SYSTEMATICS OF THE *FUSCUS* GROUP OF THE FROG GENUS *LEPTODACTYLUS* (AMPHIBIA, LEPTODACTYLIDAE)

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NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY
SCIENCE BULLETIN 29 • DECEMBER 29, 1978

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SYSTEMATICS OF THE *FUSCUS* GROUP OF THE FROG GENUS *LEPTODACTYLUS* (AMPHIBIA, LEPTODACTYLIDAE)[1]

By W. RONALD HEYER[2]

ABSTRACT: Thirteen characters of external morphology are analyzed in detail for the species comprising the *fuscus* group (genus *Leptodactylus*). The major method of data analysis is application of the multivariate stepwise discriminant function analysis. Results of the morphological analysis are compared with known information on mating calls, larvae, and karyotypes. Based on all available data, taxonomic conclusions are drawn.

The nomenclature of the group is described in detail, associating proposed names with the species units recognized in this study. Wherever possible, the original type material was re-examined for this study. Of the 19 species recognized in the *fuscus* group, 4 are described as new.

For each species, the following information is provided: a synonymy of primary names, a diagnosis for adults, adult and larval morphological characteristic summaries, diagnostic description of the mating call, diagnostic description of the karyotype, and distribution including localities and associated specimen museum numbers for the specimens examined. A key is provided at the end of the species accounts.

The composite range of the group is extensive, ranging from Texas to Argentina, on both sides of the Andes, and certain islands of the West Indies.

Several characters used in the analysis are sexually dimorphic. It is postulated that sexual dimorphism in hind limb proportions is due to differential selection, the shorter male limb the result of selection for the burrowing activity of incubating chamber formation, the longer female limb the result of selection for avoiding above ground vertebrate predators. Sexual dimorphism occurring in the lip and thigh stripes of some species is explained by the hypothesis that males are using the information to discriminate among females in mate recognition.

The ancestral stock of the *fuscus* group is presumed to have been fossorially adapted to an area with a vegetation type similar to that now found in the Gran Chaco. Evolutionary events within the species group correlate with adaptations to more mesic environments.

INTRODUCTION

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

The aim of this study is to set a new baseline for the systematic understanding of the *fuscus* group based on museum specimens and field observations. The study is based on all available specimens, exclusive of five new species in the group that are being described by South American workers.

ACKNOWLEDGMENTS AND MUSEUM ABBREVIATIONS

A study of this kind is impossible without the cooperation of people in charge of collections who freely give their help. I thank the following for the loan of specimens, tape recordings, and/or information regarding specimens: Dr. Beer, Naturwissenschaftliches Museum Leipzig, Leipzig; Robert L. Bezy, LACM; Wolfgang Böhme, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; Werner C. A. Bokermann, WCAB; Antenor L. Carvalho, MNRio; Joseph T. Collins, KU; Jorge A. Cranwell, MACN; M. Diehl, Naturhistorisches Museum der Hansestadt Lübeck, Lübeck; James R. Dixon, TCWC; William E. Duellman, KU; José M. Gallardo, MACN; Alice G. C. Grandison, BMNH; Marinus Hoogmoed, RMNH; J. O. Hüsing, Martin-Luther-Universität, Halle (Saale); Eugenio Izecksohn, Rio de Janeiro; Hans-Wilhelm Koepcke, Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Hamburg; P. Kuenzer, II Zoologisches Institut und Museum der Universität, Göttingen; Raymond F. Laurent, IML; Jean Lescure, LES; Alan E. Leviton, CAS-SU; Clarence J. McCoy, CM; Edmond V. Malnate, Academy of Natural Sciences, Philadelphia; Hymen Marx, FMNH; Charles W. Myers, AMNH; Ronald A. Nussbaum, UMMZ; F. J. Obst, Staatliches Museum für Tierkunde, Dresden; Günther Peters, Museum für Naturkunde der Humboldt-Universität, Berlin; William F. Pyburn, UTA; Juan A. Rivero, UPR; R. Roux-Estève, Museum National d'Histoire Naturelle, Paris; Jay M. Savage,

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CRE; Albert Schwartz, ASFS; A. F. Stimson, BMNH; Paulo E. Vanzolini, MZUSP; Charles F. Walker, UMMZ; Ernest E. Williams, MCZ; John W. Wright, LACM; Richard G. Zweifel, AMNH.

Carolyn Cox, Smithsonian Institution, executed the drawings in figs. 2, 33, 36, 43, 48, 56, 57, 65, 66, 70. Susan Arnold labored over preparing the localities in computer format and prepared figs. 3–4, 7–10, 13–14, 17–21. Charles D. Roberts, Smithsonian Institution, patiently explained the discriminant function program to me. Ronald I. Crombie, Smithsonian Institution, discussed the work with me while it was in progress and kindly provided several translations of original descriptions from German. George R. Zug, Smithsonian Institution, helpfully criticized the manuscript.

The paper has benefitted from the constructive comments of the assigned reviewers. They are, as usual, not responsible for any flights into fantasy on my part.

The Smithsonian Research Foundation supported the research.

Museum abbreviations as used in the text are:

AMNH	American Museum of Natural History, New York
ASFS	A. Schwartz private collection, Miami
BMNH	British Museum (Natural History), London
CAS-SU	California Academy of Sciences, Stanford University Collection
CHINM	Collección Herpetólogica del Instituto Nacional de Microbiología, Buenos Aires
CM	Carnegie Museum, Pittsburgh
CRE	University of Southern California, Los Angeles
FMNH	Field Museum of Natural History, Chicago
IML	Fundación Miguel Lillo, Tucumán
KU	University of Kansas Museum of Natural History, Lawrence
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	Museu Nacional, Rio de Janeiro
MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
TCWC	Texas Cooperative Wildlife Collection, Texas A&M University, College Station
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
UPR	University of Puerto Rico, Mayaguez
USNM	National Museum of Natural History, Washington, D. C.
UTA	University of Texas at Arlington, Arlington
WCAB	W. C. A. Bokermann private collection, São Paulo

METHODS AND MATERIALS

The study represents several stages of analysis. Briefly, as many museum specimens as could be reasonably borrowed were initially analyzed with respect to external morphology. Other known biological information was added to the results of the morphological analyses. In some cases, information at that point was adequate to draw systematic conclusions. In other cases, the data were inconclusive and additional field work and/or morphological data were gathered. After the first draft of this paper was completed, Izecksohn's description of a new species of *Leptodactylus* was published. As he had allowed me to examine the specimens, the data are included in the species accounts, but are not included in the population analysis section.

The following characters were recorded for every adult specimen examined.

1) Dorsal pattern. Standards were prepared for dorsal patterns and the specimens were placed in the category they most closely resembled (fig. 1).

2) Lip stripe. The lip was coded as either having a distinct light stripe or not. In some species, information was also recorded on the distinctiveness of a dark subocular bar.

3) Thigh stripe. The posterior face of the thigh was coded as having a distinct, indistinct, or no light stripe.

4) Dorsolateral folds. The total number of dorsolateral folds was recorded for each specimen.

5) Sex.

6–8) Tibia, tarsal, and foot texture. The relative presence or absence of white tubercles was recorded separately for the tibia, tarsus, and foot elements.

9) Snout-vent length (SVL). The SVL is the distance from the tip of the snout to behind the vent.

10–14) Head length, head width, femur length, tibia length, foot length ratios. Measurements were taken for each variable and divided by the SVL of the same animal. Head length was measured from behind the angle of the jaw to the tip of the snout. Head width was measured at the angle of the jaws. The leg measurements were taken with the leg positioned in a Z pattern with the femur element at right angles to the vertebral column. The foot was measured from behind the inner metatarsal tubercle to the tip of the third digit.

In addition, the tibia pattern was recorded for members of the *L. gracilis* complex (fig. 2).

All measurements were taken with vernier calipers. A series of 10 *L. albilabris* of diverse conditions of preservation were measured on two occasions to determine the repeatability of measurements. The average differences of measurements ranged from .2 to .4 mm; measurements are repeatable within a tolerance of .5 mm. The actual error in measurement may be greater, particularly in SVL, femur, tibia, and foot length where the position of the animal in preservative may not allow the accurate measurement of the variable.

The above data were analyzed by the Stepwise Discriminant Analysis, BMDO7M, in the Biomed package produced by the University of California. Justification for using this multivariate approach to aid in distinguishing species in leptodactylid frogs, using the type of data analyzed herein, has been presented elsewhere (Heyer 1977). The number of dorsolateral folds was not used in the computer analysis because the condition could not

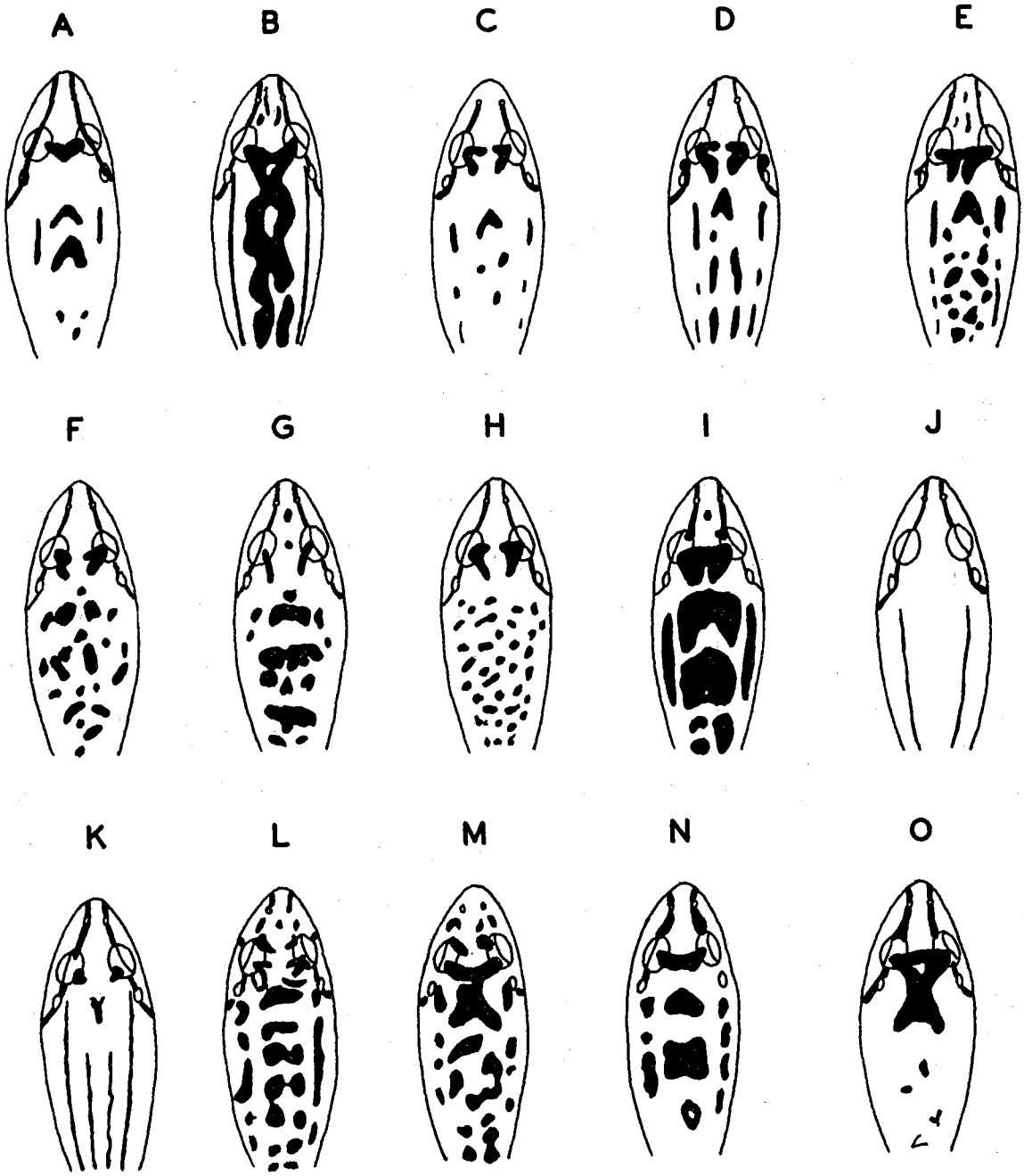

FIGURE 1. Dorsal pattern standards utilized for the *Leptodactylus fuscus* species group.

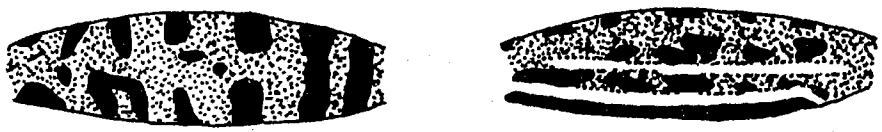

FIGURE 2. Tibia pattern standards utilized for the *Leptodactylus gracilis*-complex. Left, barred condition; right, striped condition.

be determined in a number of poorly preserved individuals. Tibial texture was also omitted from all analyses except for *L. labialis* because of slight interspecific variation. The number of variables used differs slightly from group to group. The information on group size and number of variables analyzed is presented case by case in the next section. Some members of the study group are sexually dimorphic; the male and female data were run separately. For the female *L. albilabris*-complex data, standardized and non-standardized data were analyzed. The non-standardized data were simply the raw values punched on the computer cards. The data were standardized so that the total range of variation of each character fell between 0 and 1. The discriminant function analysis results were exactly the same using the standardized and non-standardized data; the remaining analyses were run using non-standardized data.

Atchley, Gaskins, and Anderson (1976) presented theoretical arguments against the use of ratios as variables in discriminant function analysis. In terms of the ratios used here, their argument is that dividing through by SVL does not entirely eliminate size as a factor in the variable involved. Atchley et. al. (1976) compared the results of analysis of original untransformed hypothetical data with the analysis of ratios and found striking differences. As the paper by Atchley et. al. appeared after my computer runs had been made, I tested their conclusions by reanalyzing data for four members of the *mystaceus*-complex, using the measurements as originally recorded.

Overall, the results of the two runs are very similar. The posterior classifications are identical for the female data and differ by one specimen for the male data. The plots of the first two discriminant axes are essentially the same. The cumulative proportions of total dispersion accounted for by successive discriminant axes are nearly identical in both runs, in marked contrast to the runs of Atchley et. al. For example, for the female data using ratios, the cumulative proportion of dispersion of the first discriminant axis is .807 (.817 for data using measurements), .977 for the first and second axes (.978) and 1.00 for the first, second and third (1.00).

The only noticeable differences are in the entering order of the variables (Table 1). The F levels of significance cannot be interpreted literally because not all of the variables are normally distributed (see Heyer 1977, for discussion). However, the critical F-level (5%) can be used at least to screen out variables that are not adding information to the analysis. Variables having a low F value are labelled as not important (NI) in the analysis section, indicating that they are probably not statistically significant contributors to inter-group discrimination in a particular run. However, rigorous statistical interpretation is not possible. The most striking difference in variable entering order is with SVL, but overall, the orders are similar.

Corruccini (1977), in response to Atchley et. al. (1976), found analysis of ratios to be meaningful for real data sets. As Atchley et. al.'s arguments are not substantiated by real data sets, ratios are used in the discriminant function analyses of this paper.

A discriminant function analysis requires pre-formed

TABLE 1

Entering order of variables for members of the *L. mystaceus*-complex. Line indicates F significance at the 5% level (see text).

	Head and limb variables entered as ratios	Head and limb variables entered as measurements
Female data . . .	tarsal texture	tarsal texture
	foot texture	head width
	foot/SVL	foot length
	SVL	foot texture
	head length/SVL	head length
	femur/SVL	femur length
	head width/SVL	dorsal pattern
	dorsal pattern	lip stripe
	lip stripe	tibia length
	tibia/SVL	SVL
	thigh stripe	thigh stripe
Male data	tarsal texture	tarsal texture
	foot texture	foot texture
	foot/SVL	foot length
	dorsal pattern	SVL
	tibia/SVL	dorsal pattern
	lip stripe	tibia length
	femur/SVL	lip stripe
	head width/SVL	femur length
	SVL	tibia length
	head length/SVL	head width
	thigh stripe	thigh stripe

groups for analysis. The groups used are what I believed to be species units based on my observations during the data taking phase. The discriminant function analysis is used to determine whether there are demonstrable morphological differences among the units analyzed. In ten years of experience working with frogs of the genus *Leptodactylus,* I have found that consistent morphological differences among populations is indicative of species level differentiation. For purposes of this paper, if the discriminant function analysis demonstrates that the species units are morphologically distinct, no further explanation is required. If the discriminant function analysis only partly separates the groups being analyzed, then other data where available are added to see if the additional data support the species groupings as originally determined.

The use of discrete variables in the discriminant function analysis places two restrictions on the results. First, the discriminatory power of the analysis is reduced. A two state character can only discriminate two groups, a continuous character can discriminate many groups. Second, the posterior classification of individuals involves confidence limits around the centroid values for the groups as analyzed. Discrete variables do not lend themselves to meaningful confidence limits. The results of the posterior classifications are thus not robust and should not be overinterpreted. The net result of the use of discrete variables is that the discriminant function analysis results are conservative. Any differences observed are real, but there may be more differences among groups than the results indicate.

The single most useful output of the discriminant function analysis as used herein is the plot of the first two discriminant axes. This gives a visual presentation of the distinctiveness of the groups being analyzed. It is this feature that is used to demonstrate the relative morphological distinctiveness of the groups being analyzed. The results are not used to test whether or not my original sorting into species was correct. The results are used to demonstrate the relative morphological distinctiveness of the groups. For the species represented by adequate geographic samples, discriminant function analyses are performed using locality samples as groups to determine whether any of the geographic samples are morphologically distinctive. These results are interpreted very conservatively. That is, a geographic sample would have to be clearly distinctive to warrant further analysis.

The criteria used to determine the species limits for members of the *fuscus* group in the order in which I have confidence in them follow.

1. Mating calls.—The mating calls of members of this group are species specific and the kinds of differences coding species specificity have been commented on (Straughan and Heyer 1976). Where mating call information is known, those data are considered of prime importance and take precedence over the other data utilized in this study. Because mating calls are known for relatively few populations, the mating call data are used operationally in conjunction with the data of the second criterion.

2. External adult morphology.—Consistent, discrete morphological differences among populations of members of the *fuscus* group usually correlate with the mating call data. In this study, the discriminant function analysis was applied in two different ways for which I have two levels of confidence.

A. Use of the multivariate analysis with the populations I consider to represent distinct species. This analysis is utilized to show the kinds of morphological differences among the species recognized herein. Morphological overlap can be extensive for species which are clearly distinct (figs. 25 and 26 for two species which have very distinctive mating calls and karyotypes). In some cases, data not coded further separate the species groupings, particularly information on dorsolateral folds. Because all the coded data are used in these analyses, the results are interpreted liberally. That is, species groupings are considered to be morphologically distinctive and distinguishable even with a moderate amount of overlap on the discriminant axis plots.

B. Use of the multivariate analysis with geographic samples of what I consider to be the same species. In all cases, some of the variables are uniform for the analyses; thus, the analyses are based upon smaller data sets. In addition, there are no other morphological data that were not coded that will allow further discrimination. For these reasons, the results of these analyses are interpreted very conservatively. Wherever the results of this analysis show a distinctive population unit that conflicts with the mating call information, the mating call information is given priority. Where mating calls are not available, the distinctive morphological units are pointed out, but not accorded specific level recognition. I do not have enough confidence in this level of analysis to recognize species levels based on the results. The value of the technique is to point out distinctive populations that should then be sampled for mating calls before a final taxonomic decision is made. If there are taxonomic errors in this paper, they involve recognition of too few, not too many species, in my opinion.

3. Larval morphology and karyotypes.—Information from these systems is not useful in determining species limits for members of the *fuscus* species group. Too few larval samples are available to determine whether apparent differences in denticle number has systematic value. The general shapes and color patterns of all known larvae are similar. The known karyotypes for members of this group are very similar, with but a single exception. The exception is the karyotype of *L. latinasus* which is interpreted as indicating a species level difference. All other kinds of karyotypic differences reported

are as likely due to differences of preparation or interpretation as to differences of systematic value (Heyer and Diment 1974).

Within the *fuscus* group, a number of species complexes are apparent. The following complexes are recognized for purposes of discriminant function anaylses: *albilabris, labialis, fuscus, bufonius, latinasus.*

POPULATION ANALYSES

The coding of characters for computer analysis results in a loss of information in some cases. For character 1, dorsal pattern, two different codes were used. For *L. labialis,* the presence of a double dorsal chevron (fig. 1, A) was coded as a 2, any other pattern was coded as a 1. For the other species, the presence of a light middorsal stripe was coded as a 2, absence was coded as a 1. For the only analysis in which *L. labialis* is analyzed with another species group (*latinasus*), the dorsal pattern is omitted from analysis. Character 2, lip stripe, was uniformly coded as 1 for an indistinct light lip stripe, 2 for a distinct lip stripe. Character 3, thigh stripe, was uniformly coded as 1 for a distinct light stripe, 2 for an indistinct, but still discernable stripe, 3 for no stripes. Characters 6 to 8, textures of the tibia, tarsus, and sole of foot were uniformly coded as 1 for presence of any white tubercles, 2 for no white tubercles. The actual numbers for the SVL, head, and hind limb measurements were punched on cards; the head and hind limb measurements were each divided through by SVL and a new card deck punched by computer.

L. ALBILABRIS—COMPLEX

Morphology.—Members of the *L. albilabris* complex are distributed on the West Indian islands. Morphologically the group is distinct from all mainland species populations. Most taxonomic questions concerning the *L. albilabris* complex center on the question whether the different island bank systems have different species. The following variables were used in the stepwise discriminant function analysis: 1–3, 9–14. Characters 7–8 are uniform in *L. albilabris*.

Female data.—Seventy-two individuals were analyzed from five localities in Puerto Rico, two localities from the Dominican Republic and one locality each from St. Croix, St. Thomas, and Tortola. The smallest sample used consisted of three individuals from a single locality; the largest contained 16 individuals. The results (fig. 3) indicate that the Dominican Republic samples are the most distinctive, but that there is overlap with the other samples. Overlap, as used throughout, means overlap of the polygons on the plot figures of the first two discriminant axes. The first two axes account for 68% of the total variation. The variables were entered in the program in the following order (i.e. in order of descending contribution to the intergroup variation): dorsal pattern, SVL, head width ratio, tibia ratio, thigh stripe, head length ratio, foot ratio (NI), femur ratio (NI), and lip stripe (NI).

Male data.—One hundred thirty five individuals were analyzed from 7 localities in Puerto Rico and one locality each from the Dominican Republic, St. Croix, St. John's, St. Thomas, and Tortola. Four individuals from a single locality was the smallest group used, the largest was comprised of 24 individuals. The results (fig. 4) indicate that as with the females, the Dominican Republic samples are the most distinctive, but there is morphological overlap with the other samples. The first two axes account for 73% of the total variation. The variables entered in the program in the following order: dorsal pattern, tibia ratio, SVL, head width ratio, head length ratio, femur ratio, thigh stripe (NI), lip stripe (NI), foot ratio (NI).

The results of the male and female analyses both indicate that the Dominican Republic samples are the most distinctive. There is sexual dimorphism in patterns of geographic variation, as some of the variables entered the program in different orders. Part of this may be due to the fact that different numbers of localities were used for the two sexes, and only 4 localities were represented in common in the two samples.

Larvae.—Tadpole samples were examined from Puerto Rico (ASFS 7901, UMMZ 125168, 125174), St. Thomas (USNM 119038) and the Dominican Republic (USNM field 41052). All larvae examined are indistinguishable.

Mating calls.—Two calls were available for analysis: Puerto Rico: El Yunque (AMNH tape) and Dominican Republic: El Seibo Prov; 3.2 km E Sabana de la Mar (USNM tape). The calls sound similar to the human ear, but representative calls analyzed in detail show some differences. Sonagrams (fig. 5) indicate the calls have the same frequency and basic structure. The pattern of frequency modulation differs between the two calls (fig. 5). The strip chart records of individual calls (fig. 6) indicate that the initial part of the calls differ, as well as the shape of the initial part of the second portion of the call. These differences are of the kind that code species-specific information in *Leptodactylus* (Straughan and Heyer 1976), but the magnitudes of the differences (figs. 5 and 6) are not great.

No information is available on call variation within island populations or among individuals in a given population. While the calls available for analysis differ, the evidence for specific differentiation is not decisive.

Taxonomic conclusion.—The adult morphology and calls (sample size of only 2) are different for the populations from the Dominican Republic with respect to all other populations. The evidence indicates that all West Indian populations had a common ancestor: the question revolves about the degree of differentiation. I interpret the available evidence to indicate the degree of differentiation has not reached the species level.

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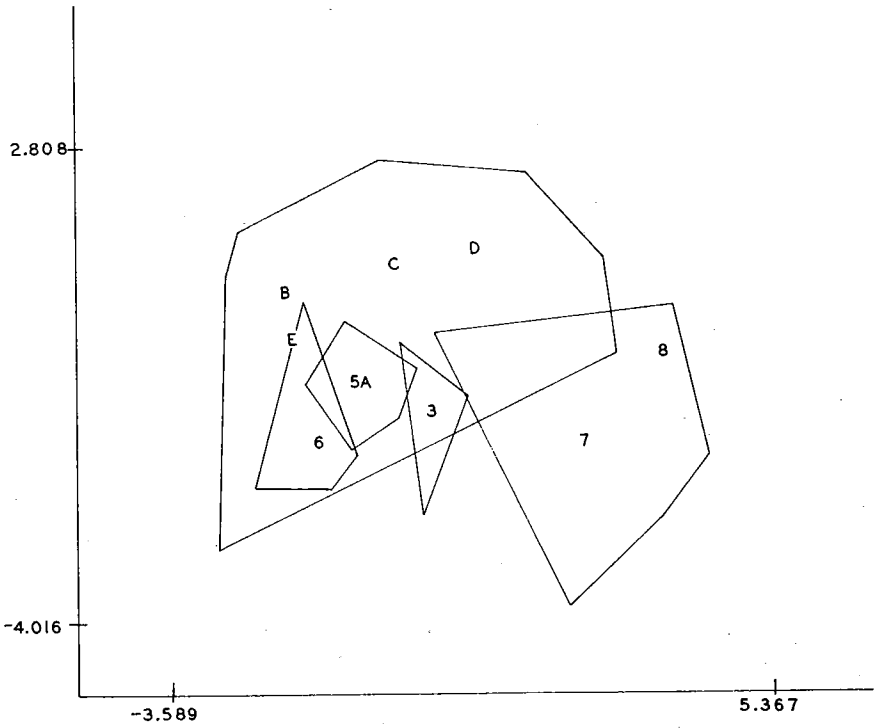

FIGURE 3. Discriminant axis plot for geographic samples of females of *Leptodactylus albilabris*. A–E = Puerto Rico, 3 = St. Croix, 5 = St. Thomas, 6 = Tortola, 7–8 = Dominican Republic. Letters and numbers placed at group means. Envelopes contain all group members by islands.

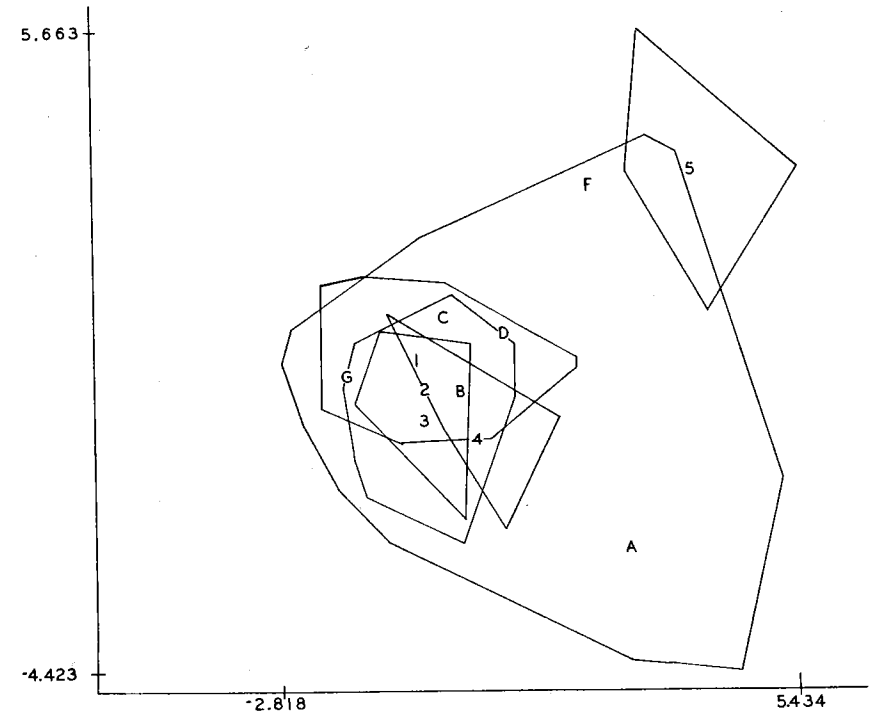

FIGURE 4. Discriminant axis plot for geographic samples of males of *Leptodactylus albilabris*. A–G = Puerto Rico, 1 = St. Croix, 2 = St. Johns, 3 = St. Thomas, 4 = Tortola, 5 = Dominican Republic. Letters and numbers placed at group means. Envelopes contain all group members by islands.

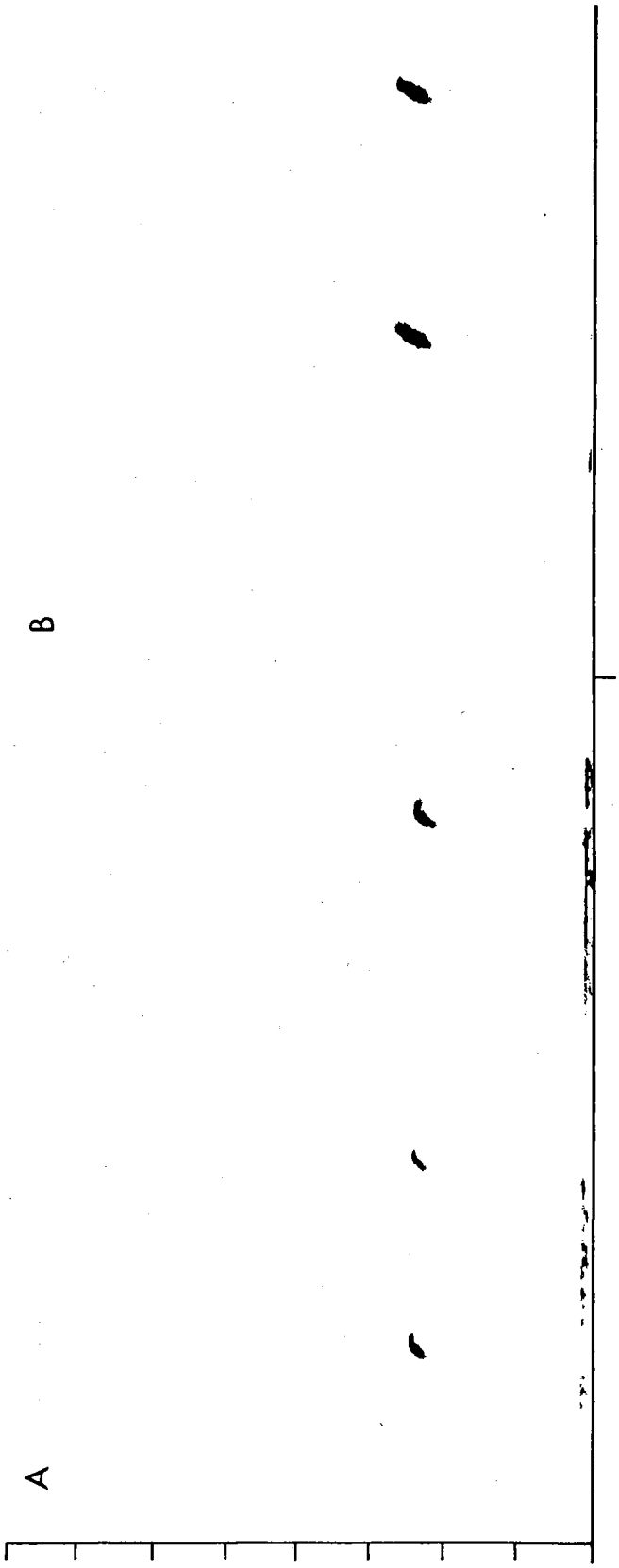

FIGURE 5. Sonagrams of the mating call of *Leptodactylus albilabris*, narrow band filter. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. A = specimen from Puerto Rico, El Yunque (AMNH tape), B = specimen from Dominican Republic, Sabana de la Mar, air temperature 20° C (R. I. Crombie recording at USNM).

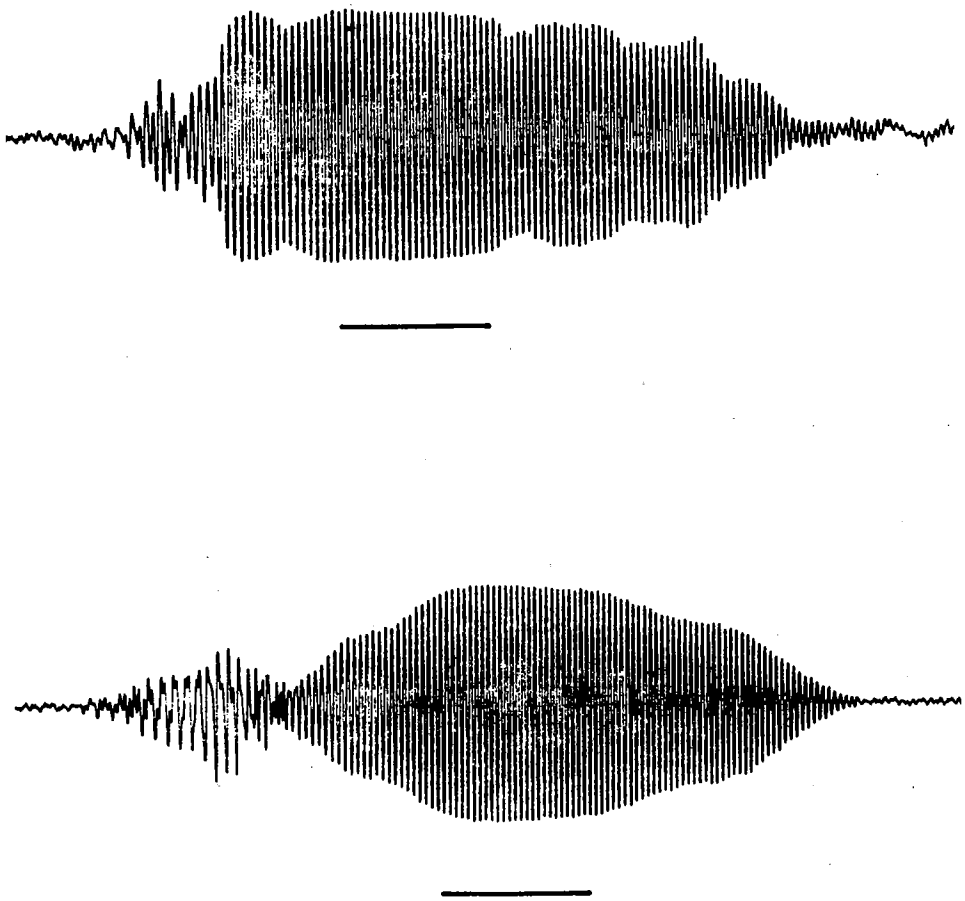

FIGURE 6. Strip chart records of the mating call of *Leptodactylus albilabris*. Line equals 0.01 s. Upper figure is note of specimen from Puerto Rico, El Yunque, lower is note of specimen from Dominican Republic, Sabana de la Mar. See legend of Figure 5 for further specimen data.

LEPTODACTYLUS LABIALIS

Morphology.—Groupings used in the computer analysis consist of specimens from single localities unless otherwise indicated. The following variables were used: 1–3, 6, 9–14. Variables 7 and 8 are uniform for *L. labialis*.

Female data.—Specimens from localities in the following political units were analyzed as follows (number of specimens in parentheses): Mexico, Campeche (47), Mexico, Michoacán (4), Mexico, Oaxaca (10), Mexico, San Luis Potosí (7), Mexico, Tamaulipas (6), Mexico, Veracruz (5), Mexico, Yucatán (4), Guatemala (3), Belize (36), Honduras, Francisco Morazán (10), Honduras (8), Costa Rica (5), Panama (4), Colombia (4), Venezuela, Apure (21), Venezuela (5). The plot of the first two discriminant axes (fig. 7) shows a complex pattern, mostly of overlapping groups. The first two axes account for 61% of the variation. The variables entered in the following order: SVL, tibia ratio, tibia texture, head width ratio, thigh stripe, foot ratio, femur ratio, lip stripe, head length ratio, dorsal pattern (NI). The northernmost Michoacán sample is the only group showing no overlap with other groups. The Costa Rican sample is also relatively distinctive. All other samples show broad overlap; generally, samples from adjacent localities are close to each other in the discriminant axis plot (fig. 7).

Male data.—Specimens from localities in the following political units were analyzed as follows (number of specimens in parentheses): Texas (3 from 2 localities), Mexico, Campeche (11), Mexico, Colima (7), Mexico, Guerrero (7), Mexico, Michoacán (6), Mexico, Morelos (3), Mexico, Tamaulipas (5), Mexico, Tamaulipas (6), Mexico, Yucatán (8), Guatemala (15), Belize (5), Honduras (7), Costa Rica, Guanacaste (6), Costa Rica, Puntarenas (5), Panama, Canal Zone (11), Panama, Coclé (7), Panama, Veraguas (8), Colombia, Antioquia (5), Colombia, Santander (5), Venezuela (9). The plot of the

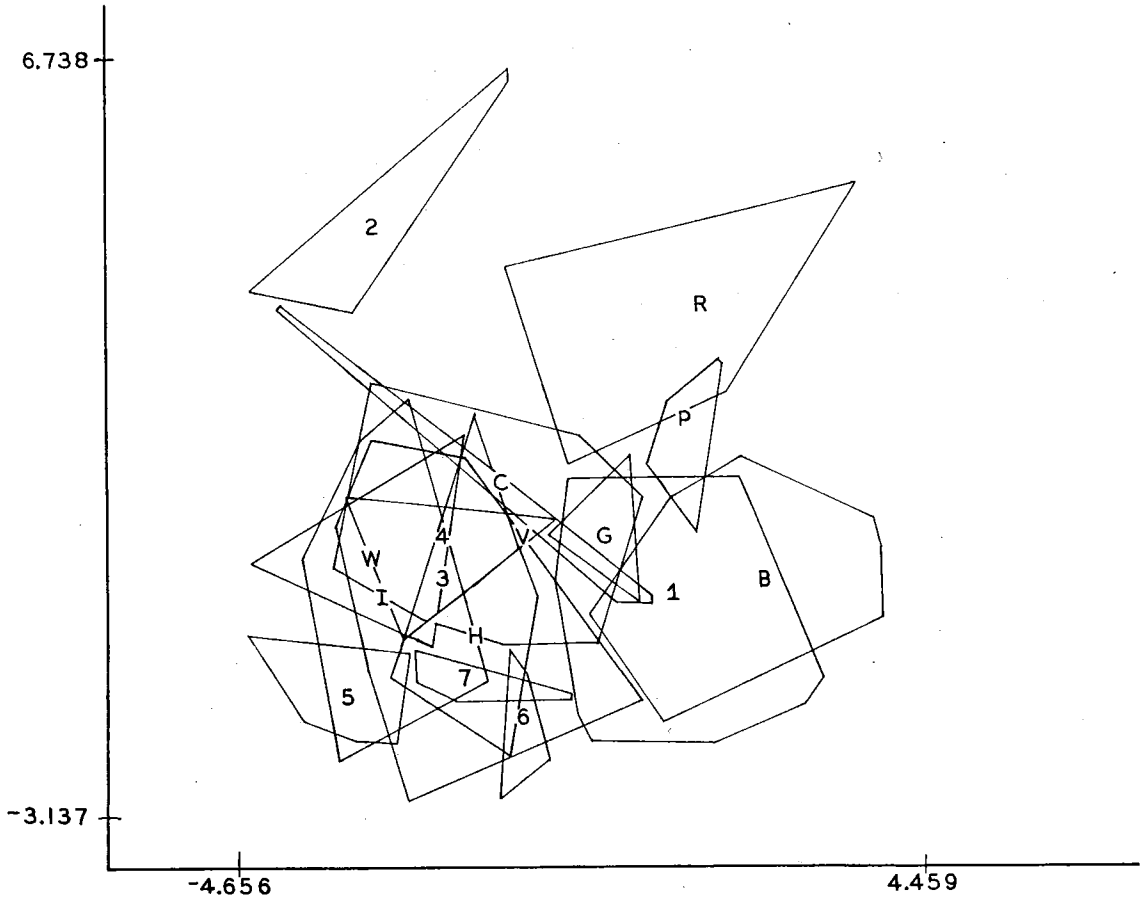

FIGURE 7. Discriminant axis plot for geographic samples of females of *Leptodactylus labialis*. 1–7 = Mexico, G = Guatemala, B = Belize, H–I = Honduras, R = Costa Rica, P = Panama, C = Colombia, V–W = Venezuela. Numbers and letters are placed at group means. Envelopes contain all group members.

first two discriminant axes (fig. 8) is comparable to the female plot (fig. 7) in that there is a complex pattern of group overlapping. The first two axes account for 58% of the total variation. The variables entered in the following order: SVL, head length ratio, foot ratio, femur ratio, thigh stripe, head width ratio, tibia ratio, tibia texture, dorsal pattern, lip stripe (NI). The only group which is completely distinct from the other groups is the northernmost group of male specimens from Mexico in the state of Colima. All other groups show varying degrees of overlap; adjacent geographic samples are usually close to each other in the plot of the discriminant axes (fig. 8).

The male and female results are similar in that: (1) SVL is the most important variable in describing the intergroup variation, and (2) the northernmost populations from west coastal Mexico are the most distinctive based on external morphology.

Larvae.—Larvae have previously been described for *L. labialis* (e.g. Heyer 1970b). During that previous study, I found no differences between larval samples from Mexico and Middle America. To my knowledge, no larval samples are available from any South American localities.

Mating call.—Straughan and Heyer (1976) summarized the call information for *labialis*, indicating a clinal trend in call characteristics from Mexico to Panama. The differences are not of the magnitude demonstrated by different species of *Leptodactylus*. No calls were available for any South American populations.

Taxonomic conclusion.—The discriminant function analysis indicates that the northwest coast Mexico population is morphologically distinguishable from all other groups. The mating call information indicates that the call of the northwest coast Mexican population is not specifically distinct from the Panamanian population call. In this case, I place more confidence in the mating call data and conclude that differentiation has not reached the species level.

LEPTODACTYLUS FUSCUS—COMPLEX

Computer analysis of the morphological data was done in two stages. The first analysis is based on data from museum specimens assembled in the laboratory.

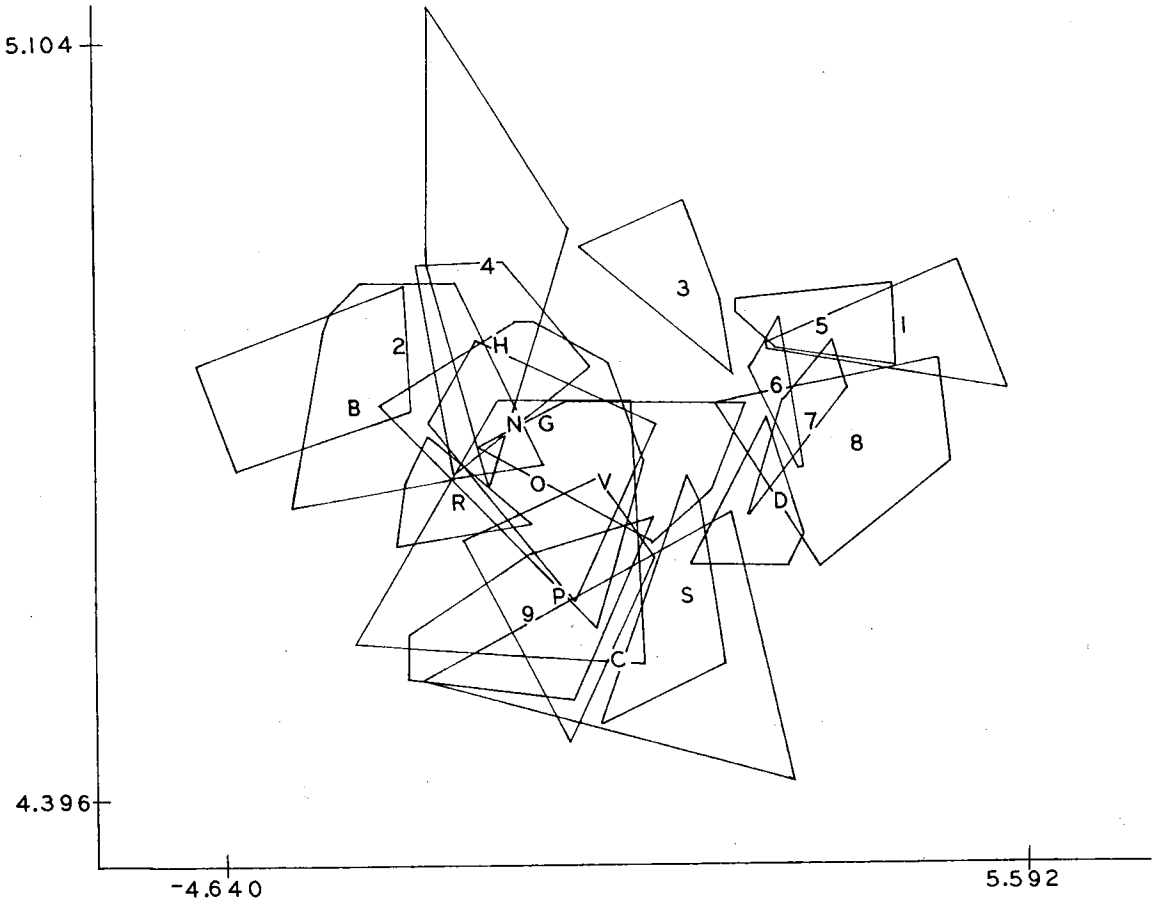

FIGURE 8. Discriminant axis plot for geographic samples of males of *Leptodactylus labialis*. 1 = Texas, 2–9 = Mexico, G = Guatemala, B = Belize, H = Honduras, R–S = Costa Rica, N–P = Panama, C–D = Colombia, V = Venezuela. Numbers and letters are placed at group means. Envelopes contain all group members.

In some cases, sample sizes were small and attempts were made to gather more data on specimens located in South American museums.

Morphology.—As discussed earlier, specimens were sorted into what appeared to be different species. The first analytic procedure was to enter each of these species units as predefined groups to determine the relative morphological distinctiveness of each of the groups. The following variables were used: 1–3, 7–14.

Female data.—the following groups were analyzed (number of specimens in parentheses): *fuscus* (178), barred *gracilis* (referring to tibial pattern) (10), striped *gracilis* (6), *longirostris* (following Rivero's (1971) identification) (15), northern *mystaceus* (76), southern *mystaceus* (12), coastal Brasil *mystaceus* (3), *poecilochilus* (83). The results (fig. 9), indicate good separation of some groups, but considerable overlap in others. Posterior classification of cases into group results are discussed below with the male data. The first two axes account for 82% of the variation. The variables entered in the following order: foot texture, tibia ratio, foot ratio, tarsal texture, head width ratio, SVL, dorsal pattern, lip stripe, head length ratio, thigh stripe, and femur ratio (NI).

Male data.—The groups analyzed were (number of specimens in parentheses): *fuscus* (214), barred *gracilis* (21), striped *gracilis* (18), *longirostris* (34), northern *mystaceus* (75), southern *mystaceus* (15), coastal Brasil *mystaceus* (3), *poecilochilus* (50). The results (fig. 10) are comparable to the female results. Seventy seven percent of the variation is accounted for in the first two axes. The variables entered in the following order: foot texture, tarsal texture, foot ratio, tibia ratio, SVL, dorsal pattern, head length ratio, lip stripe, head width ratio, thigh stripe, and femur ratio (NI).

The results of the a posteriori classification routine which assigns cases to their "most probable" groups are similar for males and females (Table 2). As indicated previously, because discrete variables were used, the results of the posterior classification should not be interpreted too finely. The results indicate that separation of the groups is good. As more specimens of *fuscus* were placed in other groups than any other species unit, the *fuscus* unit is discussed as an example to show that other

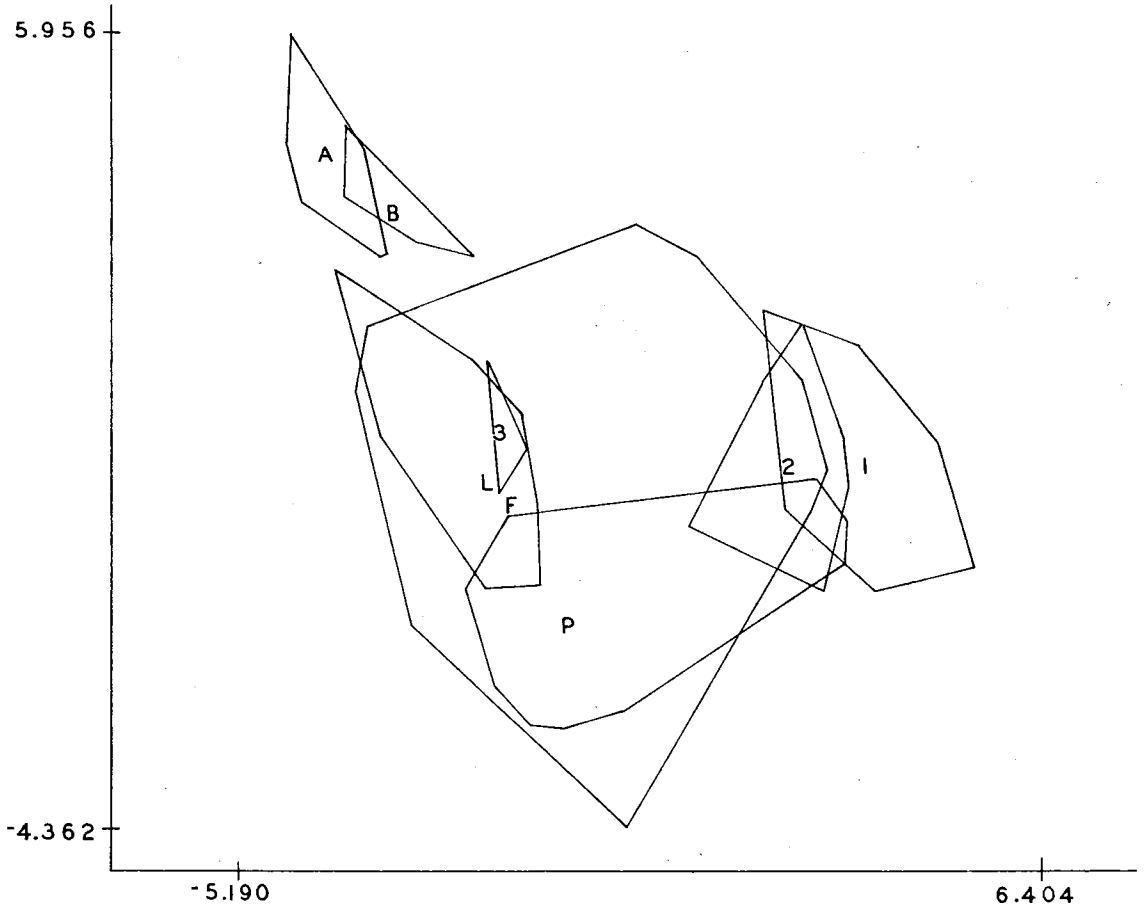

FIGURE 9. Discriminant axis plot of females of the *fuscus* complex. F = *fuscus*, A = striped *gracilis*, B = barred *gracilis*, L = *longirostris*, 1 = northern *mystaceus*, 2 = southern *mystaceus*, 3 = south coast *mystaceus*, P = *poecilochlus*. Letters and numbers placed at group means. Envelopes contain all group members.

evidence can be used to further separate the analytic units. There are two reasons why several *fuscus* specimens were assigned to other groups: (1) the variables analyzed are not sufficient in themselves to completely separate the *fuscus* specimens from specimens of the other groups, and (2) the foot texture coding is very dependent on state of preservation in this group. As noted above, foot texture was the most important distinguishing factor in the analysis for both males and females. In most of the other species, white tubercles are prominent and obviously present or conspicuously absent. In *fuscus*, however, the tubercles are at best small, are often the same color as the rest of the foot, and therefore not conspicuous. All *fuscus* probably have a tubercular foot texture, but the texture is often lost in preservation. All *fuscus* specimens classified as northern and southern *mystaceus* were coded as having foot tubercles present. Only 4 additional specimens that were coded as having foot tubercles were computer assigned to *fuscus*. Because of geographic ranges, some of the computer assignments are improbable, for example, some *fuscus* specimens from Argentina were assigned to *poecilochilus* (found in Middle America and northern South America). Improbable assignments account for 59% of the wrong assignments. As stated earlier, the information on dorsolateral folds was not included in the computer analysis because the information was missing from several specimens due to preservation. *Leptodactylus fuscus* specimens always have 6 dorsolateral folds, *mystaceus* specimens always have 4, and only *longirostris* and *poecilochilus* specimens with a light mid-dorsal stripe have 6 dorsolateral folds. When the original data were checked on the *fuscus* specimens assigned to other groups by the computer, the dorsolateral fold information resolved 77% of the cases where the computer assignments were geographically possible. Thus, out of the 129 cases in which the computer assigned *fuscus* specimens to other groups, the additional information concerning geographic improbability and state of dorsolateral folds resolved all but 14 cases.

Additional data were gathered for the *mystaceus* and *gracilis* complexes from South American museums.

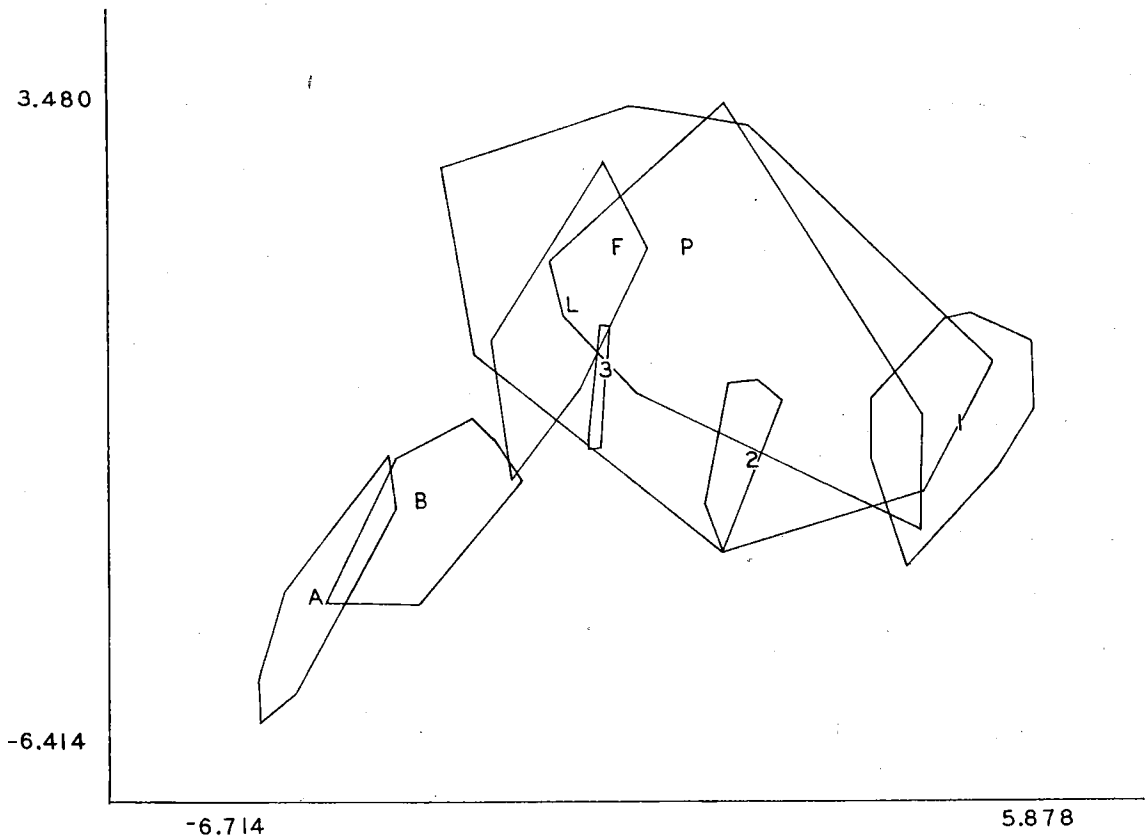

FIGURE 10. Discriminant axis plot for males of the *fuscus* complex. F = *fuscus*, A = striped *gracilis*, B = barred *gracilis*, L = *longirostris*, 1 = northern *mystaceus*, 2 = southern *mystaceus*, 3 = south coast *mystaceus*, P = *poecilochilus*. Letters and numbers placed at group means. Envelopes contain all group members.

TABLE 2

Posterior classification of members of the *fuscus* complex.

MALES

Group	Number of cases classified into group							
	A	B	C	D	E	F	G	H
A-*fuscus*	153	0	1	17	9	6	5	23
B-striped *gracilis*	0	20	1	0	0	0	0	0
C-barred *gracilis*	0	2	16	0	0	0	0	0
D-*longirostris*	0	0	0	33	0	0	1	0
E-northern *mystaceus*	0	0	0	0	75	0	0	0
F-southern *mystaceus*	0	0	0	0	1	14	0	0
G-coastal *mystaceus*	0	0	0	0	0	0	3	0
H-*poecilochilus*	6	0	0	0	4	1	0	39

FEMALES

Group	Number of cases classified into group							
	A	B	C	D	E	F	G	H
A-*fuscus*	110	1	0	31	9	4	3	20
B-striped *gracilis*	0	8	2	0	0	0	0	0
C-barred *gracilis*	0	0	6	0	0	0	0	0
D-*longirostris*	3	1	0	11	0	0	0	0
E-northern *mystaceus*	0	0	0	0	75	1	0	0
F-southern *mystaceus*	0	0	0	0	4	8	0	0
G-coastal *mystaceus*	0	0	0	0	0	0	3	0
H-*poecilochilus*	2	0	0	2	4	0	0	75

As more specimens were examined from coastal Brasil, it became evident that two taxa were present. The discriminant function analyses were performed to determine the morphological distinctiveness of these two species from the previously determined species, northern and southern *mystaceus*.

Female mystaceus-complex data.—The following groups were analyzed (number of specimens in parentheses): south coast *mystaceus* (9), east coast *mystaceus* (14), southern *mystaceus* (11), northern *mystaceus* (76). The results (fig. 11) show good separation of the groups. The first two axes account for 98% of the total dispersion. The variables entered in the following order: tarsal texture, foot texture, foot ratio, SVL, head length ratio, femur ratio, head width ratio (NI), dorsal pattern (NI), lip stripe (NI), tibia ratio (NI), thigh stripe (NI). All south coast *mystaceus* were classified posteriorly as south coast *mystaceus*, 1 east coast *mystaceus* was assigned to southern *mystaceus*, 1 southern *mystaceus* was assigned to east coast *mystaceus* and 1 southern *mystaceus* was assigned to northern *mystaceus*, 3 northern *mystaceus* were assigned to south coast *mystaceus* and 1 northern *mystaceus* was assigned to east coast *mystaceus*.

Male mystaceus-complex data.—The following groups were analyzed (number of specimens in parentheses): south coast *mystaceus* (9), east coast *mystaceus* (24), southern *mystaceus* (32), northern *mystaceus* (72). The results (fig. 12) show reasonably good separation of groups. The first two axes account for 98% of the total dispersion. The variables entered in the following order: tarsal texture, foot ratio, foot texture, head length ratio, tibia ratio, dorsal pattern, SVL (NI), femur ratio (NI), head width ratio (NI), thigh stripe (NI), lip stripe (NI). Two of the nine south coast *mystaceus* were posteriorly classified as northern *mystaceus*, 1 east coast *mystaceus* was assigned to south coast *mystaceus* and 3 east coast *mystaceus* were assigned to southern *mystaceus*, 5

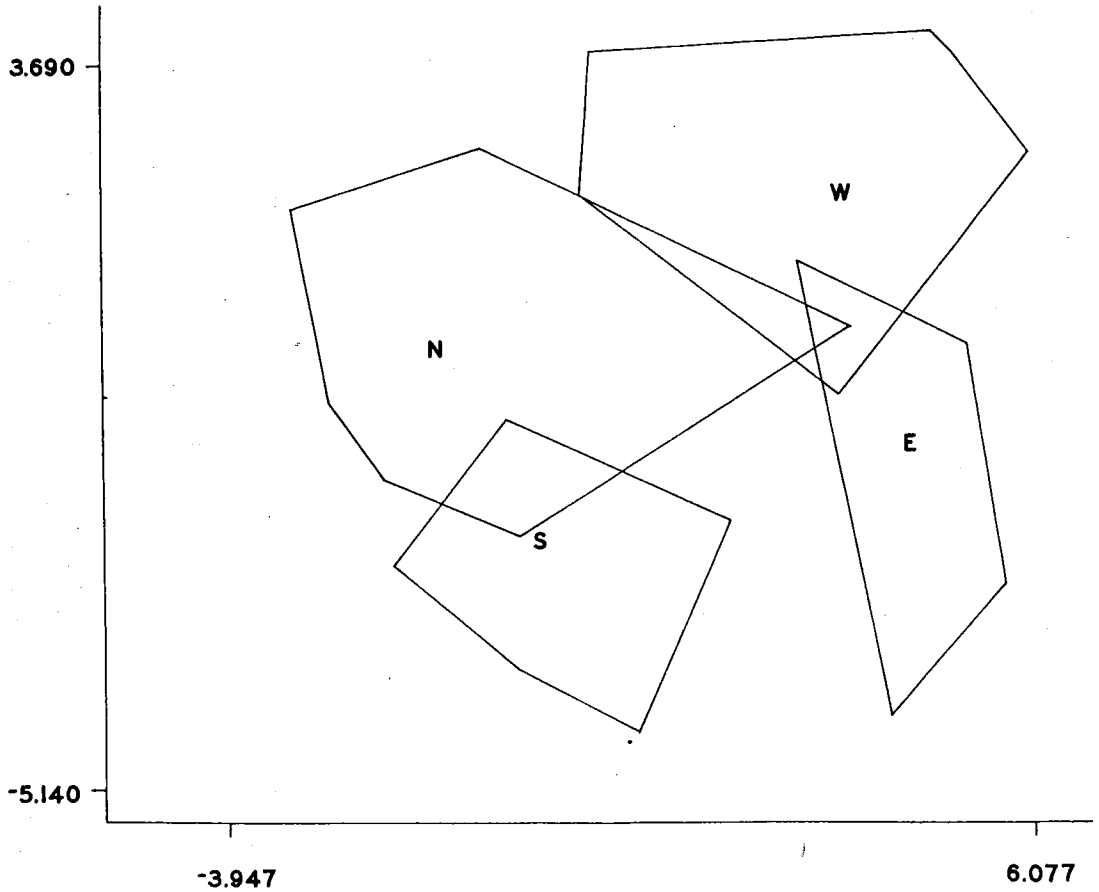

FIGURE 11. Discriminant axis plot for females of the *mystaceus* complex. E = east coast *mystaceus*, N = northern *mystaceus*, S = south coast *mystaceus*, W = southern *mystaceus*. Letters placed at group means. Envelopes contain all group members.

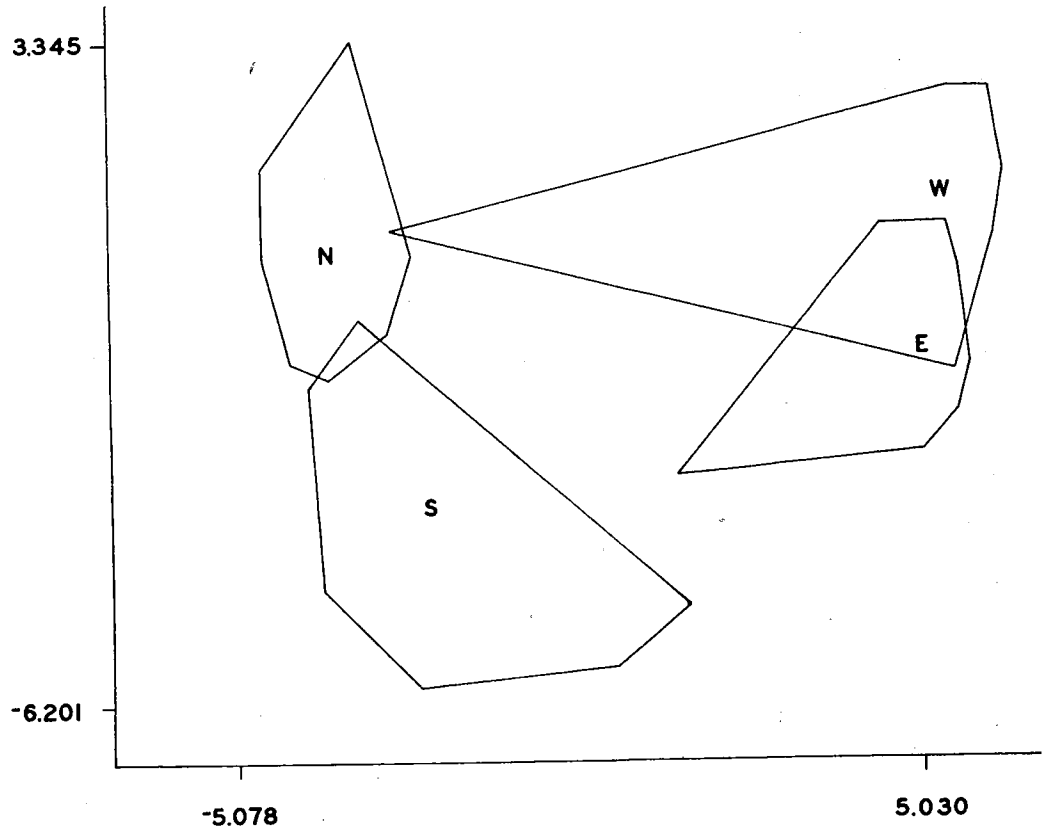

FIGURE 12. Discriminant axis plot for males of the *mystaceus* complex. E = east coast *mystaceus*, N = northern *mystaceus*, S = south coast *mystaceus*, W = southern *mystaceus*. Letters placed at group means. Envelopes contain all group members.

southern *mystaceus* were assigned to east coast *mystaceus* and 1 southern *mystaceus* was assigned to northern *mystaceus*, all northern *mystaceus* were assigned to northern *mystaceus*.

The male and female *mystaceus*-complex results are comparable. The east coast form is nearly always morphologically distinguishable from the south coast form and the northern form is nearly always morphologically distinguishable from the southern form. In a few cases the forms are not morphologically distinguishable by the discriminant function analysis, but these mostly involve completely allopatric species pairs.

The discriminant function analysis run on the larger sample sizes of barred and striped *gracilis* is similar to the analysis run on a smaller data set. For females, 22 of 23 individuals of striped *gracilis* were posteriorly classified as striped *gracilis*, 10 of 11 barred *gracilis* were classified as such. For males, 34 of 37 striped *gracilis* were classified as striped *gracilis*, 23 of 24 barred *gracilis* were classified as barred *gracilis*. The entering order of variables differs between males and females. The first three variables entered for females are head width ratio, foot ratio, and thigh stripe; the first three variables entered for males are SVL, foot ratio, and head width ratio.

The overall analysis indicates that the predetermined species units are generally separable on the basis of the morphological characters used. In some cases, additional information such as dorsolateral folds is required to make the proper species assignment.

Larvae.—Tadpoles are available or have been described for the following taxa from this complex: *L. fuscus* (Lescure 1972), striped *gracilis* (Fernandez and Fernandez 1921), northern *mystaceus* (see species accounts) and *poecilochilus* (Heyer 1970b). All larvae have similar shapes and patterns. Based on limited material, the number of denticles in the split tooth row anterior to the beak appears diagnostic at the species level, but the available larval data are not adequate to add any information to a species level discrimination analysis.

Mating calls.—Calls are known for *L. fuscus* (discussed after the following intraspecific morphological variation section), striped *gracilis*, *longirostris*, northern and southern *mystaceus*, and *poecilochilus*.

Rivero (1971) demonstrated the distinctiveness of calls of *L. fuscus*, *longirostris*, and *poecilochilus* in Venezuela. Straughan and Heyer (1976) indicated that the differences between calls of specimens from northern *mystaceus* and southern *mystaceus* populations (as used here) are indicative of species differentiation.

Barrio (1973) described the calls of *L. gracilis* and *geminus* (also see species accounts). Both species are morphologically striped *gracilis* (see nomenclature section under *L. geminus* for further discussion). W. C. A. Bokermann kindly gave me a copy of a recording of barred *gracilis*. The sonagram of this recording is visually distinctive from the sonagrams of the striped *gracilis* calls that Barrio published, confirming the distinctiveness at the species level of barred and striped *gracilis* (Bokermann and Sazima are describing the call of barred *gracilis*).

Taxonomic conclusions.—Mating calls are known for all but two members of this complex: east coast *mystaceus* and south coast *mystaceus*. All of the known calls are distinct, supporting the species level of differentiation hypothesized for these units. The east coast *mystaceus* and south coast *mystaceus* units are as morphologically distinctive as the other species in this complex and are considered to be specifically distinct.

Enough morphological data are available to study intragroup variation in the following: *L. fuscus*, northern *mystaceus*, and *poecilochilus*.

Leptodactylus fuscus

Morphology.—The groups used for analysis of variation consist of samples of individuals from single localities except for Panama. The variables used in analysis were: 1–3, 7–14.

Female data.—Groups composed of individuals from single localities were analyzed from the following political areas (numbers of specimens of each group in parentheses): Panama (3 individuals from 3 localities), Colombia (3), (10), (4), Guyana (6), (3), (6), (7), (3), (11), Surinam (3), (9), (5), (8), (9), French Guiana (5), Tobago (5), Trinidad (3), Bolivia (4), (4), (9), Brasil (3), (4), Argentina (5). The first two discriminant axes account for 69% of the variation (fig. 13). The variables entered in the following order: SVL, tibia ratio, head width ratio, foot ratio, lip stripe, head length ratio, tarsal texture (NI), dorsal pattern (NI), foot texture (NI), thigh stripe (NI), femur ratio (NI). The plot of the first two discriminant axes (fig. 13) demonstrates a complex pattern of variation, with pronounced overlap of groups. The most distinctive groups are mostly at the edges of the geographic range; Panama, Colombia, Tobago, and

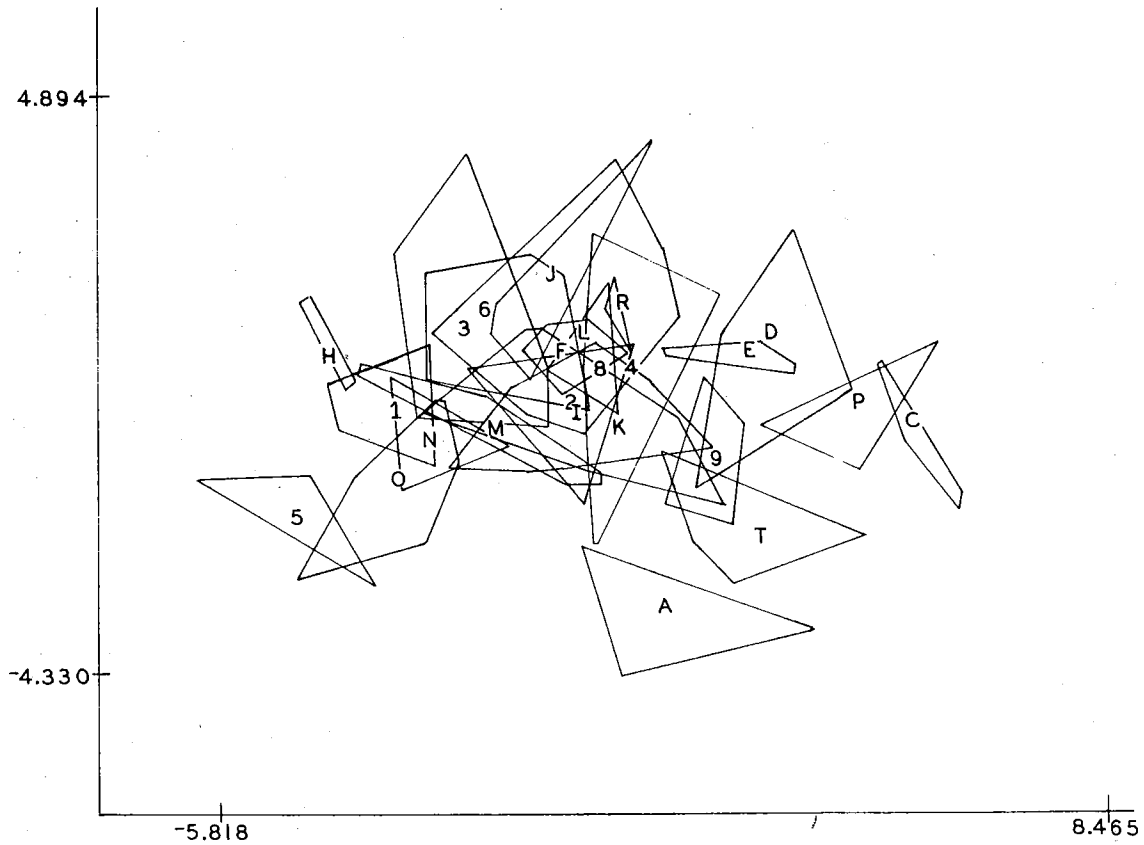

FIGURE 13. Discriminant axis plot for geographic samples of females of *Leptodactylus fuscus*. P = Panama, C–E = Colombia, 1–6 = Guyana, H–L = Surinam, F = French Guiana, T = Tobago, R = Trinidad, M–O = Bolivia, 8–9 = Brasil, A = Argentina. Letters and numbers placed at group means. Envelopes contain all group members.

Argentina. The single distinctive group from Surinam, based on three small females, is not at the edge of the geographic range.

Male data.—Groups composed of individuals from single localities were analyzed from the following political areas (numbers of specimens of each group in parentheses): Colombia (5), (4), (7), Venezuela (3), Guyana (3), (5), (3), (9), Surinam (11), (5), (3), French Guiana (13), Tobago (9), Trinidad (5), Bolivia (14), (5), (5), Brasil (3), (5), (3), (3), (4), Argentina (10), (8). The first two discriminant axes account for 72% of the variation (fig. 14). The variables entered in the following order: SVL, tibia ratio, dorsal pattern, head width ratio, head length ratio, foot texture, femur ratio, thigh stripe, lip stripe, foot ratio, tarsal texture (all variables important). One group is very distinct and 4 other groups are moderately distinctive (fig. 14). All other groups overlap in a complex manner. The single distinctive group is from a geographically extreme population in an interandean valley in Colombia and is composed of quite large individuals. The other two groups analyzed from Colombia are moderately distinctive (fig. 14), as is another geographically extreme population from Argentina. A moderately distinct group of three individuals from Brasil: Bahia is not geographically extreme.

The combined male and female results are similar in the following points: (1) The two factors which account for the most intergroup variation are SVL and tibia ratio; (2) The most distinctive populations are from the periphery of the geographic range, Panama and Colombia in the north, Argentina in the south. As these peripheral populations are the only ones that are distinctive in both male and female analyses, the populations that are distinctive in individual analyses may well be due to sampling error, as both cases involved but three specimens.

Larvae.—Geographic samples of larvae are not available. Comparisons of literature descriptions indicate no apparent differences (Kenny 1969, for Trinidad, Lescure 1972, for French Guiana).

Mating Calls.—Calls are available from a few localities throughout the geographic range. Comparison of the sonagrams (fig. 15) and strip chart records (fig. 16) with the published analyses of Lescure (1972) for French Guiana and Rivero (1971) for coastal Venezuela indicate that all calls are similar.

Taxonomic conclusion.—The morphological evidence indicates differentiation of the geographically peripheral northern and southern populations. The mating call of the southern population is not distinctive from calls throughout the range. On this basis, the conservative approach of recognizing but a single species is taken.

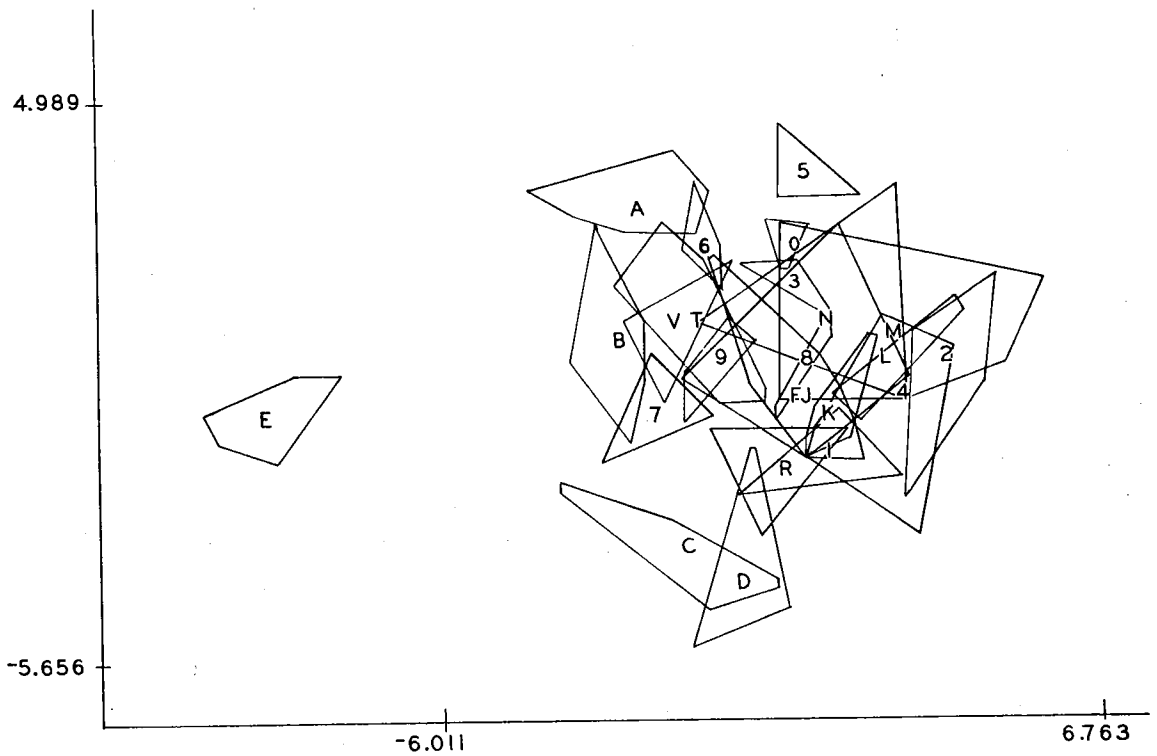

FIGURE 14. Discriminant axis plot for geographic samples of males of *Leptodactylus fuscus*. C–E = Colombia, V = Venezuela, 1–4 = Guyana, J–L = Surinam, F = French Guiana, T = Tobago, R = Trinidad, M–O = Bolivia, 5–9 = Brasil, A–B = Argentina. Letters and numbers placed at group means. Envelopes contain all group members.

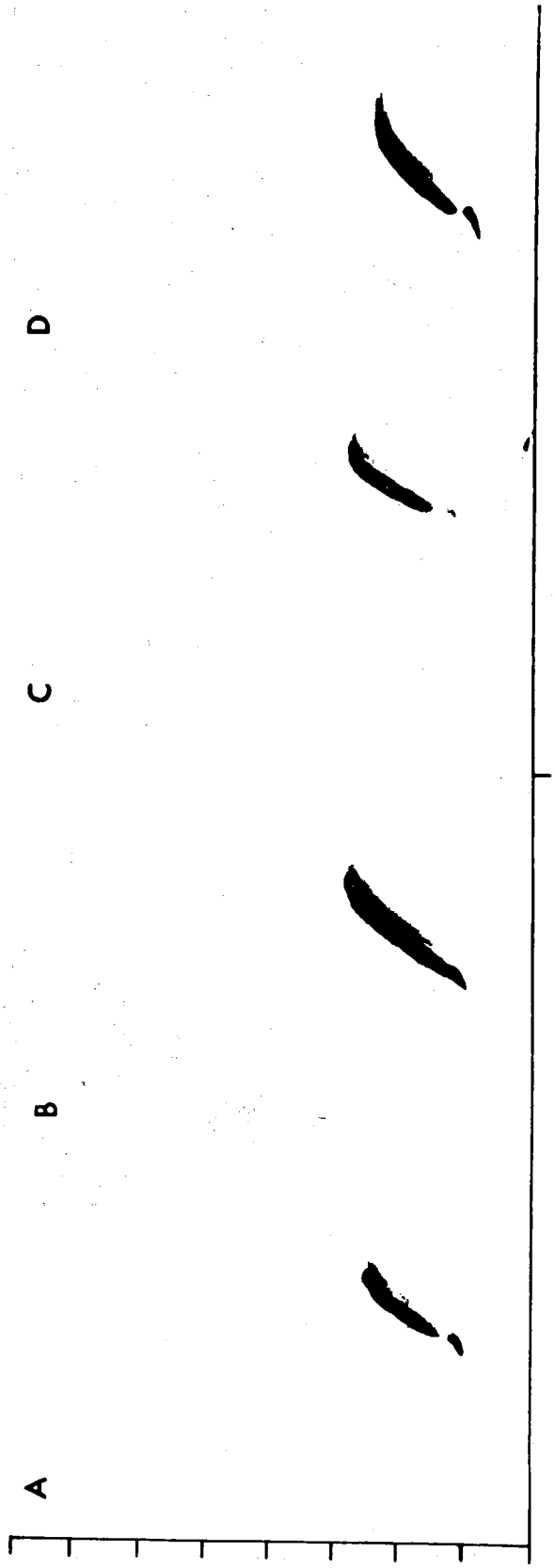

FIGURE 15. Sonagrams of representative mating calls of *Leptodactylus fuscus*, narrow band filter. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. A = specimen from Colombia, nr. Villavicencio, air temperature 23.5° C (UTA tape); B = specimen from Brasil, Manaus (USNM tape and specimen number 202506); C = Bolivia (AMNH tape recorded by William P. McLean III); D = specimen from Argentina, Embarcación (LACM tape and specimen field number WRH 1399).

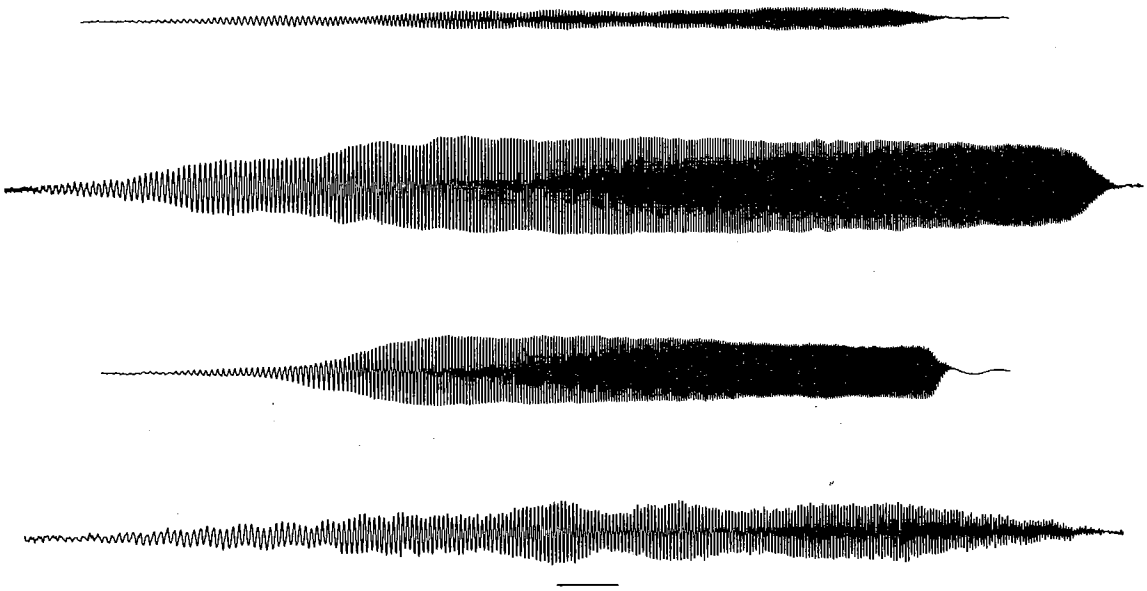

FIGURE 16. Strip chart records of the mating call of *Leptodactylus fuscus*. Line equals 0.01 s. Upper to lower figures are representative calls for specimens from Colombia, Brasil, Bolivia, and Argentina respectively. See legend of Figure 15 for further specimen data except specimen from Argentina is LACM field number WRH 1363 recorded at 21.3° C air temperature.

NORTHERN *MYSTACEUS*

Morphology.—The groups used for analysis of variation consist of individuals from single localities. The variables used in the analysis were: 1–3, 7–14. Variables 1, 7, 8 were constant for both the male and female data and do not appear in any of the analyses.

Female data.—Individuals (number in parentheses) from localities from the following areas were used as groups for analysis: Colombia (4), Guyana (5), (4), French Guiana (3), (6), Ecuador (19), Bolivia (9). The first two discriminant axes account for 81% of the variation (fig. 17). The variables entered in the following order: tibia ratio, SVL, femur ratio, head length ratio (NI), thigh stripe (NI), foot ratio (NI), lip stripe (NI), head width ratio (NI). The discriminant axis plot (fig. 17), demonstrates overlap of groups with no group distinct from any other group.

Male data.—Individuals (number in parentheses) from localities in the following areas were used as groups for analysis: Colombia (4), (3), Guyana (12), French Guiana (5), Ecuador (21). The variables entered in the stepwise discriminant function program in the following order: femur ratio, SVL, head length ratio, tibia ratio, head width ratio, lip stripe (NI), foot ratio (NI), thigh stripe (NI). The first two discriminant axes (fig. 18) account for 80% of the variation. The discriminant axis plot (fig. 18) shows extensive group overlap with the single exception of a group of three males from Vaupés, Colombia. The second Colombian sample, from Caquetá, which borders Vaupés, is well within the variation of the other samples analyzed.

The male and female data differ in the importance of variables describing the patterns of variation. This may be due to the different number of groups analyzed in each data set. Both data sets agree in that most geographic samples overlap each other with respect to morphological variation. The single exception is the sample from the state of Vaupés, Colombia. No females were available from this locality for analysis. The distinctiveness of the Vaupés sample may be due to the small sample size.

Larvae.—Tadpoles are known only from Ecuador (see species account for description).

Mating call.—Mating calls from Colombia and Ecuador are similar (Straughan and Heyer 1976).

Taxonomic conclusion.—The available evidence indicates a single species is involved.

LEPTODACTYLUS POECILOCHILUS

Morphology.—The groups used for analysis of variation consisted of individuals from single localities. The variables used were 1–3, 7–14. Variables 2 and 7 were constant for both female and male data sets; variable 8 was constant for the male data set.

Female data.—Individuals (number in parentheses) from localities in the following areas were used for analysis: Costa Rica (9), (4), Panama (3), (4), (4), Colombia (4), (14), (20). Variables entered in the stepwise dis-

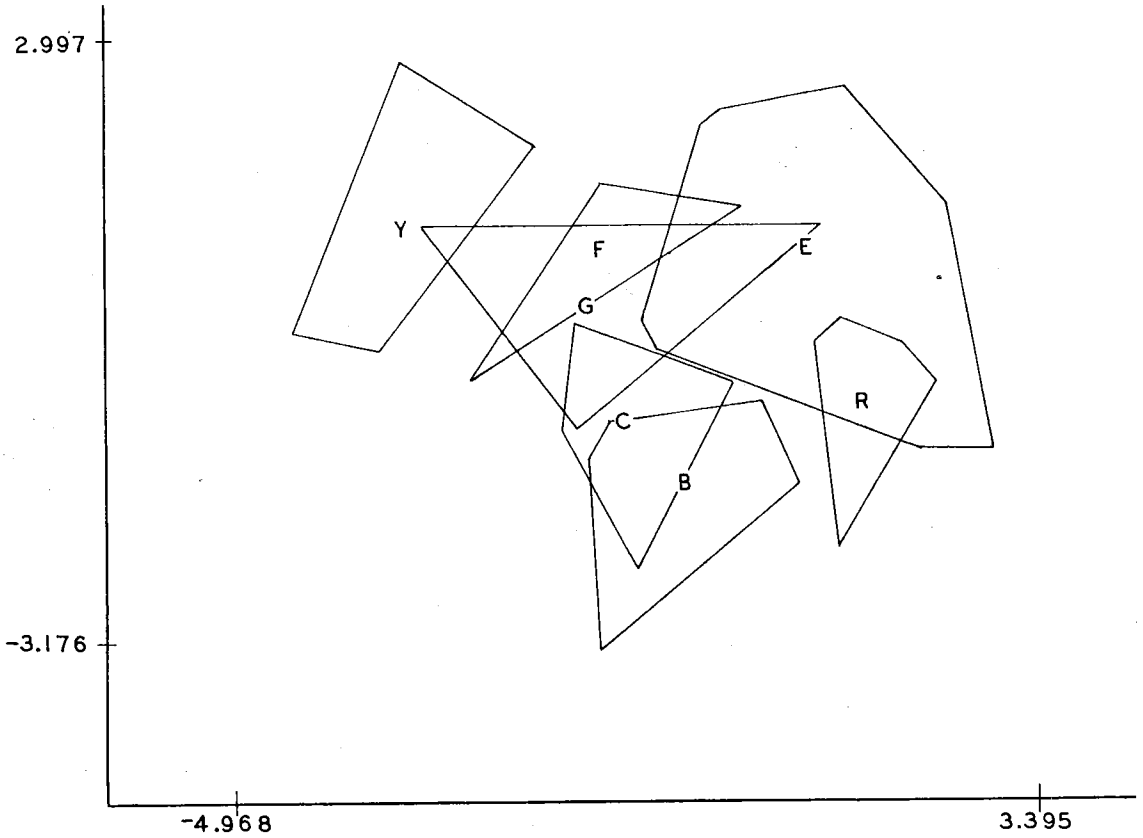

FIGURE 17. Discriminant axis plot for geographic samples of females of northern *mystaceus*. C = Colombia, G,Y = Guyana, F,R = French Guiana, E = Ecuador, B = Bolivia. Letters placed at group means. Envelopes contain all group members.

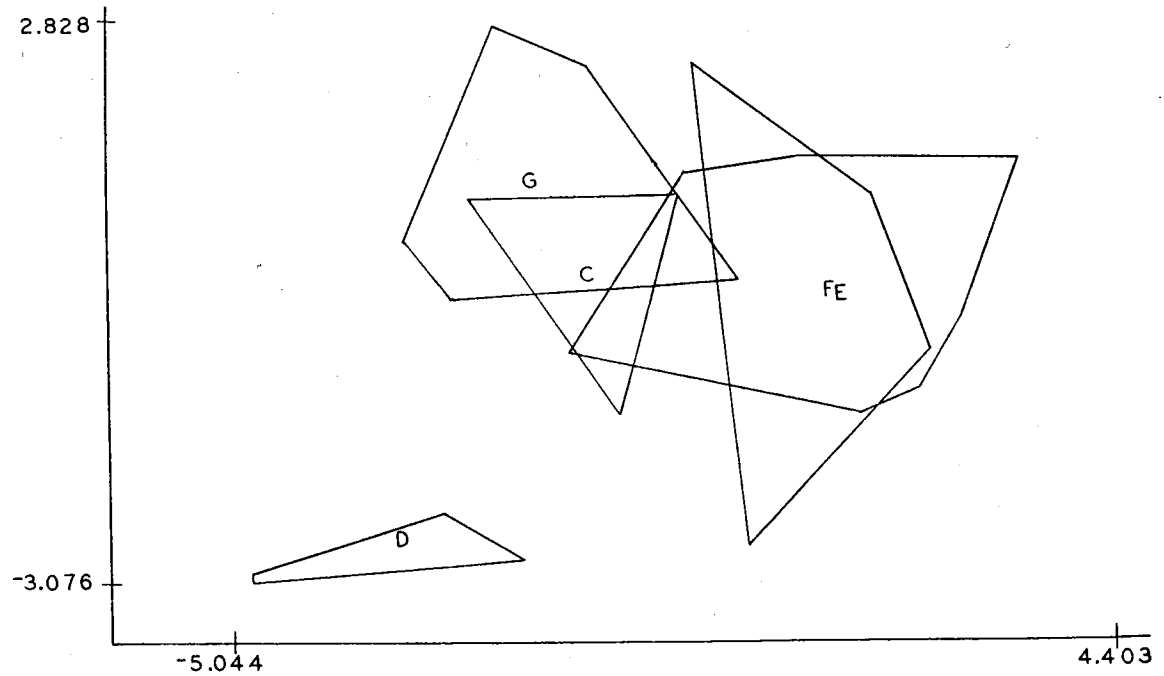

FIGURE 18. Discriminant axis plot for geographic samples of males of northern *mystaceus*. C–D = Colombia, G = Guyana, F = French Guiana, E = Ecuador. Letters placed at group means. Envelopes contain all group members.

criminant function analysis in the following order: SVL, dorsal pattern, head width ratio, tibia ratio, femur ratio, head length ratio, thigh stripe, foot texture (NI), foot ratio (NI). The first two discriminant axes account for 78% of the variation (fig. 19). The discriminant axis plot (fig. 19) shows overlap of all groups with the exception of the sample from Córdoba, Colombia.

Male data.—Individuals (number in parentheses) from localities in the following areas were used for analysis: Costa Rica (5), Colombia (5), (7), (4). Variables entered in the stepwise discriminant analysis in the following order: SVL, head length ratio, thigh stripe, head width ratio, tibia ratio, dorsal pattern, femur ratio (NI), foot ratio (NI). The first two discriminent axes account for 99% of the variation. The discriminant axis plot (fig. 20), shows overlap of the two samples from Antioquia, Colombia, and distinctive samples from Costa Rica and Córdoba, Colombia.

As there are few samples available for analysis, especially of males, the above results should be treated cautiously. Both data sets indicate the distinctiveness of the population from Córdoba, Colombia, which is a geographically peripheral population in terms of the specimens available for the present analysis.

Larvae.—Tadpoles have been previously described (Heyer 1970b) based on Middle American samples. No samples are available from South America.

Mating call.—Fouquette (1960) described the call for specimens from Panama and Rivero (1971) described the call for specimens from Venezuela. The sonagrams figured by these two authors are very different and likely represent two distinct species. At present, no calls are available from Colombia to determine whether there is a cline in call characteristics. Neither author indicated whether voucher specimens were kept for the recordings; it is therefore possible the species identifications used by Fouquette (1960) and Rivero (1971) differ from mine. Until such time as the significance of the observed call differences is resolved, I assume the reported call for *L. poecilochilus* in Venezuela to refer to a different species than that indicated as *poecilochilus* in this study.

Taxonomic conclusion.—Clearly, more information

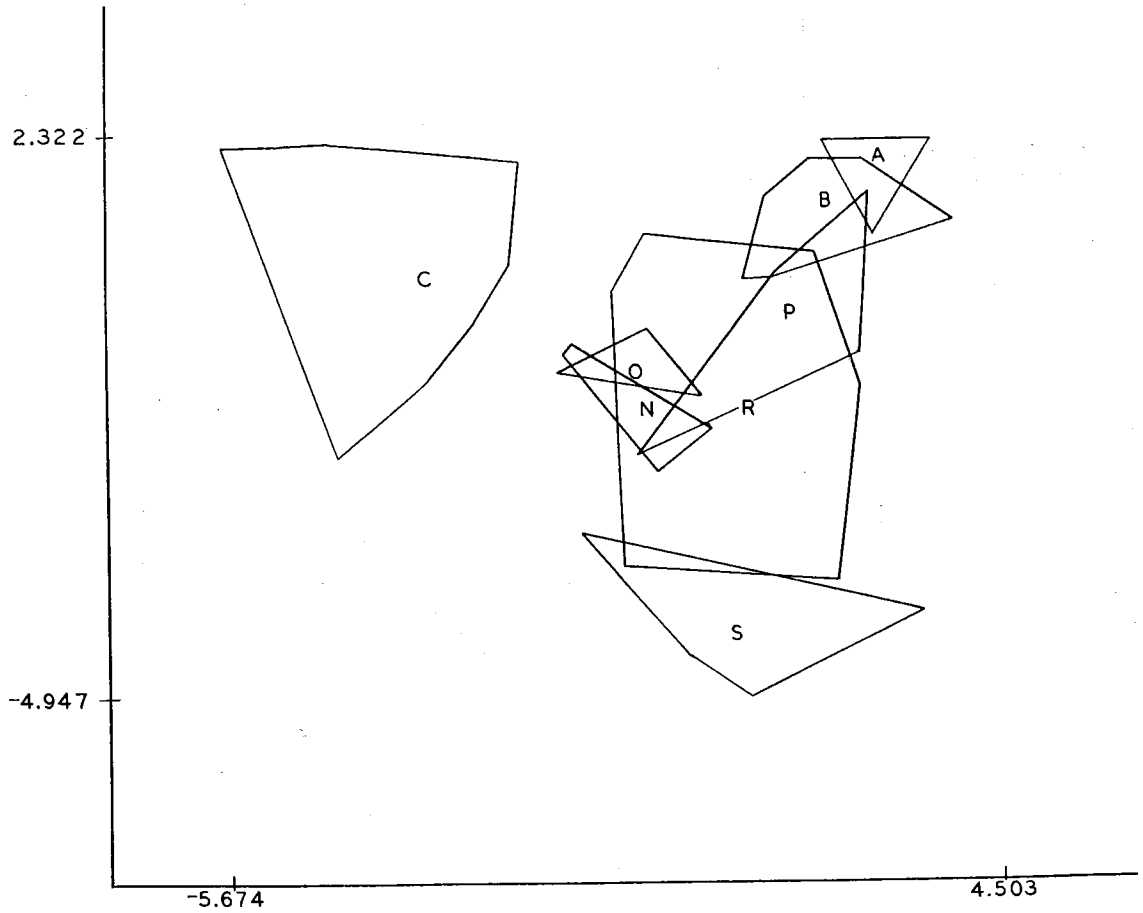

FIGURE 19. Discriminant axis plot for geographic samples of females of *Leptodactylus poecilochilus*. R–S = Costa Rica, N–P = Panama, A–C = Colombia. Letters placed at group means. Envelopes contain all group members.

bufonius are analyzed. The variables entered in the following order: foot texture, SVL, femur (NI), tibia ratio is required to understand the apparent variation in morphology and mating call. For the present, the conservative approach of recognizing a single species is taken until further field work clarifies the situation.

Leptodactylus bufonius—complex

Morphology.—The species recognized during the data gathering procedure were used as predetermined groups for the discriminant function analysis. Additional data were gathered for some group members from South American museums after the first discriminant function analysis was completed. The variables used in the computer analysis for the first set of available data were 1–3, 7–14. Variable 1 does not appear in the stepwise discriminant function results as it is uniform throughout the group. Likewise, variable 2 does not appear in the female results.

Female data.—The following groups were analyzed (number of specimens in parentheses): *bufonius* (34), *labrosus* (23), *mystacinus* (13), *ventrimaculatus* (16). The discriminant axis plot results (fig. 21) indicate good separation of the predetermined species groupings. The first two axes account for 97% of the variation. The variables entered in the following order: foot ratio, foot texture, tibia ratio, head length ratio, SVL, tarsal texture, femur ratio (NI), head width ratio (NI), and thigh pattern (NI).

Male data.—The following groups were analyzed: *bufonius* (53), northern *bufonius* (4), *labrosus* (9), *mystacinus* (44), *ventrimaculatus* (22). The discriminant axis plot results (fig. 22) also indicate good separation of the species groupings. The first two axes account for 92% of the variation. The variables entered in the following order: foot texture, lip stripe, foot ratio, head length ratio, head width ratio, tarsal texture, SVL (NI), femur ratio (NI), thigh stripe (NI), and tibia ratio (NI).

The results of the posterior classification into groups for female and male data (Table 3) also indicate that the species are morphologically distinguishable.

Data were taken on more northern and southern *bufonius* from specimens in South American museums to determine whether the initial separation based on very few northern *bufonius* specimens was substantiated.

For females, 54 southern *bufonius* and 15 northern

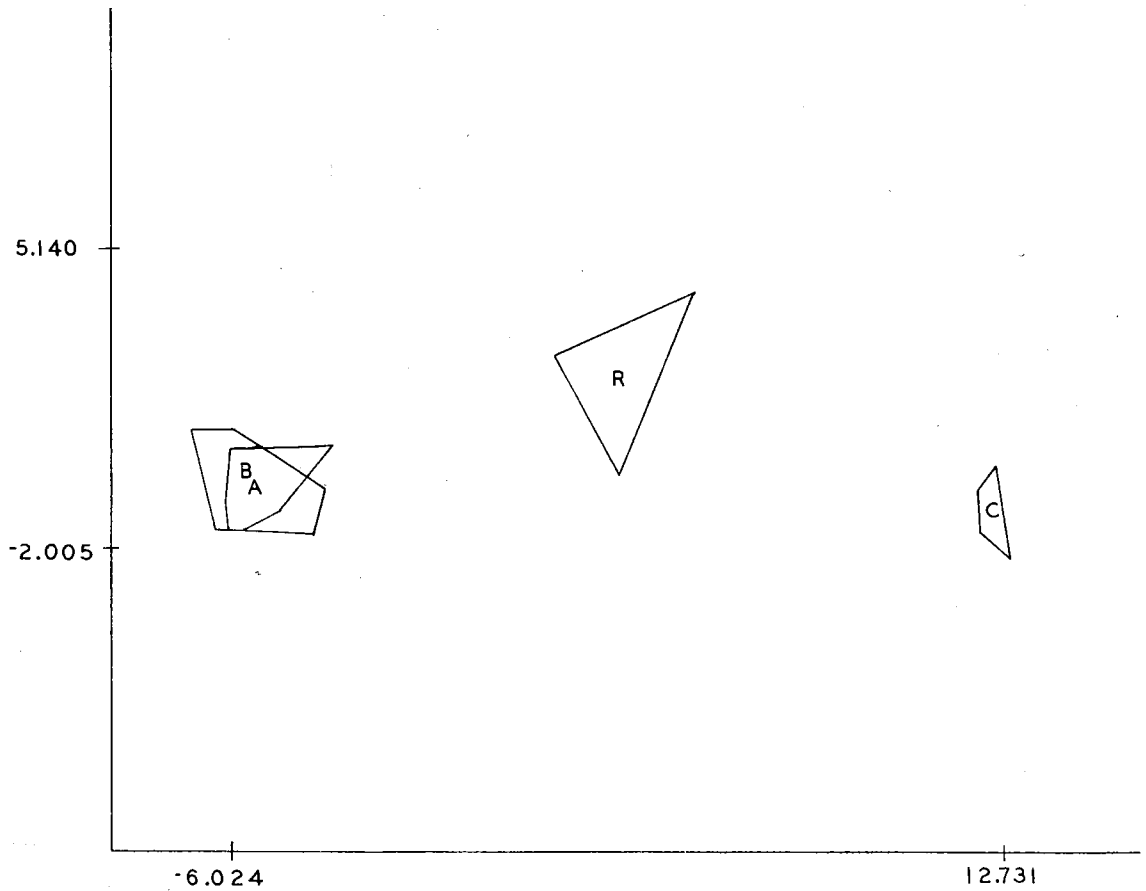

FIGURE 20. Discriminant axis plot for geographic samples of males of *Leptodactylus poecilochilus*. R = Costa Rica, A–C = Colombia. Letters placed at group means. Envelopes contain all group members.

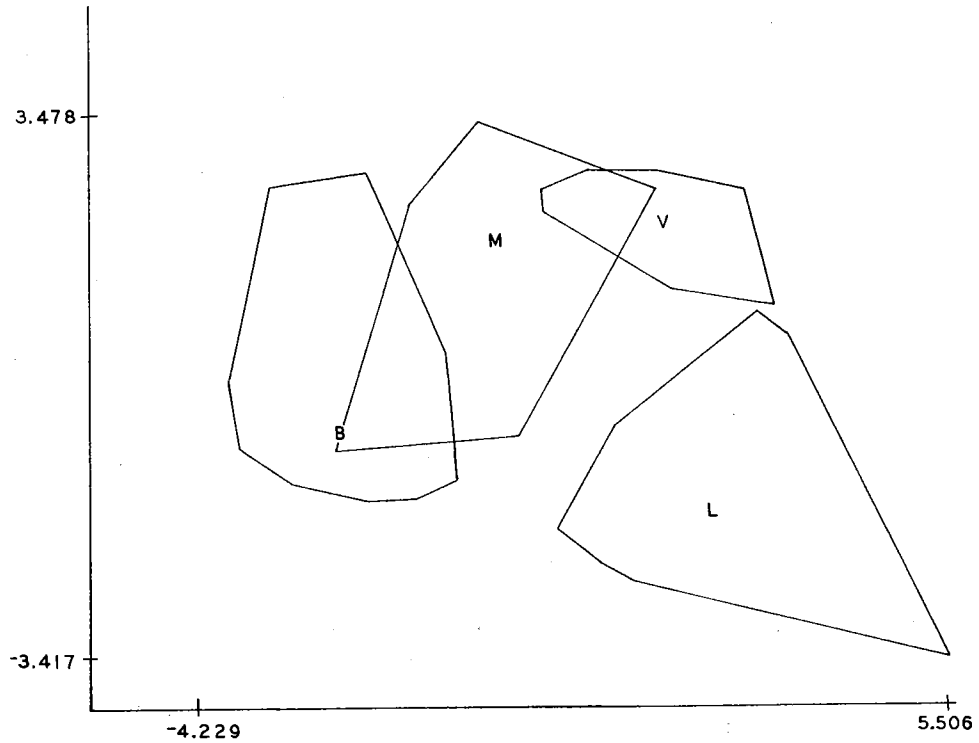

FIGURE 21. Discriminant axis plot of females of the *bufonius* complex. B = *bufonius*, L = *labrosus*, M = *mystacinus*, V = *ventrimaculatus*. Letters placed at group means. Envelopes contain all group members.

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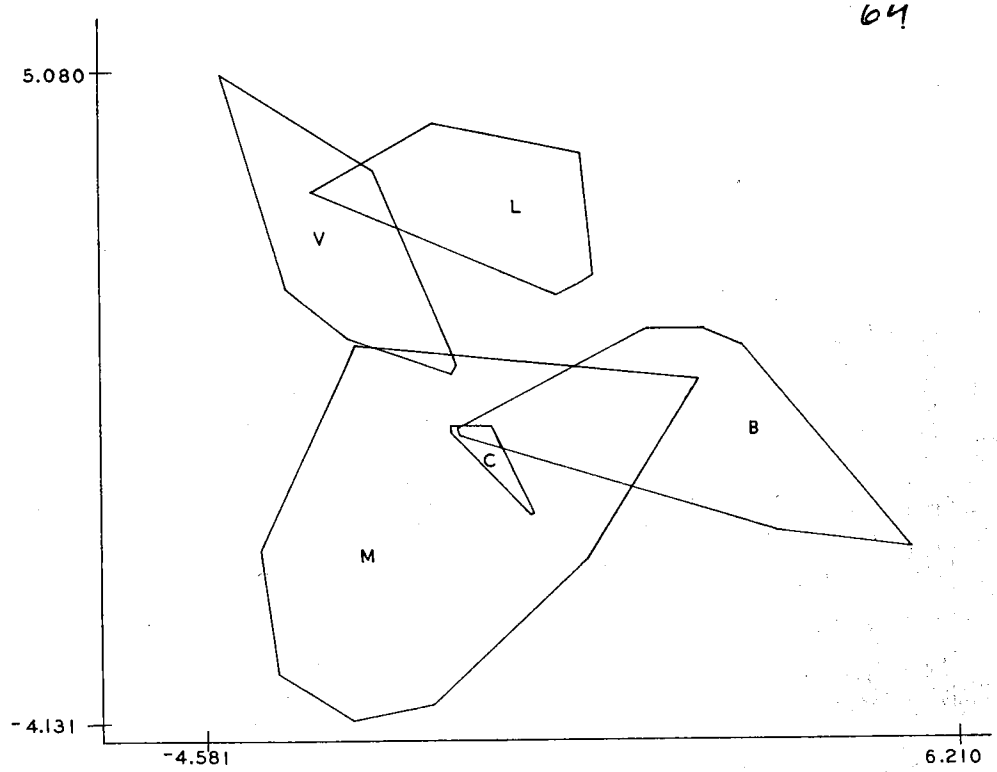


FIGURE 22. Discriminant axis plot of males of the *bufonius* complex. B = *bufonius*, C = northern *bufonius*, L = *labrosus*, M = *mystacinus*, V = *ventrimaculatus*. Letters placed at group means. Envelopes contain all group members.

TABLE 3

Posterior classification of members of the *bufonius* complex.

MALES

Group	Number of cases classified into group				
	A	B	C	D	E
A-*bufonius*	52	1	0	0	0
B-northern *bufonius*	0	4	0	0	0
C-*labrosus*	0	0	8	0	1
D-*mystacinus*	1	5	0	37	1
E-*ventrimaculatus*	0	2	0	0	20

FEMALES

Group	Number of cases classified into group			
	A	B	C	D
A-*bufonius*	33	0	1	0
B-*labrosus*	0	21	0	2
C-*mystacinus*	2	0	11	0
D-*ventrimaculatus*	0	0	1	15

(NI), head length ratio (NI), head width ratio (NI). Separation of the groups is good, but not complete. In the posterior classification, 4 of 54 southern *bufonius* are assigned to northern *bufonius*, all northern *bufonius* are assigned to northern *bufonius*.

Eighty five southern *bufonius* and 27 northern *bufonius* males comprise the groups for analysis. The variables entered in the following order: foot texture, head length ratio, head width ratio (NI), foot ratio (NI), femur ratio (NI), tibia ratio (NI), SVL (NI). As for females, separation of the groups is good, but not complete. In the posterior classification, 4 of 85 southern *bufonius* are assigned to northern *bufonius*, all northern *bufonius* are assigned to northern *bufonius*.

For both the female and male data, virtually all of the separation of groups is accounted for by the first variable, foot texture. The F values, although not statistically interpretable, give the order of magnitude differences between the importance of the first and second variables in separating the groups. For females, the F value for the first variable is 182, for the second, 10; for males, the F value for the first variable is 537, for the second, 7.

In summary, the variables used in the computer analysis distinguish the predetermined species groupings quite well. Enough data are available to study geographic trends in *L. mystacinus* only.

Female mystacinus data.—The groups and sample sizes analyzed are: Brasil, Bahia (pooled localities), 3; Brasil, São Paulo (pooled localities), 7; Brasil, Rio Grande do Sul (pooled localities), 8; Uruguay (pooled localities), 4. The variables entered in the following order: foot texture, tibia ratio, head width ratio (NI), thigh stripe (NI), foot ratio (NI), SVL (NI), femur ratio (NI), tarsal texture (NI), head length ratio (NI). The first discriminant axis accounts for 71% of the total dispersion, the first two axes account for 90%. The plot of the first against second discriminant axes indicates that the sample from the state of São Paulo is distinctive (fig. 23).

Male mystacinus data.—The groups and sample sizes analyzed are: Bolivia (pooled localities), 3, Brasil, Rio Grande do Sul (single locality), 19; Brasil, Rio Grande do Sul (remaining cases, pooled localities) 4; Brasil, São Paulo (single locality), 7; Brasil, São Paulo (remaining cases, pooled localities), 6; Argentina, Misiones (single locality), 5; Argentina (remaining cases, pooled localities), 9; Uruguay (pooled localities), 7. The variables entered in the following order: foot texture, SVL, tibia ratio, tarsal texture, thigh stripe, head width ratio, foot ratio (NI), lip stripe (NI), femur ratio (NI), head length ratio (NI). The first discriminant axis accounts for 50% of the total dispersion, the first two axes account for 80%. The plot of the first against second discriminant axes (fig. 24) gives a pattern of separation best described together with the female data.

The pictorial results of group separation for female (fig. 23) and male (fig. 24) data show similar patterns in that the samples from the state of São Paulo are distinctive. Except for the São Paulo groups, the male data groups show a geographic trend of differentiation from Rio Grande do Sul - Uruguay - Argentina. The female data indicate that this trend is not complete, as the Bahia group is morphologically similar to the Rio Grande do Sul group. The São Paulo groups thus do not fit a clinal pattern of geographic differentiation.

Larvae.—The only species in this complex for which the larvae are adequately described is *mystacinus* (Sazima 1975).

Mating calls.—Barrio (1965) figured and described the mating calls of *L. bufonius* and *L. mystacinus*. Werner C. A. Bokermann kindly gave me a copy of a recording of a northern *bufonius*. The call is very distinctive from southern *bufonius* (see species accounts for *bufonius* and *troglodytes*).

Taxonomic conclusions.—The five species recognized, *bufonius*, northern *bufonius*, *labrosus*, *mystacinus*, and *ventrimaculatus*, are morphologically distinguishable. The available mating call evidence supports

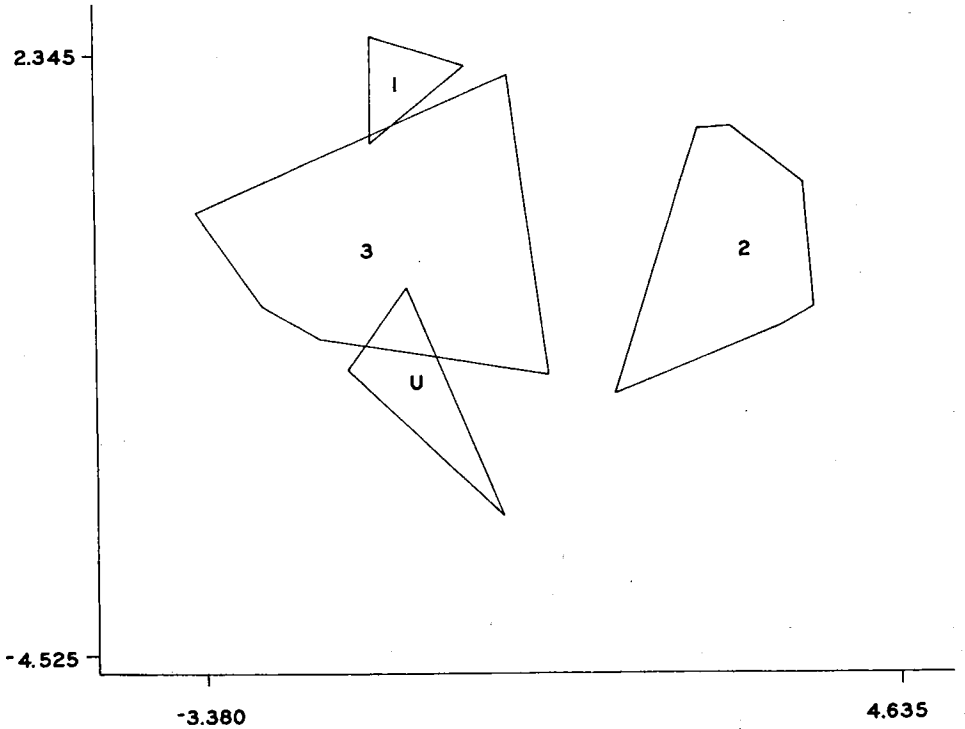


FIGURE 23. Discriminant axis plot for geographic samples of females of *Leptodactylus mystacinus*. 1 = Brasil, Bahia, 2 = Brasil, São Paulo, 3 = Brasil, Rio Grande do Sul, U = Uruguay. Numbers and letters placed at group means. Envelopes contain all group members.

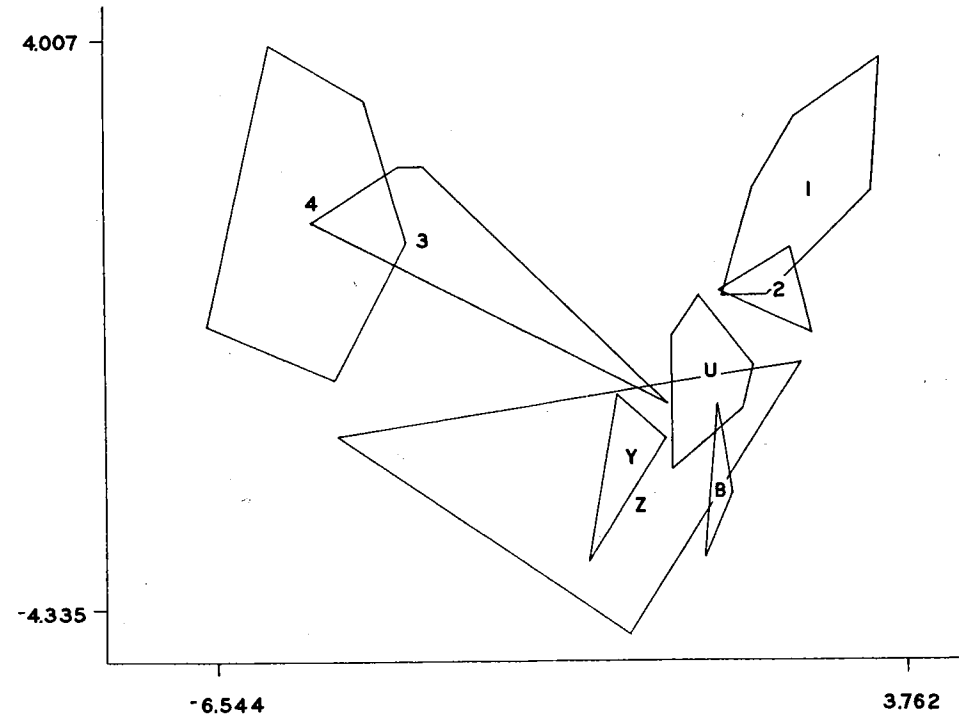


FIGURE 24. Discriminant axis plot for geographic samples of males of *Leptodactylus mystacinus*. 1–2 = Brasil, Rio Grande do Sul, 3–4 = Brasil, São Paulo, Y–Z = Argentina, U = Uruguay, B = Bolivia. Numbers and letters placed at group means. Envelopes contain all group members.

recognition of these units. Until more call information becomes available for *mystacinus*, I prefer to treat it as a single species.

LEPTODACTYLUS LATINASUS—LABIALIS

Specimens of *Leptodactylus latinasus* bear a striking resemblance to specimens of *L. labialis*. Both species usually lack well defined dorsolateral folds, are small, have prominent white tubercles on the tibia, tarsus, and foot, and have a distinct light thigh stripe. The two species are allopatric, one with a primarily Middle American distribution, the other with a primarily Chacoan distribution. Although there has never been much question regarding the specific distinctness of *labialis* and *latinasus*, I was curious to see how the stepwise discriminant function analysis would treat the morphological data. The following variables were used: 2–3, 9–14.

Female data.—The variables entered in the stepwise discriminant function analysis in the following order: lip stripe, head length ratio, head width ratio, tibia ratio, foot ratio, thigh stripe (NI), SVL (NI), femur ratio (NI). The first two discriminant axes account for all the variation. There is considerable overlap of the two groups (fig. 25). The percentage of specimens posteriorly classified in the other group amounts to 9% *labialis* assigned to *latinasus* and 24% *latinasus* assigned to *labialis*.

Male data.—The variables entered the stepwise discriminant analysis in the following order: SVL, head length ratio, tibia ratio, foot ratio, lip stripe, thigh stripe (NI), head width ratio (NI), femur ratio (NI). The first two discriminant axes account for 100% of the variation. There is considerable overlap of the two groups (fig. 26). The percentage of specimens assigned to the other group amounts to 14% for *labialis* and 9% for *latinasus*.

In contrast to the other species complexes analyzed by the stepwise discriminant function analysis (figs. 9–12, 21–22), there are no additional morphological features that were omitted from the analysis which will serve to further differentiate the two groups. The two species are very difficult to distinguish only on the basis of external morphology. The karyotypes and mating calls are distinctive however (see species accounts for *fragilis* and *latinasus*), amply verifying the specific level of distinction between the two.

LEPTODACTYLUS LATINASUS

Morphology.—The data are analyzed geographically, using the following variables: 1–3, 7–14. Three of these are constant and do not appear in the analyses: 1, 7, 8.

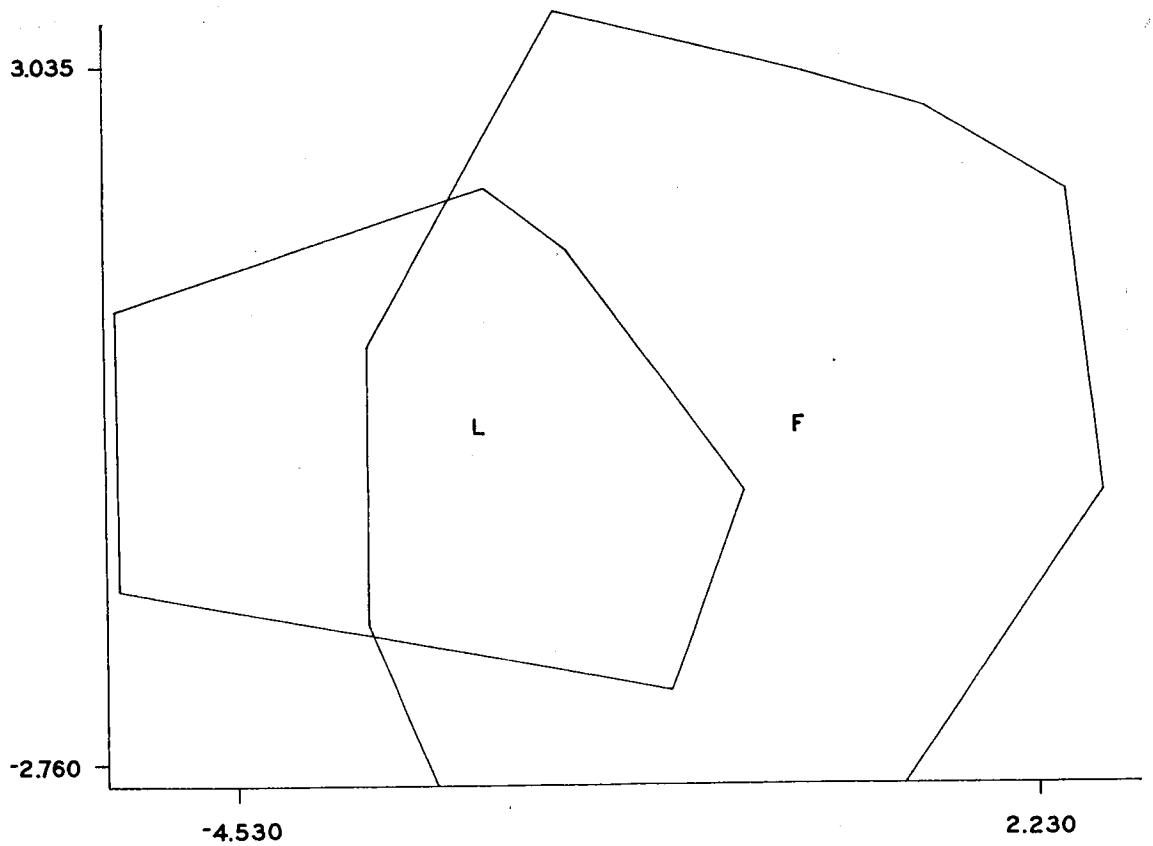


FIGURE 25. Discriminant axis plot for females of *Leptodactylus labialis* and *latinasus*. F = *labialis*, L = *latinasus*. Letters placed at group means. Envelopes contain all group members.

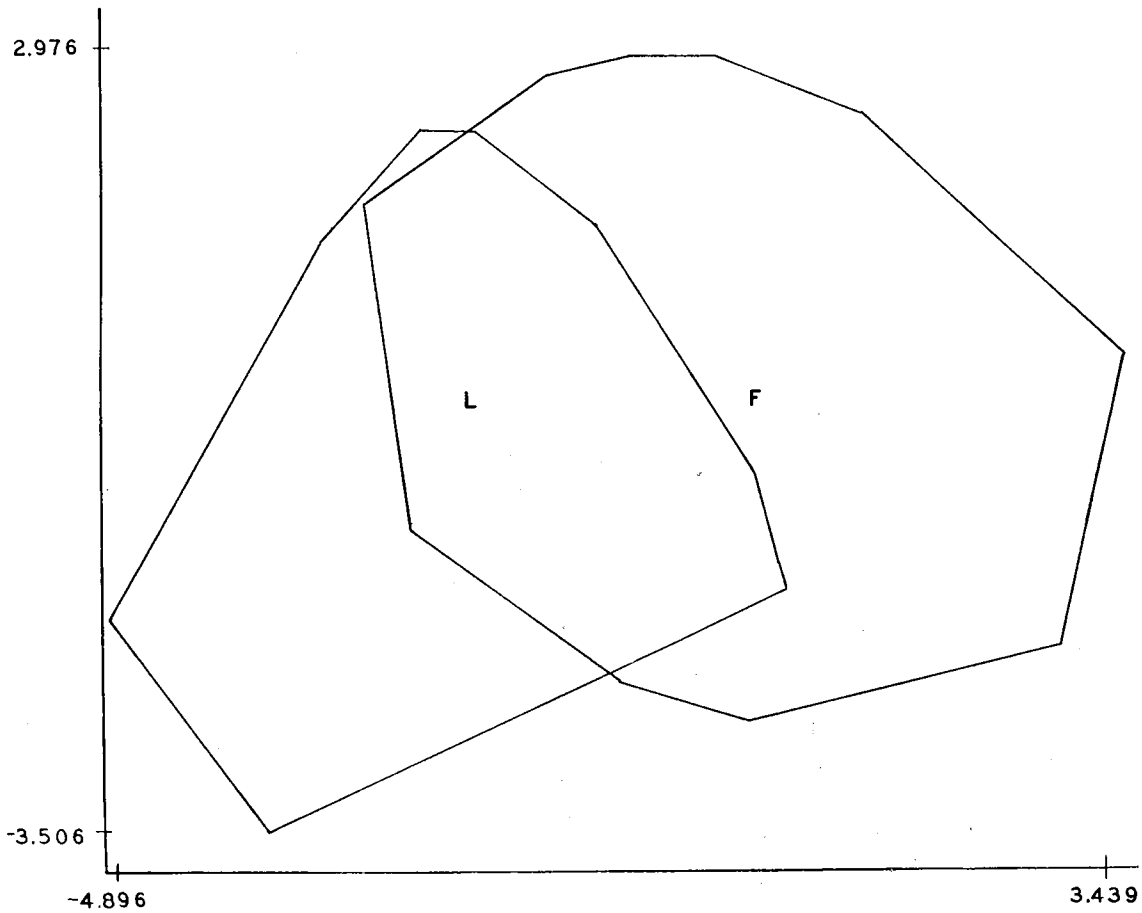


FIGURE 26. Discriminant axis plot for males of *Leptodactylus labialis* and *latinasus*. F = *labialis*, L = *latinasus*. Letters placed at group means. Envelopes contain all group members.

Female data.—The following groups and numbers of specimens comprise the samples available for geographic analysis: Argentina, Buenos Aires (pooled localities), 4; Argentina, Catamarca (pooled localities), 4; Argentina, Formosa (single locality), 7; Argentina, Salta (single locality), 7; Argentina, Salta (single locality), 9; Argentina, Tucumán (single locality), 7; Brasil, Rio Grande do Sul (pooled localities), 8; Uruguay (pooled localities), 8. The variables entered in the following order: tibia ratio, SVL, head width ratio, head length ratio, thigh stripe, femur ratio (NI), foot ratio (NI), lip stripe (NI). The first two discriminant axes account for 72% of the total dispersion. The plot of the first discriminant axis against the second (fig. 27) indicates moderate separation of the groups, generally with geographically close samples being morphologically closest also. There is no overall trend of geographic variation.

Male data.—The following groups and numbers of specimens comprise the samples available for geographic analysis: Argentina, Buenos Aires (pooled localities), 6; Argentina, Catamarca (single locality), 10; Argentina, Chaco (single locality), 7; Argentina, Corrientes (single locality), 4; Argentina, Formosa (single locality), 4; Argentina, Jujuy (single locality), 5; Argentina, Jujuy (single locality), 10; Argentina, Salta (single locality), 22; Argentina, Salta (single locality), 6; Argentina, Salta (single locality), 6; Argentina, Tucumán (single locality), 8; Argentina, Tucumán (single locality), 29; Brasil, Bahia and Espirito Santo (pooled localities), 5; Brasil, Rio Grande do Sul (pooled localities), 10; Uruguay (pooled localities), 14. The variables entered in the following order: tibia ratio, SVL, head length ratio, femur ratio, head width ratio, foot ratio, thigh stripe (NI), lip stripe (NI). The first two discriminant axes account for 69% of the total dispersion. The plot of the first discriminant axis against the second (fig. 28) shows a complex pattern in which no geographic samples are distinctive nor are any geographic trends clearly discernable.

Larvae.—Fernandez and Fernandez (1921) described the larvae of *L. latinasus* (as *prognathus*) from Argentina.

Mating calls.—Barrio (1965) described the call from

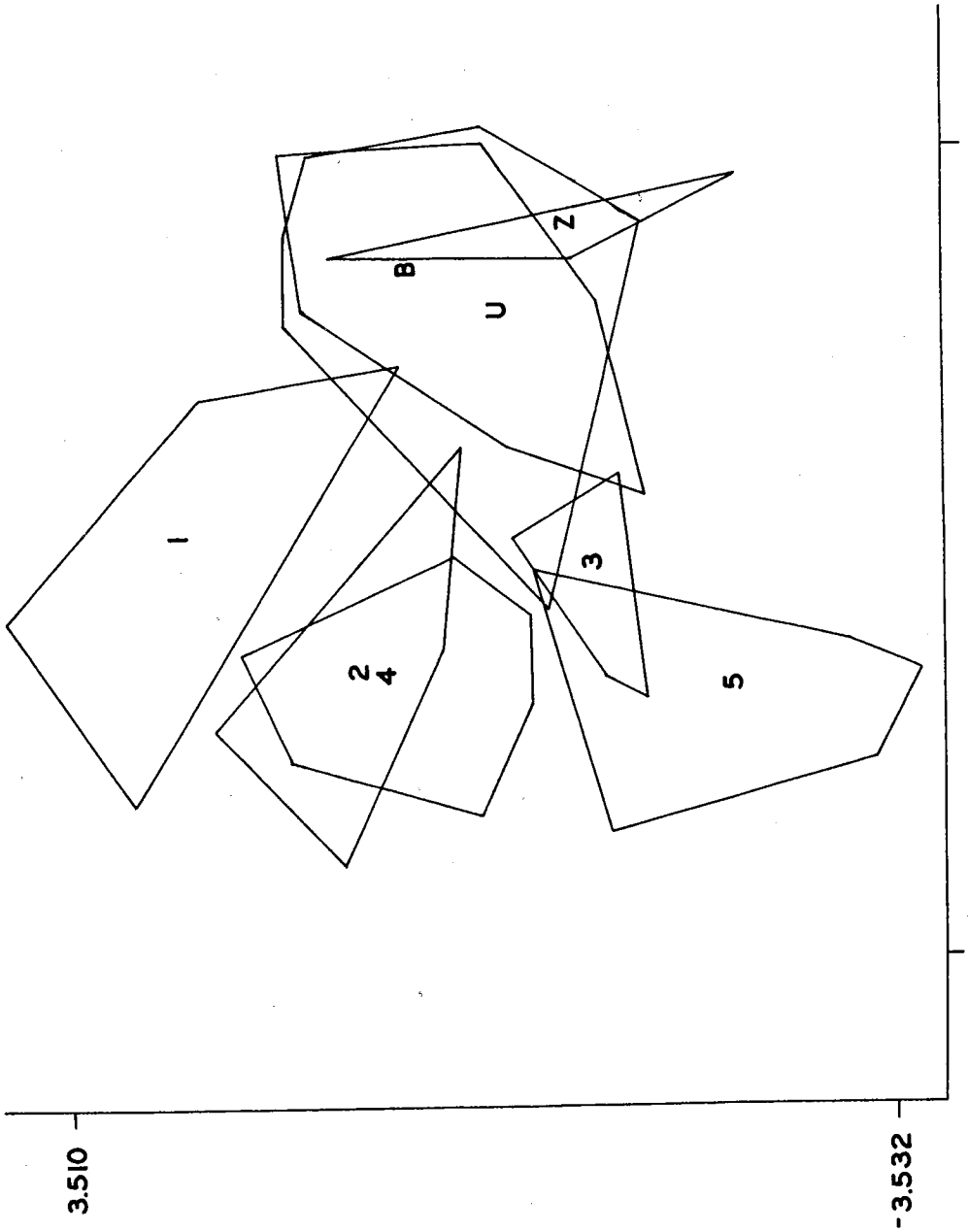


FIGURE 27. Discriminant axis plot for geographic samples of females of *Leptodactylus latinasus*. B = Brasil, Rio Grande do Sul, U = Uruguay, Z = Argentina, Buenos Aires, 1 = Argentina, Catamarca, 2 = Argentina, Tucumán, 3–4 = Argentina, Salta, 5 = Argentina, Formosa. Letters and numbers placed at group means. Envelopes contain all group members.

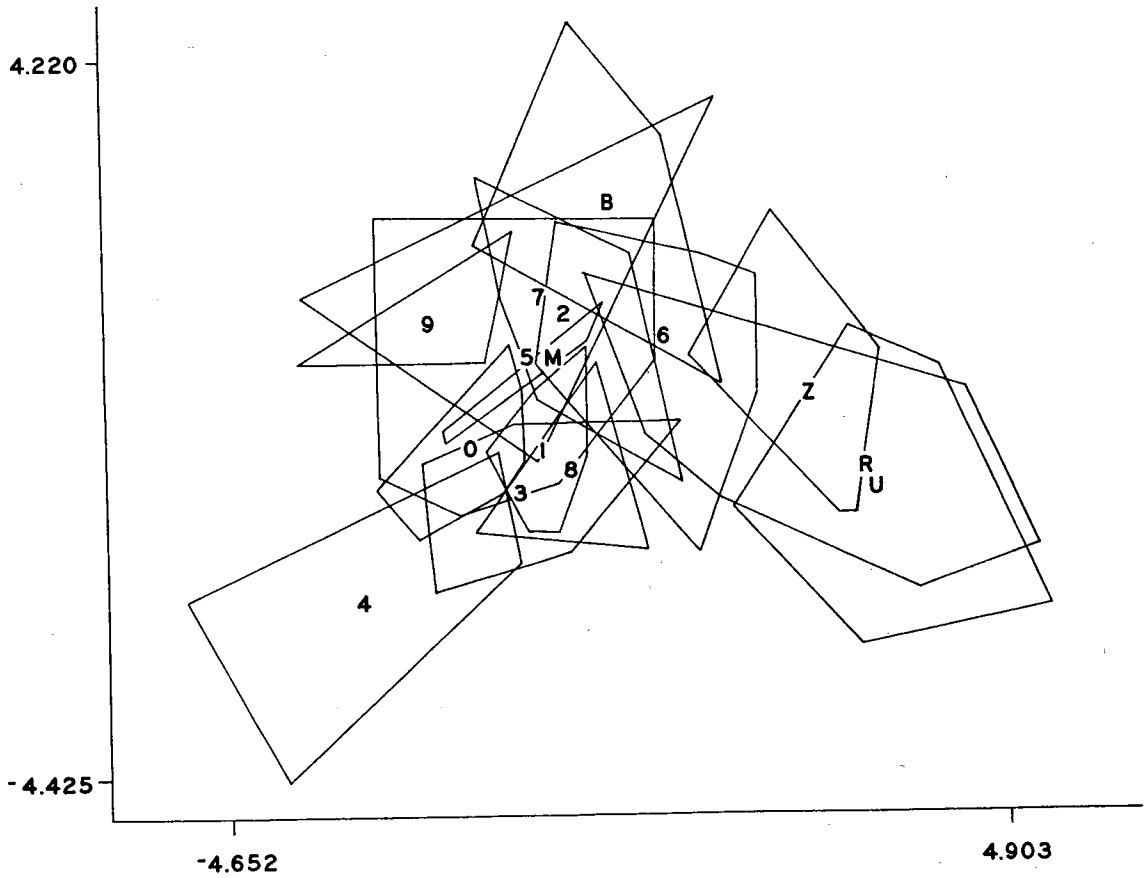


FIGURE 28. Discriminant axis plot for geographic samples of males of *Leptodactylus latinasus*. B = Brasil, Bahia and Espirito Santo, R = Brasil, Rio Grande do Sul, U = Uruguay, Z = Argentina, Buenos Aires, M = Argentina, Corrientes, 1 = Argentina, Catamarca, 2–3 = Argentina, Jujuy, 4–5 = Argentina, Tucumán, 6–8 = Argentina, Salta, 9 = Argentina, Formosa, 0 = Argentina, Chaco. Letters and numbers placed at group means. Envelopes contain all group members.

populations in two physiographically distinct areas in Argentina and concluded the calls represented the same species.

Taxonomic conclusion.—A single species is recognized.

SUMMARY OF TAXONOMIC CONCLUSIONS

Based on the available data, 17 species are recognized in the *fuscus* species group (names as used in the analysis section):

albilabris
northern *bufonius*
southern *bufonius*
fuscus
barred *gracilis*
striped *gracilis*
labialis
labrosus
latinasus
longirostris
northern *mystaceus*
southern *mystaceus*
east coast *mystaceus*
south coast *mystaceus*
mystacinus
poecilochilus
ventrimaculatus

NOMENCLATURE

Each name proposed for a member of the *fuscus* species group is discussed in chronological order.

Rana fusca Schneider 1799.—The confusion regarding this name has been commented on previously (Heyer 1968a). The neotype, Paris Museum 680, has been compared with recent material from French Guiana by Lescure (1972). He finds the specimens conspecific. This name applies to the species referred to as *L. fuscus* in the previous section.

Rana typhonia Daudin 1803.—Heyer (1968a) designated the male cotype of *Rana typhonia* Daudin as the neotype of *Rana fusca* Schneider. Lescure (1972) compared the type with recent specimens from French Guiana;

all apply to the species referred to as *L. fuscus* in the analysis section.

Rana mystacea Spix 1824.—Spix's description is based on a specimen from Bahia; he compares the described specimen with a second from Solimoens (female?). Peters (1873), the last person to examine the Spix types before they were lost, concluded that the specimens were synonyms of *Rana typhonia* Daudin. Peters (1873) clarified the Spix figure legends. Figure 3, plate 3, is an adult male from Bahia. Figure 1, plate 3, is an adult female from Solimoens. Bokermann (1966) gives the type locality of *Rana mystacea* as Salvador, Bahia. Spix's plate figures clearly pertain to members of the *mystaceus* complex as analyzed previously herein. The diagnostic characters for the *mystaceus* complex are the white tubercular conditions of the tibia, tarsus, and foot. Neither Spix nor Peters mentions these characters for any of the type specimens. In this case, geographic location of the two Spix types is sufficient for proper allocation. The taxon referred to as "east coast *mystaceus*" in the preceding analysis is the only member of the complex found in coastal Bahia; the taxon I termed "northern *mystaceus*" is the only species found along the Rio Solimões. Thus it appears that the two Spix type specimens represent different species. As all members of this complex have traditionally been called *mystaceus*, nomenclatural stability will not be improved by choosing one or the other of the two specimens as the form to which the name applies. As Spix gave the detailed description of the specimen from Bahia, I choose the specimen figured in figure 3, plate 3 as the name bearer of *mystacea*. Thus *mystacea* applies to the species called east coast *mystaceus* in the analysis section. There is enough confusion in this case that a designation of a neotype would appear to be in order. Unfortunately, no museum specimens are available from near the type locality of Salvador. As the species of the *mystaceus* complex are for the most part allopatrically distributed, the result of the action taken here should be clear to any subsequent worker in spite of not designating a neotype.

Rana sibilatrix Wied-Neuwied 1824.—Wied describes *sibilatrix* in several publications; the figure published in 1824 (Wied 1824) is usually cited for the original description of the name. The type specimen is apparently no longer extant. The figure, together with the restricted type locality of Marobá (= Vila Viçosa), Rio Peruipé (Müller 1927 as clarified by Bokermann, 1966) clearly allocates the name to the species identified as *L. fuscus* in the analysis. The figure shows a spotted dorsum with several dorsolateral folds. The species identified as *L. fuscus* is the only species along coastal Bahia to which the name can apply.

I have examined AMNH 485, a specimen from the Wied-Neuwied collection originally identied as *sibilatrix*. The specimen is a male with obvious, dark, vocal sacs; no vocal sacs are indicated in the figure of the type specimen. There is no convincing evidence that associates or disassociates AMNH 485 with Wied-Neuwied's figure. The locality given for the specimen is simply Brasil.

I can find no mention of Wied clearly associating Vila Viçosa as the collecting locality for *Rana sibilatrix* (Wied-Neuwied 1820). I have not examined museum specimens from this locality.

As this study shows no marked differences between specimens of *L. fuscus* from coastal Brasil and French Guiana, there is no need to make a final decision on whether AMNH 485 is actually the type of *Rana sibilatrix* or whether Vila Viçosa should be accepted as the type locality for the taxon.

Cystignathus gracilis Duméril and Bibron 1841.—The holotype, Paris Museum 4490, still contains the salient features to allocate the name properly. The holotype is a member of the *gracilis* complex as used by previous authors. The question is whether it is a barred or striped *gracilis*, as those terms are used in this analysis. The tibias, although soft and partly faded, clearly show the light longitudinal stripes; the name applies to the population identified as striped *gracilis* in the analysis section.

Cystignathus typhonius Duméril and Bibron 1841.—As pointed out previously (Heyer 1968a), although Duméril and Bibron indicated that the description they provided was of a new species, the name dates back to Daudin. The same specimens are involved; the lectotype of *typhonia* was designated as the neotype of *Rana fusca*. The name applies to the species identified as *L. fuscus* in the previous analysis.

Cystignathus schomburgkii Troschel 1848.—Attempts to locate the type material of this taxon have been unsuccessful. The types are not at any of the major German museums at present. The most likely depository was the collection in Leipzig. All of the herpetological material in this collection was transferred to the Staatliches Museum für Tierkunde in Dresden in 1972. F. J. Obst, the curator at the Dresden Museum, kindly informs me that Troschel's type material of *C. schomburgkii* is not in the Leipzig collection now housed at Dresden. Further, he has no knowledge of where Troschel's material might be. Troschel described two other new species in the same paper where he described *C. schomburgkii*: *Podocnemis unifilis* and *Hyla calcarata*. Duellman (1973, p. 522) was not able to locate the type of *H. calcarata*. In a brief literature search on *Podocnemis unifilis*, I find no one who refers to the type specimens. In all probability, Troschel's type specimens are lost.

Troschel's description of *C. schomburgkii* is brief and inconclusive. Three statements in the description give possible clues to the identity of *C. schomburgkii*: (1) the species is closest to *C. gracilis;* (2) color above uniform brown; (3) commonly found in dense, damp woods and in woodland swamps. The following *fuscus* group species are known from Guyana: *L. fuscus, L. longirostris,* northern *mystaceus*. Troschel's statement of close relationship with *gracilis* suggests *fuscus*. The uniform brown

dorsal color could only be *longirostris* of the Guyana members of the *fuscus* group, assuming that Troschel excluded the dorsal chevron as a uniform pattern. There is no reason to assume that Troschel and I mean the same thing by a uniform pattern, however. To my knowledge, no member of the *fuscus* group is commonly found in forests. *Leptodactylus longirostris* likely comes closest, being found in open situations in conjunction with forests. Thus *C. schomburgkii* most likely refers either to *L. fuscus* or *longirostris*. If the name applies to *fuscus*, it is a junior synonym; if it applies to *longirostris*, it is the oldest available name for that species. Historically, the name has been treated as a synonym of *sibilatrix* (= *fuscus*). As there is no proof that the types of *schomburgkii* have been destroyed, there is the remote possibility that the types still exist. As long as this possibility exists, I think the proper position to take at this point is to consider *schomburgkii* as a synonym of *L. fuscus* until such time as the status of the types can be resolved.

Cystignathus albilabris Günther 1859.—I have examined two syntypes from the series of specimens from St. Thomas, West Indies. Both specimens clearly represent the same taxon as the species referred to as *albilabris* in the analysis section. Günther's description reads as if he were looking at all the specimens, rather than describing one individual from the series. I hereby designate BMNH 1947.2.1760, an adult 35.3 mm male as the lectotype of *Cystignathus albilabris*.

Cystignathus mystacinus Burmeister 1861.—The holotype is in the collections of the Martin-Luther-Universität, Halle (Saale). Apparently no precise type locality was ever associated with the specimen other than Argentina. The specimen, although faded, is in a good state of preservation. It is a male, 51.8 mm SVL with the following diagnostic characteristics still visible: a pair of dorsolateral folds, white tubercles dorsally present in the sacral region, as well as on the dorsal surface of the tibia and lower surfaces of the tarsus and foot. The specimen is too faded to state for certain whether it has a light lip or thigh stripe, but there is no doubt that it belongs to the species identified in the analysis section as *mystacinus*.

Cystignathus poecilochilus Cope 1862.—The type specimen from Colombia is soft and faded and generally in poor condition. The light stripe on the posterior face of the thigh is still evident and the foot and tarsal surfaces are smooth. The name applies to the species identified as *L. poecilochilus* in the previous analysis.

Leptodactylus labrosus Jiménez de la Espada 1875.—Heyer and Peters (1971) discussed the type specimen. The name applies to the species identified as *L. labrosus* in the analysis.

Leptodactylus latinasus Jiménez de la Espada 1875.—Heyer (1969) discussed the type specimen. The name applies to the species identified as *L. latinasus* in the analysis.

Cystignathus fragilis Brocchi 1877.—The holotype, Paris Museum 6316, from Tehuantepec, Mexico, is clearly the same species analyzed as *L. labialis*. The specimen has tubercles on the tarsus and sole of foot, distinct light stripe on the posterior face of the thigh, indistinct light lip stripe, and somewhat distinct dorsolateral folds. The holotype compares well with other specimens collected from the Tehuantepec region.

Leptodactylus fragilis (Brocchi) is the oldest name for the species in question. Previously (Heyer 1971), I incorrectly cited the date of publication of *Cystignathus labialis* Cope as 1877. (Brocchi 1881, also thought that Cope's name predated *fragilis*.) The year 1877 is when the paper was read at the meeting, but the description was published in 1878. As discussed next, *C. labialis* Cope applies to a South American species, not to any species found in Mexico. The priority of the name, together with the misapplication of *C. labialis* for a Mexican species, leads to the conclusion that the best course of action is to use the name *L. fragilis* Brocchi for the species in question. See *C. labialis* (next) for further discussion.

Cystignathus labialis Cope 1878.—The juvenile holotype and 5 paratypes are so faded that no patterns are visible. The series demonstrates the following diagnostic character states: distinct dorsolateral folds from eye to groin; tubercles on tibia, tarsus, and sole of foot; posterior face of thigh lacking a light stripe; skin warty along sides and posterior dorsum. These states best match the species identified as *L. mystacinus* in the analysis section. Occasional individuals of specimens identified as *L. labialis* in the analysis section have uniform posterior faces of the thighs, but a series of 3 or 4 specimens always shows the light stripe. The same is true for *L. albilabris* and members of the *mystaceus* complex. The types were directly compared to faded juvenile specimens of *L. albilabris* and *L. mystacinus* (both as used in analysis section). Even in faded juvenile *albilabris*, the light thigh stripe is evident. The types match juvenile specimens of *L. mystacinus*. A faded *L. mystacinus* even has a white pin stripe along the dorsolateral folds, as do most of the *labialis* types. The type specimens thus do not pertain to the Middle American species as has always been assumed, but to the species usually called *mystacinus*.

In the original description, Cope gives the following diagnostic character states: one dermal fold on each side; skin rough; color chocolate brown; a brilliant white band extends from the anterior part of the upper lip, and describing a curve upwards, bounds the orbit below and descends to the canthus oris, from which point it continues in a straight line to the humerus, and ceases. All these states fit the species identified as *L. mystacinus* in the analysis section. The statement "color chocolate brown" better fits *mystacinus* than *labialis* (as used in analysis), as the former often has a uniform dorsum and the latter has some sort of spotting or mottling. All *mystacinus* have distinct light lip stripes; few *labialis* (as used in analysis) have brilliant white lip stripes. Cope gives the following measurements (my measurements in

meters of holotype in parentheses): length of head and body, .020 (.018); of head, .007 (.007 from tip of snout to posterior tympanum); of hind limb, .028 (.027), of hind foot, .013 (.018). The description and specimen match except for the hind foot length, which might have been a typographical error in the description.

Cope makes the following statement concerning locality, "The precise *habitat* of this species is at present uncertain. It is probably a part of Sumichrast's Mexican collection." The introductory paragraph of the paper states, "The greater number of the species described in this paper were sent to the Smithsonian Institution by its correspondents, and submitted to my examination by its Secretary, Professor Henry." Included in the paper are Mexican specimens collected by Sumichrast, Xantus, and others, Costa Rican material collected by Gabb and Franzius, Panamanian material collected by Selfridge, and a collection of 9 species, two described as new, from the following locality, "*Habitat* unknown, but supposed to be the Argentine Confederation." The species from this collection are indeed known from Argentina. Thus, it is as reasonable to assume that the specimens Cope described as *C. labialis* were part of the Argentina collection as the Sumichrast Mexican collection.

There has been confusion regarding some of the Cope types in the Smithsonian Collection. The specimens were returned to the Smithsonian after Cope died, but were not indicated especially as types. The specimens were originally recorded in the catalogue as *Cystignathus labialis* and no locality information was originally entered. Under remarks, the statement "Ret. from Cope's Estate" is recorded. Later, the following data were entered in pencil, "Probably Tehuantepec (?), [Collector] (?) Francis Sumichrast." Presumably this information was entered based on the information Cope gave in the description. Other material returned from Cope's Estate, entered in the catalog at the same time, includes some, but not all of the types Cope described in the same paper as *labialis*. Even though the specimens are now labelled as holotype and paratypes, this action seems to have been taken by a cataloguer, not a revisor in print. No further action need be taken, for if the series were still syntypes, the specimen now labelled as the holotype would clearly be the best choice to designate as lectotype.

As I have previously stated in print (Heyer 1971) that I examined the holotype and applied it to the Middle American species, comment on my previous decision is required. The 1971 statement is based upon a 1967 examination of the type specimen, when I first started systematic work on the genus. My original notes are, "Type examined 3 September 1967. The specimen is so faded that it is virtually impossible to see any pattern. Using all my imagination, I could perhaps make out a posterior thigh light stripe. The toes are not fringed, and the tarsus and sole of foot are covered with white (they could be nothing else due to the fading of the specimen) tubercles." At that time I did not look at the other type specimens. It is these specimens which clearly show the dorsolateral folds (the holotype is wrinkled along the sides due to tying the tag tightly around the waist and the dorsolateral folds do not distinctly stand out from the wrinkles). In 1967 I assumed that Mexico was the correct locality and knew that there were only two species of *Leptodactylus* in Mexico and that the holotype was certainly not *L. melanonotus*. Now that I have studied all members of the *fuscus* group, it is clear that the type specimens of *labialis* are certainly not from Mexico and that they are the same as species found in Argentina.

The evidence is reasonably conclusive. The specimens and description separately match the species identified as *L. mystacinus* in the analysis section. The holotype matches the description with the exception of the foot measurement. None of the Cope specimens can conclusively be demonstrated to be the holotype, but the evidence is most consistent with acceptance of the specimens as the types. Thus, the name *Cystignathus labialis* applies to the species identified as *L. mystacinus* in the analysis section and not to *L. labialis* as used in the analysis section.

The proper allocation of the name *C. labialis* will cause some confusion, as *Leptodactylus labialis* as currently understood is a well known species concerning which there is a sizeable body of literature. The Middle American species is mostly known to professional herpetologists, however, not to physiologists or general anatomists. The impact of the proper allocation of the name will not be felt outside of the herpetological community. The herpetological community has already endured one name change, as Kellogg's (1932) influential work considered the species in question a junior synonym of *L. albilabris*. In the long run, nomenclatural stability will best be served by the proper allocation of the type of *Cystignathus labialis* Cope.

Leptodactylus longirostris Boulenger 1882.—Boulenger based the new species upon two specimens, BMNH 76.5.26.4 and 76.5.26.5. Allocation of these specimens with the species recognized in the analysis section is not straightforward and requires discussion of the two specimens.

BMNH 76.5.26.4 is the better preserved of the two specimens. It is a 48.5 mm female, with smooth feet from Santarem, Brasil. A member of the *L. mystaceus* complex occurs in the Santarem region, but other specimens referred to as "*longirostris*" in the analysis section have not been taken that far south, the distribution of "*longirostris*" being broadly associated with the Guiana shield. The size of the specimen matches members of the Amazonian *mystaceus* complex, but is about 3 mm larger than any "*longirostris*" examined. The smooth foot matches "*longirostris*" and differs from the Amazonian *mystaceus* complex species. BMNH 76.5.26.4 has a narrow head (31% SVL) and long femur (51% SVL), tibia (59% SVL), and foot (60% SVL).

The head width is narrower than the average head widths of both "*longirostris*" and the Amazonian *mystaceus* complex species. The head width is matched by 6 individual "*longirostris*" and 2 individual Amazonian *mystaceus* complex species. The hind limb is longer than the average hind limb of both species, but individuals of "*longirostris*" match the limb proportions of the type for the femur, tibia, and foot, whereas no individuals of the Amazonian *mystaceus* complex species have the same length of either the femur or tibia. Two details of color pattern of the type specimen are matched by "*longirostris*" specimens and not by the Amazonian *mystaceus* complex species: (1) a postorbital dark triangle with the apex pointing toward the angle of the jaw, and (2) posterior continuations of the dark mid-dorsal scapular chevron.

The second specimen, BMNH 76.5.26.5 has an anomalous right leg, but is otherwise in good condition. The right femur appears shortened, the tibia is only a few millimeters long terminating in 3 misshapen toes. The female specimen resembles the other type in the following features: head length, hind limb proportions, foot texture, postorbital dark triangle. The specimen differs from the other type specimen in SVL (43.4 mm) and head width (33% SVL): both of these measurements are the same as found in specimens analyzed as "*longirostris*" in the previous section.

Both types of *L. longirostris* clearly represent the same taxon. The combined information on both specimens is most consistent with the specimens analyzed as *longirostris*. Two aspects do not allow a certain allocation of the types with the Guiana shield species analyzed as *longirostris* at this time: the large size of one of the female types and locality. Two possible conclusions may be drawn. 1) The types of *L. longirostris* represent a distinct species from the Guiana shield species analyzed as *longirostris*. This conclusion would be supported by the locality data and size differences and would require the recognition of the two as sibling species essentially indistinguishable morphologically. 2) The types of *L. longirostris* represent the same species as the Guiana shield species identified as *L. longirostris* in the analysis section. This conclusion would be consistent with the morphological data except for female size, which would have to be explained as due to small sample size of *longirostris* museum specimens or geographic variation, etc. This conclusion would also suggest that Santarem was the shipping port and the specimens were actually collected from the upper Mapuera or Trombetas rivers, for example.

I know of only two other museum specimens that resemble the types of *L. longirostris* in form and geographic provenance (MZUSP 24880, Ponta Negra, Rio Negro, Amazonas, MZUSP 37518, Tapera, Rio Negro, Amazonas) and these specimens are close geographically to the Guiana shield region. I therefore hesitate to recognize two distinct species in this assemblage, recognizing that additional data may require a re-evaluation of this position. Thus, for present purposes, I consider the types of *L. longirostris* to represent the same species as the species identified as *L. longirostris* in the analysis section. As specimen BMNH 76.5.26.4 is clearly the specimen described and figured by Boulenger, I hereby designate it as the lectotype.

Leptodactylus prognathus Boulenger 1888.—The holotype is clearly the same species identified as *latinasus* in the analysis section. Boulenger's description is misleading in one respect. He states that the 33 mm specimen is a half-grown male specimen. The specimen has vocal slits and external lateral vocal sac folds: it is a fully adult male.

Leptodactylus andicola Boettger 1891.—This name has been associated with members of the *fuscus* group (Heyer, 1974). Dr. John Lynch concurs with my current opinion that this name applies to the genus *Eleutherodactylus*. The type has been destroyed.

Leptodactylus quadrivittatus Cope 1893.—The holotype is apparently lost. The description matches recent specimens from Costa Rica. The name can only pertain to the species identified as *L. poecilochilus* in the analysis, as it is the only species in Costa Rica to have the mid-dorsal stripe color pattern phase. There is no taxonomic confusion surrounding this name and the holotype may yet be identified as such, thus there is no reason to designate a neotype for *quadrivittatus*.

Leptodactylus bufonius Boulenger 1894.—I have examined two of the four syntypes; the types are the same species called *bufonius* or southern *bufonius* in the analysis section. Boulenger gives the snout to vent measurement as 48 mm. I measure 46.4 mm on specimen BMNH 1947.2.17.72, the first specimen in the series. As this specimen is likely the one Boulenger's description is based upon, and is still well preserved, I hereby designate this female specimen as the lectotype of *Leptodactylus bufonius* Boulenger.

Leptodactylus maculilabris Boulenger 1896.—I have examined the type specimen and concur with previous workers that it represents the same species identified as *L. poecilochilus* in the analysis section.

Leptodactylus raniformis Werner 1899.—The holotype, an adult male, is clearly a member of the Amazonian Colombian population of *fuscus* as analyzed previously. The dorsolateral folds are indistinct, but the spotting pattern on the dorsum is characteristic of *fuscus* as is the tarsal and foot surfaces (smooth with light pigment spots).

Leptodactylus ventrimaculatus Boulenger 1902.—The type series was previously commented on (Heyer and Peters, 1971). The name applies to the species identified as *L. ventrimaculatus* in the analysis section.

Leptodactylus diptychus Boulenger 1918.—The holotype has the following diagnostic character states: light stripe on posterior face of thigh, smooth tarsus and foot; 2 distinct dorsolateral folds; lips with dark brown spots;

45.4 mm female. There is only one species in Venezuela that this combination of character states can apply to: the species identified as *L. poecilochilus* in the analysis section. It is the only species with brown lip spots with the other character states mentioned. The type locality, Andes of Venezuela, is probably in slight error, as *L. poecilochilus* is known only from the coastal plain region of Venezuela. As discussed in the analysis section, the presumed mating calls of Middle American and Venezuelan *poecilochilus* are distinctive. If two species are actually involved, *diptychus* would apply to the Venezuelan form.

Leptodactylus curtus Barbour and Noble 1920. Heyer and Peters (1971) discussed the allocation of this name. The name applies to the species identified as *L. labrosus* in the analysis section.

Leptodactylus dominicensis Cochran 1923.—The type is clearly a member of the *L. albilabris* complex. As but one species is recognized in this complex, the name is a synonym of *albilabris*. As noted before, the Dominican Republic population is distinctive. If further work demonstrates that the Dominican Republic population is distinct at the species level, then *dominicensis* would apply to this form.

Leptodactylus troglodytes Lutz 1926.—The specimen labelled as the type in the Adolfo Lutz collection is completely faded in any exposed areas. It is impossible to tell whether the foot and tarsus are tuberculate or not. It is clear, however, that the name applies to the form identified as northern *bufonius* in the analysis section as the type locality is Pernambuco. As northern *bufonius* is recognized as a distinct species herein, *troglodytes* applies to this species.

Leptodactylus plaumanni Ahl 1936.—I have been unable to examine the holotype. Mertens (1967) considered *plaumanni* a synonym of *sibilator* (= *fuscus* as used here). The original description appears to better match what is here recognized as striped *gracilis*, particularly in details of dorsal and tibia color pattern. In order to point out that *plaumanni* may refer to another species than *fuscus*, I prefer to place *L. plaumanni* in the synonym of *L. gracilis* until such time that I am able to examine the holotype. Also see *L. geminus*.

Leptodactylus anceps Gallardo 1964.—Gallardo described *anceps*, indicating that it had a Chacoan distribution, whereas *prognathus* (= *latinasus*) had a coastal distribution. I have examined paratypes of *L. anceps* and specimens identified by Gallardo as *anceps*. The name certainly applies to the group of frogs analyzed herein as *latinasus*. In order to examine the morphological distinctiveness of *anceps*, a discriminant function analysis was run, using specimens from geographic areas clearly within the range of *anceps* or *latinasus* as defined by Gallardo (1964).

The sample sizes for females are 20 *latinasus* and 34 *anceps*. The variables entered in the following order: tibia ratio, SVL, femur ratio, head length ratio (NI), foot ratio (NI), thigh stripe (NI), head width ratio (NI). Two of 20 latinasus were posteriorly classified as *anceps*, 1 of 34 *anceps* classified as *latinasus*. This classification separation is also shown in the plot of the first two discriminant axes, where 100% of the dispersion is accounted for by the first axis (fig. 29).

Male sample sizes are 35 *latinasus* and 107 *anceps*. The variables entered as follows: tibia ratio, SVL, head width ratio, head length ratio (NI), lip strip (NI), femur ratio (NI), thigh stripe (NI). Three *latinasus* were posteriorly classified as *anceps*, 8 *anceps* were classified as *latinasus*. All of the dispersion is accounted for by the first discriminant axis (fig. 30).

The female and male results complement one another. The species Gallardo described as *anceps* is morphologically distinctive from *latinasus*, but there is some morphological overlap. The complexity of the overlap is better seen in figs. 27 and 28 where the pattern of geographic variation is complex and not easily interpretable. Interestingly, Gallardo distinguished *anceps* in large part by differences in snout shape. The head ratios used here do not reflect those differences. Although the Chacoan populations are morphologically differentiated from the coastal populations, there is some morphological overlap (as specimens from questionable, intermediate localities were omitted from the analysis, the degree of overlap may be even greater than evidenced in the analysis). This morphological overlap, together with similarity of mating call (Barrio 1965) is interpreted to mean that a single species is involved and that *anceps* is a synonym of *latinasus*.

Leptodactylus gualambensis Gallardo 1964. Gallardo (1964) described *gualambensis* as a species of the *fuscus* group with a Chacoan distribution. I have examined specimens Gallardo identified as *gualambensis* and find them morphologically identical to *fuscus*. The geographic analysis of *fuscus* (figs. 13 and 14) did not demonstrate a morphological distinctiveness of the Chaco populations of *fuscus*. In order to specifically test for the morphological distinctiveness of *gualambensis*, a discriminant function analysis was run on individuals from the Chaco, including specimens Gallardo identified as *gualambensis* and non-Chaco individuals. Any specimens from possible intermediate localities were not used in this analysis. There are enough data for analysis of males only.

Sample sizes are 30 *gualambensis* and 163 *fuscus*. The variables entered in the following order: tibia ratio, SVL, dorsal pattern, thigh stripe, foot texture, femur ratio (NI), head width ratio (NI), head length ratio (NI), tarsal texture (NI), lip stripe (NI). Four *gualambensis* were posteriorly classified as *fuscus*, 22 *fuscus* were classified as *gualambensis*. The first discriminant axis accounts for 100% of the total dispersion (fig. 31). The results show that the Chaco populations are moderately distinctive, but fall within the range of morphological variability of the other populations of *fuscus*. Barrio

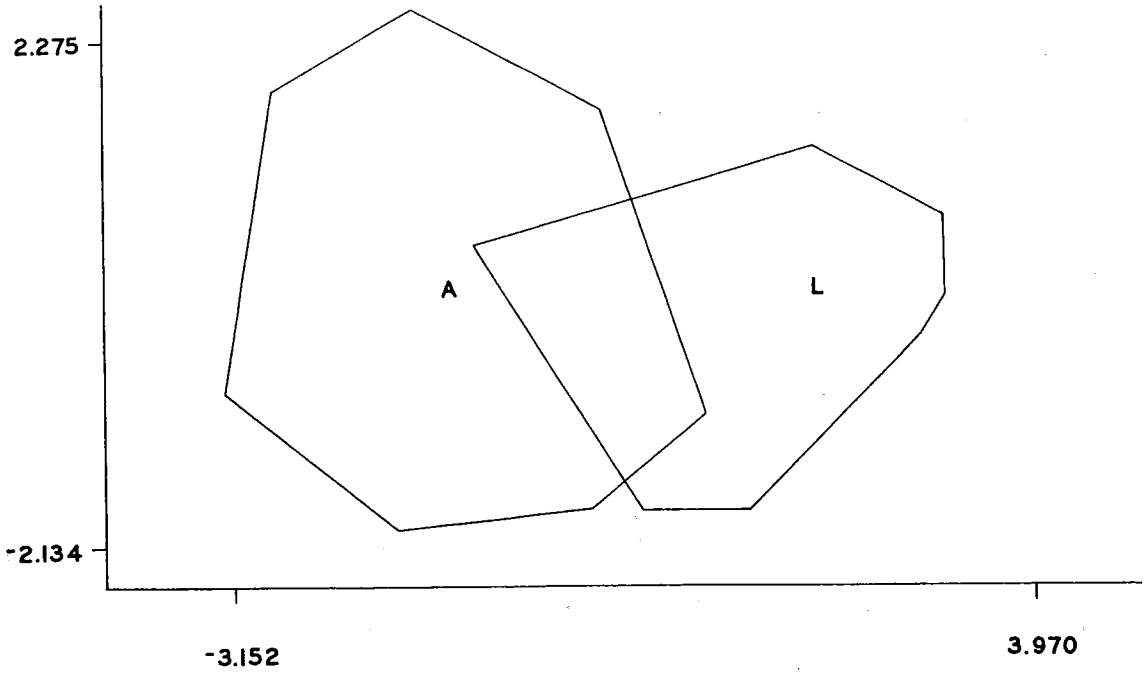


FIGURE 29. Discriminant axis plot for females of *Leptodactylus anceps* and *latinasus*. A = *anceps*, L = *latinasus*. Letters placed at group means. Envelopes contain all group members.

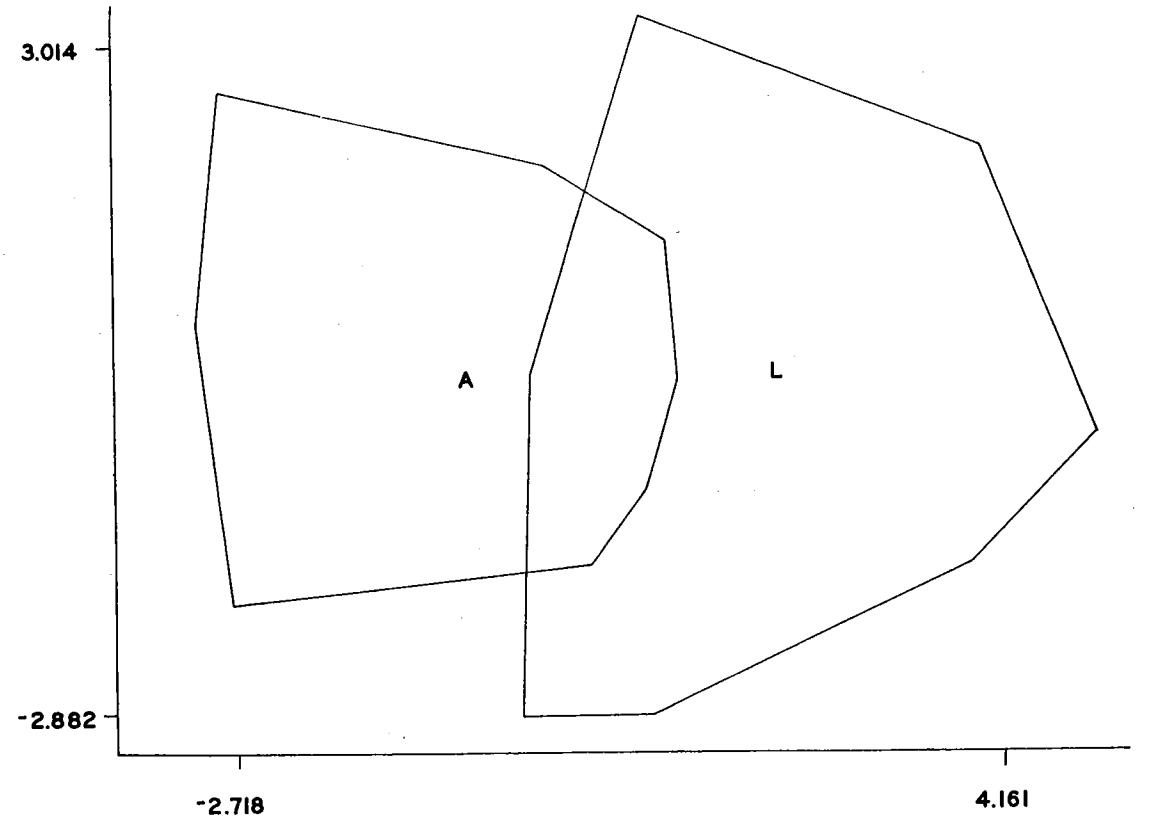


FIGURE 30. Discriminant axis plot for males of *Leptodactylus anceps* and *latinasus*. A = *anceps*, L = *latinasus*. Letters placed at group means. Envelopes contain all group members.

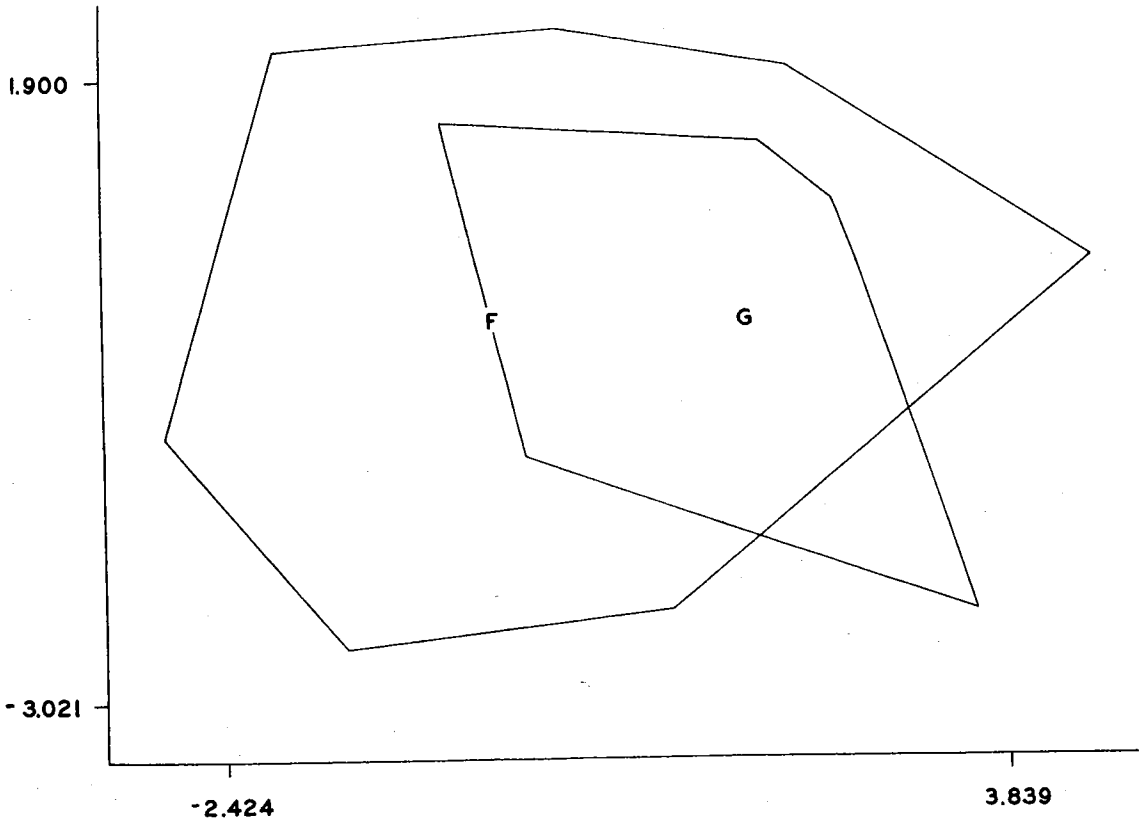


FIGURE 31. Discriminant axis plot for males of *Leptodactylus fuscus* and *gualambensis*. F = *fuscus*, G = *gualambensis*. Letters placed at group means. Envelopes contain all group members.

(1965) indicated that the call of *gualambensis* is not distinctive from the call of southeastern Brasil *fuscus*. This, together with the fact that there is morphological overlap of *gualambensis* and *fuscus* leads to the conclusion that but one species is involved.

Leptodactylus gracilis delattini Müller 1968.—Data were taken on the holotype and two paratypes (MZUSP). The data on the three specimens are compared with data on male barred and striped *gracilis* in a discriminant function analysis. The results of the plot of the first two discriminant axes are adequate for discussion (fig. 32). The subspecies is clearly morphologically closest to striped *gracilis*. The dorsal surface of the tibia has the folds characteristic of striped *gracilis*, but lacks the stripes themselves. The tibia pattern of the types are thus barred *gracilis*. Most morphological evidence is consistent with striped *gracilis:* the subspecies is considered here as belonging to striped *gracilis*, but the island population is distinctive.

Leptodactylus geminus Barrio 1973.—Barrio differentiated *geminus* from *gracilis* based solely upon distinctive features of the mating call, pointing out that the external morphologies and karyotypes of the two taxa are practically identical. I have not been able to examine the type specimens of *geminus* in detail. Barrio's figures show light longitudinal stripes on the tibia on both *geminus* and the *gracilis* he compared *geminus* with. Barrio's call data clearly indicate that two species are included in what I have recognized as "striped *gracilis*" in the analysis section. Pending further morphological analysis, *L. geminus* is recognized on the basis of its distinctive call, but subsequent discussions of specimens will not differentiate between *geminus* and *gracilis*. A further nomenclatural complication is that *L. plaumanni* may refer to either striped *gracilis* or *geminus*. The type description suggests that *plaumanni* would pertain to striped *gracilis*.

Leptodactylus marambaiae Izecksohn 1976.—Izecksohn distinguished the new species from *L. gracilis* on the basis of a shorter leg, smaller size, and color pattern. The species is very similar to striped *gracilis* as analyzed herein. Werner C. A. Bokermann kindly gave me a copy of a recording of the mating call (recorded by Izecksohn). The call is distinctive from striped *gracilis* and *geminus* (see species accounts).

All of the proposed names apply to 13 of the species recognized in the analysis section plus two species not recognized in that section. Thus, four species remain unnamed. Descriptions for these new species are included in the accounts below.

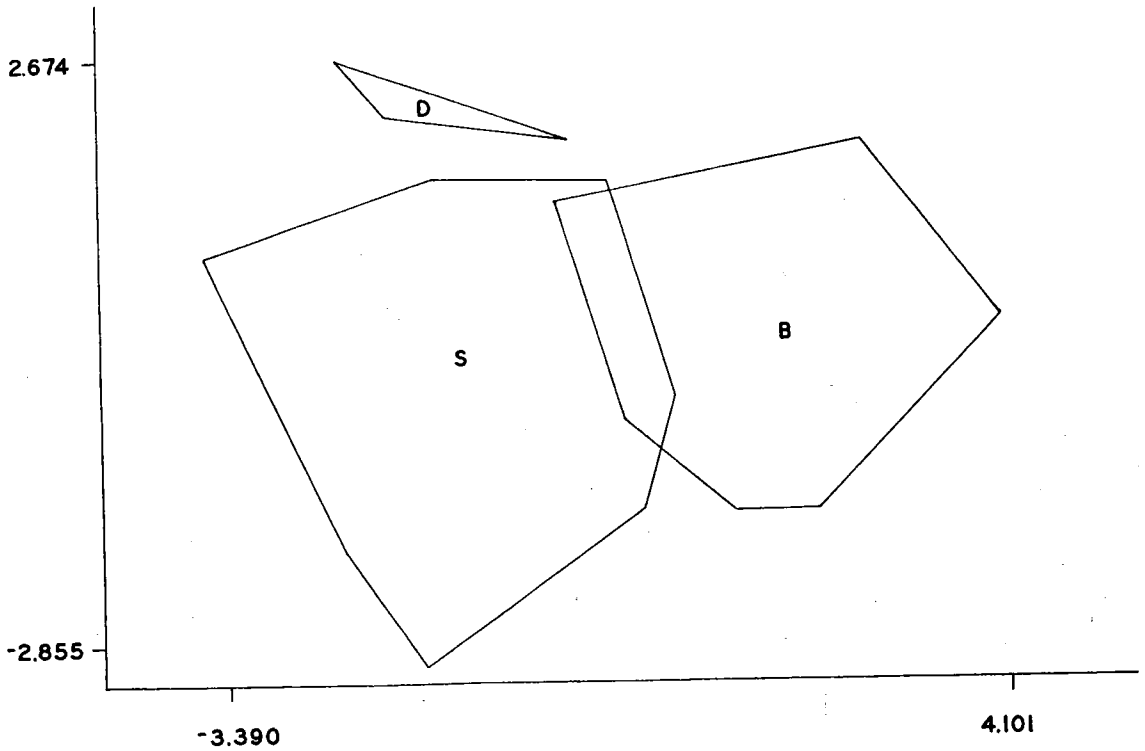


FIGURE 32. Discriminant axis plot for males of *Leptodactylus gracilis delattini,* striped *gracilis,* and barred *gracilis*. B = barred *gracilis,* D = *gracilis delattini,* S = striped *gracilis*. Letters placed at group means. Envelopes contain all group members.

SPECIES ACCOUNTS

Members of the fuscus group of *Leptodactylus* are small to moderate sized frogs; the toes lack fringe or web, the head is of normal width proportions, and the males lack thumb spines. All members of the *melanonotus* and *ocellatus* groups have fringe on the toes. All members of the *pentadactylus* group are moderate to large frogs having broad heads and in most species the males have thumb spines.

In the descriptions, only the holotypes of new species are described in detail. The characteristics used to describe the adults and larvae are those which differentiate the member species (which are the same characters used in the analysis section for the most part).

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 are quite similar morphologically; all have a denticle formula of $\frac{1}{3}\frac{1-1}{1-1}$ or $\frac{1}{2}\frac{1-1}{1-1}$, an entire oral disk with an anterior papillary gap, a median anus, sinistral spiracle, a pond type larval morphology, and an indistinct, mottled body and tail pattern. These features are not repeated in the species accounts.

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 maps are computer generated and are based on localities for which longitudes and latitudes could be found.

LEPTODACTYLUS ALBILABRIS (GÜNTHER) 1859

Cystignathus albilabris Günther 1859:217. (Type locality, West Indies, St. Thomas. Lectotype BMNH 1947.2.1760, adult male.)

Leptodactylus dominicensis Cochran 1923:184–185. (Type locality, Dominican Republic; El Seibo Province, Las Cañitas. Holotype USNM 65670, adult male.)

Diagnosis—The other species which have a light stripe on the posterior face of the thigh and obvious white tubercles on the tarsus and foot are *elenae, fragilis, latinasus, mystaceus,* and *mystacinus*. The dorsal surface of the tibia is covered with obvious white tubercles in *albilabris,* white tubercles are lacking or indistinct on the dorsal surface of the tibia in *elenae*. *Leptodactylus albilabris* has a pair of distinct dorsolateral folds, in *fragilis* and *latinasus* the folds, if present, are indistinct. *Leptodactylus albilabris* is also larger (males 30.3–43.1 mm, females 34.9–45.4 mm) than either *fra-*

gilis (males 25.9–43.0, females 28.7–43.6 mm) or *latinasus* (males 27.9–37.9 mm, females 29.0–36.3 mm), but smaller than *L. mystacinus* (males 43.6–58.8 mm, females 53.8–64.3 mm). *Leptodactylus albilabris* has a shorter tibia (male mean 43% SVL, female 44%) and foot (male mean 49% SVL, female 50%) than *L. mystaceus* (tibia—male mean 51% SVL, female 52%; foot—male mean 55% SVL, female 55%). *Leptodactylus albilabris* is the only group member found in the West Indies.

Adult Characteristics (N = 268)—Dorsum with dorsal chevrons, blotches, or confluent chevrons and blotches (fig. 1, A, B); mid-dorsal light stripe present in 17% of individuals, presence not sexually dimorphic ($X^2 = 1.05$, $P > .05$); light lip stripe almost always distinct (94%), rarely indistinct (6%), distinctiveness not sexually dimorphic ($X^2 = 0.58$, $P > .05$); dark suborbital bar absent; light stripe on posterior face of thigh present, distinct (56%) or indistinct (44%), distinctiveness not sexually dimorphic ($X^2 = 0$, $P > .05$); tibia barred; 2 distinct dorsolateral folds; dorsal surface of tibia usually covered with many white tubercles, sometimes scattered with white tubercles; posterior surface of tarsus with many white tubercles; sole of foot with many white tubercles; male SVL 35.2 ± 2.7 mm, female 40.7 ± 3.1 mm, females larger than males ($t = 15.19$, $P < .01$); male head length/SVL ratio .380 ± .013, female .372 ± .015, male head longer ($t = 4.64$, $P < .01$); male head width/SVL ratio .354 ± .014, female .354 ± .015, not sexually dimorphic ($t = .354$, $P > .05$); male femur/SVL ratio .400 ± .024, female .414 ± .024, female femur longer ($t = 4.68$, $P < .01$); male tibia/SVL ratio .431 ± .022, female .442 ± .025, female tibia longer ($t = 3.80$, $P < .01$); male foot/SVL ratio .487 ± .025, female .495 ± .028, female foot longer ($t = 2.45$, $P < .02$).

Larval Characteristics—Eye diameter 9–11% head-body length; oral disk width 20–25% head-body length; oral papilla gap 48–56% oral disk width; 42–67 denticles in anterior split tooth row on one side; head-body length 33–43% total length; total length, stage 36, 42.6 mm (fig. 33).

Mating Call (figs. 5 and 6)—Dominant (= fundamental) frequency modulated between 2000–2800 hz; no harmonic structure in call; each note of two pulses, a lower frequency and intensity pulse of .004 to .013 s duration followed without pause by a pulse of higher frequency and intensity of .038 to .040 s duration.

Karyotype—Bogart (1974) described the karyotype as diploid number 22; 7 pair median, 3 pair submedian, 1 pair subterminal; secondary constriction in chromosome pair 8.

Distribution—Known from the Virgin Islands, Puerto Rico and eastern Dominican Republic (fig. 34).

ANEGADA. MCZ 4198–4202, 4208–224.

DOMINICAN REPUBLIC. No specific locality, AMNH 20925, 20937, 20943, 20951–52, 20958, 20961–64.

EL SEIBO: Sabana de La Mar, AMNH 34402–411; 3.2 km E Sabana de La Mar, USNM field 41045–051.

PUERTO RICO. Adjuntas, USNM 25607; Aguada, CM 36058 (10); Aguadilla Rincon, CM 46462; Aguas Buenas, USNM 25628–631; Aibonito, AMNH 10030–39, USNM 25759, Añasco, USNM 25726–27; Arecibo, 23 km W, USNM 86560; Arroyo, USNM 25728–731; Bayamón, MCZ 4104–110, 21865 (5), USNM 25772–75; Cabo Rojo, 3 km E, MCZ 30790; Canóvanas, 10 km S, MCZ 19023–050; Caguas, USNM 25740; Cartagena Lagoon, MCZ 19014–19; Catalina Plantation, USNM 26894; Cayey, MCZ 18976, 18978–985 (5); Cayo Santiago, MCZ 31576–78; Coamo Springs, MCZ 19020–22; Culebra Island, MCZ 18963–65; Desengano, FMNH 12384–86; Húcares, USNM 26091–92; Humaco, USNM 27775, 86602–09; Lares, USNM 62933; Luquillo, USNM 27053; Mameyes, USNM 26820–23, 26825–833, 26835, 26981–82; Mayagüez, CM 46418–425, 46457, 46500, FMNH 12379, 12413–15, MCZ 30791, 34052–57, USNM 27749–758, 29357– 362, 29390–91, 100901; Ponce, MCZ 2756 (3), USNM 27313; Pueblo Viejo, USNM 26817–19, 86559; Río Piedras, FMNH 38582, MCZ 19001–013, 21893; Santa Barbara, USNM 31089; San Germán, USNM 86561–64; San Juan, MCZ 2187 (52); Utuado, MCZ 9352, USNM 27227–236; Vieques Island, USNM 27084–099, 27103–138; El Yunque, KU 79231; Zugillo Mtns, MCZ 18986–19000 (3).

ST. CROIX. No specific locality, CM 18821 (11), KU 94395–96, MCZ 3706–09, USNM 115898–5906; Bethlehem, USNM 162238–243; Caledonia, MCZ 24146.

ST. JOHN ISLAND. No specific locality, MCZ 18949–958 (27); Annaberg, KU 45629.

ST. THOMAS. No specific locality, AMNH 52653–57 (11), FMNH 11290 (3), 42076–080, MCZ 18959–962, USNM 15403–08, 52499–2503, 52512–524, 52527, 119036–37, 161011; near Magens Bay, USNM 52504–06; near Smith Bay, USNM 103163 (tadpoles).

TORTOLA. No specific locality, AMNH 77503–05, FMNH 11284 (6), MCZ 4225–235, 189666–69, 189671, 189673–75 (15).

LEPTODACTYLUS AMAZONICUS NEW SPECIES

Figure 35

Holotype: LACM 92111, an adult male from Ecuador; Napo Province, Limoncocha, 0° 24′ S, 76° 37′ W, elevation 260 m. Collected by Keith A. Berven and W. Ronald Heyer on 15 July 1971.

Paratopotypes: LACM 92067–070, 92072–75, 92077–085, 92087, 92090–92, 92094–95, 92098, 92102–05, 92108, 92112–15, 92117–20, 92122–25, MCZ 56309, 56312, a series of adult specimens collected by various collectors on different dates from the type locality. LACM 92067, 92072, 92090, 92105 were karyotyped.

Diagnosis.—The only species in which some or all individuals share the combination of a distinct light posterior thigh stripe, posterior surface of the tarsus smooth and sole of foot with prominent white tubercles are *amazonicus, mystaceus,* and *notoaktites*. Most individuals of *mystaceus* also have white tubercles on the posterior surface of the tarsus. Some individuals of *mystaceus* have a mid-dorsal light stripe, no *amazonicus* have a mid-dorsal light stripe. *Leptodactylus amazonicus* are found throughout the greater Amazon Basin, *mystaceus* occur along the east coast of Brasil from Bahia to Rio de Janeiro. Some individuals of *notoaktites*

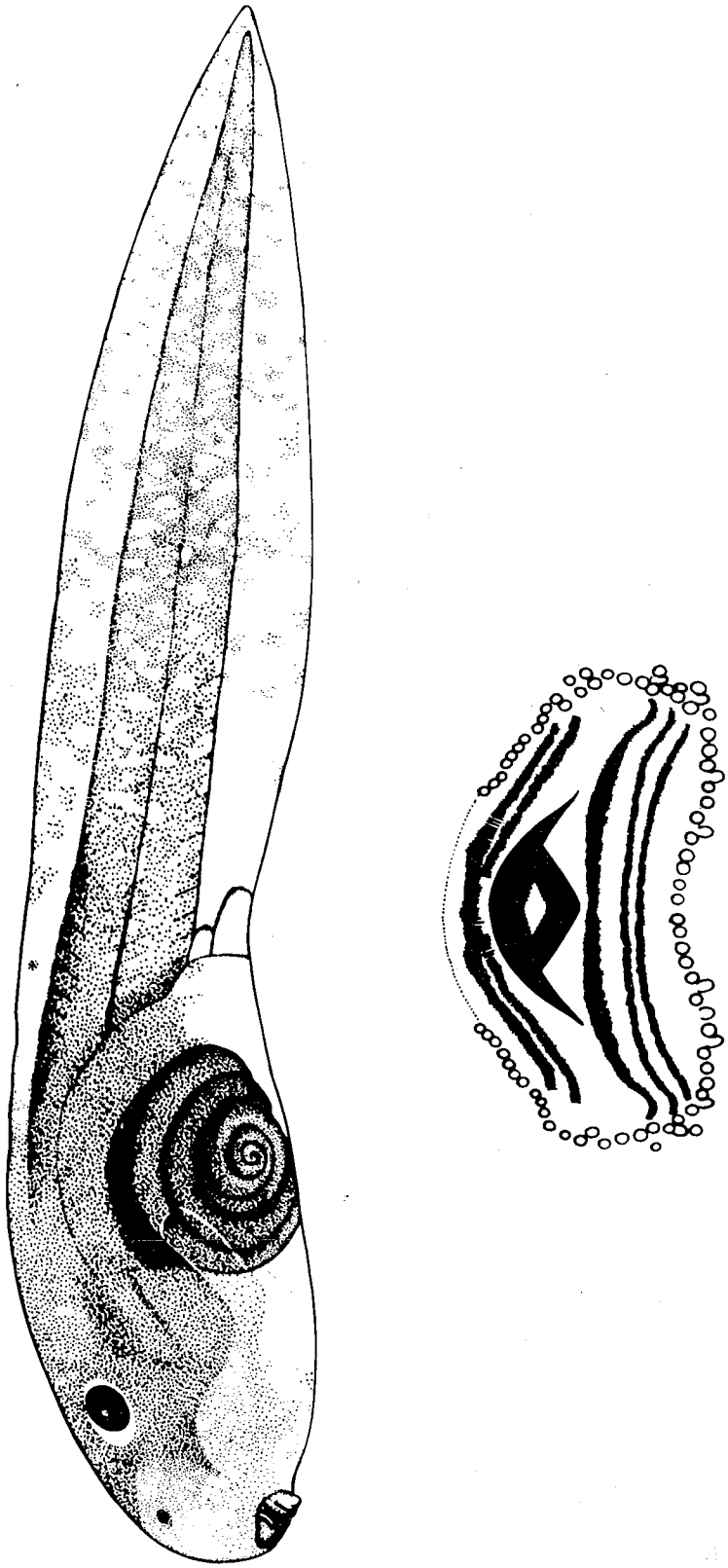


FIGURE 33. Lateral view and mouthparts of tadpole of *Leptodactylus albilabris*. Semidiagrammatic figure based on specimens from Puerto Rico.

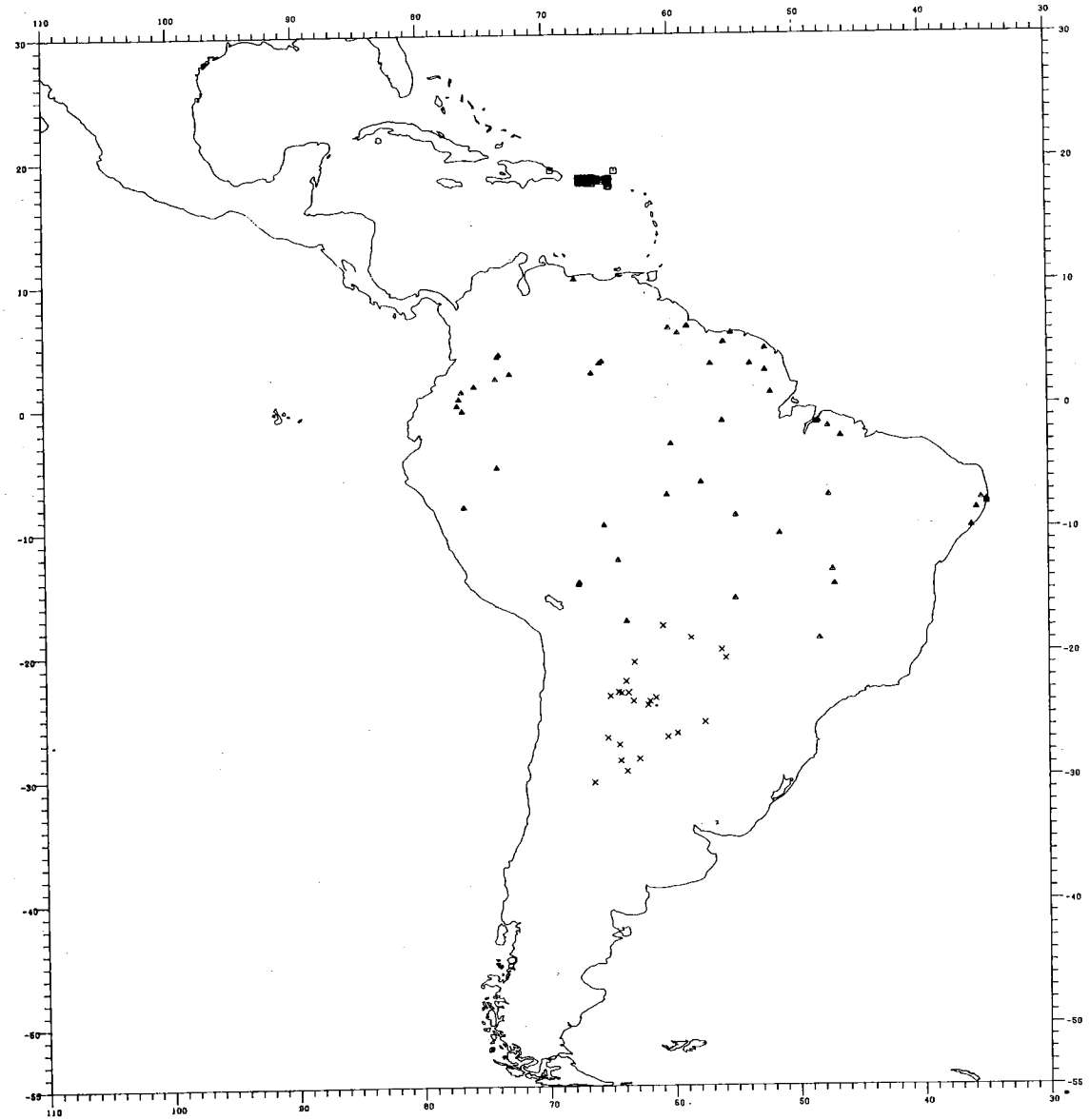


FIGURE 34. Distribution map of *Leptodactylus albilabris* (squares), *amazonicus* (triangles) and *bufonius* (Xs).

lack white tubercles on the sole of the foot; some *notoaktites* have light mid-dorsal stripes; the distribution of *notoaktites* is southern coastal Brasil from São Paulo to Santa Catarina.

Description of Holotype.—Snout subelliptical from above, acute in profile; canthus rostralis indistinct; loreal slightly concave; tympanum distinct, greatest diameter about ½ eye diameter; vomerine teeth in arched series posterior to choanae; vocal slits present; pair of external lateral vocal folds; finger lengths in order of decreasing size I≈III > II≈IV, first finger much longer than second; inner metacarpal tubercle ovoid, flat, smaller than large, flat, rounded outer metacarpal tubercle; no nuptial asperities; dorsum smooth; one pair of dorsolateral folds from back of eye to groin; supratympanic fold from eye to humerus; ventral surfaces smooth; belly disk fold well developed; toe tips not expanded; toes free, lacking fringe or web; subarticular tubercles moderately well developed; outer metatarsal tubercle small, round, about ¼ large, ovoid inner metatarsal tubercle; tarsal fold indistinct; no metatarsal fold; posterior surface of tarsus smooth; sole of foot with several large, white tubercles.

SVL 50.3 mm, head length 19.7 mm, head width 18.0 mm, interorbital distance 3.1 mm, eye-nostril distance 4.6 mm, femur 24.5 mm, tibia 26.5 mm, foot 26.8 mm.

Dorsum brown with darker brown markings including interorbital bar and 2 mid-dorsal chevrons; dorsolateral

FIGURE 35. Dorsal view of the holotype of *Leptodactylus amazonicus*.

folds outlined with dark and light pin stripes; light upper lip stripe indistinct; limbs barred; underside of chin dark edged; belly light; posterior surface of thigh blotched above, dark with distinct light longitudinal stripe below.

Etymology—Named in reference to the distribution pattern characteristic of the species.

Remark.—This is the species referred to as "northern *mystaceus*" in the morphological analysis.

Adult Characteristics ($N = 148$).—Dorsum spotted, spots very rarely fused (fig. 1, A, B, C); no light middorsal stripe, light upper lip stripe usually distinct (56%) (fig. 57), often indistinct (44%), more females with distinct lip stripes than males ($X^2 = 8.66$, $P = .003$); no dark suborbital bar; light stripe on posterior face of thigh almost always distinct (93%), rarely indistinct (7%), distinctiveness not sexually dimorphic ($X^2 = 1.81$, $P = .18$); tibia barred; usually 2 or 4 well defined dorsolateral folds; dorsal surface of tibia lacking white tubercles; posterior surface of tarsus almost always lacking white tubercles (99%), very rarely present (1%), presence not sexually dimorphic ($X^2 = .001$, $P = .98$); sole of foot with many or scattered white tubercles (100%); male SVL 47.4 ± 2.4 mm, female 50.2 ± 2.6 mm, females larger than males ($F_{1, 146} = 47.8$, $P < .001$); male head length/SVL ratio .386 ± .011, female .380 ± .013, male head longer than female ($F_{1, 146} = 7.38$, $.005 < P < .01$); male head width/SVL ratio .352 ± .013, female .347 ± .013, male head broader than female ($F_{1, 146} = 4.34$, $.025 < P < .05$); male femur/SVL ratio .433 ± .027, female .447 ± .033, not sexually dimorphic ($F_{1, 146} = .43$, $P > .05$); male tibia/SVL ratio .515 ± .020, female .526 ± .026, female tibia longer than male ($F_{1, 146} = 7.82$, $.005 < P < .01$); male foot/SVL ratio .532 ± .021, female .539 ± .026, not sexually dimorphic ($F_{1, 146} = 2.96$, $P > .05$).

Larval Characteristics.—Eye diameter 9–14% head-body length; oral disk width 22–26% head-body length; anterior oral papilla gap 50–70% oral disk width; 50–70 denticles on one side of split tooth row anterior to beak; head-body length 33–40% total length; total length, stage 40, 36.2 mm (fig. 36).

Mating Call.—Dominant frequency modulated from 700–1400 hz (fig. 37); call without harmonic structure; call pulsatile, about 15 pulses per note (fig. 38); note duration about 0.2 s; note repetition rate 1.78 per second.

Karyotype.—Diploid number 22, 5 pair median, 3 pair submedian, 3 pair subterminal (Bogart 1974) or 4 pair median, 4 pair submedian, 3 pair subterminal (Heyer and Diment 1974); secondary constriction in chromosome pair 8.

Distribution.—Throughout the greater Amazon Basin, Guianas, northern Atlantic forest, and cerrados bordering the Amazon Basin (fig. 34).

BOLIVIA. BENI: Boca del Baures, AMNH 79096; Reyes, UMMZ 64107; Rurrenabaque, UMMZ 64109.

SANTA CRUZ: Buenavista, CM 3885, 3967, MCZ 12896, UMMZ 63832 (4), 64025 (3), 66478, 66481, 66492.

BRASIL. ALAGOAS: Usina Sinimbu, S. Miguel, WCAB 2775.

AMAPÁ: Serra do Navio, LACM 44711–12, WCAB 2308, 35229–231.

AMAZONAS: Rio Canabari, Rio Tucano, WCAB 34225; Ducke Reserve, KU 129942; Prainha, Aripuanã R., MZUSP 36886.

GOIÁS: Flôres, MZUSP 25348, USNM 121271; Mun. de Aliança, Jatobasinho, MNRio 2699 (5); mouth São Domingos River, MZUSP 25347.

MARANHÃO: Aldeia Araçu, igarapé Gurupi-Una, MZUSP 24954, 24958; Aldeia Javariuhu, igarapé Gurupi-Una, MZUSP 25014; Carolina, WCAB 6692–93.

MATO GROSSO: Chapada dos Guimarães, WCAB 15382; Pimentel River, Serra do Roncador, MZUSP 1358; mouth Tapirapés River, MZUSP 25276.

MINAS GERAIS: Uberlândia, MZUSP 12136.

PARÁ: As Pedras, Cuminá-Miri River, MZUSP 28400; Belém, MNRio 1470, MZUSP 11478; Belém-Brasilia road, km 43, MZUSP 24946; Benevides, KU 127397; Cachimbo, MZUSP 21835, 21876; IPEAN, KU 127395–96; Jacareacanga, WCAB 6645–46.

PERNAMBUCO: Agua Azul, Vicência, MZUSP 36837; Bonito, UMMZ 132459–460; Iguarassú, MNRio 2363; Recife, MZUSP 25029.

RONDÔNIA: Lg. Marmelo (near Abunã), WCAB 9840.

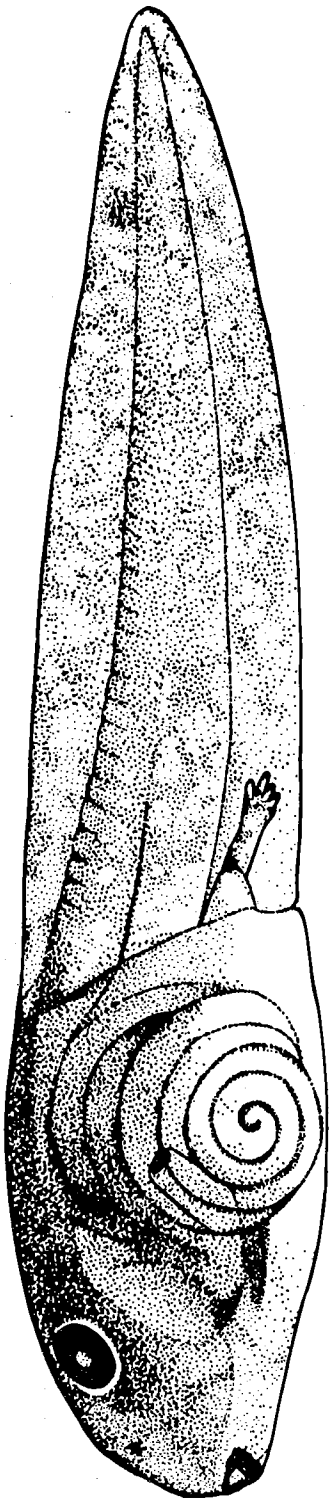
RORAIMA: Serra de Parima, MZUSP 24937–941.

COLOMBIA. CAQUETÁ: Florencia, USNM 147039–047.

META: Acacías, USNM 17048–050; Caño Losada, upper Río Guayabero, USNM 146346, 150488–89; Villavicencio, USNM 146433–35, 147396.

PUTUMAYO: about 7 km SE Mocoa, near Río Pepino, AMNH 84862–64; Santa Rosa de los Kofanes, about 30 minutes walking below San Antonio del Guamés, along middle course of Río Guamés, tributary of Upper Putumayo, CM 50647–650.

VAUPÉS: Río Ariari and Río Guaviare, UTA 2777, 2780, 3717, 3938–941, 3954.



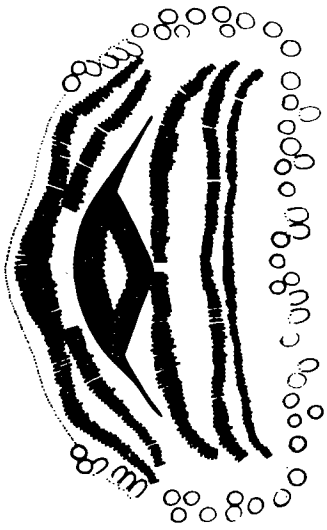


FIGURE 36. Lateral view and mouthparts of tadpole of *Leptodactylus amazonicus*. Semidiagrammatic figure based on specimens from Santa Cecilia, Ecuador.

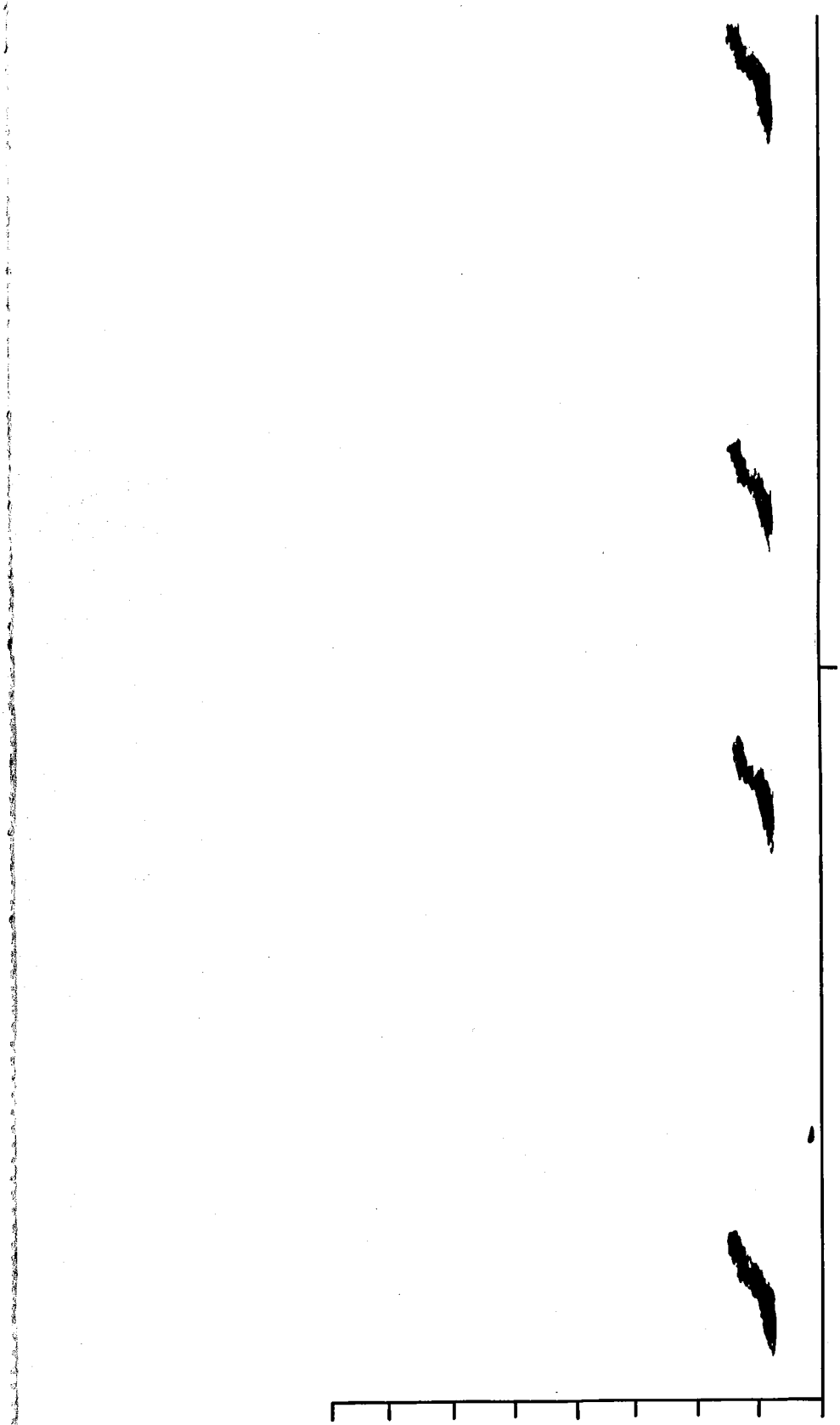


FIGURE 37. Sonagram of the mating call of *Leptodactylus amazonicus*, narrow band filter. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. Call from holotype, air temperature 22.9° C (LACM tape and specimen).

FIGURE 38. Strip chart record of the mating call of the holotype of *Leptodactylus amazonicus*. Line equals 0.01 s.

VICHADA: Anaben, UPR 91.

ECUADOR. NAPO: Limoncocha, LACM 92067–095, 92098–2125, MCZ 56308–317; Santa Cecilia, MCZ 56320–21, UMMZ 129282.

FRENCH GUIANA. Antécume-Pata (Haut Maroni), LES 1210–11; Cacao (Riv. Comté), LES 216–18; Embouchure, Haut Oyapock, Riv. Yaroupi, LES 1501; Saut Verdun et Grigel (Ouaque, Haut Maroni), LES 1447–49; Trois-Sauts (Haut Oyapock), LES 177; Village Pina (Haut Oyapock), LES 1150–54, 1161; Village Zidok (Haut Oyapock), LES 1285–89, 1291, 11204–05, 11207.

GUYANA. Issano, UMMZ 83584 (2); Kalacoon, Mazaruni River, AMNH 3988; Kartabo, AMNH 39593–94, 39651–56, 39658–59, 39661–62, 39665–68, 39672, CM 4065, UMMZ 83583 (3), USNM 118058; Kurupung, Upper Mazaruni Dist., UMMZ 83585; Rupununi, N of Acarahy Mts., W of New River, KU 69675–680, 69701–07; Shudi-kar-wau, AMNH 49250, 53488 (7); Yacarascine, LES 1494.

PERU. LORETO: Valley of Río Huallaga, AMNH 43198; Tapiche-Río Utoquinia, AMNH 43225, 43381.

SAN MARTÍN: Tocache Nuevo, Río Huallaga, USNM 195998–99.

SURINAM. Brokolonko Loksihattie, Saramacca, FMNH 134736–38, 134740; Kaiserberg Airstrip, Zuid River, FMNH 128826, 128841–42, 128924; Mataway, CM 44267–270; Paramaribo, USNM 158961–62.

VENEZUELA. AMAZONAS: Capibara, 106 km SW Esmeralda, Brazo Casiquiare, 130 m, USNM field 19585, 19588; La Culebra, UPR 3048; Monte Marahuaca, UPR 98–99.

ARAGUA: Maracay, near Rancho Grande, AMNH 70665–66.

LEPTODACTYLUS BUFONIUS BOULENGER 1894

Leptodactylus bufonius Boulenger, 1894: 348. (Type locality, Paraguay, Asunción. Lectotype BMNH 1947.2.17.72, female.)

Diagnosis.—The species with a combination of no distinct light stripe on the posterior face of the thigh and the posterior surface of the tarsus covered with obvious white tubercles are: *bufonius, labrosus, mystacinus, troglodytes,* and *ventrimaculatus*. A pair of distinct dorsolateral folds (indicated at least in color pattern in poorly preserved specimens) characteristic of *labrosus, mystacinus,* and *ventrimaculatus,* distinguish them from *bufonius,* which lacks well defined dorsolateral folds. The sole of the foot is covered with white tubercles in *troglodytes,* the sole of the foot is almost always smooth in *bufonius*. *Leptodactylus bufonius* has a Chacoan distribution, *troglodytes* occurs in NE Brasil.

Adult Characteristics (N = 139).—Dorsum spotted or blotched (fig. 1, C, E, F, L, M); mid-dorsal light stripe absent (100%); light lip stripe absent (100%); dark suborbital bar present; light stripe on posterior face of thigh absent (100%); tibia barred; a pair of indistinct dorsolateral folds present or (usually) absent; dorsal surface of tibia with white tubercles; posterior surface of tarsus with many or scattered white tubercles (100%); sole of foot rarely with white tubercles (6%), usually absent (94%), presence not sexually dimorphic (X^2 = 0.08, P = .77); male SVL 51.6 ± 2.0 mm, female 53.6 ± 2.3 mm, females larger ($F_{1, 137}$ = 29.86, $P < .001$); male head length/SVL ratio .366 ± .011, female .361 ± .011, male head longer ($F_{1, 137}$ = 6.58, $.01 < P < .025$); male head width/SVL ratio .346 ± .011, female .341 ± .012, not sexually dimorphic ($F_{1, 137}$ = 3.89, $.10 > P > .05$); male femur/SVL ratio .374 ± .024, female .377 ± .017, not sexually dimorphic ($F_{1, 137}$ = 0.82, $P > .05$); male tibia/SVL ratio .400 ± .018, female .398 ± .019, not sexually dimorphic ($F_{1, 137}$ = 0.41, $P > .05$); male foot/SVL ratio .381 ± .019, female .382 ± .020, not sexually dimorphic ($F_{1, 137}$ = 0.08, $P > .05$).

Larval Characteristics.—Available materials are insufficient for an adequate description.

Mating Call.—Dominant frequency modulated from 1000 to 2000 hz (fig. 39); note lacking harmonic structure (fig. 40); note either non-pulsed (fig. 40) or partially pulsed (Straughan and Heyer 1976, fig. 1); note duration 0.2 s; 1.25 notes/second.

Karyotype.—Diploid number 22, 7 pair median, 2 pair submedian, and 2 pair subterminal (Bogart, 1974) or 6 pair median, 2 pair submedian, and 3 pair subterminal (Heyer and Diment, 1974); secondary constriction in chromosome pair 8.

Distribution.—Found throughout the Gran Chaco and surrounding areas (fig. 34).

ARGENTINA. CHACO: Laguna Limpia, IML 562; Río Teuco, Estancia La Fidelidad, IML 122 (18); Roque Sáenz Peña, IML 588 (5).

FORMOSA: Ingeniero Juárez, IML 980 (55), LACM 91935, 91945–47, 91959–962, MCZ 35584; Bañados del Río Teuco, Depto. Bermejo, IML 1050 (29); La Florencia, Teuquito, IML 968 (9); Palma Sola, IML 1057.

JUJUY: Valle Grande, IML 1790.

LA RIOJA: Between Olta and Chamical, MCZ 33970–79.

SALTA: Abra Grande—Orán, IML 1696 (5); Aguaray, IML 560 (2); Embarcación, LACM 91925–27, 91929–932, 91934, 91937–940, 91942–44, 91948–950, 91953–58, 91963–65; Hickmann, IML 442 (39), 841 (128), 844 (64), 981 (27), KU 128857–58, MCZ 35336–345, USNM 159753; La Unión, IML 1755; Pocitos, MACN 4495; Saucelito, IML 1517.

SANTIAGO DEL ESTERO: Huyapampa, IML 819 (7), MCZ 32766–68; 46 km S Loreto, MCZ 33710–13; Ojo de Agua, IML 1139; Simbol Bajo, MACN 4999.

TUCUMAN: Los Gómez, IML 634 (3); Río Urueña (nr. Salta), IML 1761 (3); Tucumán, MZUSP 13783–84.

BOLIVIA. CHUQUISACA: 30 km SE Carandaiti, LACM 37705–06.

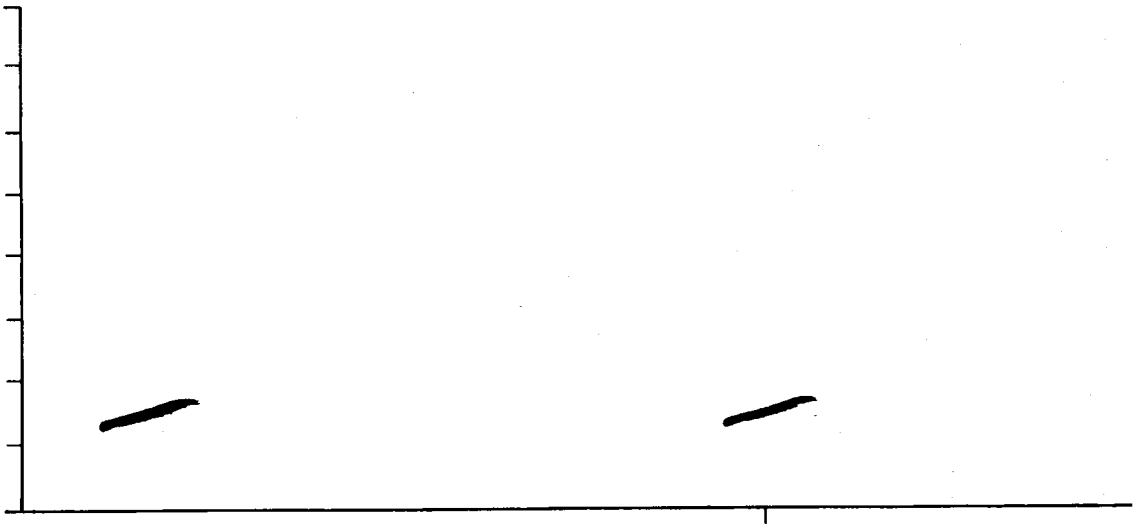


FIGURE 39. Sonagram of the mating call of *Leptodactylus bufonius,* narrow band filter. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. Specimen from Argentina, Embarcación, air temperature 24.8° C (LACM tape and specimen field number WRH 1411).

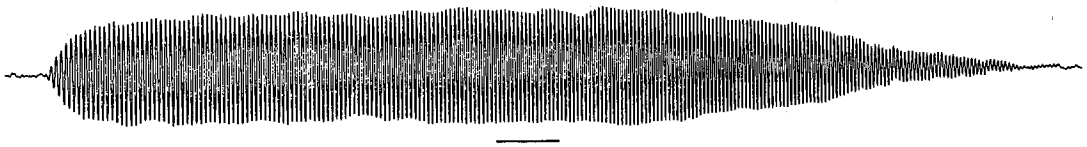


FIGURE 40. Strip chart record of the mating call of *Leptodactylus bufonius*. Line equals 0.01 s. See legend of Figure 39 for specimen data.

SANTA CRUZ: El Carmen, CM 36159–160, 36187, MCZ 29962–66; San José de Chiquitos, CM 36229, MCZ 29967–973, MZUSP 21340–41; Parapetí, KU 92902–04.

BRASIL. MATO GROSSO: Carandázal, MZUSP 127; Fazenda Cruzeiro, Aquidauana, MZUSP 16201.

PARAGUAY. Colonia Nueva Italia, MCZ 25806; Río Pilcomayo, MCZ 25819–821.

LEPTODACTYLUS ELENAE NEW SPECIES

Figure 41

Holotype: LACM 92096, an adult female from Argentina; Salta, Embarcación. Collected by Keith A. Berven, Laura M. Heyer, Miriam H. Heyer, and W. Ronald Heyer on 4 January 1972.

Diagnosis.—The species sharing the combination of a distinct light stripe on the posterior surface of the thigh and obvious white tubercles on the sole of the foot in some or all individuals are *albilabris, amazonicus, elenae, fragilis, fuscus, latinasus, mystaceus, notoaktites*. *Leptodactylus elenae* has no white tubercles on the dorsal surface of the tibia, differing from *albilabris, fragilis, latinasus,* and *mystaceus*. *Leptodactylus elenae* has 2 or 4 distinct (at least indicated in color pattern) dorsolateral folds, *fuscus* has 6. *Leptodactylus elenae* usually has white tubercles on the posterior tarsus, the tarsus is smooth in *amazonicus* and *notoaktites*. *Leptodactylus elenae* has a Chacoan distribution, *L. notoaktites* a SE Brasilian distribution.

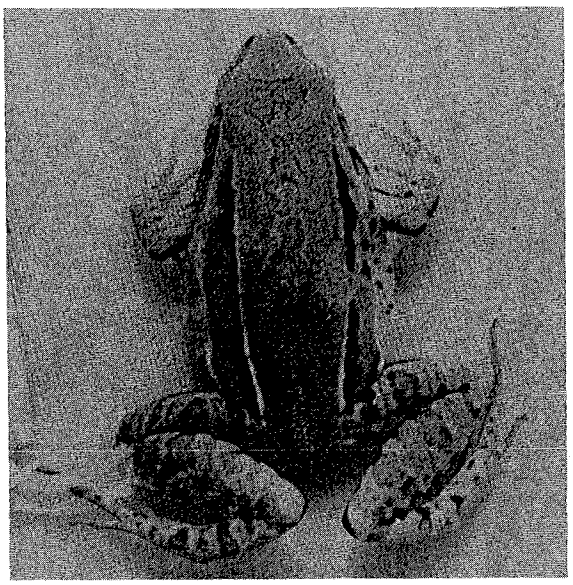


FIGURE 41. Dorsal view of the holotype of *Leptodactylus elenae*.

Description of Holotype.—Snout subelliptical from above, rounded-acute in profile; canthus rostralis slightly

obtuse; loreal slightly convex; tympanum distinct, greatest diameter just more than ½ eye diameter; vomerine teeth in slightly arched series posterior to choanae; finger lengths in order of decreasing length I≃III > II≃IV, I >> II; inner metacarpal tubercle flat, oval, smaller than flat, heart shaped outer metacarpal tubercle; dorsal surfaces smooth; 2 pair of dorsolateral folds (indicated by color pattern); ventral texture smooth; belly disk fold distinct; toe tips just wider than adjacent portion of toes; toes free, lacking fringe or web; subarticular tubercles moderately distinct; outer metatarsal tubercle small, round, about ⅓ oval inner metatarsal tubercle; tarsal fold extends about ¾ length of tarsus; no metatarsal fold; posterior surface of tarsus with scattered, barely visible light tubercles; sole of foot with many distinct white tubercles.

SVL 43.5 mm, head length 15.6 mm, head width 14.3 mm, interorbital distance 2.6 mm, eye-nostril distance 4.2 mm, femur 18.4 mm, tibia 20.6 mm, foot 22.1 mm.

Dorsum tan with darker tan markings consisting of an irregular interorbital bar and 2 dorsal blotches; inner broken light pin stripe bordered by outer irregular dark brown stripe along dorso-lateral fold from back of eye to groin; broken light pin stripe along lateral fold; dark brown canthal stripe from tip of snout across upper tympanum to humeral region; distinct light upper lip stripe; limbs faintly barred; venter immaculate; tarsal fold highlighted by a white line; posterior surface of thigh blotched with distinct light longitudinal stripe.

Etymology.—Named for my daughter, Elena, who shares my enthusiasm for encountering frogs in nature.

Remarks.—This is the species referred to as "southern *mystaceus*" in the morphological analysis.

Adult Characteristics (N = 43).—Dorsum spotted, spots rarely fused (fig. 1, A, B, C); no light mid-dorsal stripe; light lip stripe usually distinct (77%), sometimes indistinct (23%), distinctiveness not sexually dimorphic ($X^2 = .77$, $P = .38$); dark suborbital bar absent; light stripe on posterior face of thigh distinct (100%); tibia barred; usually 4 well defined dorsolateral folds; no white tubercles on dorsal surface of tibia; many or scattered white tubercles usually present on posterior surface of tarsus (91%), sometimes lacking (9%), presence not sexually dimorphic ($X^2 = 3.16$, $P = .08$); sole of foot with many or scattered white tubercles (100%), male SVL 42.7 ± 2.5 mm, female 42.8 ± 3.1 mm, not sexually dimorphic ($F_{1, 41} = .02$, $P > .05$); male head length/SVL ratio .375 ± .011, female .374 ± .009, not sexually dimorphic ($F_{1, 41} = .15$, $P > .05$); male head width/SVL ratio .338 ± .013, female .336 ± .019, not sexually dimorphic ($F_{1, 41} = .20$, $P > .05$); male femur/SVL ratio .406 ± .021, female .404 ± .034, not sexually dimorphic ($F_{1, 41} = .08$, $P > .05$); male tibia/SVL ratio .468 ± .020, female .470 ± .030, not sexually dimorphic ($F_{1, 41} = .06$, $P > .05$); male foot/SVL ratio .501 ± .027, female .491 ± .030, not sexually dimorphic ($F_{1, 41} = .95$, $P > .05$).

Larval Characteristics.—Larvae unknown.

Mating Call.—Barrio (1965) described and figured the call (as *L. mystaceus* from Villa Angela, Chaco). The fundamental frequency modulates from 700–1500 hz, note duration 0.3 s, call repetition rate 2 notes per second.

Karyotype.—Diploid number 22, no terminal pairs (no further interpretations can be made from the karyotype prepared from LACM 92097, from the type locality).

Distribution.—Found in the Gran Chaco and adjacent areas to central Brasil and Río Huallaga, Peru (fig. 42).

ARGENTINA. JUJUY: Ruta Yuto-Ledesma, near Arroyo Quemado, IML 1275, Ruta Yuto-Ledesma, 7 km from bifurcation, IML 1274.

SALTA: Campo Aguaray, IML 1472 (2); El Saucelito, 50 km S Orán, IML 1624 (5) near Embarcación, LACM 92026–27, 92127; Río Pescado, IML 1401 (9).

BOLIVIA. BENI: Lake Rogoagua, UMMZ 64108; Río Mamoré, about 10 km W San Pedro, AMNH 79095.

LA PAZ: Ixiamas, UMMZ 64106 (2).

SANTA CRUZ: Buenavista, CM 3889, 4345, 4352, 4432, UMMZ 63832 (4), 66491, 66543 (2); El Carmen, MCZ 29985; San José de Chiquitos, CM 36118, MCZ 29987–88.

BRASIL. MATO GROSSO: Carandázal, MZUSP 139; Corumbá, CM 36162; Rosario Oeste, WCAB 15628–632; Salobra, USNM 133011–12; Santo Antônio do Leverger, WCAB 15102–05; Parque Indígena do Xingu, Posto Diauarum, MZUSP 49543, WCAB 37186.

PERU. SAN MARTÍN: Tocache Nuevo, Río Huallaga, USNM 195998–99.

LEPTODACTYLUS FRAGILIS (BROCCHI) 1877

Cystignathus fragilis Brocchi 1877:182–184. (Type locality, Mexico, Tehuantepec. Holotype Paris Museum 6316, female.)

Remark.—This is the species referred to as *labialis* in the analysis section and in the herpetological literature for the past 30 years.

Diagnosis.—The species demonstrating a combination of a distinct light stripe on the posterior surface of the thigh, and obvious white tubercles on the posterior surface of the tarsus and sole of foot in some or all individuals are *albilabris, elenae, fragilis, latinasus,* and *mystaceus*. *Leptodactylus elenae* has a smooth dorsal tibial surface, the dorsal surface of the tibia is covered with white tubercles in *fragilis*. *Leptodactylus albilabris* and *mystaceus* have distinct dorsolateral folds (indicated by color pattern in poorly preserved specimens), *fragilis* has indistinct dorsolateral folds or lacks them. *Leptodactylus fragilis* and *latinasus* have considerable morphological and color pattern overlap (fig. 43), *fragilis* being a slightly larger species (maximum male SVL 43 mm, female 43.6 mm) than *latinasus* (maximum male SVL 37.9 mm, female 36.3 mm). *Leptodactylus fragilis* has a Middle American and north coast South American distribution, *L. latinasus* has a southern South American distribution.

Adult Characteristics (N = 591).—Dorsum spotted or blotched, blotches rarely confluent (fig. 1, A, B, C,

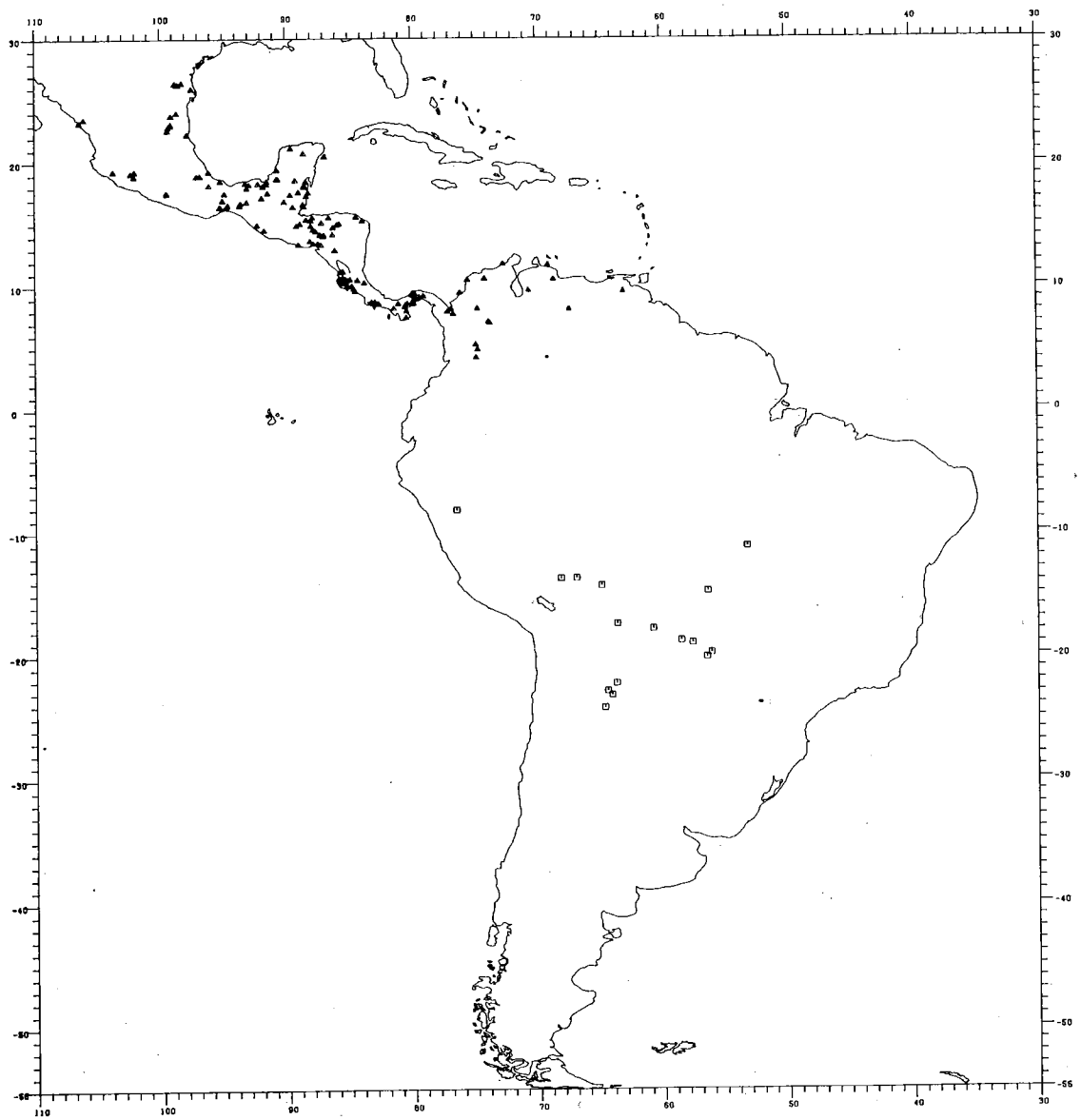


FIGURE 42. Distribution map of *Leptodactylus elenae* (squares) and *fragilis* (triangles).

D, E); mid-dorsal light stripe absent; light lip stripe usually indistinct (97%), rarely distinct (3%), distinctiveness not sexually dimorphic ($X^2 = .01$, $P = .94$); dark suborbital bar absent; light stripe on posterior face of thigh usually very distinct (66%), often moderately distinct (33%), rarely absent (1%), expression not sexually dimorphic ($X^2 = 2.70$, $P = .26$); tibia barred; dorsolateral folds usually indistinct, 2 or 4 present when visible; dorsal surface of tibia usually covered with many white tubercles, sometimes scattered with white tubercles; posterior surface of tarsus with many white tubercles (89%), rarely absent (11%), presence of tubercles not sexually dimorphic ($X^2 = 2.50$, $P = .11$); sole of foot always with many white tubercles (100%); male SVL 34.7 ± 2.9 mm, female 34.2 ± 2.6 mm, not sexually dimorphic ($F_{1, 589} = 3.23$, $P > .05$); male head length/SVL ratio .379 ± .017, female .376 ± .013, male head longer ($F_{1, 589} = 9.22$, $.001 < P < .005$); male head width/SVL ratio .336 ± .019, female .333 ± .016, male head wider ($F_{1, 589} = 4.64$, $.025 < P < .05$); male femur/SVL ratio .389 ± .028, female .399 ± .025, female femur longer ($F_{1, 589} = 22.19$, $P < .001$); male tibia/SVL ratio .451 ± .026, female .456 ± .026, female tibia longer ($F_{1, 589} = 44.43$, $P < .001$); male foot/SVL ratio .494 ± .033, female .502 ± .030, female foot longer ($F_{1, 589} = 10.03$, $.001 < P < .005$).

Larval Characteristics.—Eye diameter 12–16% head-body length; oral disk width 17–22% head-body length; oral papilla gap 53–67% oral disk width 46–101 denticles in one side of split tooth row anterior to beak;

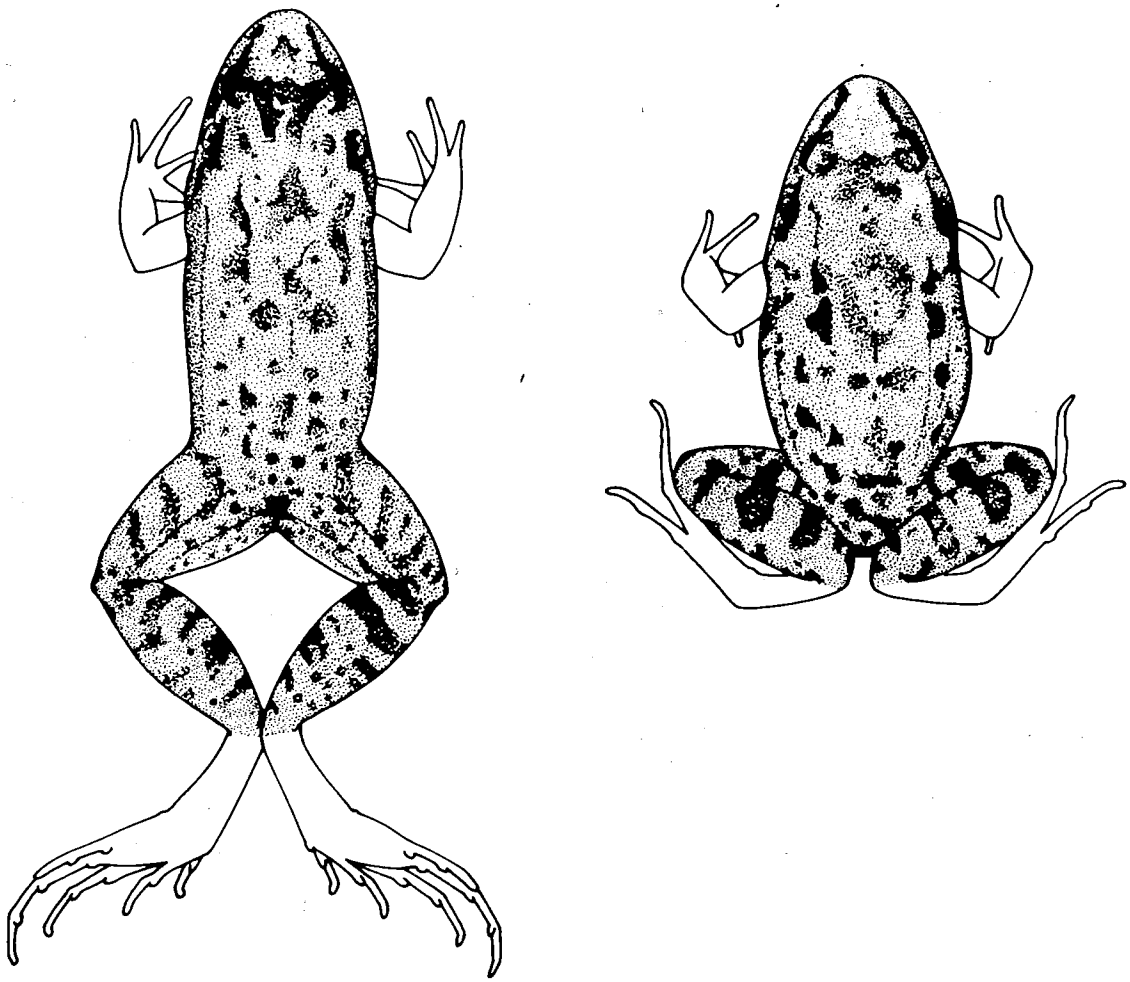


FIGURE 43. Dorsal views of *Leptodactylus fragilis* (left, KU 116833) and *latinasus* (right, LACM 92039).

head-body length 31–40% total length; total length, stage 41, 41 mm (Heyer 1970b, figs. 7, 12, 17).

Mating Call.—Dominant frequency modulates from 600–1200 hz (Texas) to 1000–2200 hz (Panama); call lacking harmonic structure; call with a pulsatile and non-pulsatile portion; pulsatile portion .170 s duration immediately followed by non-pulsatile portion of .023 s duration; note repetition rate 1.5 per second (Straughan and Heyer 1976, fig. 3).

Karyotype.—Bogart (1974) described the karyotype as diploid number 22; 7 pair median, 1 pair submedian, 3 pair subterminal; secondary constriction in chromosome pair 8.

Distribution.—From southernmost Texas throughout lowland Middle America along the north coast of South America as far as Venezuela, including the Magdalena Valley of Colombia (fig. 42).

BELIZE. Belize, FMNH 4392, 4398, 4732, UMMZ 124744 (3); Corozal, (A. Ross collection numbers) 2975–981, 2984, 2986–88, 2991–92, 2998–3036, 3046–058; Gallon Jug, MCZ 37863, 37873–74; Kates Lagoon, FMNH 49060; Manatee, FMNH 4263; Monkey River, Swazey Branch, MCZ 37867–872; Otro Benque, USNM 194891–99, 194931; Tower Hill, USNM 167739, 194081–83.

COLOMBIA. ANTIOQUIA: Casabe, USNM 147079; Chigorodó, near Turbo, USNM 153915–17; Golfo de Urabá, N Turbo, LACM 50198, USNM 150491–0515; Nechí, FMNH 54572, 54575–76.

BOLÍVAR: Cartagena, Bocagrande, CM 50603; Isla Fuerte, FMNH 74937, USNM 150516–19.

CHOCÓ: Atrato, Sautatá, FMNH 74920 (2).

CUNDINAMARCA: Beltrán, USNM 145743.

GUAJIRA: near Pájaro, USNM 151306.

MAGDALENA: Fundación, UMMZ 48489–492, 48495–99, 48503–04, 48509, 48511, USNM 102409.

NORTE DE SANTANDER: Catatumbo, USNM 145088–092; Río Zulia, USNM 147071, 147074–75.

SANTANDER: El Centro, FMNH 81760, USNM 144839–842, 147091–92; Río Zulia, USNM 147051–52.

TOLIMA: Espinal, MCZ 15065–66, 15069–070, 15072–75 (2); Mariquita, FMNH 81835, 81838, USNM 150516–19.

COSTA RICA. ALAJUELA: Los Chiles, CRE 7215, 7217 (2).

GUANACASTE: Arenal, CRE 6251 (2); 2.4 mi N. Bagaces, CRE 8193; near Cañas, CRE 2902 (2), 8009, 8181; 50

km S Cañas, CRE 249; Finca Jiménez, CRE 3088 (2), 3091, 3094 (2), 3095 (8), 3097, 3099 (2); 7.6 mi S La Cruz, CRE 8091; near Liberia, CRE 107, 2888, 8015 (3), 8140, 8153, 8162 (2), 8163–64; 21.3 mi SW Liberia, CRE 8215; 35.5 mi N Liberia, CRE 8196; between Liberia and Cañas, USNM 192558; near Nicoya, CRE 8229–230; near Playa del Coco, CRE 6504, 6512–14, 6516 (2), 8012 (4); near Santa Cruz, CRE 8218; Hacienda Taboga, CRE 6297, 6439.

LIMÓN: Los Diamantes, FMNH 176916.

PUNTARENAS: near Barranca River, CRE 254, 739 (4); base of Peninsula, CRE 253 (4); Coto, km 47 on rail from Golfito, CRE 176–78, 180 (5); Esterillos Oeste, 15 km SE Jacó, CRE 2873 (3); Golfito, CRE 7231; Río Grande de Tárcoles, 6.1 km NE mouth, SW Orotina, CRE 817; Villa Neily, 75 m, CRE 8039 (6); 13.6 mi NW Villa Neily, CRE 8005.

EL SALVADOR. LA PAZ: Los Blancos, FMNH 65121-22.

MORAZÁN Divisadero, USNM 73285-86.

GUATEMALA. EL PETEN: near La Libertad, CM 13020, MCZ 21455; Pacomon, USNM 71333; near Poptún, UMMZ 117989 (7), 124377 (8), 124378 (2), 124379 (4), 124380 (2); Tikal UMMZ 117988.

RETALHULEU: Hacienda Casa Blanca, UMMZ 107886, 107887 (7).

HONDURAS. CHOLUTECA: 2 mi NE Choluteca, LACM 60525–28.

COMAYAGUA: 2–3 mi S Comayagua, LACM 47522, 47532, 3½ mi WSW Siguatepeque, LACM 47531.

COPÁN: Copán, FMNH 40864; 6 mi SW La Florida, LACM 47523.

CORTÉS: Lake Ticamaya, E San Pedro, FMNH 4656–660; Lake Yojoa, MCZ 26407–09 (8); 2½–4½ mi ENE Villanueva, LACM 47524–530.

EL PARAÍSO: 1 km N Santa María, LACM 45084–85.

FRANCISCO MORAZÁN: 8.6 mi NW Comayaguela, LACM 60529–532; El Hatillo, 1400 m, LACM 72074; El Picacho, Tegucigalpa, MCZ 28887–898; El Zamorano, 2700 ft, LACM 39757; near Río Yeguare, MCZ 25964–69 (8), 26466 (30).

GRACIAS A DIOS: Ahuás, LACM 45245; Tansín, 15 km NW Puerto Lempira, LACM 47511–16.

OLANCHO: 8.6 mi E Catacamas, LACM 45101–03; 7.6 mi SW Juticalpa, LACM 45238–240; ½ mi SE San José de Río Tinto, LACM 45178, 45194–99.

SANTA BÁRBARA: Quimistán, USNM 128058–59.

VALLE: near Río Guascorán, LACM 45064, 47520–21; 5.5 mi E San Lorenzo, LACM 48374.

YORO: 1.5 km W Olanchito, LACM 47517–19; Subirana Valley, FMNH 21821–24, MCZ 21260–69 (4).

MEXICO. CAMPECHE: Balchacah, FMNH 108273, 108276, 108279–280, 108282–87, 108289–291, 108298–8301, 108306, 108310–11, 108315–16, 108319, 108322–27, 108329–330, 108333–35, 108337, 108340–41, 108344, 108355, 108357, 108362, 108364–371, 108376, 108380–81 108385, 108388, 108390–92, 108395–98, 108401, 108408, 108410–11, 108413–15, 108422–24, 108426; Champotón, MCZ 21452; Escárcega, 5 mi W "El Tormento," CM 40106–07; Matamoros, FMNH 38588; Pital, FMNH 108271, 108312, 108348, 108352, 108361, 108373, 108383, 108409, 108421; Tres Brazos, FMNH 108288, 108320.

CHIAPAS: near Asunción, FMNH 108443; El Censo, MCZ 28255; El Real, 600 m, MCZ 28271 (4); near San Ricardo, FMNH 108436, 108444–45, 108461, 108467; near Tapachula, FMNH 108435; near Tonda, FMNH 108460; near Tuxtla Gutiérrez, FMNH 108449.

COLIMA: 7.5 mi SW Colima, LACM 37265–66, 37430–34.

GUERRERO: 2 mi S Garropata, 44 mi S Chilpancingo, FMNH 108454; near Palo Blanco, S of Chilpancingo, FMNH 108427, 108430, 108432, 108446, 108452, 108459, 108462, 108464–65.

MICHOACÁN: Apatzingán, FMNH 38806–817; 11.7 mi S Cuatro Caminos, LACM 37049, 37429; Hacienda El Sabino, FMNH 108438, 108448, 108458, 108466.

MORELOS: near Antiguo, FMNH 108431, 108434, 108450, 108457, 108483.

OAXACA: Barrio, USNM 30241–42; Matías Romero, AMNH 52139–140 (3), 69508; Mixtequilla, AMNH 13922; Niltepec, CM 52739–742; 10 mi W Río Ostuta, FMNH 72427–28; Tehuantepec, AMNH 65633–35, MCZ 15767, USNM 10018–19, 27765, 114229–231; Tolosa, AMNH 53608–09; Tuxtepec Soyaltepec, LACM 74753.

QUINTANA ROO: Isla Cozumel, 12 km SW San Miguel, CM 41315; Laguna Chacanacab, 86 km W Chetumal, CM 45231–32.

SAN LUIS POTOSÍ: El Salto Falls, 12 mi W Nuevo Morelos, UMMZ 99518 (7).

TABASCO: 2.5 mi NE Comalcalco, AMNH 60317; Encarnación, FMNH 106351, 108272, 108274–75, 108278, 108281, 108292–97, 108302–05, 108307, 108309, 108313–14, 108317–18, 108321, 108328, 108331–32, 108336, 108338–39, 108342–43, 108345–47, 108349–351, 108353, 108358–360, 108363, 108372, 108374–75, 108377–79, 108382, 108384, 108386–87, 108389, 108393–94, 108399–8400, 108402–07, 108412, 108416–18, 108420, 108425, 108456; Tenosique, USNM 114217–18; 43 mi N Villa Hermosa, USNM 192539.

TAMAULIPAS: Arroyo Los Almos, 3 mi SE Rio Grande City, FMNH 108429; Ciudad Victoria, N on Highway 101, LACM 64151; La Laguna Doña Ana, MCZ 24982–86 (2); between Monterrey and Ciudad Victoria, FMNH 108481; Ocampo, AMNH 62065–66; Pano Ayuctle, 5 mi NE Gómez Farías, UMMZ 98948, 102913, 110714 (4); Rancho Sta. Ana, MCZ 24973–77 (2); Río Corona, MCZ 24966–68; 3 mi W San Gerardo, UMMZ 110712 (2), 110713 (3); 10 mi E jct highways 80 and 85 to Tampico, LACM 65752; 10 mi N Victoria, FMNH 105279, 108442, 108451, 108453, 108472, 108477, 108479–480, 108482, 108487.

VERACRUZ: Hacienda La Oaxaqueña, 30 km S Jesús Carranza, on Coatzacoalcos River, AMNH 43926–29; Orizaba, USNM 16547; Potrero near Córdoba, USNM 32410–12; Potrero Viejo, FMNH 108277, 108468–69, 108471, USNM 114210–16; Río Chiquito at San Lorenzo, USNM 123528–29; near San Andrés Tuxtla, AMNH 69505, FMNH 108437; near San Gerónimo, FMNH 108433, 108440, 108455; Tierra Colorado, FMNH 108428; Veracruz, MCZ 4651–52.

YUCUTÁN: Chichén Itzá, FMNH 26962–64, 36567 (7); Cozumel Id., UMMZ 78548 (14); Dzibichaltún, Cenote Xcalah, CM 45230.

NICARAGUA. MATAGALPA: near Sebaco, LACM 9430–34.

PANAMA. CANAL ZONE: Alhajuela, CM 7391, 7407; Balboa, AMNH 41759, MCZ 17378, Fort Kobbe, USNM 193338 (3); Fort Sherman, MCZ 16017; Gatun, MCZ 35645; Laguna to Mendoza, Madden Dam road, AMNH 55398; 2 mi W Locona, KU 67949–951; Majanál, MCZ 10729; Rosseau, KU 67948; Summit, FMNH 22976–77, KU 115292–301.

CHIRIQUÍ: 3.3 mi E Concepción, AMNH 69723.

COCLÉ: 3.2 km W Aguadulce, 15 m, KU 115291; 1 km NE El Caño, 40 m, KU 115290; El Valle de Antón, AMNH 59585–87, 59589, 69721–22, FMNH 22985, KU 76519; near Penonomé, 30–70 m, KU 115281–89, 116833, 116835–37.

COLÓN: Achiote, 40 m, KU 76517–18; 3.5 km SE Puerto Pilón, 260 m, KU 116834.

LOS SANTOS: Los Santos, CM 43570; Tonosí, 40 m, KU 108617–624.

PANAMÁ: 14.4 km SSW Bejuco, 40 m, KU 115302; Capitán, near Chepo, USNM 192622; near La Chorrera, CM

23483; Nueva Gorgona, AMNH 69720; Panama City, MCZ 17580; about 8 mi W Playa Coronado, road to Laguna, FMNH 67893–95; near Puerto la Chorrera, UMMZ 95477; Tapia, AMNH 18932, 22838.

VERAGUAS: Cerro Lute, near Santa Fe, FMNH 67896–7908; Mojara, USNM 129843–44; Río Corobora, USNM 140877.

UNITED STATES. TEXAS: Cameron County; Brownsville, FMNH 27150 (12); Hidalgo County; 10 mi NW Edinburg, USNM 101143–44; 15 mi W Mission, UMMZ 98905; Starr County; 13 mi SE Rio Grande City, Arroyo El Salado, AMNH 46014, FMNH 107556–57.

VENEZUELA. APURE: Hato La Cuanota, 4 km W San Fernando de Apure, TCWC 45229–260, 45262–67, 45269–278; Río Apure at San Fernando de Apure, UMMZ 85112.

FALCÓN: Boca de Yaracuy, 28 km WNW Puerto Cabello, USNM field 1543–48; 19 km NW Urama, km 40, USNM field 5176–182.

MONAGAS: 42 km SE Maturín, LACM 31380–81.

TRUJILLO: Sabana de Mendoza, UMMZ 57478–482.

YARACUY: San Felipe, BMNH 1973.2274–75.

LEPTODACTYLUS FUSCUS SCHNEIDER 1799

Rana fusca Schneider 1799:130–131. (Type locality not specified. Neotype Paris Museum 680, male [lectotype of *Rana typhonia* Daudin 1803 and *Cystignathus typhonius* Duméril and Bibron 1841]).

Rana typhonia Daudin 1803:55–56, plate 17, fig. 3. (Type locality, Surinam. Lectotype Paris Museum 680, male.)

Rana sibilatrix Wied-Neuwied 1824: fig. 2. (Type locality originally undesignated, designated by Müller (1927) as Vila Viçosa, rio Peruipé. Type material apparently lost.)

Cystignathus typhonius Duméril and Bibron 1841:402–404. (Type locality, French Guiana and Surinam. Lectotype Paris Museum 680, male.)

Cystignathus schomburgkii Troschel 1848:659. (Type locality, British Guiana. Type material apparently lost.)

Leptodactylus raniformis Werner 1899:479–480. (Type locality, Colombia; Llanos, Río Meta. Holotype II Zoologisches Institut und Museum der Universität, Göttingen, no number, male.)

Leptodactylus gualambensis Gallardo 1964:46–50, plate 2, fig. 1. (Type locality, Argentina; Salta, Urundel, 43 km W Orán, Río Santa María. Holotype MACN 9752, male.)

Diagnosis.—The species having a combination of a light stripe on the posterior surface of the thigh and 6 distinct dorsolateral folds (almost always recognizable in *fuscus*) in some or all individuals are *fuscus, geminus, gracilis, laurae, longirostris, marambaiae, mystaceus, notoaktites,* and *poecilochilus*. Of these, only *fuscus* has individuals that have 6 dorsolateral folds without a light mid-dorsal stripe; in all of the other species, the individuals with 6 dorsolateral folds also have a light mid-dorsal stripe (this feature allows positive identification when series of specimens are available). Individuals of *L. fuscus* rarely have distinct white tubercles on the sole of the foot and posterior surface of the tarsus, but small light spots are present on these surfaces indicating the presence of weakly developed tubercles. The posterior surface of the tarsus and sole of foot are smooth and uniform in coloration in *geminus, gracilis, laurae, longirostris, marambaiae,* and *poecilochilus*. *Leptodactylus mystaceus* usually has well developed, distinct white tubercles on the posterior surface of the tarsus and sole of foot. *Leptodactylus notoaktites* has a smooth posterior surface of the tarsus.

Adult Characteristics (N = 392).—Dorsum spotted or blotched (fig. 1, C, D, E, F, G, H, I); mid-dorsal light stripe sometimes present (20% of individuals), presence not sexually dimorphic ($X^2 = 1.98$, $P = .15$); light lip stripe usually indistinct (81%), sometimes distinct (19%), more females with distinct light lip stripes than males ($X^2 = 19.18$, $P < .001$); dark suborbital bar absent; light stripe on posterior face of thigh usually very distinct (77%), often moderately distinct (23%), distinctiveness not sexually dimorphic ($X^2 = 3.67$, $P = .06$); tibia barred; usually 6 distinct dorsolateral folds; dorsal surface of tibia usually lacking white tubercles, few rarely present; posterior surface of tarsus rarely with distinct white tubercles (4%), but scattered light spots associated with tubercles almost always present, presence of distinct tubercles not sexually dimorphic ($X^2 = .39$, $P = .53$); sole of foot rarely with distinct white tubercles (8%), but many to scattered light spots associated with tubercles almost always present, presence of distinct tubercles not sexually dimorphic ($X^2 = .83$, $P = .36$); male SVL 42.8 ± 4.0 mm, female 43.6 ± 4.4 mm, not sexually dimorphic ($F_{1, 390} = 3.47$, $P > .05$); male head length/SVL ratio .374 ± .015, female .376 ± .021, not sexually dimorphic ($F_{1, 390} = 1.12$, $P > .05$); male head width/SVL ratio .336 ± .015, female .332 ± .017, male head broader than female ($F_{1, 390} = 4.55$, $.025 < P < .05$); male femur/SVL ratio .426 ± .024, female .436 ± .028, female femur longer than male ($F_{1, 390} = 14.61$, $P < .001$); male tibia/SVL ratio .510 ± .031, female .521 ± .030, female tibia longer than male ($F_{1, 390} = 12.46$, $P < .001$); male foot/SVL ratio .509 ± .028, female .514 ± .032, not sexually dimorphic ($F_{1, 390} = 3.75$, $P > .05$).

Larval Characteristics.—Lescure (1972) described and figured the larvae.

Mating Call.—Dominant frequency modulates between 1000–2800 hz (fig. 15); no harmonic structure in call; call pulsed or partially pulsed (fig. 16); note duration .16–.17 s, note repetition rate 1 per second.

Karyotype.—Diploid number 22; 7 pair median, 3 pair submedian, 1 pair subterminal (Bogart, 1974) or 5 pair median, 3 pair submedian, 3 pair subterminal (Heyer and Diment 1974); secondary construction on chromosome pair 8.

Distribution.—Known from a broad geographic range from Panama, throughout lowland South America east of the Andes (fig. 44).

ARGENTINA. CORRIENTES: Ituzaingó, Isla Apipé, IML 711, 768, 914; Manantiales, IML 778, MACN 13422–23, MCZ 35586.

FORMOSA: Esteros Lacuna Oca, IML 2195; Ingeniero Juárez, IML 700, 1102, 2194.

JUJUY: Ruta Yuto-Ledesma, near Arroyo Quemado, IML 1277–78, 1280.

MISIONES: Caraguatay, FMNH 9304; El Bonito, IML

FIGURE 44. Distribution map of *Leptodactylus fuscus*.

2045; Mártires, MACN 13644–46; Oberá, IML 769; Río Paranay, FMNH 9395–98, 9400, 9454, 9456–57; San Ignacio, IML 707.

SALTA: Agua Blanca, IML 1686; Campo Aguaray, IML 1470; near Embarcación, LACM 92010–030; near Hickmann, IML 448, 454, 660, 699; Los Toldas, Santa Victoria, IML 2252; Orán, Abra Grande, IML 1584, 1691, 2212; Río Pescado, IML 1403 (3); Tobantirenda, N Aguaray, IML 555, 1481.

BOLIVIA. BENI: Beni, FMNH 140212; Rurrenabaque, MCZ 10092–93, UMMZ 58831 (18).

COCHABAMBA: Villa Tumarí Road, km 58, Chapare Prov., USNM 146508–512.

SANTA CRUZ: Buenavista, CM 3883–84, 3954–55, 3957, 3976, 4241, 4392, 4431, 4433–34, 4436, 4439–440, UMMZ 60633 (5), 60634 (4), 60637; El Carmen, CM 36247; San José de Chiquitos, CM 36230 (8), MCZ 30032–38.

BRASIL. AMAZONAS: Coarí, MZUSP 28129, 39845–861, 40805–0950; Igarapé Belém, rio Solimões, MZUSP 24599–4600; Manacapuru, MZUSP 15951; Manaus, FMNH 64220, MCZ 295; Tefé, MZUSP 39919.

BAHIA: near Barreiras, UMMZ 109999, 110000 (2), 110001–03; Bom Jesus da Lapa, UMMZ 109996–98 (3), 110004.

CEARÁ: Crato, MNRio 409.

DISTRITO FEDERAL: Brasilia, MNRio 2716 (3).

ESPÍRITO SANTO: Itá, MZUSP 24601–610, 24669, USNM 121267–69; Linhares, MZUSP 25096.

GOIÁS: Aruanã, MZUSP 4993, 7549–551; Barra R. S. Domingos, MZUSP 24622–25, USNM 121299; Cana Brava, MZUSP 24628–646, USNM 121289–291, 121297–98; Fazenda Transvaal, Rio Verde, MZUSP 12511; Flôres, MZUSP 24626; Jaraguá, MZUSP 1419; Rio Verde, MZUSP 25340–42; Sta. Isabel, Ilha do Bananal, MZUSP 24627.

MARANHÃO: Perimirim, WCAB 8816.

MATO GROSSO: Buritĺ, Chapada dos Guimarães, MZUSP 37459–460; Corumbá, CM 36231–32, MCZ 30030–31, MZUSP 25496; Dumbá, MZUSP 1433; Fazenda Cruzeiro, Aquidauana, MZUSP 16206–07; Local do Massacre, MZUSP 4279–280, 14747–48; Mato Verde, rio Araguaia, MZUSP 24611–621; Santa Luzia (ex. Juti), MZUSP 28552; São Domingos, rio das Mortes, MZUSP 1080, 1093, 1394, 1397; São Luiz de Cáceres, MNRio 3073 (6), MZUSP 3638, 22160–67; mouth, Tapirapés River, MZUSP 25277–281; Três Lagoas, MZUSP 25221, 25227; Urucum, MZUSP 21382–85; Utiariti, MZUSP 25207– 211; Parque Indígena do Xingu, Posto Diauarum, MZUSP 49491–9500.

MINAS GERAIS: Arinos, MZUSP 25050–51; Belo Horizonte, MNRio 1060–62, UMMZ 109994 (3); Januária, rio Pandeiros, MZUSP 24647–668, USNM 121287; Lagoa de Curralinho, Lassance, USNM 97015, 98210; Lagoa Santa, MZUSP 25076, 25080–81; Morro da Garça, MZUSP 25087; Ouro Preto, USNM 98028–044; Passa Quatro, MNRio 3898 (4); Pirapora, USNM 98268–271; Piraporinha, UMMZ 109995, USNM 98548; Rib. Confins, Buritís, MZUSP 25070; Rio Pandeiros, MZUSP 24152, USNM 121288, 121294–96; Sete Lagoas, MZUSP 25085; Uberlândia, MZUSP 12090–2122.

PARÁ: Barreira, rio Tapajós, MZUSP 35805; Cachimbo, MNRio 2860 (3), MZUSP 21596–97, 21836–37, 21849–853, 21874; Cachoeira do Araří, Ilha de Marajó, MZUSP 24973–74; Igarapé Taperebá, Ilha de Marajó, MZUSP 24961, 24963–64, 24966–67, 24969–971; João Cativo, km 149 da Rede Cearense, 12 km a oeste de Itapipoca, MNRío 3901; Rio Trombetas, headwaters, 15 km from Surinam, KU 128029–033.

RIO DE JANEIRO: Caxias, MNRio 2240; Campo Belo, USNM 96944–45; Itaguaí, MCZ 32699–2700; Itatiaia, Vale Paraíba, MNRio 3555, 3561; Niteroi, Saco de São Francisco, USNM 99119; São João da Barra, MNRio 2539 (6); Teresópolis, USNM 97678–79.

RIO GRANDE DO SUL: Rio Pardo, MZUSP 21682–83; 39 km W Rio Pardo, FMNH 80332–33; Santa Maria, UMMZ 83133; Santo Augusto, Baixada da Olaria, MNRio 3844 (6).

RONDÔNIA: Pôrto Velho, MZUSP 16917–17365; Forte Príncipe da Beira, MZUSP 25160–61.

SÃO PAULO: Botucatú, MZUSP 4156; Emas, USNM 129176–77; Eugênio Lefévre, MZUSP 14906; Ituai, FMNH 83274; Jurumirim, MZUSP 24672; Piracicaba, MZUSP 1302; Piraçununga, Cachoeira de Emas, CM 33436, MNRio 2114; MZUSP 2294, 2440, 2442, 2860, 2862–65, 2867–68, 4606–612, 4614–15, 4617–626, 9035–37, 11105–155, 11224, 24670–71; Pôrto Martins, MZUSP 116–17, 281, 1963, 1966; Rio Pardo, Botucatú, MZUSP 3868; Rio Preto, MZUSP 24674; São Paulo, MZUSP 24677–686.

COLOMBIA. ANTIOQUIA: Nechí, FMNH 54569–570, 54573–74, 54577–78; Villa Arteaga, FMNH 78141.

BOLÍVAR: Río Viejo, USNM 145777–79; Tierra Alta, FMNH 61806; Tolu Viejo, MZUSP 5438, 5442.

BOYACÁ: Miraflores, USNM 153920–21.

CUNDINAMARCA: Cambao, USNM 147080–82; Villeta, USNM 151878.

MAGDALENA: Fundación, MCZ 8968–69; Ciénaga, USNM 144159–160.

META: 11.6 mi E Candilejas, UTA 3951; Granada, on Río Ariari, S of Villavicencio, USNM 151495–97; Loma Linda, UTA 3716; Macarena, upper Río Guejar and El Meco, USNM 144894; Mapiripán, UTA 3943, 3945; Menegua, E Puerto López, USNM 147275; near Puerto López, USNM 146197–99, UTA 3713, 3942; San Juan de Arama, Los Micos, FMNH 81330–31; Villavicencio, FMNH 30574, 30813, 174078, 174081, 174085–86, MCZ 64699, UMMZ 71223, USNM 144895, 147083–87, 147397–98, UTA 3748, 3944, 3946–47, 3949–950, 3952–53.

NORTE DE SANTANDER: Astillero, USNM 147088–89.

SANTANDER: Puerto Wilches, USNM 142805.

TOLIMA: Mariquita, FMNH 81836–37, USNM 144896–4900, 147093–94.

VAUPÉS: Cerro Yapoboda, Río Cuduyarí, USNM 146432.

VICHADA: Puerto Carreño, CM 55655 (5).

FRENCH GUIANA. Kourou, LES 50–61, 285–290; Montsinéry, LES 664–669, 752–53; Rochambeau, LES 1018; Stoupan, LES 62.

GUYANA. Atkinson, USNM 162880–88, 162890–93; Demerara, FMNH 3299; Essequibo River, UMMZ 79476 (7); Georgetown, FMNH 174462–471, UMMZ 43968, 80416; Lethem, MCZ 50710–13; Manari, near Lethem, FMNH 174602–04; upper Rupununi River, AMNH 46495 (4); Wismar, UMMZ 76680 (19), 104473.

PANAMA. HERRERA: Parita, USNM 127261.

PANAMÁ: Capitán, near Chepo, USNM 192621; Nueva Gorgona, AMNH 69735; Río Tocumen, MCZ 10036.

SURINAM. Berlijn, RMNH 15054; Blakawatra, RMNH 17522; Christian Kondre, MZUSP 24759–760, 24762–63; 24766; Coronie Road, RMNH 17568; Enmore Estate, USNM 162943–49, 162951–965; Langaman Kondre, Marowijne, MZUSP 24583–598; Lawa River, MZUSP 24773, 24777; Lelydorp, RMNH 17551 (3), 17561 (3); Moengo Tapoe, RMNH 17536; Paramaribo, CM 49483, RMNH 15132 (2), 15140, 15158, 17534, 17548, 17550 (2), 17552, USNM 158953–960; Powakka, CM 44266, 4949[illegible]–92; Sipaliwini, RMNH 15171, 15189, 17523, 17541–46; Tibiti, RMNH 17553, 17554 (2), 17556–57, 17559–560, 17562, 17564, 17567; 43 km S Paramaribo on Zanderij Highway, CM 49487; Zanderij, CM 50484–85, 50559.

TOBAGO. Bloody Bay, Charlotteville Road, USNM 167493, 167507–08, 167513, 192748 (5), 194989, 195005, 195017–19.

TRINIDAD. Aripo Savanna, MCZ 3299–3302; Brickfield, FMNH 49666; La Veroraca, USNM 141545; Piarro, USNM 166617–621; Port of Spain, USNM 102392–99; Quare River, CM 4535.

VENEZUELA. AMAZONAS: Misión Coromoto-Atures, USNM 137193; Puerto Ayacucho, FMNH 175466–67, 190627 (3).

APURE: Hato Cariben, 46 km NE Puerto Páez, Río Cinaruco, USNM field 5482, 5668.

ARAGUA: Pie del Cerro (La Victoria), USNM 121148.

BOLÍVAR: Los Patos, 25 km SE El Manteco, USNM field 7587, 7589, 7590, 7592.

GUÁRICO: Calabozo, MCZ 50709; Estación Biológica de los Llanos, 9 km SE Calabozo, 100 m, USNM field 24619; Hato La Palmita, USNM 162700–01; Laguna de los Patos, UMMZ 131704–05; 10 km SE Valle de la Pascua, USNM 128839.

MONAGAS: 42 km SE Maturín, LACM 31375–79.

NUEVA ESPARTA: Salamanca, Margarita Island, USNM 137346.

SUCRE: Cumanacoa, CM 9064; Guaraúnos, KU 150799.

TÁCHIRA: Maracoi, FMNH 125406, 176331.

YARACUY: San Felipe, BMNH 2272–73.

LEPTODACTYLUS GEMINUS BARRIO 1973

Leptodactylus geminus Barrio 1973:199–206, figs. 2, 4, 6, 8. (Type locality, Argentina; Misiones, Bernardo de Irigoyen. Holotype CHINM 5860, male.)

Diagnosis.—Apparently morphologically identical to and indistinguishable from *L. gracilis* (see diagnosis for *gracilis*). At present *geminus* and *gracilis* can be differentiated only on the basis of call; the note repetition rate for *geminus* is faster (22 per second) than for *gracilis* (4 per second).

Adult Characteristics.—Specimens not examined by author.

Larval Characteristics.—Unknown.

Mating Call.—Dominant frequency modulated from 2700–3100 hz (fig. 45); 16–31 notes per call group; call without harmonic structure; call pulsatile, 2–4 pulses per note (fig. 46); note duration from about 0.02 s (beginning notes) to 0.03 s (mid-call); note repetition rate 22 per second.

Karyotype.—Diploid number 22; 5 pair median, 4 pair submedian, 2 pair subterminal; secondary constriction in chromosome pair 8 (Barrio 1973).

Distribution.—Known from the northeastern part of the province of Misiones, Argentina (fig. 47).

LEPTODACTYLUS GRACILIS DUMÉRIL AND BIBRON 1841

Cystignathus gracilis Duméril and Bibron 1841:406–407. (Type locality, Uruguay, Montevideo. Holotype Paris Museum 4490, male.)

Leptodactylus plaumanni Ahl 1936:389–390. (Type locality, Brasil; Santa Catarina, Nova Teutônia. Holotype Senckenberg Museum 22469, male.)

Leptodactylus gracilis delattini Müller 1968:48–52, figs. 2, 3. (Type locality, Brasil; Ilha Campeche. Holotype originally Saarbrucken 4080 now in MZUSP.)

Diagnosis.—The species with light longitudinal stripes on skin folds on the dorsal surface of the tibia (fig. 48) (if light stripes indistinct, folds are present where stripes occur in other individuals) are *geminus, gracilis,* and *marambaiae*. *Leptodactylus gracilis* has a longer leg (e.g. tibia average 58% SVL in males, 57% in females) than *marambaiae* (e.g. tibia 50% SVL). At present, *geminus* and *gracilis* can be differentiated only on the basis of call. The note repetition rate for *gracilis* is slower (4 per second) than for *geminus* (22 per second).

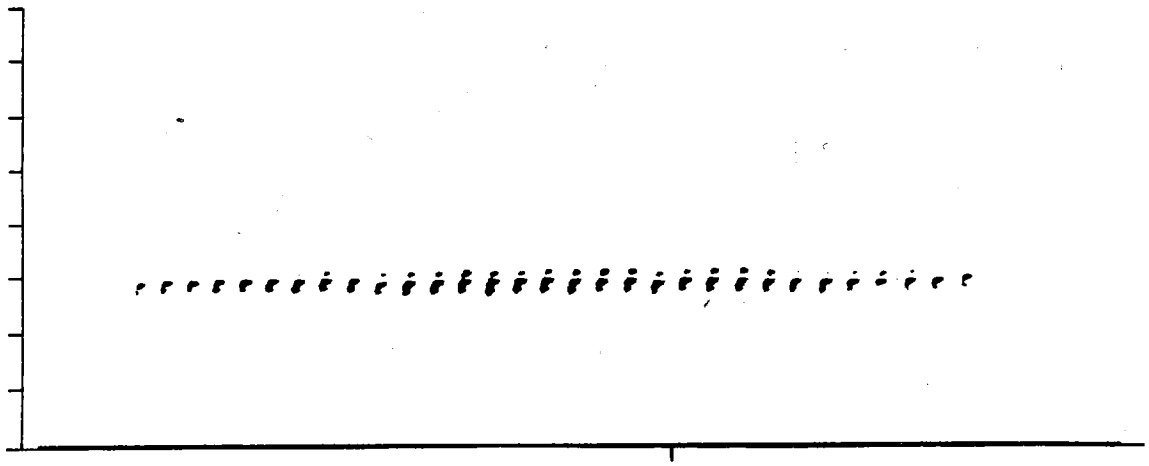


FIGURE 45. Sonagram of the mating call of *Leptodactylus geminus,* narrow band filter. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. Specimen from Argentina (Barrio tape copy).

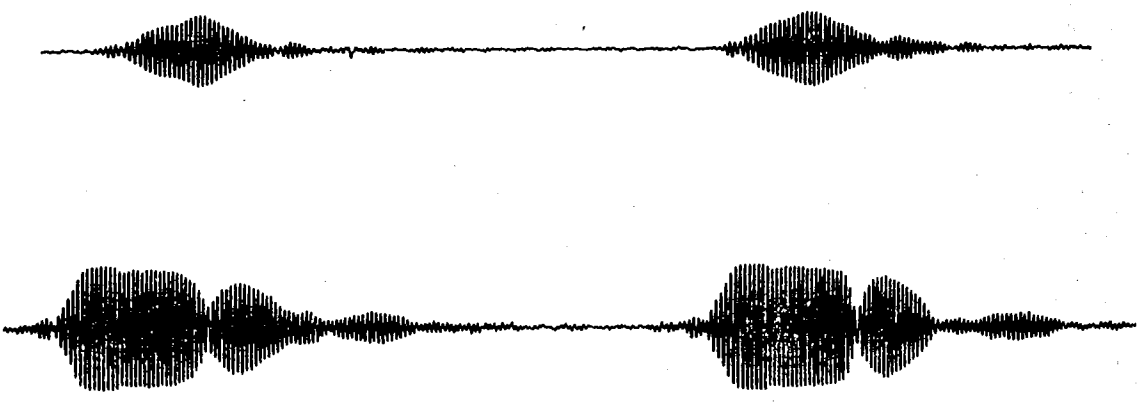


FIGURE 46. Strip chart records of the mating call of *Leptodactylus geminus*. Upper figure of initial two notes in call sequence, lower figure of two notes in middle of call sequence. Line equals 0.01 s. See legend of Figure 45 for specimen data.

FIGURE 47. Distribution map of *Leptodactylus geminus* (circle) and *gracilis* (triangles).

Adult Characteristics (N = 60).—Dorsum spotted or striped (fig. 1, F, G, H, striped pattern not figured); mid-dorsal light stripe always present (100%), light upper lip stripe almost always distinct (95%), rarely indistinct (5%), distinctiveness not sexually dimorphic ($X^2 = .18, P = .67$); no dark suborbital bar; light stripe on posterior face of thigh usually distinct (72%), sometimes indistinct (27%), rarely absent (2%), distinctiveness not sexually dimorphic ($X^2 = 1.19, P = .55$); tibia partially barred with light longitudinal pin stripes present; 6 well defined dorsolateral folds, sometimes an additional 2 or 4 ill defined folds (total 8 or 10); upper surface of tibia lacking white tubercles; posterior surface of tarsus lacking white tubercles (100%); sole of foot lacking white tubercles (100%); male SVL 43.0 ± 4.8 mm, female 43.0 ± 3.7 mm, not sexually dimorphic ($F_{1, 58} = .002$, $P > .05$); male head length/SVL ratio .373 ± .013, female .369 ± .014, not sexually dimorphic ($F_{1, 58} = 1.37, P > .05$); male head width/SVL ratio .324 ± .013, female .317 ± .010, male head broader than female ($F_{1, 58} = 5.79, .01 < P < .025$); male femur/SVL ratio .476 ± .031, female .480 ± .028, not sexually dimorphic ($F_{1, 58} = .31, P > .05$); male tibia/SVL ratio .579 ± .038, female .573 ± .032, not sexually dimorphic ($F_{1, 58} = .38, P > .05$); male foot/SVL ratio .593 ± .029, female .598 ± .022, not sexually dimorphic ($F_{1, 58} = .52, P > .05$).

Larval Characteristics.—Fernandez and Fernandez (1921) described and figured the larvae.

Mating Call.—Dominant frequency modulates be-

FIGURE 48. Dorsal views of *Leptodactylus gracilis* (left, MZUSP 26801) and *laurae* (right, KU 74216).

tween 500–2400 hz (fig. 49); call without harmonic structure; call partially pulsed (fig. 50); note duration 0.04 to 0.05 s; note repetition rate about 4 per second.

Karyotype.—Diploid number 22; 5 pair median, 4 pair submedian, 2 pair subterminal (Barrio 1973) or 5 pair median, 5 pair submedian, 1 pair subterminal (Bogart 1974); secondary constriction on chromosome pair 8.

Distribution.—The following records and distribution are based on museum specimens which may contain both *L. geminus* and *L. gracilis*. The (combined) distribution is Argentina through southeast Brasil (fig. 47).

ARGENTINA. BUENOS AIRES: Ernestina, Ptdo. 25 de Mayo, MACN 20970–74; Lincoln, Estancia Triunfo, MACN 4688; Tigre, AMNH 11959, MACN 3692.

CATAMARCA: near Balcosna, IML 2263.

CHACO: Laguna Limpia, IML 406.

CÓRDOBA: Achiras, AMNH 51906; btwn La Falda and Río Ceballos, IML 1340; Puesto El Cura, IML 25.

CORRIENTES: Colonia Carlos Pellegrini, MACN 4760; Ituzaingó, IML 916, MACN 4352.

MISIONES: Yacú-poí, 30 km E Pto. Bemberg, on Río Uruguaí, MACN 12341.

SANTA FÉ: Roldán, MACN 4911; Tostado, MACN 1831.

TUCUMÁN: Tacanas, IML 532.

BRASIL. PARANÁ: Bituruna, MNRio 3712 (5).

RIO GRANDE DO SUL: Corrientes, MCZ 32701; Gramado, Taquara, MZUSP 16038; Ipanema, MZUSP 16051; Itaqui, MZUSP 348; Osório, CAS 85689–690, 94560, CM 39033, MNRio 2723, 3781, MZUSP 21684–85; near Pôrto Alegre, KU 154549, MZUSP 16059; Restinga Sêca, MZUSP 24692; Santa Maria, MCZ 22954, 22958, 22959, MZUSP 24691, USNM 121265–66; São Lourenço, MZUSP 90, 96; Tramandaí, MZUSP 26801.

SANTA CATARINA: Bôca da Serra, mun. Bom Jardim da Serra, 1200 m, MZUSP 35572–580; Nova Teutônia, MZUSP 8711–12; Novo Horizonte, 400–800 m, MZUSP 35307–330; São Bento, USNM 97174–75.

SÃO PAULO: França, MZUSP 610; Ipiranga, CM 33791; Perus, MZUSP 604; Ribeirão Pires, MZUSP 584; São Paulo, MZUSP 33, 453, 4532, 14897; Serra da Cantareira, MZUSP 24676.

URUGUAY. CERRO LARGO: 6 km SE Melo, AMNH 71176.

COLONIA: Santa Ana-Artilleros, MZUSP 22926.

DURAZNO: 18 km NE Paloma, Arroyo del Estado, CM 57038–39.

LEPTODACTYLUS LABROSUS ESPADA 1875

Leptodactylus labrosus Jimenez de la Espada 1875:36. (Type locality, Ecuador; Los Ríos, Pimocha, shores of Río Daule. Lectotype Museo Nacional de Ciencias Naturales, Madrid, no number, female.)

Leptodactylus curtus Barbour and Noble 1920:405–406. (Type locality, Peru; Cajamarca, Bellavista. Holotype MCZ 5281.)

Diagnosis.—The species lacking a distinct light stripe on the posterior surface of the thigh in some or all individuals are *albilabris, bufonius, labrosus, mystacinus,* and *troglodytes*. The sole of the foot is usually smooth in *labrosus* (fig. 69), the sole of the foot has distinct

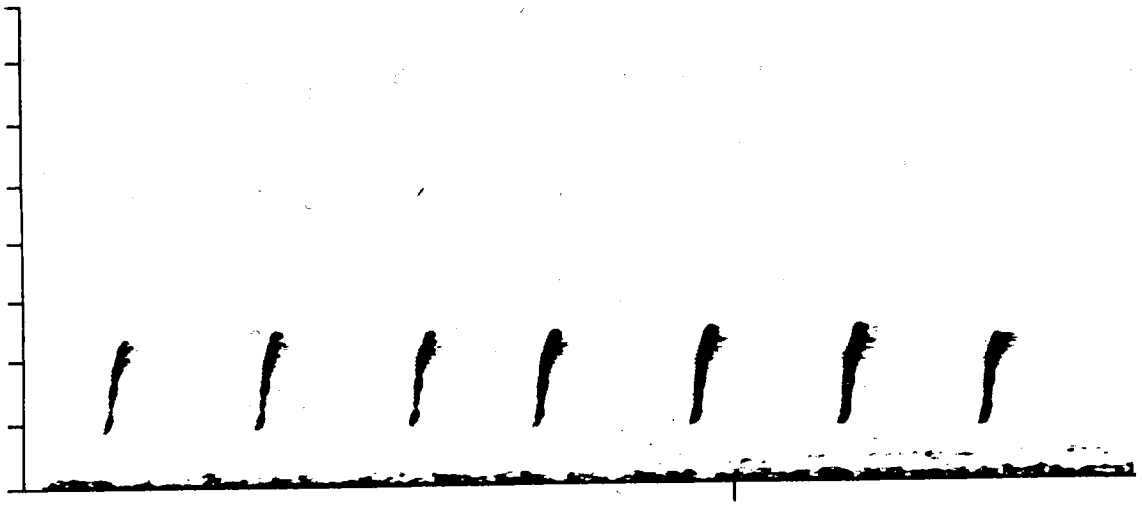


FIGURE 49. Sonagram of the mating call of *Leptodactylus gracilis,* narrow band filter. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. Specimen from Argentina, Buenos Aires (Barrio tape copy).

FIGURE 50. Strip chart record of the mating call of *Leptodactylus gracilis*. Line equals 0.01 s. See legend of Figure 49 for specimen data.

white tubercles in *albilabris, troglodytes, ventrimaculatus* and some *mystacinus* individuals. *Leptodactylus labrosus* is found along dry coastal South America from mid-Ecuador to Peru; *albilabris* is in the West Indies, *troglodytes* in NE Brasil, *ventrimaculatus* along wet east coast South America from Colombia to mid-Ecuador, *mystacinus* occurs in southern South America east of the Andes. *Leptodactylus labrosus* has a pair or two of distinct dorsolateral folds (indicated at least by color pattern in poorly preserved specimens), *bufonius* lacks distinct dorsolateral folds.

Adult Characteristics (N = 32).—Dorsum spotted or rarely uniform, spots rarely fused (fig. 1, A, B, C, J); no light mid-dorsal stripe; no distinct light upper lip stripe; dark suborbital bar present or absent; light stripe on posterior face of thigh almost always absent (94%), rarely indistinct (6%), presence not sexually dimorphic ($X^2 = .01$, $P = .92$); tibia barred; dorsolateral folds often absent or 4 indistinct folds present; dorsal surface of tibia usually with many or scattered white tubercles, sometimes absent; posterior surface of tarsus usually with scattered white tubercles (78%), sometimes absent (22%), presence not sexually dimorphic ($X^2 = .26$, $P = .61$); sole of foot usually lacking white tubercles (91%), rarely present (9%), not sexually dimorphic ($X^2 = .22$, $P = .64$); male SVL 54.6 ± 5.3 mm, female 53.3 ± 6.3 mm, not sexually dimorphic ($F_{1, 30} = .30$, $P > .05$); male head length/SVL ratio .356 ± .013, female .361 ± .016, not sexually dimorphic ($F_{1, 30} = .60$, $P > .05$); male head width/SVL ratio .344 ± .008, female .347 ± .013, not sexually dimorphic ($F_{1, 30} = .68$, $P > .05$); male femur/SVL ratio .400 ± .019, female .417 ± .022, female femur longer than male ($F_{1, 30} = 4.38$, $.025 < P < .05$); male tibia/SVL ratio .430 ± .007, female .442 ± .025, not sexually dimorphic ($F_{1, 30} = 1.84$, $P > .05$); male foot/SVL ratio .459 ± .014, female .481 ± .032, not sexually dimorphic ($F_{1, 30} = 3.81$, $P > .05$).

Larval Characteristics.—Unknown.

Mating Call.—Unknown.

Karyotype.—Unknown.

Distribution.—Mostly associated with dry west coast South America from mid-Ecuador to northern Peru, including the dry interandean valley of northern Peru (fig. 51).

ECUADOR. EL ORO: 7 km SE Buena Vista, USNM 196728; near Machala, USNM 196729–730 (3); Río Jubones, AMNH 16241.

GUAYAS: near Guayaquil, KU 120296, USNM 66876–880, 164327–333; Río Puyango, AMNH 16206, 16228.

LOJA: Casanga Valley, USNM 196731; La Toma, USNM 196732.

LOS RÍOS: Quevedo, WCAB 40161; 56 km N Quevedo, KU 146181–85, 147569, 152576–77.

PERU. ANCASH: 4.5 km SSE Río Casma, LACM 49161.

CUZCO: Río Cosñipata, 4 km SW Santa Isabel, 1700 m, KU 46443, 46603.

LIBERTAD: Río Jequetepeque, 2 km N Cruce de San José, LACM 49148–154, 49280.

PIURA: 1.5 km S Las Lomas, Río Chipillico, LACM 49155–160, 49281, 77005; near Sullana, USNM 153799.

LEPTODACTYLUS LATINASUS ESPADA 1875

Leptodactylus latinasus Jiménez de la Espada 1875:40. (Type locality, Uruguay; Montevideo. Holotype Museo Nacional de Ciencias Naturales, Madrid, jar number 335, female.)

Leptodactylus prognathus Boulenger 1888:187. (Type locality, Brasil; Rio Grande do Sul. Holotype BMNH 1947.2.17.52, male.)

Leptodactylus anceps Gallardo 1964:100–105, plate 1, fig. 2, plate 2, fig. 2. (Type locality, Argentina; Tucumán, Tucumán. Holotype MACN 531, male.)

Diagnosis.—The species having a combination of a distinct light stripe on the posterior face of the thigh and obvious white tubercles on the posterior surface of the tarsus and sole of foot in some or all individuals are *albilabris, elenae, fragilis, latinasus, mystaceus. Leptodactylus latinasus* lacks distinct dorsolateral folds, distinct dorsolateral folds (indicated by color pattern in poorly preserved individuals) are found in *albilabris, elenae,* and *mystaceus. Leptodactylus latinasus* and *fragilis* have considerable morphological and color pattern overlap (fig. 43), *fragilis* being a slightly larger species (maximum male SVL 43.0 mm, female 43.6 mm) than *latinasus* (maximum male SVL 37.9 mm, female 36.3 mm). *Leptodactylus latinasus* has a southern South American distribution, *fragilis* has a Middle American and north coast South American distribution.

Adult Characteristics (N = 233).—Dorsum spotted or blotched (fig. 1, A, B, C, E, N); mid-dorsal light stripe absent; light lip stripe usually indistinct (66%), more females with distinct lip stripes than males ($X^2 = 11.67$, $P < .001$); dark suborbital bar absent; light stripe on posterior face of thigh usually very distinct (90%), sometimes indistinct (10%), distinctiveness not sexually dimorphic ($X^2 = .11$, $P = .74$); tibia barred; dorsolateral folds indistinct, when present usually 2, sometimes 4; dorsal surface of tibia usually with many, sometimes scattered, white tubercles, very rarely absent; posterior surface of tarsus with many distinct white tubercles (100%); sole of foot with many distinct white tubercles (100%); male SVL 31.2 ± 1.7 mm, female 33.0 ± 1.9 mm, females larger than males ($F_{1, 231} = 51.75$, $P < .001$); male head length/SVL ratio .372 ± .012, female .368 ± .013, male head longer than female ($F_{1, 231} = 3.85$, $P = .05$); male head width/SVL ratio .343 ± .013, female .343 ± .012, not sexually dimorphic ($F_{1, 231} = .06$, $P > .05$); male femur/SVL ratio .388 ± .028, female .394 ± .023, not sexually dimorphic ($F_{1, 231} = 2.08$, $P > .05$); male tibia/SVL ratio .451 ± .023, female .455 ± .029, not sexually dimorphic ($F_{1, 231} = 1.36$, $P > .05$); male foot/SVL ratio .476 ± .024, female .475 ± .027, not sexually dimorphic ($F_{1, 231} = .02$, $P > .05$).

Larval Characteristics.—Fernandez and Fernandez (1921) described and figured the larvae as *L. prognathus.*

Mating Call.—Dominant frequency modulates from

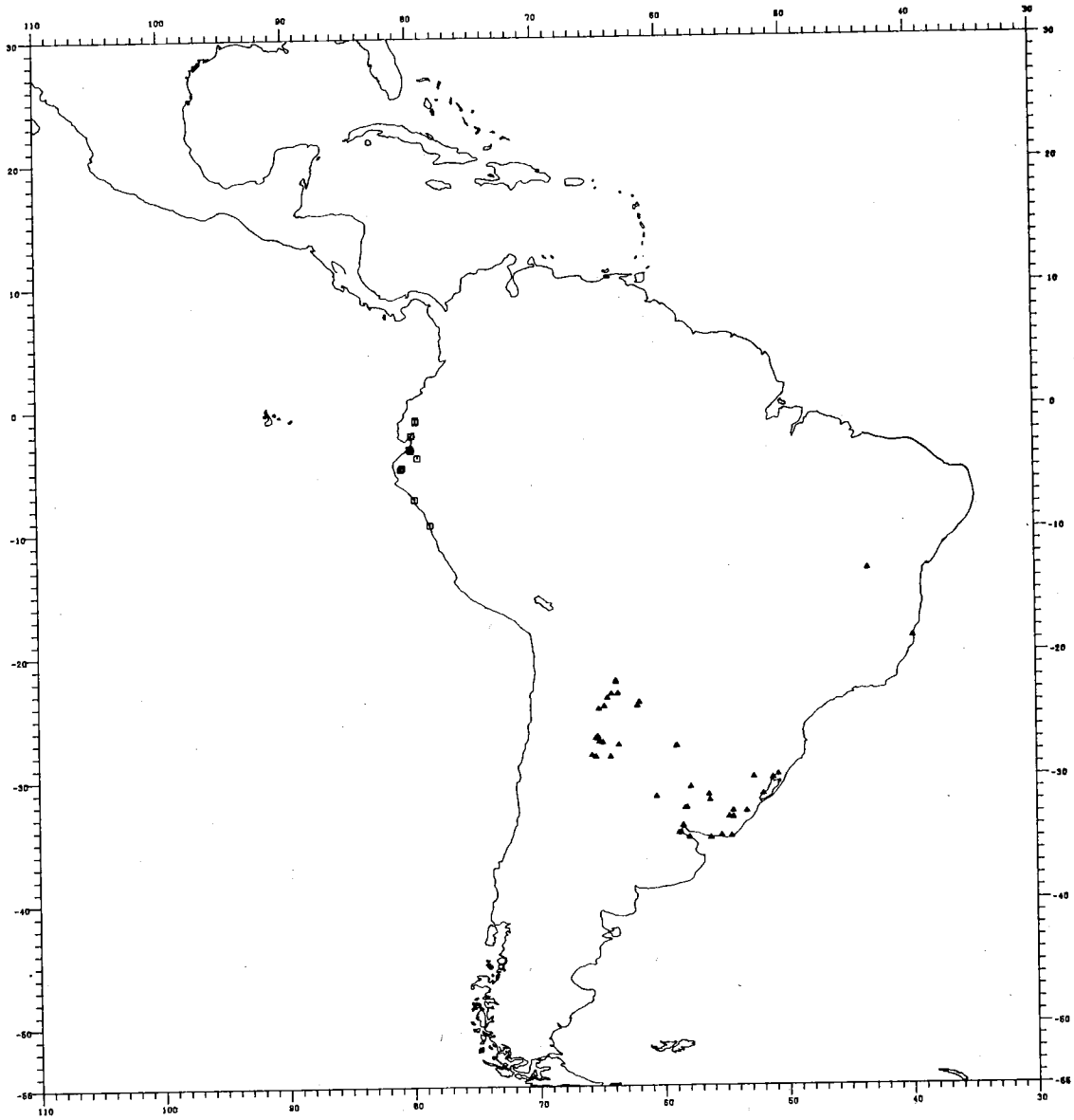


FIGURE 51. Distribution map of *Leptodactylus labrosus* (squares) and *latinasus* (triangles).

3100–4000 hz (fig. 52); call lacking harmonic structure; note non-pulsed (fig. 53); note duration 0.06 s; note repetition rate 2.3 per second.

Karyotype.—Bogart (1974) described the karyotype as diploid number 22; 5 pair median, 3 pair submedian, 2 pair subterminal, 1 pair terminal; secondary constriction on chromosome pair 8.

Distribution.—Found throughout the Gran Chaco and littoral zone of Argentina, central and coastal Brasil (fig. 51).

ARGENTINA. BUENOS AIRES: Bancalari, UMMZ 98837 (3); Ensenada, UMMZ 98838; José C. Paz, IML 854, 4475.

CATAMARCA: El Alto, IML 1442; near La Merced, IML 2261 (13).

CHACO: Barranqueras, MZUSP 26325–333.

CORRIENTES: Corrientes, MACN 4605 (4).

ENTRE RÍOS: Concepción del Uruguay, MACN 4530 (3).

FORMOSA: Ingeniero Juárez, LACM 92044; Río Bermejo, La Florencia, IML 651 (11).

JUJUY: Arroyo Los Naranjos, 8.3 km SSW Perico del Carmen, KU 43866–870; Ruta Yuto-Ledesma, near Arroyo Quemado, IML 1276 (11).

SALTA: Campo Aguaray, IML 1479 (3); El Saucelito, 50 km S Orán, IML 1627 (2); near Embarcación, LACM 92031–32, 92034–043, 92045–46, 92048–054, 92057–065; near Hickmann, IML 307 (3), 311 (4), 652 (8); Parque El Rey, Pozo Los Lobitos, IML 2393 (2); Tobantirenda, N of Aguaray, IML 1482 (7); Urundel, IML 9.

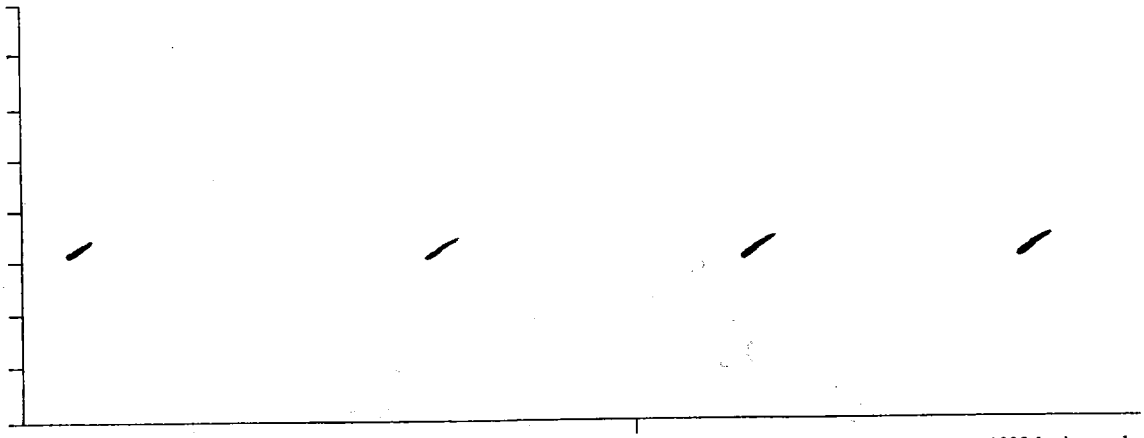


FIGURE 52. Sonagram of the mating call of *Leptodactylus latinasus*, narrow band filter. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. Specimen from Argentina, Embarcación, air temperature 21.3° C (LACM tape and specimen field number WRH 1361.)

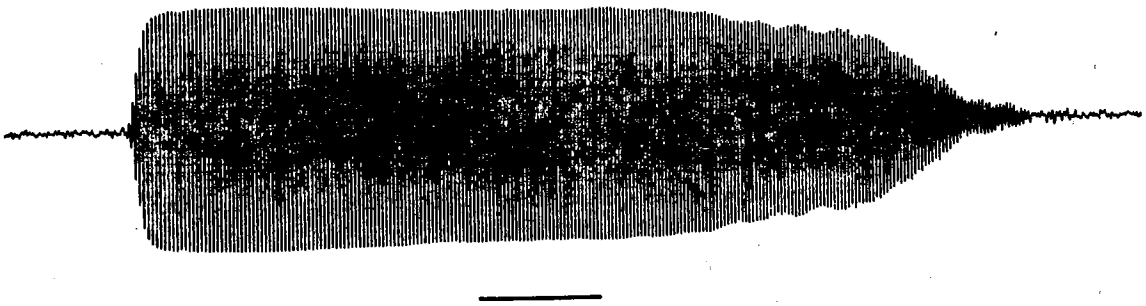


FIGURE 53. Strip chart record of the mating call of *Leptodactylus latinasus*. Line equals 0.01 s. See legend of Figure 52 for specimen data.

SANTA FÉ: Bañados del Rincón, CM 38728.

SANTIAGO DEL ESTERO: Bañado de Figueroa, ± 6 km N Caspi Corral, KU 43961–62; S. Loreto, MCZ 33714–16.

TUCUMÁN: El Cadillal, IML 2297, 2410 (15), KU 44045–062, 44065–66; El Durazno, IML 1902; Hualinchai, 8 km W S. P. de Colalao, IML 1783; Río Urueña, near Salta, IML 1429 (2); Saladillo, IML 467 (3); San Javier, IML 1599 (2); Soledad de Maria-Lamadrid, IML 37; Tacanas, IML 534; Tucumán FMNH 69077, IML 1427, UMMZ 109751 (8).

BRASIL. BAHIA: Bom Jesus da Lapa, UMMZ 109991 (2); Itiúba, MZUSP 38556–564.

ESPÍRITO SANTO: São Mateus, MCZ 1298.

MINAS GERAIS: Rio Grande at São José, UMMZ 109992.

RIO GRANDE DO SUL: Pôrto Alegre, FMNH 80347–351, 80354–59, 83289; 39 km N Rio Pardo, MZUSP 21699–1701; 39 km W Rio Pardo, FMNH 80352–53; São Lourenço, MZUSP 93; Vila Nova, São Sepé, MZUSP 27303–06.

URUGUAY. 30 Y 3: 8 mi E 30 y 3, FMNH 10435, 10463; Boca del Rio Tacuarí, AMNH 71189; Quebrada de los Cuervos, 45 km N 30 y 3, FMNH 10489–491.

ARTIGAS: 6 km NNW Belén, AMNH 71181.

CANELONES: Montevideo, USNM 196655.

COLONIA: Nueva Palmira, Arroyo del Sauce, CM 57046–47.

LAVALLEJA: Río de Averías, Depto. Minas, FMNH 10251.

MALDONADO: Sierra de Animas, MZUSP 24567–570.

RÍO NEGRO: Arroyo Neapo, 15 km S Paysandú, AMNH 71178–180.

ROCHA: Arroyo Garzón, 10 km NW Garzón, FMNH 10251.

SAN JOSÉ: Arazatí, S of Cocilda, FMNH 10623, 10628.

TACUAREMBÓ: 40 km NW Tacuarembó, AMNH 71182–88; 3 km NE Tambores, Pozo Hondo, CM 55394–98.

LEPTODACTYLUS LAURAE NEW SPECIES

Figure 54

Holotype: MZUSP 130, an adult male from Brasil: Minas Gerais; Agua Limpa, Juiz de Fora. Collected by Joaquim Venancio on 27 November 1947.

Diagnosis.—The species with a combination of a distinct light stripe on the posterior surface of the thigh and smooth surfaces on the posterior tarsus and sole of the foot in some or all individuals are *fuscus, geminus, gracilis, laurae, longirostris, marambaiae, notoaktites,* and *poecilochilus. Leptodactylus laurae* lacks light stripes on the dorsal surface of the tibia, such stripes are found in *geminus, gracilis,* and *marambaiae* (fig. 48). All individuals of *L. laurae* have a light mid-dorsal stripe and at least 6 dorsolateral folds; only individuals with a light mid-dorsal stripe have 6 dorsolateral folds in *longiros-*

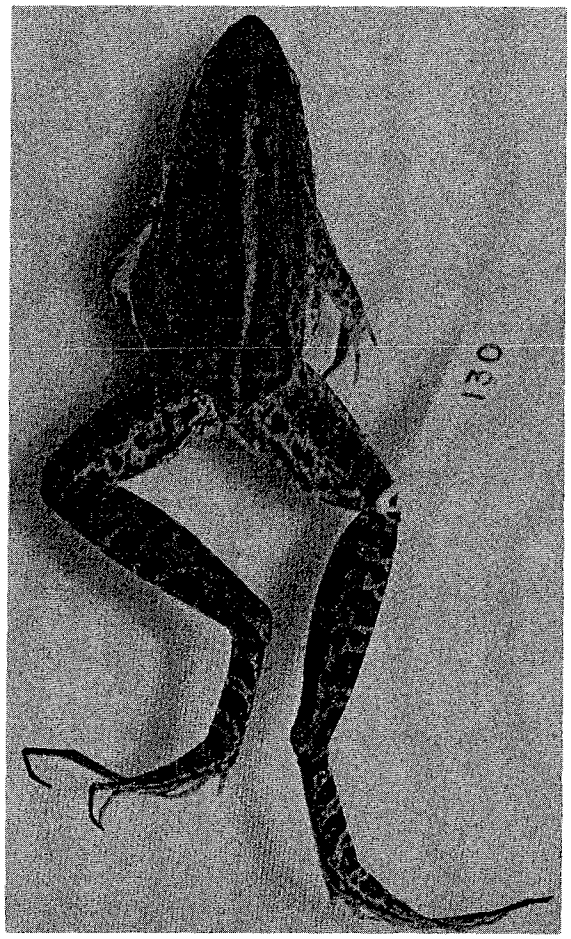


FIGURE 54. Dorsal view of the holotype of *Leptodactylus laurae*.

tris, notoaktites, and *poecilochilus,* most *fuscus* individuals lack a light mid-dorsal stripe. The leg of *laurae* is longer (e.g. male foot/SVL ratio .649 ± .039, female .628 ± .028) than *fuscus* (male foot/SVL ratio .509 ± .028, female .514 ± .032), *longirostris* (male foot/SVL ratio .545 ± .026, female .553 ± .031), *notoaktites* male foot/SVL ratio .587 ± .033, female; .583 ± .036), and *poecilochilus* (male foot/SVL ratio .514 ± .029, female .508 ± .029). *Leptodactylus laurae* has a mid-east and southern South American distribution, *L. poecilochilus* and *L. longirostris* occur in northern South America. Many individuals of *notoaktites* have distinct white tubercles on the sole of the foot.

Description of Holotype.—Snout pointed from above, rounded-acute in profile; canthus rostralis indistinct; loreal slightly concave; tympanum distinct, greatest diameter just greater than ½ eye diameter; vomerine teeth in slightly arched series posterior to choanae; vocal slits present; internal vocal sac; finger lengths in order of decreasing size I ≃ III > II ≃ IV, I >> II; inner metacarpal tubercle flat, oval, smaller than large, flat, outer metacarpal tubercle; no nuptial asperities; dorsal surfaces smooth; 3 pair of dorsolateral folds; ventral texture smooth; belly disk fold distinct; toe tips not expanded; toes free, lacking fringe or web; subarticular tubercles moderately developed; outer metatarsal tubercle small, indistinct, smaller than indistinct, oval, inner metatarsal tubercle; tarsal fold indistinct; no metatarsal fold; posterior surface of tarsus smooth; sole of foot smooth.

SVL 40.4 mm, head length 14.5 mm, head width 12.1 mm, interorbital distance 1.5 mm, eye-nostril distance 3.4 mm, femur 19.5 mm, tibia 24.6 mm, foot 27.4 mm.

Dorsum tan with lighter and darker brown markings including a light mid-dorsal stripe bordered by an irregular dark stripe on either side; series of dark spots parallel other dorsolateral folds; upper lip dark edged bordered above by distinct light stripe from tip of snout passing under eye to tympanum; limbs barred; venter immaculate; posterior surface of thigh blotched, light stripe more distinct on left than right side; light tarsal fold stripe; posterior tarsus and sole of foot mottled.

Etymology.—Named for my daughter Laura, a friend to all animals, including frogs.

Remarks.—This is the species referred to as "barred *gracilis*" in the morphological analysis.

Adult Characteristics (N = 35).—Dorsum spotted or striped (fig. 1, F, H, striped pattern not figured); mid-dorsal light stripe always present (100%); light upper lip stripe usually distinct (71%), often indistinct (29%), distinctiveness not sexually dimorphic ($X^2 = .27$, $P = .60$); no dark suborbital bar; light stripe on posterior face of thigh distinct (51%) or indistinct (49%), distinctiveness not sexually dimorphic ($X^2 = .71$, $P = .40$); tibia barred; 6 well defined dorsolateral folds; dorsal surface of tibia without white tubercles; posterior surface of tarsus without white tubercles (100%), sole of foot without white tubercles (100%); male SVL 36.1 ± 2.3 mm, female 40.7 ± 3.3 mm, females larger than males ($F_{1, 33} = 22.5$, $P < .001$); male head length/SVL ratio .379 ± .014, female .365 ± .011, male head longer than female ($F_{1, 33} = 7.53$, $.01 < P < .025$); male head width/SVL ratio .313 ± .013, female .304 ± .007, male head broader than female ($F_{1, 33} = 4.34$, $.025 < P < .05$); male femur/SVL ratio .485 ± .030, female .489 ± .023, not sexually dimorphic ($F_{1, 33} = .12$, $P > .05$); male tibia/SVL ratio .591 ± .038, female .594 ± .032, not sexually dimorphic ($F_{1, 33} = .03$, $P > .05$); male foot/SVL ratio .649 ± .039, female .628 ± .028, not sexually dimorphic ($F_{1, 33} = 2.55$, $P > .05$).

Larval Characteristics.—W. C. A. Bokermann and Ivan Sazima are in the process of describing the larvae of *L. laurae*.

Mating Call.—W. C. A. Bokermann and Ivan Sazima are describing the call of this species (pers. comm.).

Karyotype.—Unknown.

Distribution.—Southeast and central Brasil (fig. 55).

BRASIL. DISTRITO FEDERAL: Brasilia, MZUSP 25349. MATO GROSSO: Serrinha, 120 km W Mortes River, MZUSP 4275.

FIGURE 55. Distribution map of *Leptodactylus laurae* (squares), *longirostris* (triangles), and *marambaiae* (circle).

MINAS GERAIS: Agua Limpa, MZUSP 130; Serra do Caraça, MZUSP 13516.

PARANÁ: Curitiba (Xaxim), USNM 125499.

RIO GRANDE DO SUL: Santa Maria, MCZ 22951–53, 22955–57, 22959 (2), MZUSP 24688–690.

SÃO PAULO: Botucatú, MZUSP 14482; Campo Grande, Santo André, CAS 93822–23, KU 9209–212, 74215–16, MZUSP 516; Emas, MZUSP 9034; Eugênio Lefévre, MZUSP 11328; Itanhaem, MZUSP 625; Paranapiacaba, MZUSP 846; Rio Grande, MZUSP 1967; São Paulo, MZUSP 906; Serra da Bocaina, MCZ 15849, MZUSP 24136–39, 25467, USNM 81133, 96614–16; Alto da Serra de Cubatão, USNM 96813, 124588–89.

LEPTODACTYLUS LONGIROSTRIS BOULENGER 1882

Leptodactylus longirostris Boulenger 1882:240, plate 16, fig. 3. (Type locality, Brazil; Santarem. Lectotype BMNH 76.5.26.4, female.)

Diagnosis.—The species having a combination of a distinct light stripe on the posterior surface of the thigh and smooth surfaces on the posterior tarsus and sole of foot in some or all individuals are *fuscus, geminus, gracilis, laurae, longirostris, marambaiae, mystaceus. notoaktites,* and *poecilochilus. Leptodactylus longirostris* has a barred tibia, the dorsal surface of the tibia has light longitudinal stripes in *geminus, gracilis,* and *marambaiae*. Only individuals of *L. longirostris* with light mid-dorsal stripes have 6 dorsolateral folds (fig. 56), all *fuscus* have 6 dorsolateral folds (individual *L. longirostris* with the light mid-dorsal stripe are morphologically difficult to distinguish from *fuscus*). All individuals of *laurae* have a light mid-dorsal stripe and 6 dorsolateral folds; the leg of *longirostris* is shorter (e.g. male foot/