

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

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## TABLE OF CONTENTS

ABSTRACT .....	1
INTRODUCTION .....	1
ACKNOWLEDGMENTS AND MUSEUM ABBREVIATIONS .....	1
METHODS AND MATERIALS .....	2
POPULATION ANALYSES .....	6
<i>Leptodactylus albilabris</i> .....	6
<i>Leptodactylus labialis</i> .....	9
<i>Leptodactylus fuscus</i> -complex .....	10
<i>Leptodactylus bufonius</i> -complex .....	22
<i>Leptodactylus latinasus</i> - <i>labialis</i> .....	26
<i>Leptodactylus latinasus</i> .....	26
SUMMARY OF TAXONOMIC CONCLUSIONS .....	29
NOMENCLATURE .....	29
SPECIES ACCOUNTS .....	37
<i>Leptodactylus albilabris</i> .....	37
<i>Leptodactylus amazonicus</i> — <i>new species</i> .....	38
<i>Leptodactylus bufonius</i> .....	44
<i>Leptodactylus elenae</i> — <i>new species</i> .....	45
<i>Leptodactylus fragilis</i> .....	46
<i>Leptodactylus fuscus</i> .....	50
<i>Leptodactylus geminus</i> .....	52
<i>Leptodactylus gracilis</i> .....	53
<i>Leptodactylus labrosus</i> .....	56
<i>Leptodactylus latinasus</i> .....	57
<i>Leptodactylus laurae</i> — <i>new species</i> .....	59
<i>Leptodactylus longirostris</i> .....	61
<i>Leptodactylus marambaiae</i> .....	64
<i>Leptodactylus mystaceus</i> .....	64
<i>Leptodactylus mystacinus</i> .....	65
<i>Leptodactylus notoaktites</i> — <i>new species</i> .....	68
<i>Leptodactylus poecilochilus</i> .....	69
<i>Leptodactylus troglodytes</i> .....	71
<i>Leptodactylus ventrimaculatus</i> .....	73
AN ARTIFICIAL KEY TO THE ADULT MEMBERS OF THE <i>LEPTODACTYLUS FUSCUS</i> GROUP .....	75
THE SIGNIFICANCE OF SEXUAL DIMORPHISM IN MEMBERS OF THE <i>LEPTODACTYLUS FUSCUS</i> GROUP .....	76
RELATIONSHIPS .....	78
ZOOGEOGRAPHY .....	79
EVOLUTIONARY HYPOTHESES .....	82
PRELIMINARY COMMENT ON SIBLING SPECIES .....	82
RESUMEN .....	83
LITERATURE CITED .....	84

SYSTEMATICS OF THE *FUSCUS* GROUP OF THE FROG  
GENUS *LEPTODACTYLUS* (AMPHIBIA, LEPTODACTYLIDAE)<sup>1</sup>

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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.

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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 Herpetológica 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, BMD07M, 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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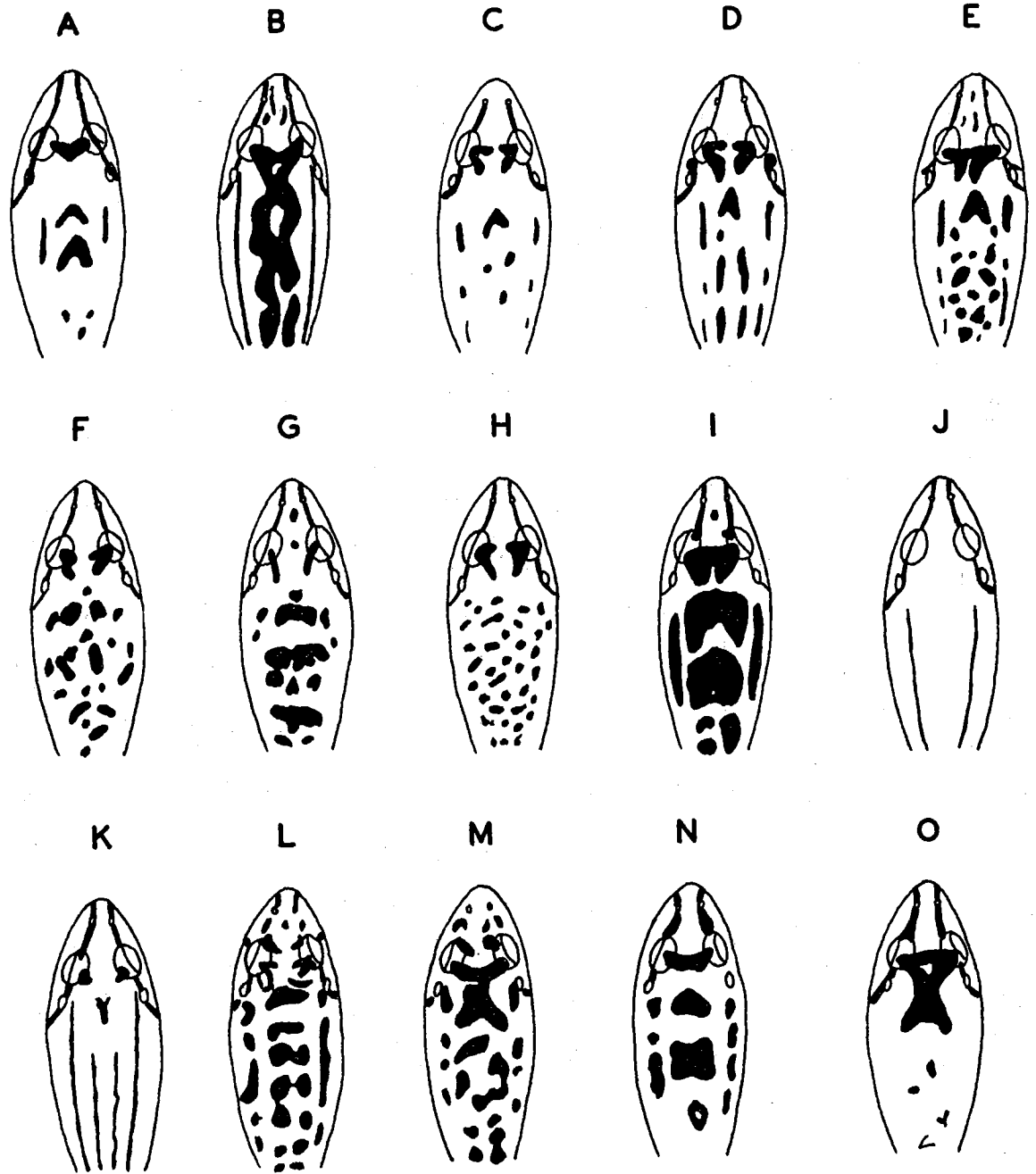


FIGURE 1. Dorsal pattern standards utilized for the *Leptodactylus fuscus* species group.

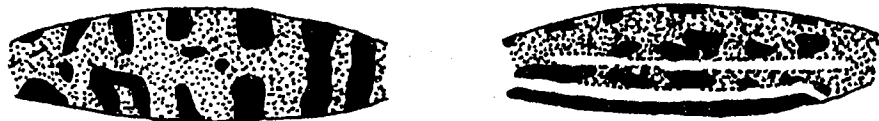


FIGURE 2. Tibia pattern standards utilized for the *Leptodactylus gracilis*-complex. Left, barred condition; right, striped condition.

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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
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 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

