *rhodonotus. Leptodactylus rhodonotus* is a moderate-sized species (maximum adult SVL 90 mm) with two spines per thumb in males; *fallax, labyrinthicus, pentadactylus,* and *knudseni* are large species (mini-

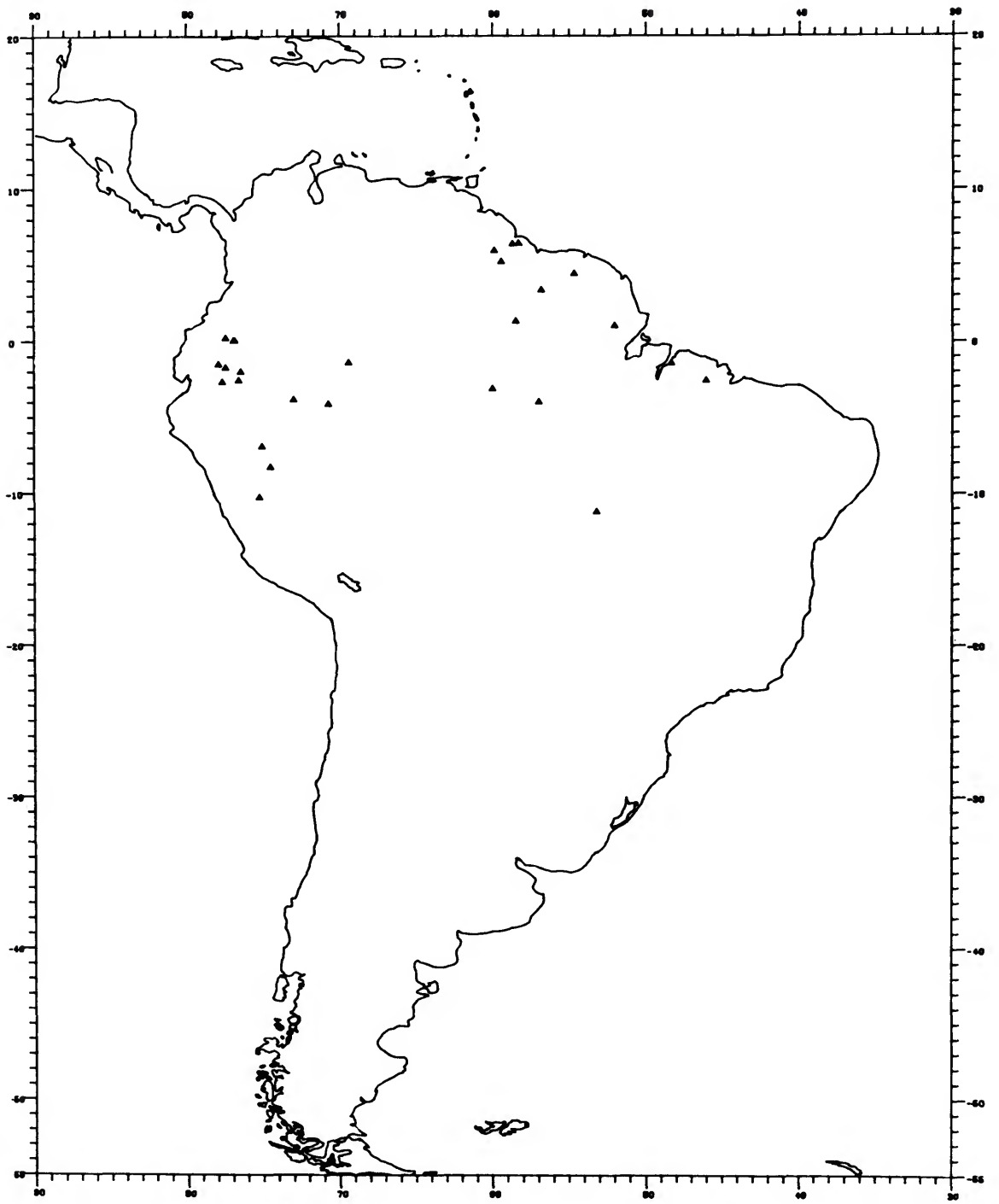

FIGURE 15.—Distribution map for *Leptodactylus rhodomystax*.

mum adult SVL 97 mm) with one spine per thumb in males. *Leptodactylus flavopictus* is also a large species (minimum adult SVL 112 mm) with smooth upper tibial surfaces contrasting with the tuberculate upper tibial surfaces of *rhodonotus*. The posterior surface of the thigh is variously mottled in *rhodonotus* but never has the pattern of discrete, distinct light spots on a dark background found in *rhodomystax*. *Leptodactylus rhodonotus* is a smaller species (males 54–79 mm SVL, females 67–90 mm SVL) with male thumb spines present; *stenodema* is a larger species (males 83–100 mm SVL, females 82–100 mm SVL) lacking male thumb spines. The dorsum of *rhodonotus* often has a distinctive pattern; the dorsum of *stenodema* is patternless.

Adult Characteristics (N=87).—Dorsum uniform, with scattered small dots or blotches to complex lattice network (Figure 1, C, I); lip with dark triangular patterns, uniform, or rarely with a distinct light stripe (Figure 2, A–C, E, L, M); posterior surface of thigh almost uniform, mottled, or with contrasting light and dark pattern (Figure 3, A, C, D, P); upper tibia with distinct or indistinct bars or uniformly patterned (Figure 4, D, E); a pair of dark outlined dorsolateral folds from eye to sacrum or groin; dark outlined fold from eye over tympanum to shoulder; dark outlined fold from above tympanum to side of body present or absent, continuous or interrupted; male thumb with two spines per hand; male chest usually with spines, all specimens 65 mm SVL or larger with spines; upper tibial and distal tarsal surfaces with scattered to many white- or black-tipped tubercles; sole of foot usually with scattered black-tipped tubercles, sometimes smooth or with scattered white tubercles; female SVL 75.0±5.8 mm, maximum 89.5 mm, male 67.8±6.7 mm, maximum 79.0 mm; female interorbital distance/head length ratio 0.20±0.02, male 0.20±0.02; female eye-nostril distance/head length ratio 0.24±0.01, male 0.24±0.02; female head length/SVL ratio 0.35±0.01, male 0.36±0.01; female head width/SVL ratio 0.37±0.02, male 0.37±0.02; female femur/SVL ratio 0.40±0.03, male 0.40±0.02; female tibia/SVL ratio 0.42±0.02, male 0.43±0.02; female foot/SVL ratio 0.45±0.02, male 0.46±0.03.

Distinctive Colors in Life.—Ventral hind limb surfaces are often pinkish orange. The tips of the digits and the subarticular tubercles are orange (from field notes of J. P. Bogart, R. Etheridge, and D. B. Wake).

Larval Characteristics.—Eye diameter 9–12 percent head-body length; oral disk subterminal; oral disk entire; oral disk width 17–24 percent head-body length; oral papilla gap 46–62 percent oral disk width; split tooth row anterior to beak just less than ½ length entire tooth row anterior to beak; 150–167 denticles in split tooth row anterior to beak; tooth row formulae $\frac{1}{1-1}$ or $\frac{1}{1-1}$; head-body length 34–37 percent total length; maximum length stage 40, 59 mm.

Mating Call.—Unknown.

Karyotype.—Diploid number 22, 7 pair median, 3 pair submedian, 1 pair subterminal; secondary constructions in chromosome pair 2 and 7 (Bogart, 1974).

Distribution (Figure 16).—This species is known from a limited geographic area in Amazonian Peru and Bolivia.

BOLIVIA. Cochabamba: Tarate (UMMZ 68187(3)).

PERU. Cuzco: Quince Mil (FMNH 140470, 140508, 141035); Río Cosñipata, 4 kw SW Santa Isabel, 1700 m (KU 138883). Huanuco: Chinchao, 5700′ (FMNH 3544); Divisoria, 1600 m (FMNH 56308–13); Exito, valley of the Cayumba (FMNH 5587); Tingo Maria (USNM 196003–11(5)); about 12 km (by Huanuco Rd) S of Tingo Maria, Sector Cueva de las Pavas, Parque National de la Bella Durmiente (USNM 196002). Junin: Chancharia, on Río Perene, 2.5 hrs by motor boat below Pampa Silva and approximately 5 mi above entrance of Río Ipok, about 700 m (USNM 196001); Chanchamayo (FMNH 40582–83, 134511); San Ramon, 800 m (KU 135506, MCZ 22823, 22825–26); Tarma, valley of Vitoc R 900 m (FMNH 36832–37). Loreto: Iparia (MCZ 75039–40). Madre de Dios: Avispal (FMNH 140923); La Pampa (FMNH 40289). Pasco: Iscozazin Valley, Chontilla (LACM 40608–47). Puno: Bella Pampa (FMNH 40280); Camp 4 (FMNH 40287–88); Juliaca (AMNH 6129); Sagrario, Río Quitún (FMNH 40270–79); Santo Domingo (FMNH 40281–86). Sandia: Tambopata, San Juan (FMNH 64930–32). San Martín: Moyobamba (MCZ 4780); Tocache Nuevo, Río Huallaga (USNM 196000).

Leptodactylus rugosus Noble, 1923

Leptodactylus rugosus Noble, 1923:297. [Type-locality: near Kaieteur Falls, British Guiana. Holotype: AMNH A-1169, adult male.]

Diagnosis.—As the name implies, most individuals of *rugosus* are rugose. The degree of dorsal wartiness of most *rugosus* is only approached by some *labyrinthicus*, but the condition in *labyrinthicus* is glandular, not tubercular as in *rugosus*. *Leptodactylus*

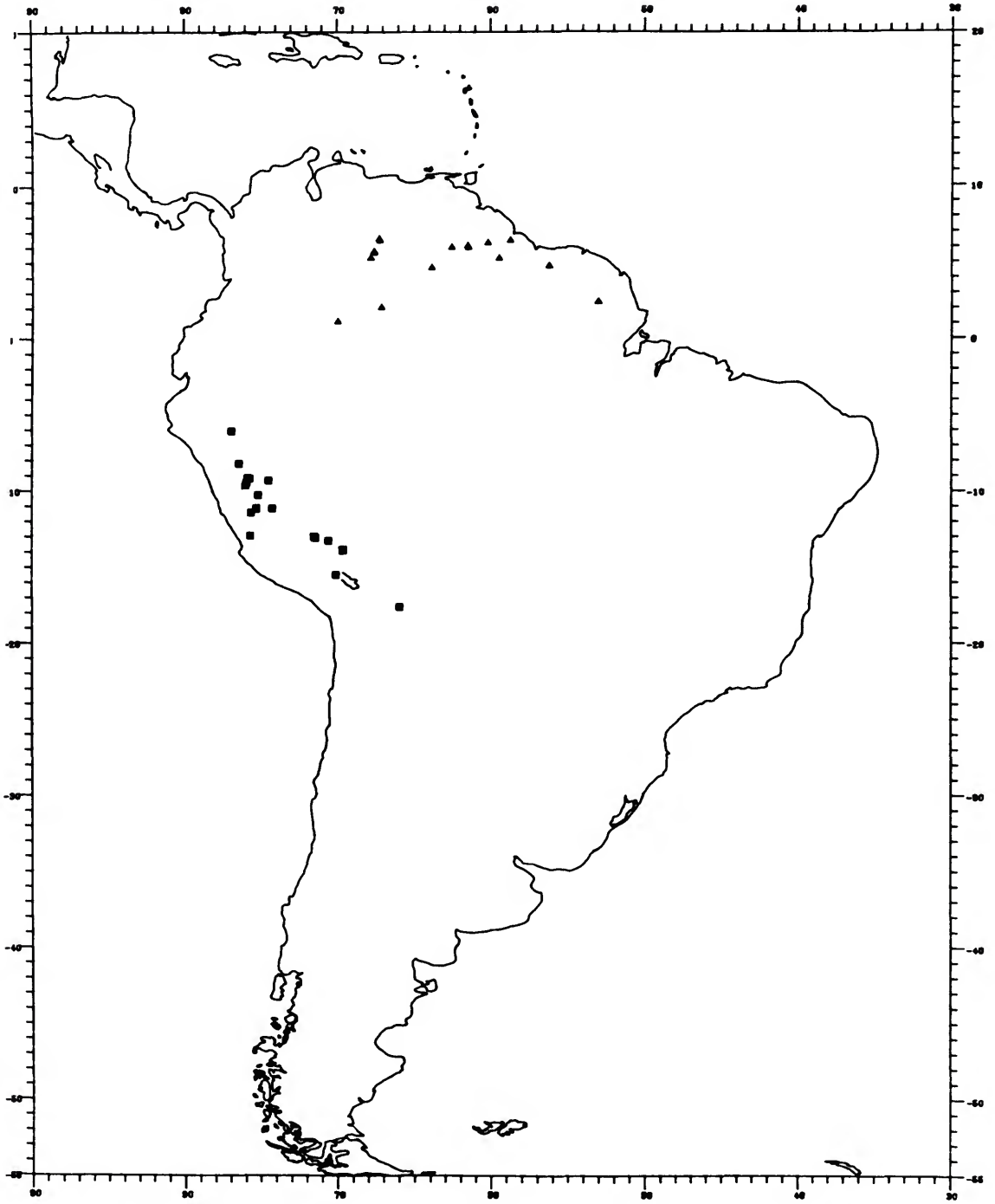

FIGURE 16.—Distribution map for *Leptodactylus rhodonotus* (squares) and *L. rugosus* (triangles).

rugosus is a moderate-sized species (maximum adult SVL 86 mm) that usually lacks dorsolateral folds. *Leptodactylus fallax, flavopictus, labyrinthicus, pentadactylus,* and *knudseni* are large species (minimum adult SVL 97 mm) with distinct dorsolateral folds (a few *labyrinthicus* lack dorsolateral folds). *Leptodactylus laticeps* has a tile-like dorsal pattern (Figure 1, F) and is larger (minimum adult SVL 91 mm) than *rugosus,* which does not have a tile-like pattern. *Leptodactylus rhodomystax* has a distinct light stripe on the upper lip; *rugosus* does not have a distinct light lip stripe. The dorsolateral folds are interrupted in the few *rugosus* that have folds; all *rhodonotus* and *stenodema* have continuous folds. Most *rugosus* have smooth soles of the foot; most *syphax* have tuberculate soles of the foot.

ADULT CHARACTERISTICS (N=42).—Dorsum uniform, spotted, or blotched (Figure 1, C, D, H–K); lip uniform or usually with a complex dark and light pattern (Figure 2, A, C, E, F, J, K, M, N); posterior surface of thigh variously mottled (Figure 3, A, C, D, J, P, R); upper tibia distinctly or indistinctly barred (Figure 4, A, C, E); usually no dorsolateral folds, rarely an interrupted pair of folds from eye to midbody; fold from eye above tympanum to shoulder not dark outlined; no fold from above tympanum to shoulder; male thumb usually with one spine per hand, sometimes two; male chest spines present or absent; upper tibial and distal tarsal texture smooth or with scattered to many white- or black-tipped tubercles; sole of foot smooth or scattered with white- or black-tipped tubercles; female SVL 68.2±8.9 mm, maximum 85.7 mm, male 59.8±5.3 mm, maximum 68.3 mm; female interorbital distance/head length ratio 0.16±0.02, male 0.16±0.02; female eye-nostril distance/head length ratio 0.24±0.01, male 0.24±0.01; female head length/SVL ratio 0.38±0.01, male 0.38±0.01; female head width/SVL ratio 0.39±0.01, male 0.39±0.01; female femur/SVL ratio 0.45±0.03, male 0.44±0.02; female tibia/SVL ratio 0.45±0.03, male 0.45±0.02; female foot/SVL ratio 0.47±0.03, male 0.47±0.03.

DISTINCTIVE COLORS IN LIFE.—Throat and belly of females white and ventral surfaces of hind limbs cream with gray suffusion. (W. E. Duellman, pers. comm.)

LARVAL CHARACTERISTICS.—Eye diameter 12–14 percent head-body length; oral disk subterminal; oral disk laterally indented; oral disk width 20–28 percent head-body length; anterior oral papilla gap 80–88 percent oral disk width; split tooth row anterior to beak just less than ½ length of entire tooth row anterior to beak; 37–65 denticles in split tooth row anterior to beak; tooth row formula $\frac{1}{1-1}$ $\frac{1-1}{2}$ head-body length 26–32 percent total length; maximum total length, stage 41, 41.3 mm.

MATING CALL.—Dominant frequency modulates from between 600–2300 Hz to 700–2700 Hz (Figure 17); no harmonic structure in call; call complexly pulsed and partially pulsed (Figure 18); a short, approximately 0.03 s pulse of lower frequency (600–700 Hz) (Figure 18) immediately followed by a 0.49 to 0.64 s pulse train of higher frequency (1300–2300 Hz to 1500–2700 Hz) (Figure 17 shows this part of call only, Figure 18 shows both lower and higher frequency components).

KARYOTYPE.—Unknown.

DISTRIBUTION (Figure 16).—This species is restricted to granitic rock outcroppings in the Guiana shield region from Colombia to French Guiana.

COLOMBIA. VAUPÉS: Cerro Patava (UTA 3724–25, 3772–85, 3857, 3859–61, 3863–77).

FRENCH GUIANA. Montagne St Marcel (LES 426b); Peolaeu (Haut-Oyapock) (LES 4197).

GUYANA. Kartabo (AMNH 70904–08, USNM 118063–64, 129537–38); Kurupung, upper Mazaruni Dist (UMMZ 85211); Membaro Creek, upper Mazaruni R (UMMZ 85155–57, 85210, USNM 118684); Tukeit Hill, below Kaiteur Falls, Tumong Dist (AMNH 1166–68, 3789).

SURINAM. Raleighvallen–Voltzberg Nature Reserve, Voltzberg Camp, W bank Coppename R (MCZ 92363).

VENEZUELA. AMAZONAS: Misión Coromoto-Atures (USNM 137186–92); Puerto Ayacucho (AMNH 23209–19, FMNH 175460–65, 176197–222, USNM 80634, 80665–73, 133186); Puerto Sanariapo (USNM 80635–39). APURE: Hato Caribén, 46 km NE Puerto Páez, Río Cinaruco (USNM field 5625–26, 5820). BOLIVAR: 3 km E Canaiama (KU 117125); 85 km SSE El Dorado, km 125 (USNM field 8107, USNM 162698–99); km 104–151 on El Dorado-Santa Elena de Uairén Rd (KU 166498–524, 166531–544); Laja, at mouth of Río Parguaza, 100 m (AMNH 62168); Mt Auyantepui, 1100 m (AMNH 46038–39); Paso de El Danto (KU 166525–30); W Wiaka-Piapo Mt, 20 mi from Guyana border, 5000′ (UMMZ 85158, 85209). GUAINÍA: Río Negro opposite Casiquiare and Guainía (AMNH 23160–62).

Leptodactylus stenodema Jiménez de la Espada, 1875

Leptodactylus stenodema Jiménez de la Espada, 1875:64. [Type-locality: San José de Moti, Napo, Ecuador. Lectotype:

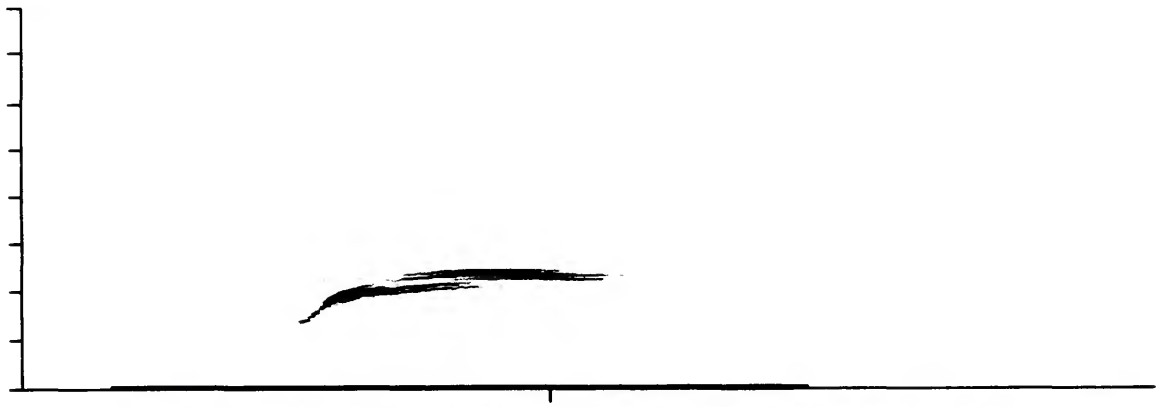

FIGURE 17.—Sonogram of mating call of *Leptodactylus rugosus,* narrow band filter. (Vertical scale marks at 1000 Hz intervals; horizontal scale mark at 1 s; KU tape 1270 from km 104 El Dorado–Santa Elena de Uairén Road, Bolivar, Venezuela; air temperature 22°C.)

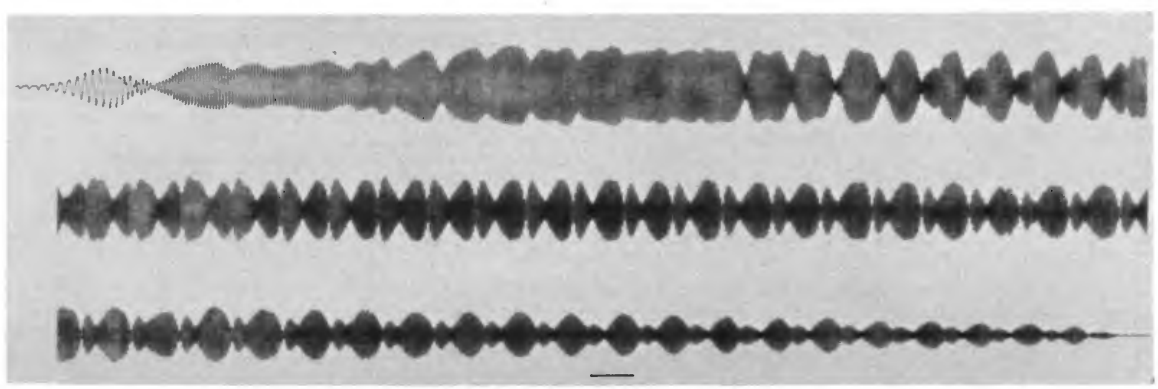

FIGURE 18.—Strip chart record of mating call of *Leptodactylus rugosus.* (Line = 0.01 s; tape data same as Figure 17.)

Museo Nacional, Madrid, 190, adult female.]
Leptodactylus vilarsi Melin, 1941:52. [Type-locality: Taraqua, Amazonas, Brazil. Holotype: Göteborg Naturhistoriska Muséet, Ba. ex., 498, adult female.]

DIAGNOSIS.—Specimens of *stenodema* have dark-outlined dorsolateral folds extending from the eye to the sacrum or groin. This condition also occurs in some or all individuals of *fallax, flavopictus, labyrinthicus, pentadactylus, knudseni, rhodomystax, rhodonotus,* and *rugosus.* The distinct light upper lip stripe of *flavopictus* and *rhodomystax* distinguishes those species from *stenodema,* which lacks such a stripe. The dorsum of *stenodema* is patternless, the size is moderate (maximum adult SVL 100 mm), and the males lack thumb spines; the dorsums of *fallax, labyrinthicus, pentadactylus,* and *knudseni* are usually patterned, the sizes are large (minimum adult SVL 97 mm), and the males have thumb spines. The dorsum of *rhodonotus* is often patterned, the males have thumb spines, and the size of *rhodonotus* (males 54–59 mm SVL, females 67–90 mm) is smaller than that of *stenodema* (males 83–100 mm SVL, females 82–100 mm). Most *rugosus* lack dorsolateral folds; when present, the folds are interrupted, contrasting with the continuous folds of *stenodema.*

ADULT CHARACTERISTICS (N=13).—Dorsum uniform or with small dark spots, no bars or distinct pattern (Figure 1, C); lip with dark triangular bars (Figure 2, A, B, D); posterior surface of thigh uniform, with uniform patches, or mottled (Figure 3, C, G, L, M); upper tibia with wide or narrow bars

(Figure 4, A, D) or uniformly dark; a pair of dark, outlined dorsolateral folds extending from behind eye to midbody or groin; dark outlined fold from eye over tympanum to shoulder; no fold from above tympanum to side of body; no male thumb spines; no male chest spines; upper tibial and distal tarsal surfaces with many white- or black-tipped tubercles; sole of foot usually smooth, sometimes with very scattered white- or black-tipped tubercles; female SVL 91.1±6.5 mm, maximum 100.3 mm, male 89.9±5.4 mm, maximum 99.7 mm; female interorbital distance/head length ratio 0.21±0.01, male 0.19±0.01; female eye-nostril distance/head length ratio 0.28±0.01, male 0.26±0.01; female head length/SVL ratio 0.36±0.02, male 0.36±0.01; female head width/SVL ratio 0.36±0.02, male 0.37±0.01; female femur/SVL ratio 0.38±0.02, male 0.36±0.02; female tibia/SVL ratio 0.39±0.02, male 0.38±0.01; female foot/SVL ratio 0.40±0.03, male 0.39±0.01.

Distinctive Colors in Life.—Life colors are yellow/brown to brown with no contrasting bright colors.

Larval Characteristics.—Unknown.

Mating Call.—Dominant frequency modulates between 760–900 Hz (Figure 19); no harmonic structure in call; call partially pulsed (Figure 20); call duration about 0.36 s.

Karyotype.—Unknown.

Distribution (Figure 21).—Apparently found throughout the greater Amazon Basin.

BRAZIL. Amazonas: Restauração (USNM field 3764).

COLOMBIA. Caquetá: Río Mecaya (FMNH 69752). Putumayo: Mocoa, about 7 km SE, near Río Pepino (AMNH 84866–67). Vaupés: Wacará (UTA 3722, 3833, 3835, 4007, 4072).

ECUADOR. Morona-Santiago: Cusuime, 320 m (AMNH 93704). Napo: Puerto Libre, Río Aguarico, 570 m (KU 122582). Pastaza: Andoas (AMNH 71023); Puyo (USNM 196752–53); Río Rutuno, tributary of Rio Bobonaza (USNM 196754).

PERU. Amazonas: Mouth of Río Santiago (AMNH 42399).

Leptodactylus syphax Bokermann, 1969

Leptodactylus syphax Bokermann, 1969:13. [Type-locality: Cuiabá São Vincente, Mato Grosso, Brazil. Holotype: WCAB 16141, adult male.]

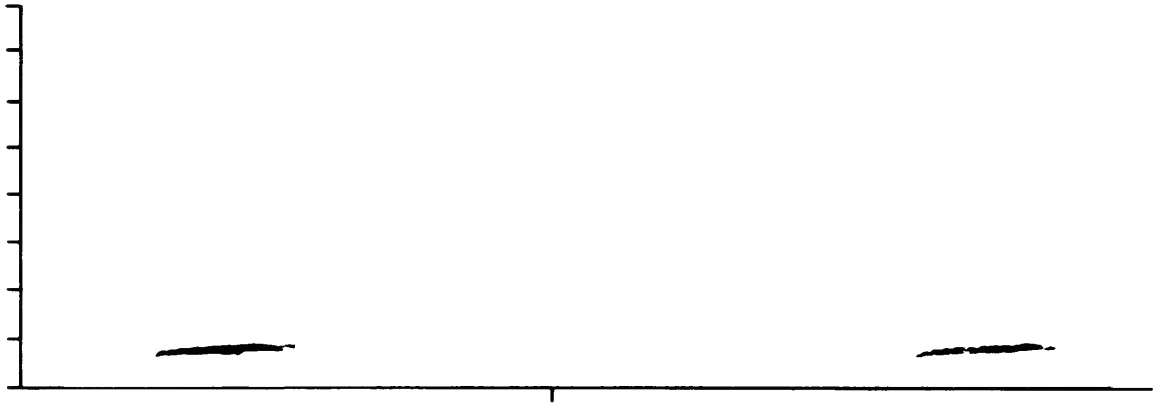

Figure 19.—Sonagram of mating call of *Leptodactylus stenodema*, narrow band filter. (Vertical scale marks at 1000 Hz intervals; horizontal scale mark at 1 s; specimen UTA A-3833.)

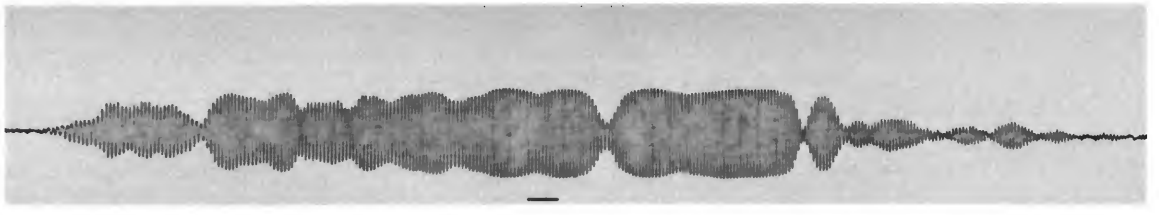

Figure 20.—Strip chart record of mating call of *Leptodactylus stenodema*. (Line = 0.01 s; specimen data same as Figure 19.)

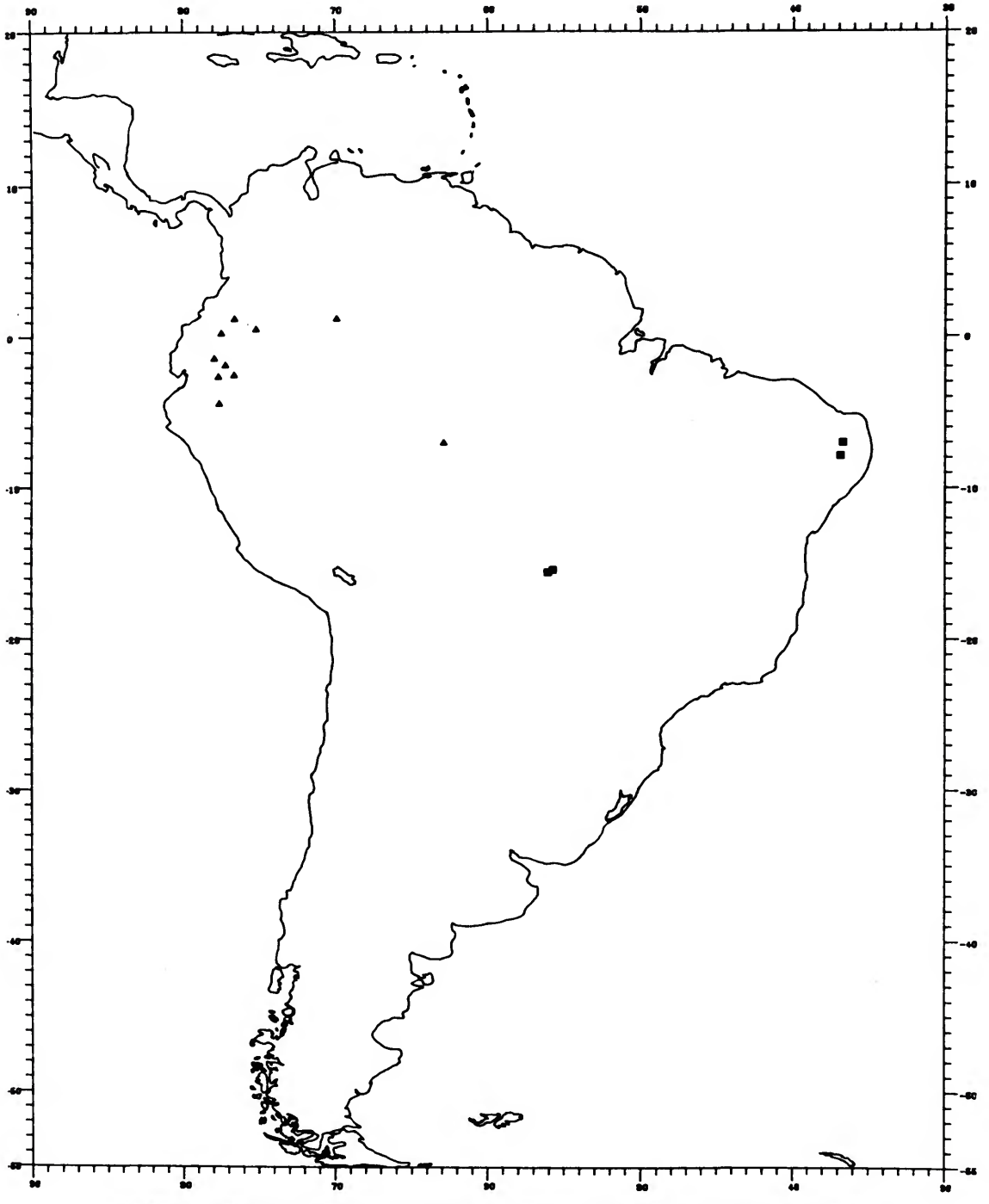

FIGURE 21.—Distribution map for *Leptodactylus stenodema* (triangles) and *L. syphax* (squares).

DIAGNOSIS.—*Leptodactylus syphax* lacks dorsolateral folds. The other species in which some or all individuals lack dorsolateral folds are *labyrinthicus, laticeps,* and *rugosus.* Most *labyrinthicus* have dorsolateral folds; *labyrinthicus* is a large species (minimum adult SVL 117 mm) with a single thumb spine in males contrasting with the smaller size of *syphax* (maximum adult SVL 78 mm) and the two spines per thumb on the hands of the males. The dorsum of *laticeps* has a tile-like pattern (Figure 1 F), and *laticeps* is larger (minimum adult SVL 91 mm) than *syphax,* which does not have a tile-like dorsal pattern. Most *rugosus* have a tuberculate dorsum and a smooth sole of the foot; the dorsum of *syphax* is not rugose and the sole of the foot is usually tuberculate.

ADULT CHARACTERISTICS (N=18).—Dorsum blotched (Figure 1, E); lip uniform, with dark triangular bars, or a complex dark and light pattern (Figure 2, A, E, K); posterior surface of thigh with distinct mottled pattern (Figure 2, A, D); upper tibia distinctly or indistinctly barred (Figure 3, A) or uniform with small dark spots; no dorsolateral folds; fold from eye over tympanum to shoulder not dark outlined; no fold from above tympanum to side of body; thumb of male with two spines per hand; chest of male usually with spines, always present in males 65 mm SVL or larger; upper tibial and distal tarsal surfaces with scattered to many white- or black-tipped tubercules; sole of foot smooth or scattered with white- or black-tipped tubercles; female SVL 73.7±4.8 mm, maximum 77.1, male 70.0±5.8 mm, maximum 77.4 mm; female interorbital distance/head length ratio 0.14±0.01, male 0.15±0.01; female eye-nostril distance/head length ratio 0.26±0.01, male 0.26±0.01; female head length/SVL ratio 0.38±0.01, male 0.36±0.01; female head width/SVL ratio 0.41±0.01, male 0.36±0.02; female femur/SVL ratio 0.42±0.01, male 0.40±0.01; female tibia/SVL ratio 0.42±0.01, male 0.42±0.01; female foot/SVL ratio 0.44±0.02, male 0.42±0.02.

DISTINCTIVE COLORS IN LIFE.—Intense to barely visible brick red ventrally and in groin.

LARVAL CHARACTERISTICS.—Unknown.

MATING CALL.—Dominant frequency modulates between 500–1900 Hz (Figure 22); no harmonic structure in call; call with initial higher intensity portion followed by nonpulsatile portion (Figure 23); call duration about 0.08 s.

KARYOTYPE.—Unknown.

DISTRIBUTION (Figure 21).—This species is restricted to rock outcroppings in the open formations from central to northwest Brazil.

BRAZIL MATO GROSSO: Chapada dos Guimaraes, Salgapeiro, 400 m (AMNH 81354, USNM 202686, WCAB 15336, 15339–44); Cuiabá (KU 92950, WCAB 16134–38, 16141). MINAS GERAIS: Serra do Cipó (WCAB, no number). PARAÍBA: Junco do Seridó (MZUSP field 760900–01).

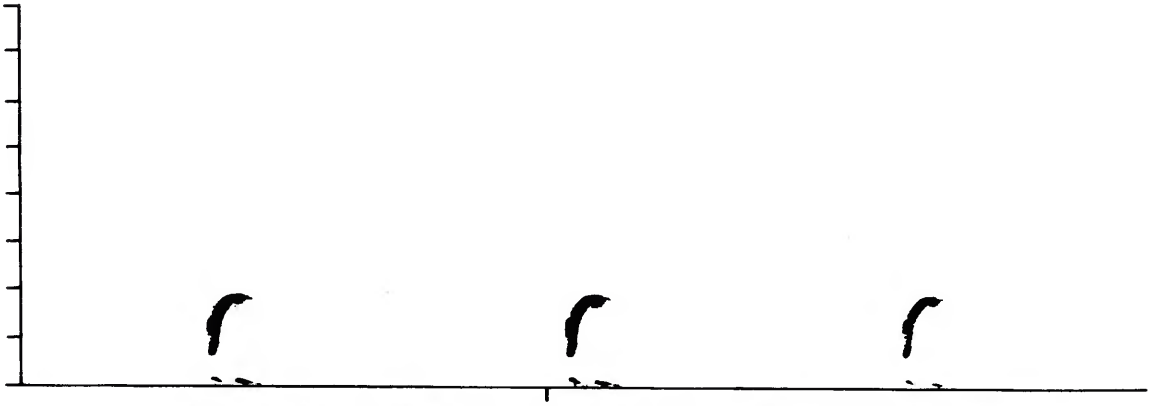

FIGURE 22.—Sonagram of mating call of *Leptodactylus syphax,* narrow band filter. (Vertical scale marks at 1000 Hz intervals; horizontal scale mark at 1 s; specimen WCAB 15336 from Chapada dos Guimerães, Mato Grosso, Brazil; air temperature 28°C.)

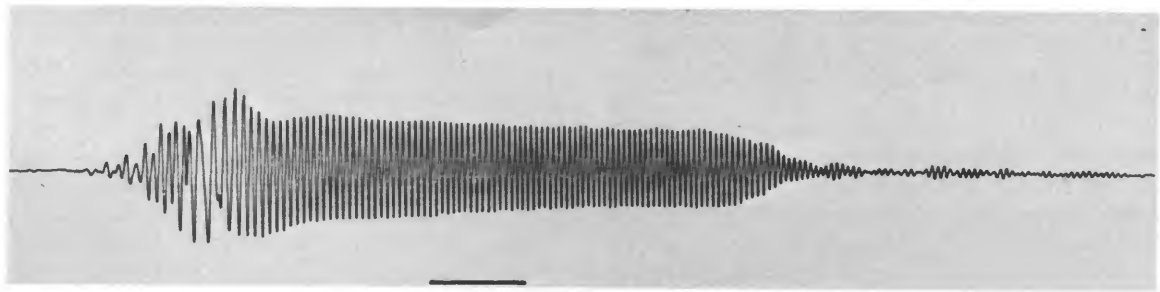

FIGURE 23.—Strip chart record of mating call of *Leptodactylus syphax*. (Line = 0.01 s; specimen data same as Figure 22.)

Artificial Key to Adult Members of *Leptodactylus pentadactylus* Group

1. Dorsal pattern of dark squares and rectangles on a white (yellow in life) background (Figure 1, F); Argentine Chaco ..... ***L. laticeps***
   Dorsal pattern various, background tan to brown, never white (yellow in life); Misiones region of Argentina and north throughout much of South America, the Lesser Antilles, and Middle America to Honduras 2
2. Posterior surface of thigh pattern consisting only of discrete, distinct light spots on a dark background (Figure 3, R, S) ..... ***L. rhodomystax***
   Posterior surface of thigh uniform or variously mottled, never with only discrete, distinct light spots 3
3. No distinct dorsolateral folds, adult size not over 90 mm SVL 4
   Distinct dorsolateral folds present, or if absent, minimum adult size over 100 mm SVL 5
4. Dorsum usually tuberculate; sole of foot usually smooth; northern South America from Colombia, Venezuela, Surinam, and French Guiana ..... ***L. rugosus***
   Dorsum warty or smooth but not tuberculate; sole of foot usually tuberculate; Brazil ..... ***L. syphax***
5. Light longitudinal stripe on the upper lip (Figure 2, G, H) ..... ***L. flavopictus***
   Upper lip variously marked, not with a light longitudinal lip stripe 6
6. No pattern between dorsolateral folds; male without thumb spines ..... ***L. stenodema***
   Usually some sort of dorsal pattern between dorsolateral fold region; male with thumb spines 7
7. Size moderate, adults not exceeding 90 mm SVL ..... ***L. rhodonotus***
   Size large, adults at least 95 mm SVL 8
8. Distinct fold from above tympanum to side of body, usually dark outlined for extent ..... ***L. pentadactylus***
   No fold from above the tympanum to the side of the body 9
9. Dorsolateral folds often extending to groin; tibia and foot longer, usually 50% SVL or longer; Lesser Antilles ..... ***L. fallax***
   Dorsolateral folds not extending past sacrum; tibia and foot shorter, usually less than 50% SVL; mainland South America 10
10. Upper lip often with light vertical bars; dorsolateral folds often interrupted; larger, adults to 200 mm SVL; non-Amazonian distribution ..... ***L. labyrinthicus***
    Upper lip never with light vertical bars; dorsolateral folds continuous; smaller, adults not exceeding 170 mm SVL; Amazonian distribution ..... ***L. knudseni***

Hypothetical Speciation Events, Ancestors, and Mode of Evolution within the *Leptodactylus pentadactylus* Species Group

There are too few characters for which primitive states can be determined to undertake a rigorous analysis of relationships. Examination of the available data does suggest some general trends that are discussed below. The zoogeography of the group is discussed elsewhere (Heyer and Maxson, in prep.).

The absence of dorsolateral folds is likely a derived condition within this group. This condition is shared by *L. laticeps, rugosus,* and *syphax. Leptodactylus rugosus* and *syphax* are morphologically quite similar, whereas the color pattern of *L. laticeps,* associated with toxic skin secretions (Abalos, 1967), is the most distinctive within the genus.

Facultatively carnivorous tadpoles are known for *L. flavopictus, labyrinthicus,* and *pentadactylus.* This derived tadpole condition, together with foam nest placement, produces an adaptively plastic life history mode different from all other members of the genus (Cardoso and Sazima, 1977; Heyer et al., 1975; Muedeking and Heyer, 1976). The adult morphologies and patterns of *L. fallax* and *knudseni* are very similar to those of *L. flavopictus, labyrinthicus,* and *pentadactylus.* Together, these five species form a natural association within the species group.

There remain three species that do not seem to share any particular features that would indicate either close relationships among themselves or with any other members of the species group: *L. rhodomystax, rhodonotus,* and *stenodema.* Of these three, the tadpole is known only for *rhodonotus,* which has a generalized tadpole morphology.

The species can be arranged in the following four groups.

Leptodactylus laticeps (Group 1): This is the single most distinctive species in the entire genus. The species is xeric adapted and is distributed in the Chaco environment.

Leptodactylus rugosus and *syphax* (Group 2): The species share similar adult morphologies. The larvae of *rugosus* are stream adapted, the larvae of *syphax* are unknown. Both species are restricted to rock outcroppings. Whether the adaptations to a rocky outcropping way of life represent a common ancestry or convergence is not discernible with the present data. Discovery of the larvae of *L. syphax* might shed some light on the relationships of these two taxa.

Leptodactylus fallax, flavopictus, knudseni, labyrinthicus, and *pentadactylus* (Group 3): Members of this group have the widest collective geographic distribution and occur both in forest and open formations. The forest adaptations of members of this group include phototactic response adaptations (Jaeger and Hailman, 1973). The members of this group likely share their closest relationships with each other.

Leptodactylus, rhodomystax, rhodonotus, and *stenodema* (Group 4): The relationships among these three species are unclear. The available data suggest all three are forest forms.

Cei and his associates have analyzed the seroproteins and skin proteins of some members of the *L. pentadactylus* group (Cohen de Hunau, Cei, and Castro, 1967; Cei, Erspamer and Roseghini, 1967; and other papers cited therein). Most of their results have established that differences occur among the forms treated as species herein. Two of their results yield information on relationships. *Leptodactylus laticeps* is not closely related to *L. labyrinthicus* (Cohen de Hunau, Cei, and Castro, 1967). *Leptodactylus stenodema* shows a closer relationship to *pentadactylus* than *labyrinthicus* (Cei, 1972).

The biochemical data are overall consistent with the groupings proposed above with the exception of tying groups 3 and 4 closer together with the relationship of *pentadactylus* and *stenodema.* The data suggest that the members of group 4 approximate the ancestors of members of group 3.

Based on the above groupings with the insights provided by the biochemical data, the following speculations are presented as hypotheses for further testing.

The presence of dorsolateral folds is associated with forest environments, the absence of dorsolateral folds is associated with open formations. The correlation does appear to be valid for this group (it is not valid for the *fuscus* group), as *L. labyrinthicus,* a species with reduced or rarely absent folds, is an open formation species. The function of the folds is not known.

The ancestor of the *pentadactylus* group was a moderate-sized species. The available data do not distinguish whether the ancestor was a forest or open formation inhabitant. The habitat restrictions of members of groups 1, 2, and 4 to either forest or

open vegetation formations suggest that the ancestor was not a forest ecotone species as is *L. pentadactylus*. The ancestor of members of group 3 was a moderate-sized forest species with a generalized pond tadpole, most similar to members of group 4. The lack of thumb and chest spines in male *L. stenodema* suggests that this might be the primitive state for the *pentadactylus* species group.

Adult morphological evolution in the *pentadactylus* group has been conservative. Male adult measurements were analyzed to determine whether the slope regressions for size-related comparisons differed.

The slopes for the 11 species were analyzed for seven comparisons: (1) interorbital distance versus head length, (2) eye-nostril distance versus head length, (3) head length versus SVL, (4) head width versus SVL, (5) femur length versus SVL, (6) tibia length versus SVL, and (7) foot length versus SVL. An analysis of covariance for the 11 species was run to test the homogeneity of the slopes. In all seven regressions, the results were not statistically significant, indicating that the slopes of the 11 species did not differ for each of the comparisons. Next, an analysis of covariance was run on the 11 species in which a common slope was assumed. The results for all seven comparisons were the same: (1) the groups differed statistically and (2) the regressions were statistically significant. The r-square values for the comparisons are high, indicating that the single slope model for each of the comparisons explains most of the variation. The lowest r-square value is for interorbital distance versus head length, 0.91. The other r-square values range between 0.96–0.98. These results indicate that the large species are simply projections of the smaller species. The same growth processes and dynamics are involved. Selection has likely operated with respect to size, whereas growth processes have determined shape.

In contrast to the moderate evolution of the adult morphology within the group is the striking morphological differences found in the larvae. There are three very different adaptive types of the known larvae. First, at least one species, *L. rhodonotus,* has a generalized pond tadpole. Second, the larva of *L. rugosus* has a stream adapted larva with a large sucking disk and an attenuate tail with reduced fin. Third, the larvae of *L. flavopictus, labyrinthicus,* and *pentadactylus* are facultative carnivores with a strong tail and the mouthparts located anteriorly. The key evolutionary adaptations within the species group apparently have occurred at the larval portion of the life cycle, rather than the adult portion. This situation contrasts with that found in the *Leptodactylus fuscus* group, in which the known larvae are all similar and differences of adult body size and shape have been the evolutionarily important morphological features of the life cycle (Heyer, 1978).

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