

Distributions, Relationships, and Zoogeography of Lowland Frogs The *Leptodactylus* Complex in South America, with Special Reference to Amazonia

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ABSTRACT An analysis of the distributions and evolutionary relationships of lowland frogs of the species-rich *Leptodactylus* complex is presented. Composite species distributions are derived and carefully examined for general patterns. Centers of species diversity are defined and compared with the present distribution of morphoclimatic domains. The high species diversity observed in the *Leptodactylus* complex is attributed to the occurrence of two major ecological groupings of frogs and three distinct adaptive patterns of these frogs.

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Evolutionary relationships among representative *Leptodactylus* species based on comparative studies of albumin sequence differentiation are also described. This work reveals that speciation events are Tertiary, not Pleistocene events, and that there exists some intraspecific variation that appears to extend back into the Pliocene.

The refuge theory accounts for very few distributional events and no speciation events in the *Leptodactylus* complex.

The *Leptodactylus* complex of frogs has been the subject of extensive systematic analyses by the senior author for the past twelve years. More recently we have initiated biochemical analyses of these same species in hopes of providing new insights into the relationships among this interesting but enigmatic assemblage of frogs. This symposium has provided us the impetus to synthesize our current understanding of the distributions and evolutionary relationships of the members of the *Leptodactylus* complex. Because much systematic and biochemical work is still going on, what we present here must be construed as a progress report. However, we believe that at this time we are able to make some basic statements concerning the distribution, evolutionary relationships, and zoogeography of the group.

The focus of this symposium is the testing of what has come to be called the refuge theory (Simpson & Haffer 1978), based on studies of avifaunas primarily in

Amazonia (Haffer 1969). Additional vertebrate evidence supporting this theory comes from studies of iguanid lizards (Vanzolini & Williams 1970). The group of frogs that we are studying possesses some unique features which help to provide a different perspective for an understanding of the zoogeography of the Amazon basin.

The leptodactylid frogs are quite different from those organisms used to develop the refuge theory. Previous zoogeographic analyses of Amazonian frogs that discussed the refuge theory used the theory as an uncritical explanation of the patterns identified in the studies (e.g., Duellman 1972; Heyer 1973). We attempt here to make some zoogeographic statements based on patterns of distributions and relationships. We then compare the results of our analysis with predictions drawn from the refuge theory. As will develop, the frogs we are studying differ from other groups of organisms in aspects of both zoogeography and speciation. Only through study of a variety of plant and animal groups will the total zoogeography of any region be understood. This is especially true for a region as old and complex as the Amazon basin.

The distributions and ecological affinities of the frogs we study suggest that they are ideal candidates for a zoogeographical analysis centering on the Amazon basin. Collectively, the species range throughout tropical and subtropical lowland South America. Some species occur only in the Amazon basin. Others occur only outside the basin. Still others occur broadly throughout the basin and adjacent areas. Some species occur only within the rainforests proper. Others occur only in open vegetation. Others occur in the forests, at forest edges, and in the open.

We do not believe that analysis of members of the *Leptodactylus* complex will allow a total understanding of the zoogeography of the Amazon basin. On the other hand, we think that any zoogeographic construct of the Amazon basin will be incomplete unless it includes the data derived

from frogs, and that members of the *Leptodactylus* complex comprise an exemplary system for an analysis of frog zoogeography in Amazonia.

Methods and Materials

Two kinds of data are used in the analysis: distributional data and comparative molecular data.

The distributional data are based on the point locality maps published elsewhere (Heyer 1970, 1973, 1978, 1979). General distribution maps were produced by circumscribing the individual localities. The criterion used for determining where the species boundary lines should be drawn was that reasonable fidelity had to be maintained to the previously published point locality maps. Thus, someone who compares a range map produced for this study with a previously published point locality map can determine that the range map is indeed a general reflection of the point locality map and further, comparison will show where and how decisions were made on whether to consider any given point as a part of a large distribution pattern or as an isolated outlier population (for example, compare figure 20.6 in this paper with figure 27 in Heyer 1973). One other practical method was used in drawing boundary lines. Ab'Saber's (1977a) morphoclimatic domain map of South America was compared with the individual point location maps. If one of the morphoclimatic domain boundary lines (or any part thereof) would describe the boundary line for the point distributions as well as a smoothly curved boundary line, the former was used. Use of morphoclimatic domain distributions introduces other factors in the analysis. The disadvantage introduced is that of a certain amount of subjectivity.

This amount of subjectivity is not critical, as the morphoclimatic domain boundary lines were used only where there were point localities which supported using those boundaries. Where point distributions did not coincide with a morphoclimatic domain, a smooth curve was drawn around the point localities. The advantage introduced is generality. For those species represented in collections by many specimens from many localities, it is clear that Ab'Sáber's morphoclimatic domains correlate best with the actual data. We do not have enough data to perform intricate correlation analyses, but we are convinced by the correlations we see. The purpose of our analysis is to identify some general distribution patterns. To do this, we have gone from specific point distribution maps to general range maps, sacrificing precision, but gaining generality. The point distribution maps are not predictive in terms of what species can be found in an as yet unsampled locality—the general distribution maps are.

Until recently, the species comprising the genera *Adenomera* and *Vanzolinius* also were included in the genus *Leptodactylus*. As far as the distributions are known for these groups (Heyer 1970, 1973), they are included in this analysis.

Certain species are excluded from analysis. As the focus of this paper is on South America, particularly Amazonia, all species having primarily or entirely Middle American or West Indian distributions are omitted. These are *Leptodactylus albilabris*, *L. fallax*, *L. fragilis*, *L. melanonotus*, and *L. poecilochilus*.

Five species are known from too few localities to estimate a distribution range: *Adenomera lutzi*, *Leptodactylus dantasi*, *L. geminus*, *L. marambaiae*, *L. syphax*.

Two species that have been reviewed have since been found to be a composite of at least two species whose ranges are not individually known: *Adenomera bokermanni* and *Leptodactylus wagneri*.

Member of the *Leptodactylus ocellatus* group have not been reviewed recently at the group level so no detailed locality maps

are available for the members of this group. Two members of this group occur in the Amazon basin. The names currently associated with this complex are: *Leptodactylus bolivianus*, *L. chaquenis*, *L. macrosternum*, *L. ocellatus*, and *L. viridis*.

With the above exceptions, the distributional analyses are based on the 30 remaining known members of the *Leptodactylus* complex: *Adenomera andreae*, *A. hylaedactyla*, *A. marmorata*, *A. martinezi*, *Leptodactylus amazonicus*, *L. bufonius*, *L. elenae*, *L. flavopictus**, *L. fuscus**, *L. gracilis**, *L. knudseni**, *L. labrosus*, *L. labyrinthicus**, *L. laticeps**, *L. latinasus**, *L. laurae*, *L. longirostris*, *L. mystaceus*, *L. mystacinus*, *L. notoakites*, *L. pentadactylus**, *L. podocipinus*, *L. pustulatus*, *L. rhodomystax*, *L. rhodonotus*, *L. rugosus*, *L. stenodema**, *L. troglodytes*, *L. ventrimaculatus*, and *Vanzolinius discodactylus*.

The molecular data were obtained using the quantitative immunochemical technique of microcomplement fixation (MC'F) to compare sequence similarities of the serum albumin proteins of the frogs. Purified albumin from *Leptodactylus fuscus* (Brazil: São Paulo; Boracéia) and *L. pentadactylus* (Panama: Canal Zone; Frijoles) were used to prepare antiserum for comparisons with other species of *Leptodactylus*. Plasma and phenoxylethanol preserved muscle tissue from representatives of nine species of *Leptodactylus* were used as sources of albumin for comparisons with the two antisera. Those species in the preceding list that are marked with asterisks were used in the MC'F studies: Voucher specimens of all species used in this study are now or will be deposited in the Smithsonian collections. The details of the MC'F procedure can be found in Champion et al. (1974), and Maxson, Highton, and Wake (1979). The MC'F derived data are reported in immunological distance units. For albumin one unit of immunological distance is roughly equivalent to one amino acid substitution (Maxson & Wilson 1974). The mean evolutionary rate of albumin approximates one immunological distance

unit per 0.54 million years (Carlson, Wilson, & Maxson 1978) and this relationship was used in drawing the time scales in figures 20.11 and 20.12.

Certain terms as used in the text are defined as follows:

Domain. A morphoclimatic domain in the sense of Ab'Sáber (1977a). Of particular interest are the forested domains of Amazonia and the Atlantic forests of Brazil and open formation Chaco, Cerrado, and Caatinga domains.

Vegetation. This is the actual vegetation at a given site. Two major kinds of vegetation are discussed; forest vegetation and open formation vegetation. The forest vegetation has a closed canopy, the open formation vegetation an open canopy, including vegetations characteristic of the cerrados and caatingas as well as natural and man-made clearings.

Delimited taxa. These are taxa limited to certain vegetation types. Of importance are forest delimited taxa, which occur in and are limited to forest vegetations and open formation delimited taxa which occur in and are limited to open formation vegetations.

An example of how these terms are used is that the forested domain of Amazonia contains a broad expanse of forest vegetation and it also contains a network of open formation vegetation.

Species Distributions

We first examine composite distributions of species to look for general patterns and then examine some specific distributions to clarify the general patterns or to raise ques-

tions concerning these patterns. The patterns of overlapping species distributions are not viewed as analytic panaceas, but as an analytic approach that may give rise to interesting patterns and questions.

The composite map was made by tracing each species distribution on a single base map. Only contiguous ranges were used; individual outlying localities were omitted for the analyses leading to figures 20.1, 20.3, 20.4 and 20.5 only. The composite distribution map (fig. 20.1) is presented with a map (fig. 20.2) extracting some of the major morphoclimatic zones recognized by Ab'Sáber (1977a), which was used as an aid to delimit individual species ranges. The patterns of lines resulting from the composite ranges is complex, but two general statements can be drawn from figure 20.1. First, the distributions of members of the *Leptodactylus* complex in the Amazon are rela-



Figure 20.1 Composite distributions of 30 species of the *Leptodactylus* complex. Heavy lines indicate where three or more species boundaries coincide.

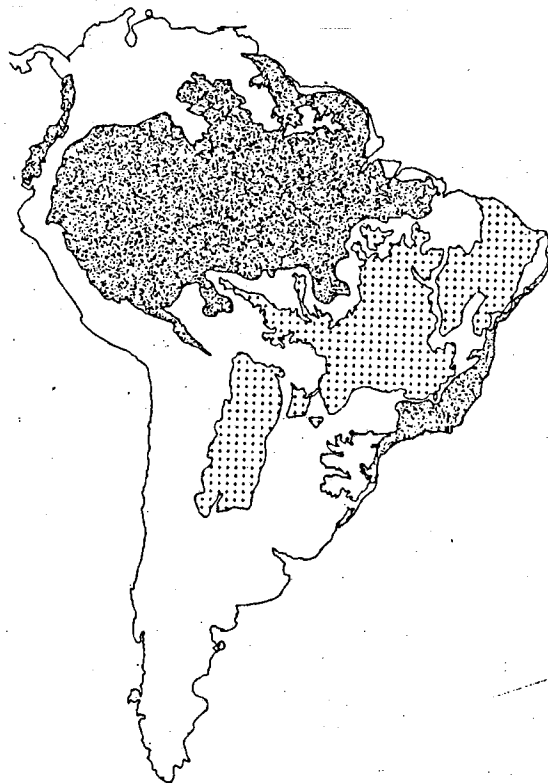


Figure 20.2 Selected morphoclimatic domains (Ab' Sáber, 1977a) pertaining to distributions of species in the *Leptodactylus* complex. Heavy, uneven stippling indicates the forested domains of (left to right) the Pacific Equatorial Domain, the Amazon Equatorial Domain (Amazonia), and Atlantic Tropical Domain (Atlantic Forests). Crosses indicate the open vegetation formation domains of (lower left to upper right) Central Chaco Domain, Cerrados Domain, and Caatingas Domain. Normal stippling indicates Araucaria Domain.

tively homogeneous. Second, the domain where the greatest number of species ranges coincide is the Amazon Equatorial Domain, or Amazonia.

A map of isophenes of species densities is presented in figure 20.3. The pattern shows a diversity gradient, with the highest diversity generally occurring in the middle of the composite range and lower diversity around the periphery. If the Middle American species were included, the species diversity in northwestern South America would be higher and the number of species would decrease from Costa Rica to south-

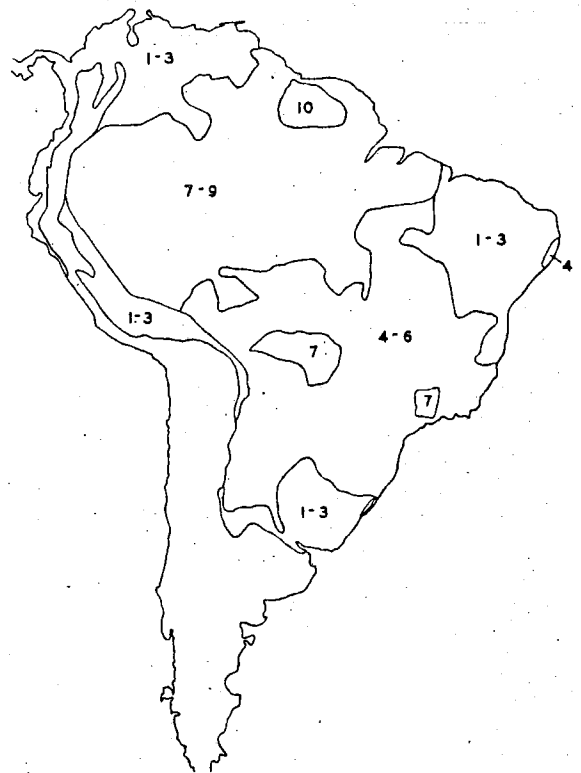


Figure 20.3 Species density map for 30 species of the *Leptodactylus* complex. Isophene contour lines of intervals of three species derived from figure 20.1. An example of how to read the figure is that Amazonia has 7-9 species; the Roraima area has 10 species.

ernmost Texas. It is clear that Amazonia has a high species density and that the zoogeography of the *Leptodactylus* complex in Amazonia is a key step to understanding the zoogeography of the complex throughout its range. The four areas of highest diversity are rather different in terms of habitats and ranges. Those of Amazonia (broad region with 7-9 species in figure 20.3) and the Atlantic Forest of Brazil (area with 7 species in southeast Brazil in figure 20.3) represent major morphoclimatic domains and most of the species represented have their centers of distribution in those domains. In north-central South America 10 species ranges overlap in an area where two morphoclimatic domains interdigitate (see fig. 20.2); this area represents an overlapping of species ranges whose centers of

distribution lie elsewhere. The area in south-central South America (area of 7 species where Brazil, Bolivia, and Argentina border each other) is a transition area between three major morphoclimatic domains. No species is restricted to that area; their centers of distribution lie elsewhere.

A basic tenet to understanding the zoogeography of the frogs of Amazonia is the recognition of forest and open formation delimited taxa (Heyer 1976, as tutored by Vanzolini, pers. comm.). We know of two species that occur both in open formation and forest vegetations: *Adenomera marmorata* and *Leptodactylus pentadactylus*. These, together with *L. knudseni*, *longirostris*, *mystaceus*, *rhodonotus*, and *ventrimaculatus*, for which we have no information, are omitted from this analysis. There remain 5 species which are forest delimited taxa (fig. 20.4) and 18 which are open formation delimited taxa (fig. 20.5).



Figure 20.4 Species density map for 5 forest delimited species of the *Leptodactylus* complex.

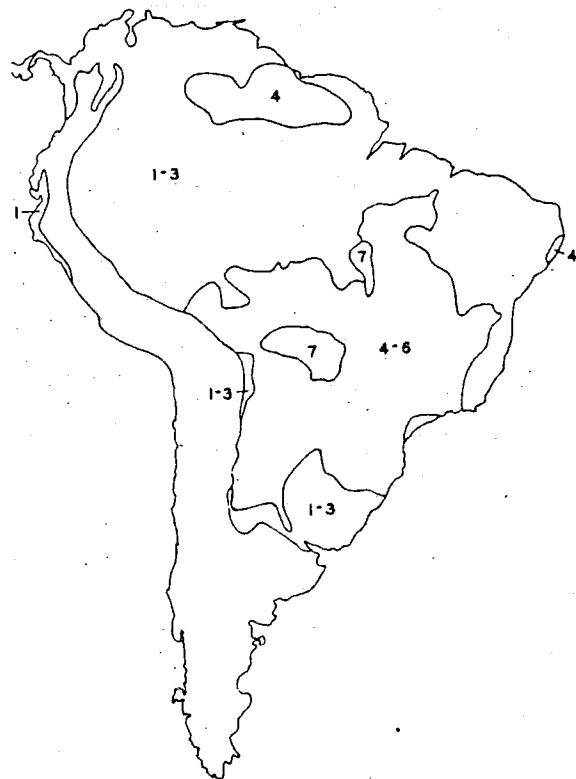


Figure 20.5 Species density map for 17 open formation delimited species of the *Leptodactylus* complex. Field observations for *Leptodactylus notoaktites* were made after the figure was prepared. Addition of this species does not appreciably change the pattern (distribution of *L. notoaktites* shown in fig. 20.8).

As expected, the forest delimited species occur in and are restricted to forest domains (fig. 20.4). The diversity pattern of forest delimited taxa (fig. 20.4) differs from the total pattern (fig. 20.3), in that the density pattern of the forest delimited species is a subset of the total pattern, but is not the same as any part of the total pattern. The pattern of open formation delimited species (fig. 20.5) is similar to the total pattern (fig. 20.3) in the open formation domains of South America. The differences lie in the forest domain regions. In contrast to the limitation of forest delimited frogs to forested domains, some open formation delimited species also occur in forest domains. The high species densities found in the forested domains of South America are



Figure 20.6 Distribution map of *Adenomera andreae*. Hatching indicates homogeneous, differentiated populations.



Figure 20.7 Distribution map of *Adenomera hylaedactyla*. Hatching indicates homogeneous, differentiated population.

due to the overlap of the two ecological groupings, forest and open formation delimited taxa.

In order to better understand the nature of the open formation delimited taxa occurring in forested domains, we need to examine some specific distribution patterns.

Of all the members of the *Leptodactylus* complex analyzed to date, intraspecific variation has been studied in detail only for members of the genus *Adenomera* (Heyer 1973). This is because several species of *Adenomera* have considerable color pattern polymorphism not matched in *Leptodactylus* or *Vanzolinius* species. Two examples show the kind of variation encountered, as well as the distributions of species delimited to forest and open formation vegetation.

Adenomera andreae occurs on the leaf litter of the forest floor. Individuals are ac-

tive in the daytime and most specimens have been collected diurnally. The distribution coincides with the Amazonian forest domain (fig. 20.6). Two homogeneous and differentiated population systems were recognized previously (fig. 20.6 extrapolated from Heyer 1973). Notice that there are two isolated locality records outside the major area of distribution of this species. These records, as well as isolates of other species (certain of following maps) are somewhat troublesome. The distributions of the species involved would be easier to understand without them. Either they represent errors in locality data (which we have tried to confirm), misidentifications, or isolated, disjunct populations. The topic of disjunct isolates is discussed further in the zoogeography section. *Adenomera hylaedactyla* is a nocturnal species found in areas of open vegetations, such as river edges and agri-

