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

By W. RONALD HEYER

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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

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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

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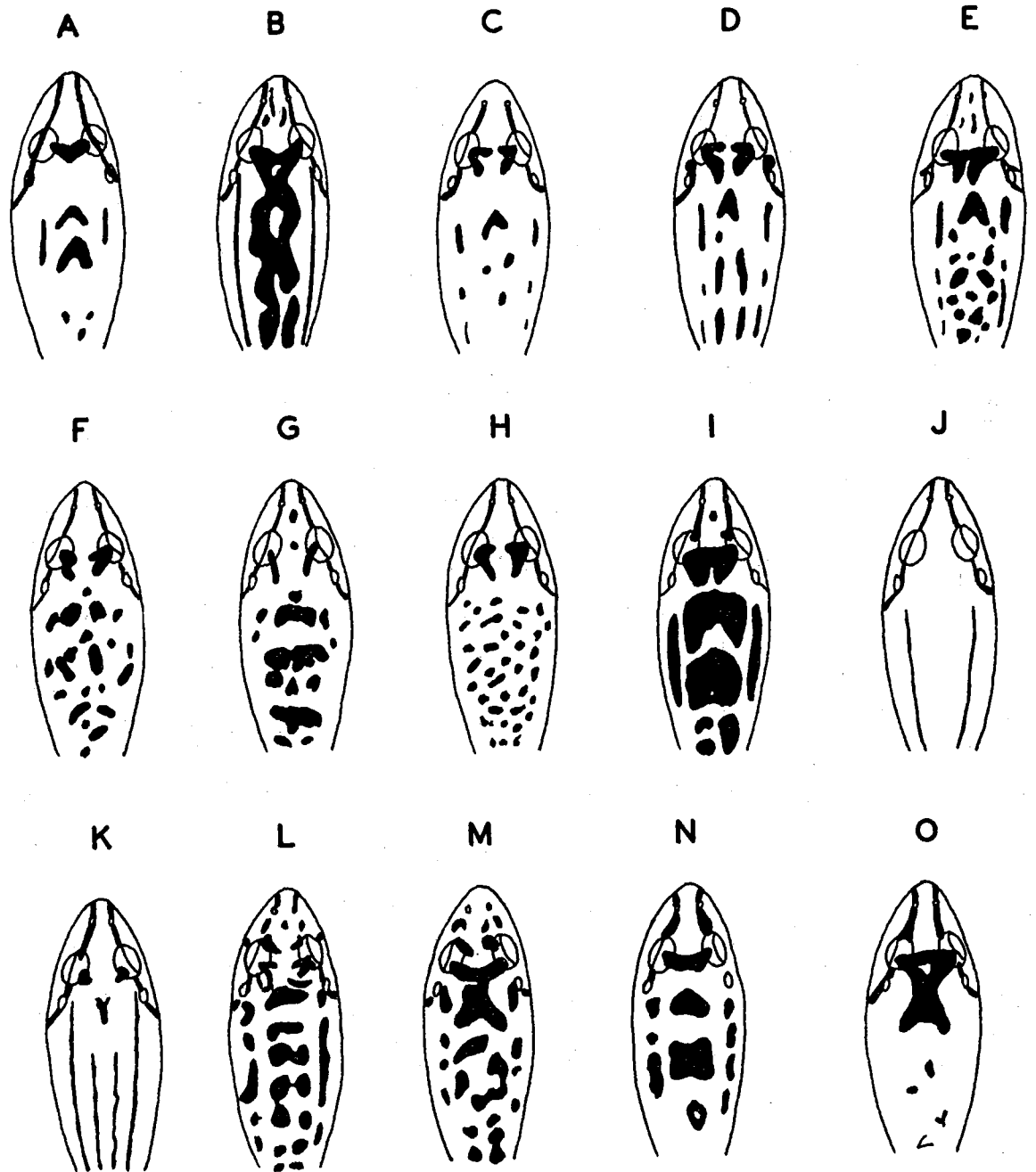ackage
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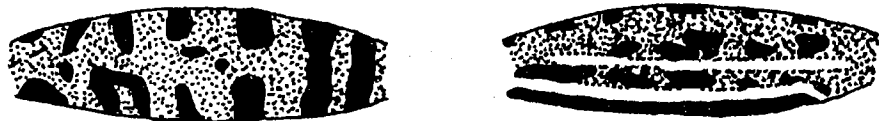FIGURE 1. Dorsal pattern standards utilized for the *Leptodactylus fuscus* species group.

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

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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 distinct. 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 uti-

lized 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 mid-dorsal 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 pat-

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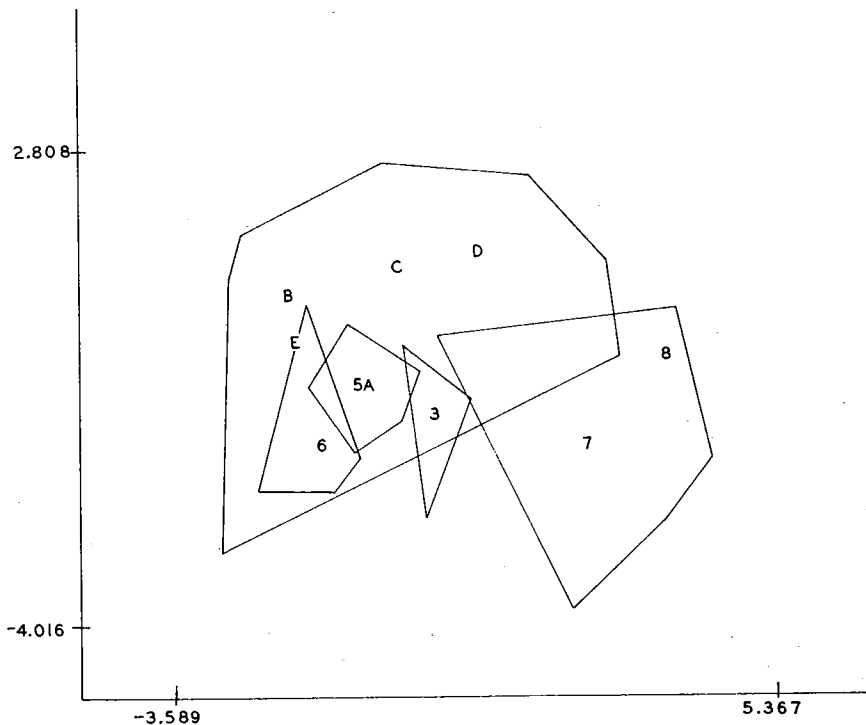spect to
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FIGURE 3. Discriminant axis plot for geographic samples of females of *Leptodactylus albilabris*. A–E = Puerto Rico, 3 = St. Croix, 5 = St. Thomas, 6 = Tortola, 7–8 = Dominican Republic. Letters and numbers placed at group means. Envelopes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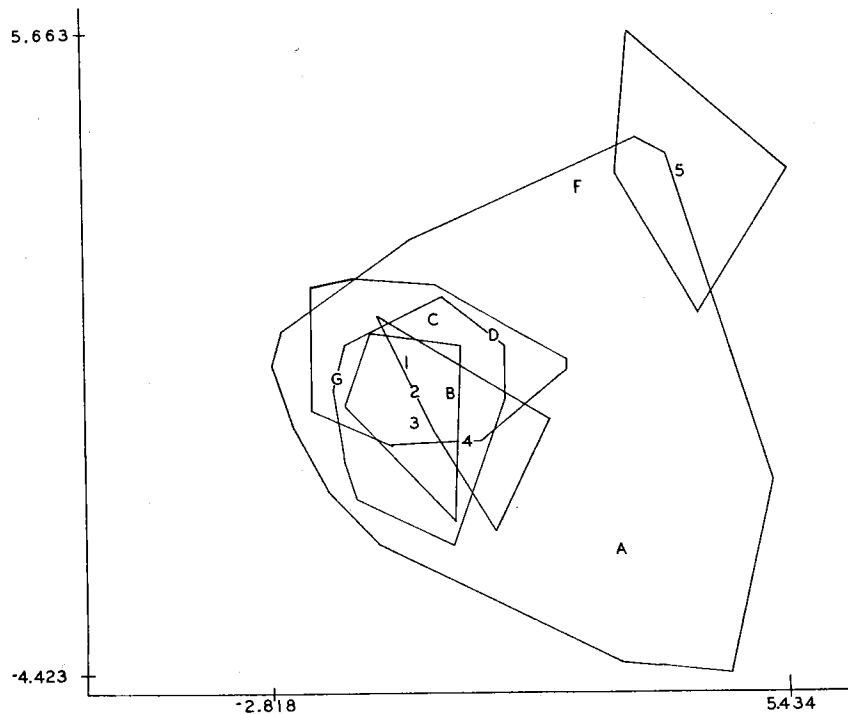

FIGURE 4. Discriminant axis plot for geographic samples of males of *Leptodactylus albilabris*. A–G = Puerto Rico, 1 = St. Croix, 2 = St. Johns, 3 = St. Thomas, 4 = Tortola, 5 = Dominican Republic. Letters and numbers placed at group means. Envelopes contain all group members by islands.
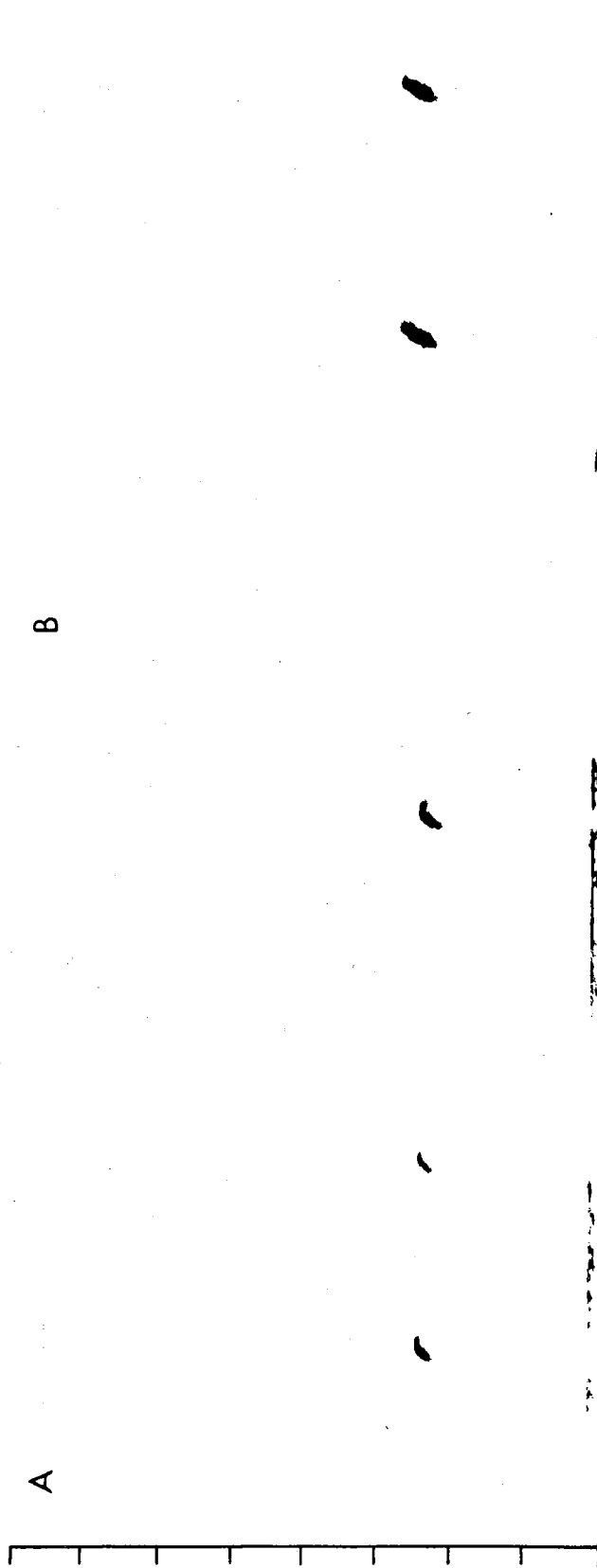
FIGURE 5. Sonagrams of the mating call of *Leptodactylus albilabris*, narrow band filter. Vertical scale marks at 1000 hz intervals. Horizontal scale mark at 1 s. A = specimen from Puerto Rico, El Yunque (AMNH tape), B = specimen from Dominican Republic, Sabana de la Mar, air temperature 20° C (R. I. Crombie recording at USNM).
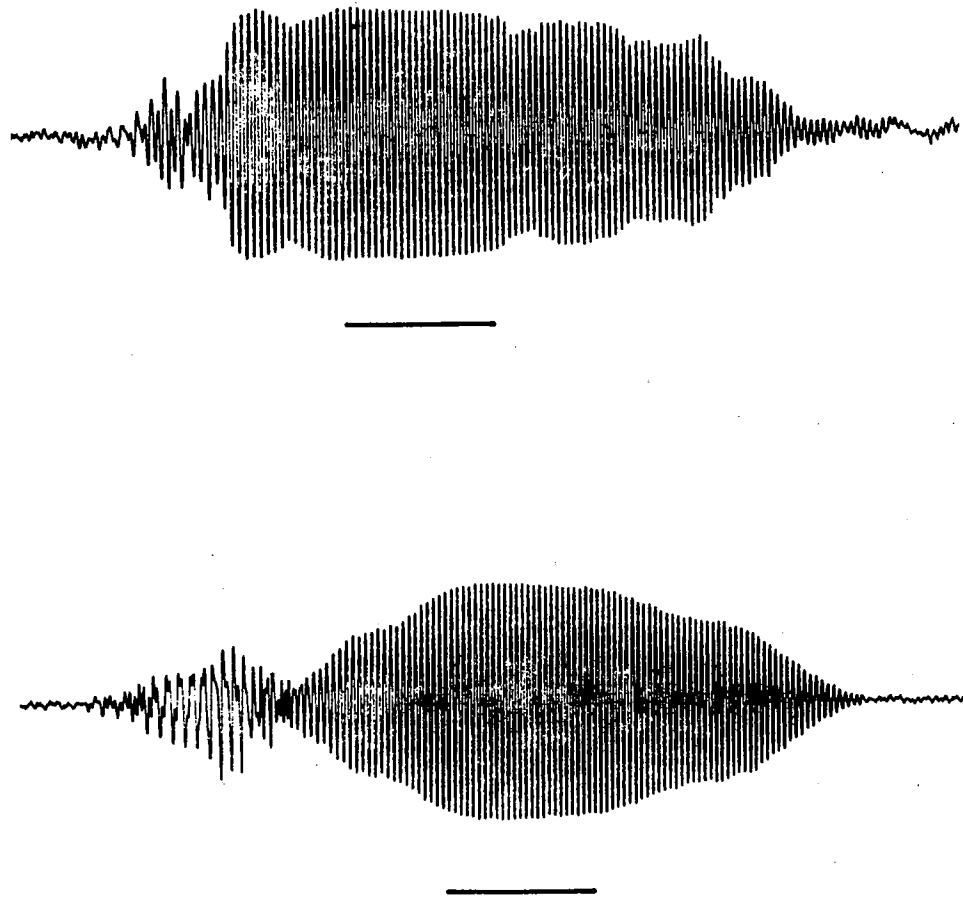
FIGURE 6. Strip chart records of the mating call of *Leptodactylus albilabris*. Line equals 0.01 s. Upper figure is note of specimen from Puerto Rico, El Yunque, lower is note of specimen from Dominican Republic, Sabana de la Mar. See legend of Figure 5 for further specimen data.

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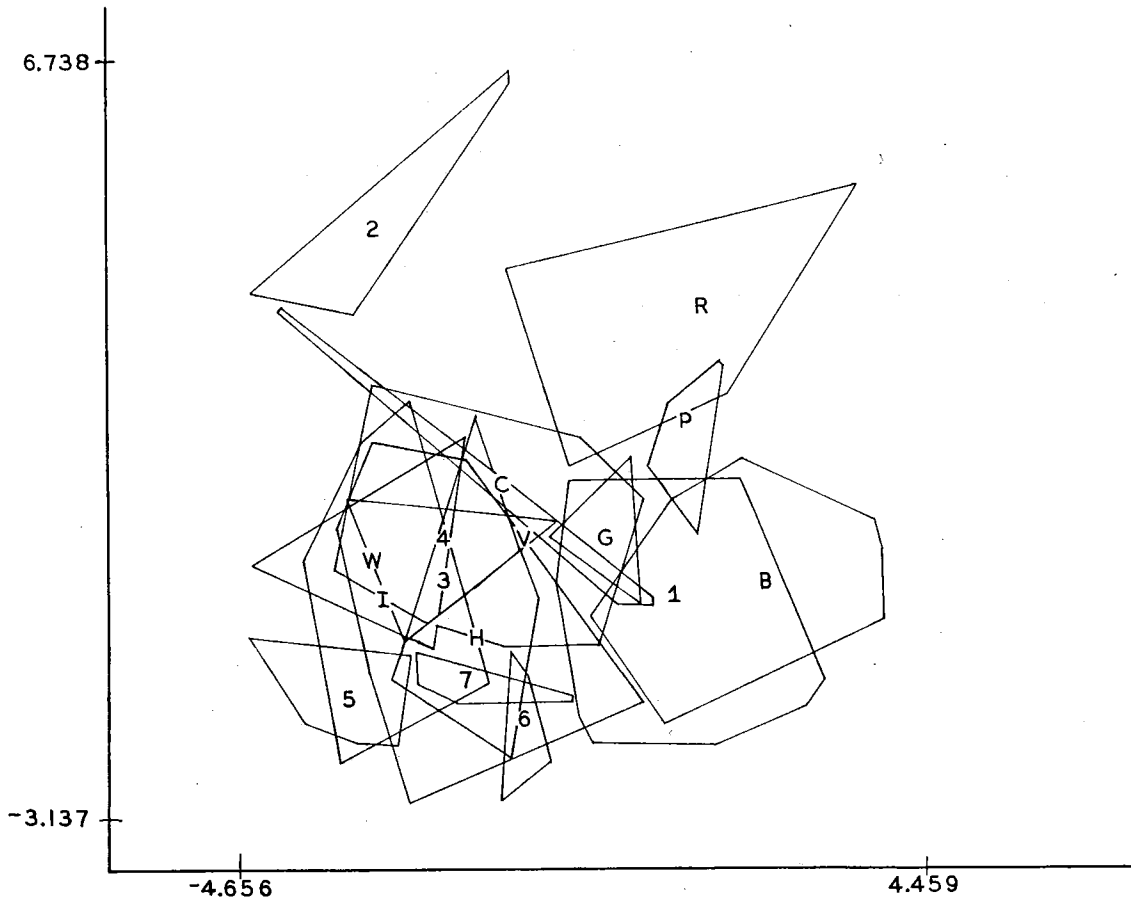
FIGURE 7. Discriminant axis plot for geographic samples of females of *Leptodactylus labialis*. 1–7 = Mexico, G = Guatemala, B = Belize, H–I = Honduras, R = Costa Rica, P = Panama, C = Colombia, V–W = Venezuela. Numbers and letters are placed at group means. Envelopes contain all group members.

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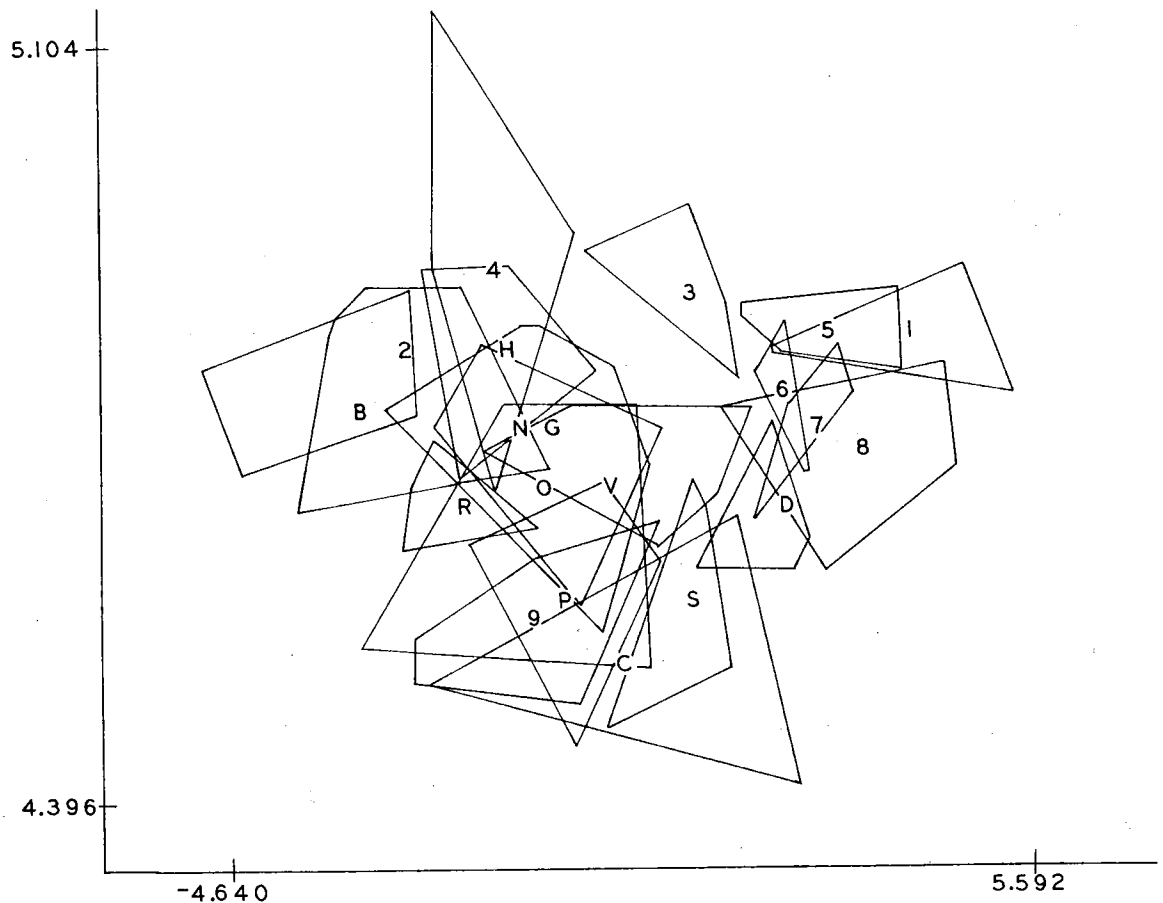
FIGURE 8. Discriminant axis plot for geographic samples of males of *Leptodactylus labialis*. 1 = Texas, 2–9 = Mexico, G = Guatemala, B = Belize, H = Honduras, R–S = Costa Rica, N–P = Panama, C–D = Colombia, V = Venezuela. Numbers and letters are placed at group means. Envelopes contain all group members.

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
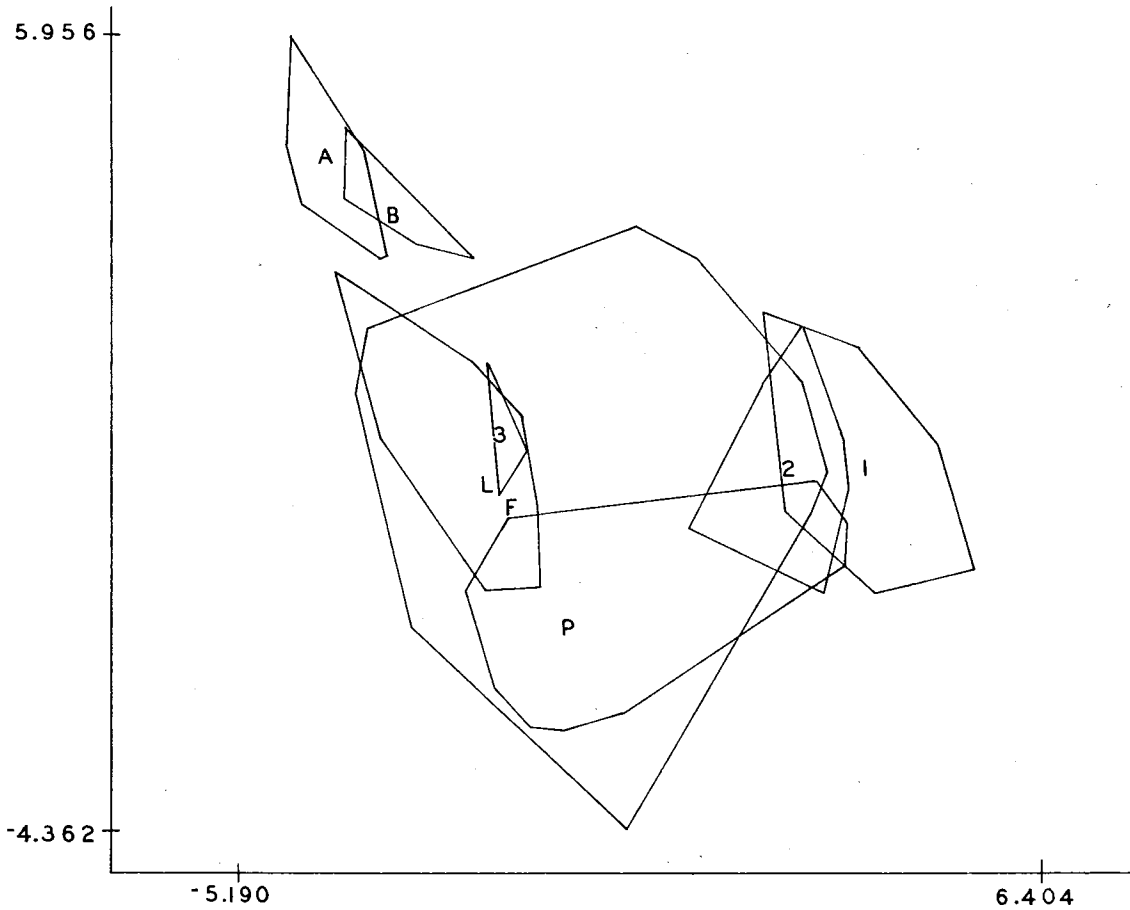
FIGURE 9. Discriminant axis plot of females of the *fuscus* complex. F = *fuscus*, A = striped *gracilis*, B = barred *gracilis*, L = *longirostris*, 1 = northern *mystaceus*, 2 = southern *mystaceus*, 3 = south coast *mystaceus*, P = *poecilochlus*. Letters and numbers placed at group means. Envelopes 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.
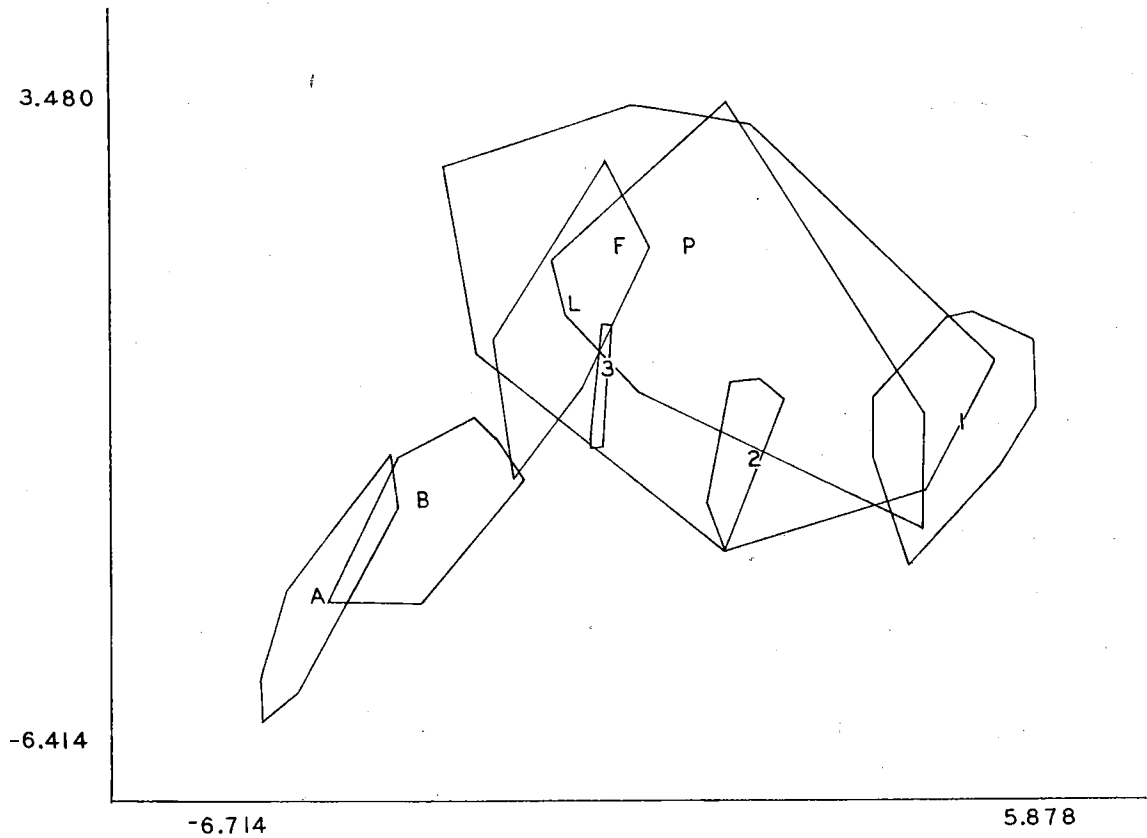
FIGURE 10. Discriminant axis plot for males of the *fuscus* complex. F = *fuscus*, A = striped *gracilis*, B = barred *gracilis*, L = *longirostris*, 1 = northern *mystaceus*, 2 = southern *mystaceus*, 3 = south coast *mystaceus*, P = *poecilochilus*. Letters and numbers placed at group means. Envelopes contain all group members.

TABLE 2

Posterior classification of members of the *fuscus* complex.

MALES

Number of cases classified into group

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

Number of cases classified into group

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
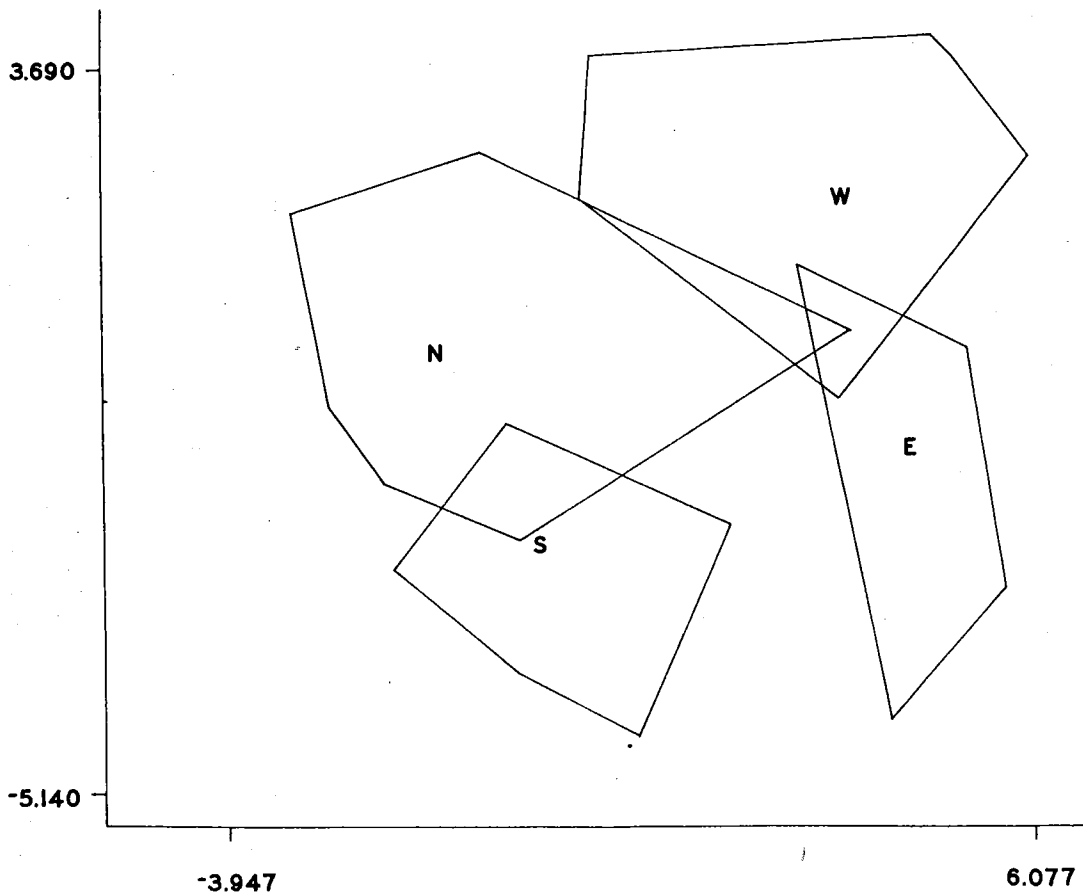

FIGURE 11. Discriminant axis plot for females of the *mystaceus* complex. E = east coast *mystaceus*, N = northern *mystaceus*, S = south coast *mystaceus*, W = southern *mystaceus*. Letters placed at group means. Envelopes contain all group members.