

Neotropical Frog Biogeography: Paradigms and Problems¹

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SYNOPSIS. The distributions and relationships of exemplary species groups of the Neotropical frog genera *Cycloramphus* and *Leptodactylus* are discussed in terms of current biogeographic models. From this exercise, the following conclusions emerge: (1) frog biogeography is and will remain primarily a correlative science; (2) both morphological and genetic data are required to choose among alternate biogeographic models; (3) frog speciation events significantly predate recent distributional events complicating the understanding of past and recent distributions; (4) both data and theory are inadequate to completely understand Neotropical frog biogeography at present.

INTRODUCTION

The basic adaptations of a jumping morphology and amphibious life cycle suggest that frogs are a distinctive eco-evolutionary vertebrate unit wherever they occur. Thus, study of frog biogeography would be predicted to add an additional perspective to the total biogeographic picture for any area of consideration. Frogs are a major component of Neotropical ecosystems, especially in the wet lowlands and lower Andean slopes. Ideally, this paper would represent a synthesis based on the distributions and relationships of the almost one thousand species of frogs occurring in South America (Duellman, 1979). The available data base does not allow the luxury of having too much data to effectively manipulate, however.

The systematic knowledge of Neotropical frogs is just beyond the initial exploratory phase. Generally, names are available and can be associated for most Neotropical frog species. However, when

individual collections are identified or groups revised, the inadequacy of the systematic base is clear. For example, in a collection of 74 species of frogs from the Rio Madeira and Rio Purus, Brasil, 58 were confidently identified, seven were tentatively identified, two were described as new, and seven were unidentifiable and probably represented new species (Heyer, 1977). As another example, until recently the genus *Cycloramphus* from the Atlantic Forests of Brasil was thought to have 7-9 species (Lynch, 1971). In a revision in progress, 21 species are recognized (Heyer, 1982). Needless to say, we need to know what the evolutionary units (species) are before the relationships among them can be determined.

Biogeographical analyses also depend upon accurate distributional and ecological data. These data are partially available for most species of Neotropical frogs. Reasonably accurate distributions are available only for abundant species which have been recently revised based upon examination of all available museum materials, including materials from South American museums. A most fundamental piece of ecological data, the species habitat fidelity, is not available for most Neotropical frogs. Species habitat fidelities throughout the

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geographical distributional ranges must be known before important insights such as Vanzolini's on vanishing refuges (Vanzolini, 1981) can be made.

The approach of this paper is thus limited by the nature of the data base. Our approach is to choose clusters of species, as examples, for which the following criteria are met. First, the clusters must represent the closest relationships among themselves based on gross morphological analysis. Second, the examples must have been recently revised and have reasonably well known distributions. Third, the species clusters must have genetic data on relationships among the species.

The examples chosen for this study are two species clusters of the genus *Leptodactylus* and two species clusters of the genus *Cycloramphus*. Members of these genera are well represented in museum collections and the morphological variation among and within species is reasonably well understood.

Although the focus of this study is narrow in terms of number of species analyzed, the results do provide an example of how frog biogeographic patterns fit current biogeographical paradigms and what problems remain in our lack of understanding of Neotropical frog biogeography both in terms of lack of adequate data and theory.

We have an obvious bias in our biogeographic studies. We are interested in understanding the biogeography of Neotropical frogs using whatever methods and models seem appropriate to further that aim.

METHODS

Distributional and relationship data for the species clusters are presented; these data are then examined for congruence with the current biogeographical paradigms.

The distributional data are of two scales. The first is large scale geographic distribution, plotting localities on a map from museum specimen records. The second is small scale distribution; that of habitat at any locality. Of major importance in terms of frogs is whether species are restricted to

either forest or open formation vegetations (Heyer, 1976; Heyer and Maxson, 1982).

The relationship data are those derived from micro-complement fixation (MCF) analysis of the serum protein, albumin. Antisera to pure albumins were made according to established procedures (Maxson *et al.*, 1979) for *Leptodactylus flavopictus*, *L. labrosus*, *L. labyrinthicus*, *L. pentadactylus*, *Cycloramphus brasiliensis*, and *C. sp.* As sources of albumin, plasma or skeletal muscle preserved in a phenoxethanol solution (Karig and Wilson, 1971) were used. The preserved voucher specimens are deposited in the National Museum of Natural History collections. MCF studies with the albumins of the members of each of the species clusters were performed (Champion *et al.*, 1974) and the results are given as immunological distance units. One unit of immunological distance between two species of frogs represents roughly one amino acid difference in the albumins of these two species (Maxson and Wilson, 1974). As a basis for comparison, previous anuran studies reported distances from 0–120 units within a genus (Maxson, 1976; Scanlan *et al.*, 1980). Frog genera typically differ immunologically by 100 units, although in some cases different hylid genera (*Acris* and *Hyla*, *Pseudacris* and *Hyla*) differ by as few as 45–60 units (Maxson and Wilson, 1975). Reliability of MCF is quite good particularly for the range 0–100 units (± 2 ID units), but may lessen somewhat from 100 to the upper limit of 200 units.

DATA

Leptodactylus labrosus cluster

The four defined species of this morphological cluster are *L. bufonius*, *labrosus*, *troglydytes*, and *ventrimaculatus* (Heyer, 1978). The four species have essentially allopatric geographic distributions (Figs. 1 and 2).

Leptodactylus bufonius has a distribution centering on the Gran Chaco (Fig. 1); *L. troglydytes* has a distribution centering on the caatingas of northeastern Brasil (Fig. 1). Both of these species occur in open for-

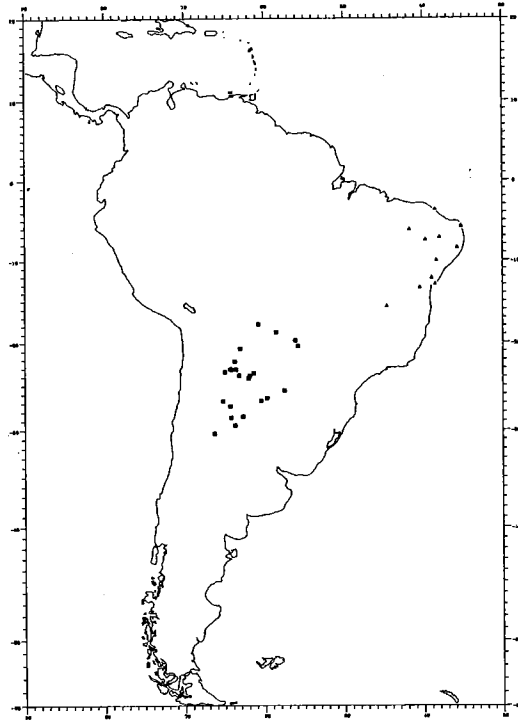


FIG. 1. Distribution of *Leptodactylus bufonius* (squares) and *L. troglodytes* (triangles).

mation vegetations (open in terms of canopy) characteristic of the Chaco and caatingas, secondary growth, natural and man-made clearings.

Leptodactylus labrosus and *ventrimaculatus* occur along west coastal South America, essentially allopatric, but with a single known site of sympatry (Fig. 2). All habitat and relationship data are drawn from specimens at the site of sympatry. There are two other known populations of this species cluster that are most similar to *L. labrosus* and *ventrimaculatus*, which can not be assigned to either species or determined as new with certainty. The more northern (Fig. 2, northern hexagon) population is represented by two poorly preserved specimens. The condition of the specimens precludes accurate determination, but they resemble *L. ventrimaculatus* more than *labrosus*. The more southern population (Fig. 2, southern hexagon) was previously examined (Heyer, 1978), and considered conspecific with *L. labrosus*, but the speci-

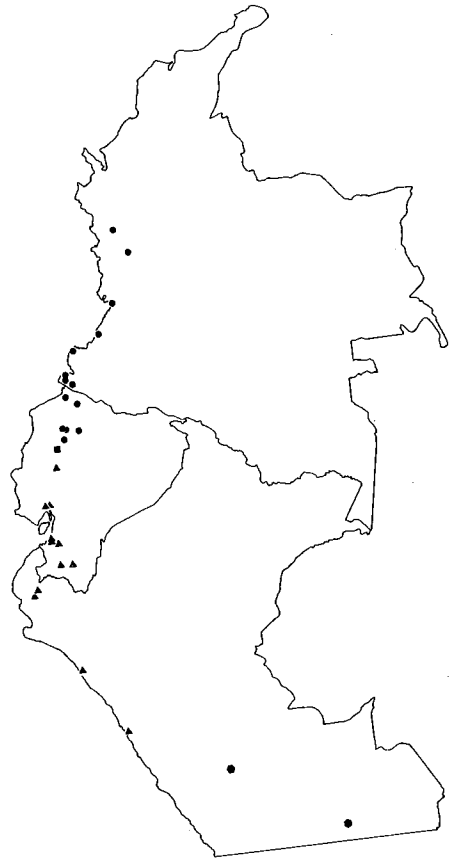


FIG. 2. Distribution of *Leptodactylus labrosus* (triangles and square) and *L. ventrimaculatus* (square and circles). Hexagons indicate two problematic populations of this species cluster (see text).

mens were lost in the mails when borrowed for re-examination. These two most southern populations are not considered further for purposes of this paper, although their distributions are curious.

Leptodactylus ventrimaculatus is restricted to closed forest vegetation, *L. labrosus* occurs in open formation vegetation, second growth, and clearings. At the site of sympatry, the habitat segregation of these two is more pronounced and complete than the morphological differences found between them (McDiarmid and Miyata, personal communication and in preparation).

Morphologically, the four species form two pairs; *bufonius-troglodytes* and *labrosus-ventrimaculatus*. The morphological differences between the members within each



FIG. 3. Distribution of *Leptodactylus flavopictus* (squares) and *L. knudseni* (triangles).

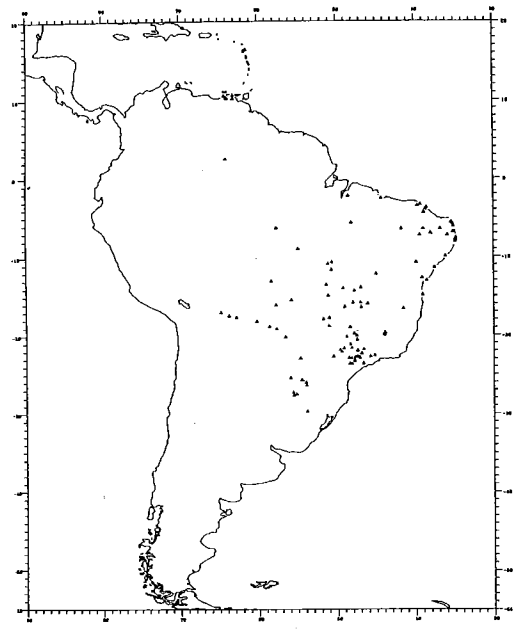


FIG. 4. Distribution of *Leptodactylus labyrinthicus*.

pair are trivial, but the advertising calls are distinctive (Heyer, 1978; Heyer and McDiarmid, in preparation).

The distribution of *L. labrosus* and *ventrimaculatus* is suggestive that clinal variation would be present between these two species. No such clinal relationship is obvious (Heyer and McDiarmid, in preparation).

Antiserum is available only for *L. labrosus*, which differs from *ventrimaculatus* by six immunological distance (ID) units, from *bufonius* by at least 80 ID units, and from *trogodytes* by at least 84 units. As we have no antisera to either *bufonius* or *trogodytes*, the genetic relationships between them are unknown.

Leptodactylus pentadactylus cluster

This cluster includes five species, *L. fallax*, *flavopictus*, *knudseni*, *labyrinthicus*, and *pentadactylus* (Heyer, 1979). *Leptodactylus fallax* occurs in the Lesser Antilles, the remaining four have mainland distributions. As we lack albumin data for *L. fallax*, it is not considered further here.

Leptodactylus flavopictus occurs along east coastal Brazil (Fig. 3). The species is re-

stricted to forests. *Leptodactylus knudseni* and *pentadactylus* have broadly overlapping distributions centering on the Amazonian *Hylaea* (Figs. 3, 5). *Leptodactylus knudseni* and *pentadactylus* occur both in the forests, in disturbed areas, and in clearings adjacent to forests. *Leptodactylus labyrinthicus* has a distribution centering on the open formation vegetations of cerrados and caatingas (Fig. 4); the species does not occur in closed forest. *Leptodactylus flavopictus* and *labyrinthicus* may be found at the same general localities in some areas, but never occurring syntopically; *L. flavopictus* is in the closed forests, *labyrinthicus* in the open formations outside of the forests. *Leptodactylus labyrinthicus* occurs in cerrado enclaves within the Amazonian rainforest and is surrounded by *L. pentadactylus*. As of yet, the two have not been taken together within the cerrado enclaves.

Antisera were prepared for three of the species. The matrix of average ID values for the four species is presented in Table 1. The percent standard deviation from reciprocity (Maxson and Wilson, 1975) is 8.5%. Geographic samples are available for *L. labyrinthicus* (NE Brasil [antiserum] and State of São Paulo) and *pentadactylus*



FIG. 5. Distribution of *Leptodactylus pentadactylus*.

(Pamana [antiserum], coastal Ecuador, and Amazonian Peru) and are included in a cladogram of relationships among the samples (Fig. 6). The estimates of goodness of fit of the immunological distance data with the cladogram is 2.4% using the Fitch and Margoliash (1967) measure, 2.2% using the Prager and Wilson (1976) measure. Both of these values are lower than often found in other immunological studies from a wide variety of organisms (Prager and Wilson, 1978).

Cycloramphus fuliginosus cluster

This cluster contains the morphologically similar *C. brasiliensis* and *fuliginosus* (Heyer, 1982). The species are allopatrically distributed (Fig. 7) in southeast Bra-

TABLE 1. Matrix of average immunological distances for four species of *Leptodactylus*.

| | P | K | L | F |
|---|---|-----|-----|----|
| P | — | 32* | 36 | 53 |
| K | | — | 15* | 55 |
| L | | | — | 55 |
| F | | | | — |

* = one way only. P = *L. pentadactylus*, K = *L. knudseni*, L = *L. labyrinthicus*, F = *L. flavopictus*.

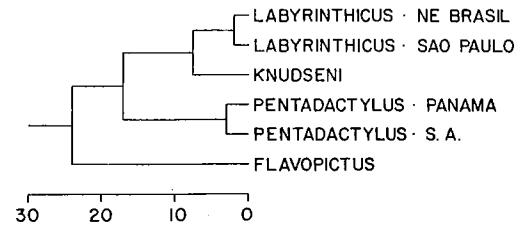


FIG. 6. Relationships among members of the *Leptodactylus pentadactylus* cluster indicated by immunological distance units of the serum protein albumin.

sil. Both species are restricted to forested mountain streams within the Atlantic Forest system.

The two species differ by 116 immunological distance units.

Cycloramphus dubius cluster

This cluster of *Cycloramphus dubius*, *semipalmatus* and a new species is restricted in distribution to a small area in southeastern Brazil (Fig. 8). *Cycloramphus dubius* is most morphologically similar to the new species; the distributions of these two species are allopatric. The morphologically more distinctive *C. semipalmatus* occurs sympatrically with both of the other two species. All three species are restricted to areas covered by Atlantic Forest vegetation. The new species is found along moderately large forested streams and wet rock outcroppings. The other two species occur along small to moderate size mountain brooks. At sites of sympatry, *C. semipalmatus* and the new species demonstrate habitat separation, whereas *C. dubius* and *semipalmatus* occur at the same places along the same brooks (Heyer, 1982).

Antiserum was produced from the new species. The new species is essentially indistinguishable from *dubius* (one ID unit) and differs from *semipalmatus* by five ID units.

PROBLEMS: DATA

The data themselves pose problems, some of which may be peculiar to this data set, others which are common to biogeographic studies in general.

Scale

There is loss of information in the transformation of the relatively precise collect-

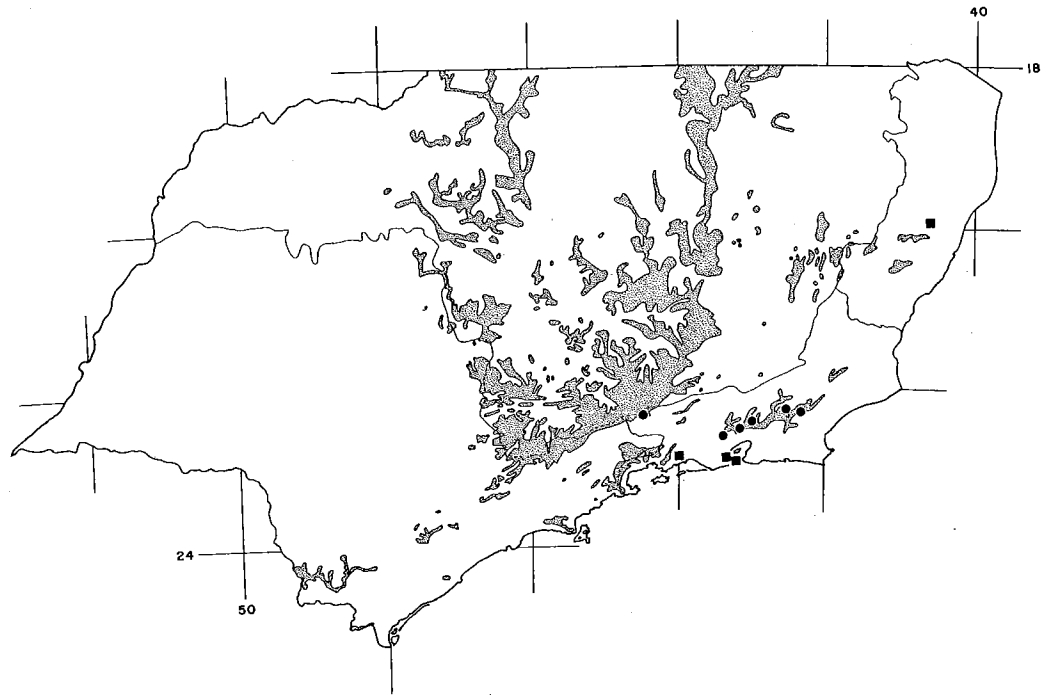


FIG. 7. Distribution of *Cycloramphus brasiliensis* (circles) and *C. fuliginosus* (squares) in southeastern Brazil. Stippled areas connect 1,000 m contour lines.

ing data and observations made in the field to the production of the distribution maps, such as presented in this paper (Figs. 1-5, 7-8). The distribution maps, which are usually the critical data on which biogeographic studies are based, sacrifice precision for generality. Of course this observation is not new, but it is worth repeating, as there are still biogeographic studies that are based on the assumption that distribution maps are precise pieces of information.

Distributional limits and continuities

The distribution maps (Figs. 1-5, 7-8) represent known occurrences of species from given localities. The distributional data for Neotropical frogs is too incomplete to factually state whether the species in question occurs at unsampled localities within the total distributional range, or what the precise distributional limits are. Predictive range maps could be made for the species discussed in this paper which would be based on experience guided by

common sense (see Heyer and Maxson, 1982, for examples), but such maps are predictive models, not statements of fact. The most difficult kind of data to collect, which may be critical to the understanding of a species distribution, is negative data; that is, documentation of a species' absence from a region. An example is a lizard which has a widespread Amazonian distribution, common in collections made along river transects for over 20 years by P. E. Vanzolini, but is entirely missing along the Rio Trombetas (P. E. Vanzolini, personal communication). We do not have this level of knowledge of distributional data for Neotropical frogs at present.

Incongruence of morphological and biochemical data

The relationships among the study organisms must be known in order to develop a robust biogeographical hypothesis for the study group (for example, Rosen, 1975). Often, relationships are deduced from an analysis of morphological fea-

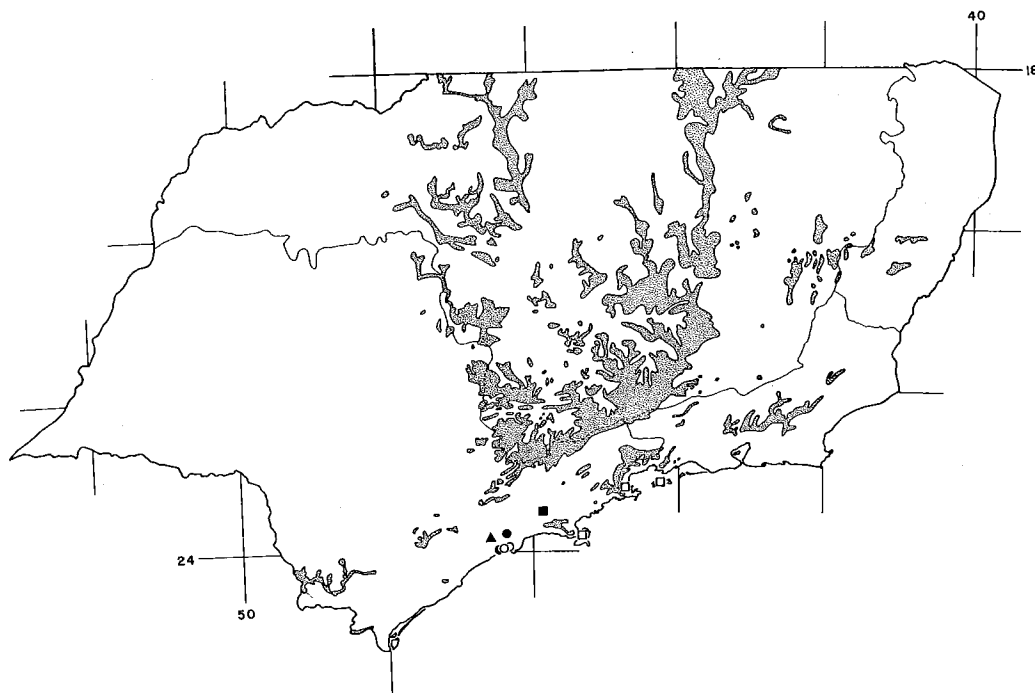


FIG. 8. Distribution of *Cycloramphus dubius* (circles), *C. semipalmatus* (solid symbols) and *C. n. sp.* (squares).

tures, as those data are the most accessible. The data presented above indicate that morphology does not always give accurate or precise information on relationships.

As stated previously, each of the species clusters discussed was determined to be a monophyletic cluster based entirely on morphological data (Heyer, 1978, 1979, 1982). The albumin data are congruent with most of the clusterings. For all *Cycloramphus* and *Leptodactylus* for which we have reciprocal immunological data (unpublished), we find no species that have smaller ID values than those observed within the *Leptodactylus labrosus* cluster, the *L. pentadactylus* cluster, and the *Cycloramphus dubius* cluster.

The obviously incongruent morphological and genetic data occur within the *Cycloramphus fuliginosus* cluster. The morphological features that separate *C. brasiliensis* and *fuliginosus* are so trivial that even some herpetologists who have had field experience with both consider them to be conspecific. The albumin data indicate that the two species are not at all closely related.

This incongruence of morphological and genetic data is not an unexpected evolutionary phenomenon (for example, Maxson and Wilson, 1974; Maxson *et al.*, 1981), and as more data are becoming available, it is clear that the incongruence is not uncommon. This means that analyses of relationships solely based on morphological features may only give a first approximation and at times may be misleading, at least in part.

At another level of detail, certain biologically critical morphological data are of no help in elucidating relationships. For example, the morphological features that distinguish the species within the *L. pentadactylus* cluster are details of color pattern and dorsolateral fold development. These data can not be used effectively in a cladistic analysis to hypothesize relationships within this cluster (Heyer, 1979). Thus, in order to develop a robust biogeographical hypothesis, genetics are needed to elucidate relationships where morphological data are inadequate.

Incongruences of methodological re-

sults, cases, or traits provide information in themselves; an incongruence is as important as a congruence in leading to a total understanding of the biogeographic system being studied.

As discussed more fully in a later section, the incongruence of morphological and genetic data sets has an important implication regarding evolutionary rates.

PARADIGMS

Several paradigms of differentiation/speciation/biogeography have been or are currently used to explain observed patterns of distributions and relationships. Each of these models is now examined to determine whether the data presented in this paper are congruent with and/or can be tested for robustness with the models. These models are not necessarily mutually exclusive, but each has a distinct emphasis.

Dispersal

This model proposes that current distributions involved historic long distance dispersal, often from a site of evolutionary origin. Dispersal is an important model in oceanic island biogeography, where biotic origins on the islands are due to the dispersal mechanism. Darlington (1957) relied heavily on the dispersal mechanism in discussing the zoogeography of the families of frogs.

The distributions and relationships presented here are not particularly concordant with the dispersal paradigm. Dispersals involving range expansions and contractions are indicated, such as the distribution of *Leptodactylus pentadactylus* in Middle America. These kinds of dispersal events are not of the magnitude associated with this model, however.

Vicariance: The forest refugia hypothesis

The vicariance model was proposed as an alternative to the dispersal model, where fragmentation and differentiation of formerly continuous distributions account for present distributions. Vicariance biogeography is more or less what used to be called allopatric speciation. Currently, vicariance biogeography lacks a rigorous definition and the term has been used for

different phenomena by various authors. There has been much interest lately in a special case of the vicariant model, that of tropical forest refugia. The refugial model proposes that presently continuous forest systems, such as the Amazonian Hylaea, were historically reduced by drier climatic conditions into small islands. These forest islands not only served as refuges for the forest biota, but also served as differentiation centers, resulting in speciation in some cases. At present, the evidence for these refugia in the Amazon indicates that there were three or four such cycles of forest contraction and expansion during the Pleistocene. The documentation of rapid differentiation in small refugia by certain forest biotic elements is now available (Vanzolini, 1981). As pointed out elsewhere (Heyer and Maxson, 1982), Pleistocene forest refugia effected distributions, but not speciation in frogs of the genus *Leptodactylus*.

The best supporting evidence for distributions correlating with refugia is current distributions which coincide with proposed refugial distributions. Ideally, refugia should be based on geomorphological data and analysis and not on biotic distribution patterns. The best fit of geomorphological evidence with refugial distributions for South America is presented in maps by Haffer (1979) and Jackson (1978). The distribution of *Leptodactylus ventrimaculatus* matches the proposed distribution of the Chocoan refuge. The distributions of *Leptodactylus knudseni* and *pentadactylus* do not show evidence of refugial distribution patterns, but as they are not forest delimited species, they would not be predicted to. The forest delimited species in addition to *Leptodactylus ventrimaculatus* are *Leptodactylus flavopictus* and the *Cycloramphus* species. *Cycloramphus dubius* and *semipalmatus* show a pattern of distributions restricted to a single forest refugium; the others have a pattern joining two refugia.

The very close relationship of *C. dubius* and the new species is consistent with Pleistocene speciation in adjacent refugia (see Jackson, 1978, fig. 38, refugia 2 and 3) and subsequent range expansion by the new species. The distribution of the closely re-

lated *C. dubius* and *semipalmatus*, while consistent with a distribution demonstrating a refugial pattern, does not conform with a vicariant model of speciation.

The refugia model also has ramifications for non-forest delimited species, although not as striking as for the forest delimited species (Heyer and Maxson, 1982). During more arid times, open formation vegetations were widespread in Amazonia. The relictual populations of *L. labyrinthicus* on north coastal Venezuela and the present cerrado enclaves in Amazonia reflect a former broader distribution explained by the refugial model. The albumin differentiation between the Northeast and São Paulo samples of *L. labyrinthicus* indicates that the species was likely *in situ* near the sampled localities at least through the Pleistocene and would likely have occurred throughout much of the Amazon basin during drier climatic phases.

Vicariance: The general model

The general vicariance model calls for a barrier separating previously contiguous populations. Much of the South American continent on which the species discussed in this paper occur lacks obvious barriers to short dispersal. The uplift of the Andes is an obvious exception. The distance of relationships between *L. bufonius-troglodytes* and *L. labrosus-ventrimaculatus* is so great that these pairs likely differentiated prior to the uplift of at least the northern, if not central portion of the Andes. The immunological distance between the Middle American and mainland Amazonian populations of *L. pentadactylus* is of a magnitude compatible with the suggestion that uplift of the northern Andes may have been the event that led to vicariant differentiation of these daughter units.

Ecological determinism

This model proposes that present day ecological factors are the major determinant of distributions, regardless of whatever historical changes in distribution have occurred through dispersal or vicariance.

Ecological determinism can be viewed at a minimum of two levels. The first is the habitat distribution of a species, the second

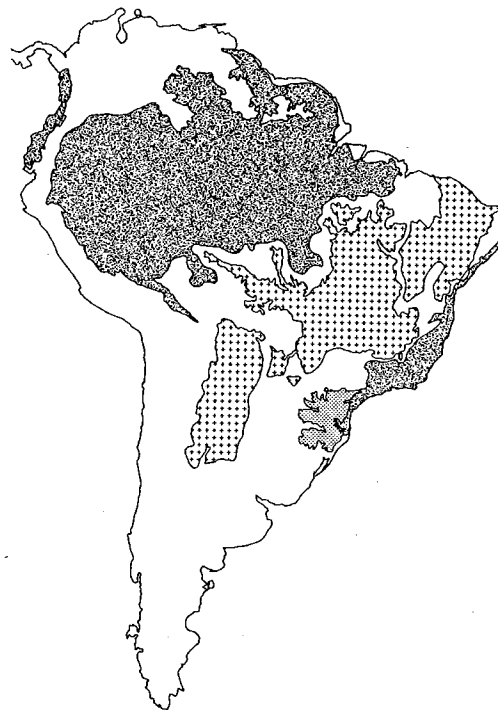


FIG. 9. Selected morphoclimatic domains (Ab'Sáber, 1977) pertaining to *Cycloramphus* and *Leptodactylus* distributions. Heavy, uneven stippling indicates the forested domains of (left to right) the Pacific Equatorial Domain, the Amazon Equatorial Domain, and the Atlantic Tropical Domain. Crosses indicate the open vegetation formation domains of (lower left to upper right) Central Chaco Domain, Cerrados Domain, and Caatingas Domain. Normal stippling indicates Araucaria Domain.

the ecogeographical distribution of a species.

Where closely related species have different ecological distributions, the distributions at a general locality are strikingly different. An example is the distribution of the forest delimited *L. ventrimaculatus* and the open formation delimited *L. labrosus* at the Río Palenque site in Ecuador. The *Cycloramphus* species provide another kind of habitat distribution. All of the species discussed in this paper are closely associated with small rushing mountain brooks. The species only occur in geographic regions where such brooks are found. These kinds of data are adequate to explain local distributions and ecological determinism is of paramount importance

at this biogeographic level. However, the model was proposed to explain larger scale, or what are here considered ecogeographical distributional patterns.

The Neotropics contain a variety of environments, even within lowland areas, ranging from deserts to rainforest. Obviously, species are limited in distribution within portions of this environmental gradient. Large scale vegetation maps are often used in understanding individual species ecogeographical distributions. We have found Ab'Sáber's (1977) morphoclimatic domain map (Fig. 9) to be the best tool in understanding the ecogeographic distributions of neotropical frogs (Heyer and Maxson, 1982). Basically, a morphoclimatic domain is defined by superposition of relief, soil, drainage, climate and vegetation. The most visible aspect is the vegetation characteristic of the particular domain involved. Comparison of the distribution maps (Figs. 1-5, 7-8) with the morphoclimatic domain map (Fig. 9) indicates (1) an extremely good fit of distributions of *L. ventrimaculatus* with the Pacific coastal tropical forest domain, *L. bufonius* with the Chaco domain, and *L. troglodytes* with the Caatinga domain; (2) several species are limited in distributions within a domain, but apparently do not occur throughout the domain—*L. knudseni* to the Amazonian domain, *L. flavopictus* and all the *Cycloramphus* to the Atlantic Forest domain; and (3) two distributions that occur in more than one domain, *Leptodactylus pentadactylus* in the cis- and trans-Andean forested domains, and *L. labyrinthicus* in the open formation domains in Brasil and northern Venezuela. At this time we can point out the correlations of frog and domain distributions. We do not know if the correlations are due to adaptations to features of the domain as defined, or solely to aspects of the vegetation characteristic of the domain. These correlations do add a great deal to our understanding of the distributions of the species in question (also see Heyer and Maxson, 1982), but they do not provide a convincing demonstration that ecological determinism is the only determining factor

in the current species distributions of the study group. If ecological determinism were the only paradigm involved, restricted distributions within morphoclimatic domains would not be predicted. The restricted distributions of the *Cycloramphus* species within the Atlantic Forest domain are more understandable, at least in part, in terms of the vicariant model than the ecological deterministic model.

Clinal speciation

Endler (1977) has recently demonstrated the theoretical possibility of parapatric or even sympatric speciation along environmental clines. The distribution of *L. labrosus* and *ventrimaculatus* along the Pacific coastal environmental gradient, together with the very close relationship of these two species are consistent with this model. The available data on the morphological variation along the environmental cline (Heyer and McDiarmid, in preparation) indicate that the nature of the variation is complex and can not be used to support or negate a clinal relationship. What would be expected is a step cline as there is a sharp environmental change along the cline.

The same clinal model of differentiation could be involved for the origin and distribution of *Leptodactylus labyrinthicus* and either *L. knudseni* or *pentadactylus* on the one side and *L. flavopictus* on the other. The distance of relationships among these taxa would require that speciation was not a recent phenomenon across the environmental gradients as they occur now or occurred throughout the Pleistocene, however.

The clinal model of parapatric or sympatric speciation is clearly not involved for the *Cycloramphus* species discussed in this paper.

Differentiation by distance

This model has been proposed to account for variation observed in organisms where there are no obvious environmental differences involved for the populations studied (area-effect speciation of White, 1978). This model is based on distribution

ranges that are orders of magnitude larger than individual home ranges, so that the effect of gene flow is limited. This model is consistent with the differentiation observed between populations sampled for albumins for *L. labyrinthicus* from NE Brazil and the State of São Paulo and *L. pentadactylus* from Panama and coastal Ecuador.

The mechanism of differentiation implied in this model would enhance any vicariant speciation model.

The island model

The island model of biogeography (MacArthur and Wilson, 1967) involving colonization of suitable environments by propagules from distant sources and faunal equilibrium, has been applied to mainland biogeography in some cases, where distinctive habitats occur in island-like distribution patterns (e.g., Brown, 1971). The model does not apply to the lowland Neotropical biota, however, as the most likely application would involve the islands of forest involved in the vicariant refugial model. As Vanzolini (1981) points out for the current mesic enclaves found in NE Brazil, "A very interesting, if incidental, consequence of the interactions of the fauna of the refuges with that of the surrounding open formation is that it precludes the direct application to small enclaves of the concepts of insular biogeography, which makes no provision for fishes foraging on trees."

Stasipatric speciation

White (1978) recently elucidated this model involving chromosomal mechanisms of speciation resulting in distributions which may lack ecogeographic congruence. The model is strongest for closely related groups of species which have major differences in karyotypic morphologies. The model calls on major chromosomal rearrangement within the karyotype. A contributing factor to the origin of the chromosomal variability that serves as a basis for the model can be catastrophic selection. The distributions resulting from this model are typically parapatric with a

narrow zone of stable hybridization. The zone of hybridization may shift geographically over time, and not strictly be correlated with environmental factors.

For the species of *Cycloramphus* and *Leptodactylus* for which karyotypes are known, the karyotypes are conservative, $2n = 22$ for *Leptodactylus*, $2n = 26$ for *Cycloramphus*. As White (1978) points out, there can be considerable chromosomal reorganization within a given karyotype morphology, but the initial karyotypic data for these genera, together with no known instances of a stable hybrid zone, suggests that this model is not appropriate for the examples discussed. This model may be involved in the frog genera *Adenomera* and *Pseudopaludicola*, which have considerable karyotypic variation.

PROBLEMS: BIOGEOGRAPHY

Data-model congruence versus proof

All of the examples discussed above either demonstrate data congruence with a model or lack of congruence. Most biogeography is correlative and like many ecological studies, suffers the same drawback, namely, that correlation does not prove cause and effect. Probably the strongest test of robustness of a biogeographic model is when falsifiable predictions can be made from the model. Generally, biogeographic models explain distributions, rather than predict, however. So far, the exceptions have been limited to unusual distribution patterns, but have been dramatic when proposed and tested (for example, the sand-dune *Liolaemus* model proposed by Vanzolini and Ab'Sáber, 1968; verified by Müller and Steiniger, 1977).

Having data of both distributions and genetic relationships allows some model alternatives to be discarded for the data under consideration. For example, the distributions of *Leptodactylus bufonius-troglo-dytes* on the one hand and *L. labrosus-ventrimaculatus* on the other is consistent with the vicariant model involving uplift of the Andes. The genetic data on relationships indicates that the separation of these taxon-groups took place before the uplift of

the northern Andes, however, falsifying the model. While the kinds of data presented in this paper can be used to falsify some models, congruence of data and model do not prove that the model is the correct explanation for the data at hand. Of course, just because a model can not be proven to be correct does not mean that it is false.

Palimpsest phenomenon

The biogeography of recently differentiated taxa is the easiest to understand. In these cases, the mode of speciation/differentiation as well as distribution may be clear and unambiguous. For taxa with longer evolutionary histories, the biogeographic picture is not simple or easily understandable. One of the examples provided in this paper demonstrates a non-congruence of morphological and genetic data. This incongruence is explained best by the hypothesis that morphological evolutionary rates are much more variable than the albumin evolutionary rates of differentiation (see Maxson *et al.*, 1981 for a complete discussion). The relative constancy of albumin differentiation allows the data to be interpreted in a time frame, with one million years of time corresponding to an average immunological distance of 1.8 units (Wilson *et al.*, 1977). When this time clock is applied to the data presented in this paper, all of the speciation events in *Leptodactylus* took place from the Eocene throughout the Miocene to the Pliocene at the latest. The differentiation between *Cycloramphus brasiliensis* and *fuliginosus* may go back to the Paleocene, while speciation occurred among the *C. dubius* members in the Pliocene and Pleistocene. Most of the speciation events in the genus *Leptodactylus* were likely Miocene events (also see Heyer and Maxson, 1982 and unpublished data). Climatic fluctuation and concomitant species range expansions and contractions have occurred frequently, at least throughout the Pleistocene. For the species with long evolutionary histories in the Neotropics, the same parchment has been written on and partially erased so often that a single biogeographic model or theory may be incorrect, incomplete, or inappropriate. It

is worth emphasizing that morphological data can not be used to estimate divergence times. Members of the *L. pentadactylus* cluster are so morphologically similar that they were either usually considered subspecies or conspecifics until recently (Heyer, 1979). Based on morphological similarities, Pleistocene speciation would be predicted. The albumins of the *Leptodactylus* cluster, however, indicate that speciation was much earlier than Pleistocene.

Distributions without a model

No one model completely explains the biogeography of any of the species clusters presented herein. One or more models explain various biogeographic component parts of many of the clusters. However, there are several details presently unexplained by any of the models for the species clusters. For the *C. fuliginosus* cluster, no current model adequately explains the origin and distribution of the component species.

Inadequacy of biogeographic theory

Our current understanding of biogeographic theory does not allow a complete understanding of the differentiation and distribution patterns of Neotropical frogs. This is not to say that we should formulate new biogeographic theory, although this may result given further analysis and synthesis of the data. For the species with long evolutionary histories, the fact that more than one currently expressed biogeographic model may apply, combined with the palimpsest phenomenon, may preclude a definitive biogeographic understanding of the species involved. For these kinds of species, it would appear hopeless to ever be able to test any biogeographic model. For most Neotropical frog data, biogeography will continue to be a correlative, non-predictive science.

CURRENT STATE OF THE SCIENCE: CONCLUSIONS AND PROGNOSIS

Biogeography has historically been based on (1) systematic studies using morphological analyses to determine species limits and relationships and (2) distribution maps that accompanied the systematic

studies. Recently, there has been an active group that uses cladistic analyses of morphological data to propose relationships which are applied to a biogeographic paradigm. Our studies indicate that any approach which uses relationship data based entirely on morphological data will give only a first approximation to any biogeographic understanding. For a more complete biogeographic picture both data on morphological variation and genetic relationships are needed to combine with precise distributional data.

In terms of Neotropical frogs (and very likely for all Neotropical groups except for birds and certain groups of butterflies), much rice and bean level of work needs to be done. We need much more locality data in order to have precise distributions; for many species the longer field work is delayed the greater the imprecision of our data will be due to habitat destruction. We need field ecological data; at the least, data on habitat occurrence and fidelity throughout the geographic range. We need basic taxonomic studies completed for most of the frogs.

When more detailed systematic studies based on analysis of morphological variation are available that have accompanying detailed distribution maps, then distribution patterns can be grouped and critical examples can be explored in further detail. The detailed examination should include an analysis of relationships based on genetic data and ecophysiological studies to understand the physiological limits to distribution. Unfortunately, the genetic and ecophysiological studies can not be done for all groups as they are expensive in terms of time and resources. The ecophysiological approach adds a finer understanding to biogeographic distributions (for an example, see Pough *et al.*, 1977, for Jamaican *Eleutherodactylus*). Currently, it is not clear why *Leptodactylus labrosus* does not penetrate the network of open formations further to the north in the Chocó. Physiological studies on water and heat stress and metabolic efficiency might provide that information.

At present, we have the first general understandings of Neotropical frog biogeog-

raphy. We can expect the picture to come into sharper focus when additional data are available. However, the traditional kinds of data used in biogeographical studies will not lead to a complete resolution of any biogeographic picture. We may be able to understand current distributions, but "It is very probable that no simple explanation will be found for many vicariant distributions in South America, and that models will eventually emerge implicating, directly or indirectly, physiological factors not currently studied" (Vanzolini, 1980). Past distributions may be beyond a comparable level of understanding for species with long Neotropical evolutionary histories.

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REFERENCES

- Ab'Sáber, A. N. 1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação. *Geomorfologia* 53:1-23.
- Brown, J. H. 1971. Mammals on mountaintops: Nonequilibrium insular biogeography. *Amer. Natur.* 105:467-478.
- Champion, A. B., E. M. Prager, D. Wachter, and A. C. Wilson. 1974. Micro-complement fixation. In C. A. Wright (ed.), *Biochemical and immunological taxonomy of animals*, pp. 397-416. Academic Press, London.
- Darlington, P. J., Jr. 1957. *Zoogeography: The geographical distribution of animals*. John Wiley and Sons, Inc., New York.
- Duellman, W. E. 1979. The numbers of amphibians and reptiles. *Herpetological Rev.* 10:83-84.

- Endler, J. A. 1977. Geographic variation, speciation, and clines. *Monogr. Pop. Biol.* 10:1-246.
- Fitch, W. M. and E. Margoliash. 1967. Construction of phylogenetic trees. *Science* 155:279-284.
- Haffer, J. 1979. Quaternary biogeography of tropical lowland South America. In W. E. Duellman (ed.), *The South American herpetofauna: Its origin, evolution, and dispersal*, pp. 107-140. Monograph 7, Museum of Natural History, University of Kansas, Lawrence.
- Heyer, W. R. 1976. Notes on the frog fauna of the Amazon Basin. *Acta Amazonica* 6:369-378.
- Heyer, W. R. 1977. Taxonomic notes on frogs from the Madeira and Purus rivers, Brasil. *Pap. Avulsos Zool.* 31:141-162.
- Heyer, W. R. 1978. Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Natur. Hist. Mus. Los Angeles County, Sci. Bull.* 29:1-85.
- Heyer, W. R. 1979. Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithsonian Contrib. Zool.* 301:1-43.
- Heyer, W. R. 1982. Variation and systematics of frogs of the genus *Cycloramphus* (Amphibia, Leptodactylidae). *Arq. Zool.* (In press)
- Heyer, W. R. and L. R. Maxson. 1982. Distributions, relationships, and zoogeography of lowland frogs: The *Leptodactylus* complex in South America with special reference to Amazonia. In G. T. Prance (ed.), *Biological diversification in the tropics*, pp. 375-388. Columbia University Press, New York.
- Jackson, J. F. 1978. Differentiation in the genera *Enyalius* and *Strobilurus* (Iguanidae): Implications for Pleistocene climate changes in eastern Brazil. *Arq. Zool.* 30:1-79.
- Karig, L. and A. C. Wilson. 1971. Genetic variation in supernatant malate dehydrogenase of birds and reptiles. *Biochem. Genet.* 5:211-221.
- Lynch, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Univ. Kansas Mus. Natur. Hist. Misc. Publ.* 53:1-238.
- MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. *Monogr. Pop. Biol.* 1:1-203.
- Maxson, L. R. 1976. The phylogenetic status of phylomedusine frogs (Hylidae) as evidenced from immunological studies of their serum albumins. *Experientia* 32:1149-1150.
- Maxson, L. R., W. R. Heyer, and R. D. Maxson. 1981. Phylogenetic relationships of the Brazilian leptodactylid frog genera *Craspedoglossa*, *Cycloramphus*, and *Zachaeus*. *Experientia* 37:144-145.
- Maxson, L. R., R. Highton, and D. B. Wake. 1979. Albumin evolution and its phylogenetic implications in the plethodontid salamander genera *Ensatina* and *Plethodon*. *Copeia* 1979:502-508.
- Maxson, L. R. and A. C. Wilson. 1974. Convergent morphological evolution detected by studying proteins of tree frogs in the *Hyla eximia* species group. *Science* 185:66-68.
- Maxson, L. R. and A. C. Wilson. 1975. Albumin evolution and organismal evolution in tree frogs (Hylidae). *Syst. Zool.* 24:1-15.
- Müller, P. and H. Steiniger. 1977. Evolutionsgeschwindigkeit, Verbreitung und Verwandtschaft Brasilianischer Erdleguane der Gattung *Liolaemus* (Sauria, Iguanidae). *Schwerp. Biogeogr. Univ. Saarlandes* 9:1-17.
- Pough, F. H., M. M. Stewart, and R. G. Thomas. 1977. Physiological basis of habitat partitioning in Jamaican *Eleutherodactylus*. *Oecologia* 27:285-293.
- Prager, E. M. and A. C. Wilson. 1976. Congruence of phylogenies derived from different proteins. *J. Molec. Evol.* 9:45-57.
- Prager, E. M. and A. C. Wilson. 1978. Construction of phylogenetic trees for proteins and nucleic acids: Empirical evolution of alternative matrix methods. *J. Mol. Evol.* 11:129-142.
- Rosen, D. E. 1975. A vicariance model of Caribbean biogeography. *Syst. Zool.* 24:431-464.
- Scanlan, B. E., L. R. Maxson, and W. E. Duellman. 1980. Albumin evolution in marsupial frogs (Hylidae: *Gastrotheca*). *Evolution* 34:222-229.
- Vanzolini, P. E. 1980. *Coleodactylus septentrionalis*, sp. n., with notes on the distribution of the genus (Sauria, Gekkonidae). *Pap. Avulsos Zool.* 34:1-9.
- Vanzolini, P. E. 1981. A quasi-historical approach to the evolution of reptiles in tropical geographic isolates. *Pap. Avulsos Zool.* 34:189-204.
- Vanzolini, P. E. and A. N. Ab'Sáber. 1968. Divergence rate in South American lizards of the genus *Liolaemus* (Sauria, Iguanidae). *Pap. Avulsos Zool.* 21:205-208.
- White, M. J. D. 1978. *Modes of speciation*. W. H. Freeman and Company, San Francisco.
- Wilson, A. C., S. S. Carlson, and T. J. White. 1977. Biochemical evolution. *Ann. Rev. Biochem.* 46:573-639.