

polytypic characters except for the character, posterior sternum. State 60, the presence of a bony style in at least some species, has a clustering value of 0.18 and appears twice in the phylogeny of Figure 9, once at the cluster basal to the leptodactylines, and once at the end point *Thoropa*. In the initial character analysis, two species of *Thoropa* were examined for the sternal apparatus. In one, *Thoropa petropolitana* (USNM 164135), the sternum is clearly the same as state 1 of character 32, or state 57 as it appears in the phylogenies: the sternum is cartilagenous, the sides are parallel proximally, and the distal portion is expanded and bifurcate (Figure 4H). The posterior sternum of *Thoropa miliaris* (USNM 97765), is quite different in appearance. Functionally, the apparatus is a sternal style, and this is how it was coded in the analysis (Figure 4P). However, there is a major difference between the sternal style of *Thoropa miliaris* and the styles of the leptodactylines. The styles of the leptodactylines are bony and appear whitish in dissection. The style of *Thoropa miliaris* is composed of calcified cartilage and appears brownish in dissection. A further differentiation is that the posterior sternal apparatus of the leptodactylines is composed of two distinct parts, a bony mesosternum and a cartilagenous xiphisterum. The sternum of *Thoropa miliaris* grades from a bony style proximally to a cartilagenous bifurcate xiphisterum distally. Thus, while the styles of *Thoropa miliaris* and the leptodactylines are functionally the same, all evidence indicates that they are not phylogenetically the same. With the sternal apparatus of *Thoropa miliaris* recoded as state 2 of character 32 or state 58 as it appears in the phylogenies, the relationships of *Thoropa* become clearer. *Thoropa* had been placed in a cluster with the leptodactylines previously at one point in the analysis of relationships. It is now clear that this clustering was made possible by the incorrect coding of the sternum in *Thoropa*, and that as suggested in Figure 9, *Thoropa* is a grypiscine, not a leptodactyline. Further, state 60 is now a unique state in the phylogeny of Figure 9, appearing only in the basal cluster of the leptodactylines.

I am actually surprised by the high number of convergences that appear in the phylogenies. I had hoped that the data would not have as much noise in it as apparently it does. Nevertheless, I am con-

vinced that the methodology used to analyze these data resulted in a phylogeny which reflects the relationships reasonably well. Perhaps one of the most critical areas of the phylogeny is in the clusters which define each of the five informal groups. Overall, these five clusters are sound. The cluster joining the ceratophrines is a monothetic cluster, although it does not contain any unique states. The telmatobines are represented by a monothetic cluster in the phylogeny of Figure 9, but with the addition of the other genera, there is no cluster that defines the group. As discussed in the zoogeography section, there is valid reason for not expecting the telmatobines to share a cluster of derived states. The cleutherodactylines have a basal, monothetic cluster with a unique state, direct development. The leptodactylines have a monothetic basal cluster with a unique state involving the sternal style. The grypiscines are the weakest group represented in the phylogeny of Figure 9, as they do not share a monothetic cluster. In fact, the relationships of the grypiscines in Figure 9 could as well be expressed with the leptodactylines as they share the states 14, 20, 57. From evidence of evolution and zoogeography, however, to be discussed below, I think the strongest case is for the closest relationships of the grypiscines to lie with the cleutherodactylines rather than the leptodactylines.

It is apparent from the nature of the data that two requirements had to be met to arrive at what I believe are meaningful conclusions. The first is adequate sample size in terms of numbers of characters. I think with the diversity represented by the genera of the family, the number of convergences in any data set is going to be high. To overcome this, the sample size of characters must be fairly large, otherwise the noise due to convergences may well override the phylogenetic information present. I think the number of characters used herein is on the low end of the sufficient number. The second is adequate sample size in terms of numbers of taxa analyzed. For instance, if *Eleutherodactylus nigrovittatus* had not been included in the sample, I would most likely have included *Barycholos* in the leptodactylines rather than the cleutherodactylines. It is for this reason that I think there will be modifications of the intragroup relationships as more information becomes available.

Evolutionary Zoogeography

The emphasis of this discussion will be at the level of the five major informal groupings for the obvious reason that the intragroup details are not worked out at present.

In formulating hypotheses on the evolutionary zoogeography of leptodactylid frogs, the basic data used are radiation centers and the broad ecological adaptations exhibited by the genera. The following radiation centers and broad ecological adaptations appear to represent the most basic units below which subdivision is not desirable. In part, the radiation centers and ecological adaptations overlap.

RADIATION CENTERS.—A radiation center is a geographic area that contains at least one endemic genus of leptodactylid frog and is further set apart by distinctive vegetation type or geographic relationships. The radiation centers correspond to the geographic areas used in the initial character analysis with the exception of the Guiana Shield (discussion follows). The nine radiation centers, the percentage of primitive states averaged for all genera found in each center, the total number of genera, and the number of endemic genera found within each center are presented diagrammatically (Figure 10). As presently understood, there are no genera endemic to Middle America. However, once the relationships within the *Eleutherodactylus*-complex become better understood, I believe there will be at least one eleutherodactyline endemic to this area. The absence of endemic leptodactylid frog genera from the Guiana Shield is surprising at first thought because the Guiana Shield is an ancient land mass that supports a number of endemic frog genera. If the Guiana Shield region is thought of in a broad sense, radiations of the following frog families are found there at present: Allophrynidae, Bufonidae, Centrolenidae, Dendrobatidae, and Hyliidae (from Savage, 1973). It is therefore instructive that the Guiana Shield region does not represent a radiation area for leptodactylid frogs. The radiation centers compare favorably with Müller's distribution centers (1973). The radiation centers recognized here encompass several of Müller's distribution centers. This is to be expected, as the unit of analysis for the radiation center is the genus, while that of Müller's distribution center was the species and subspecies.

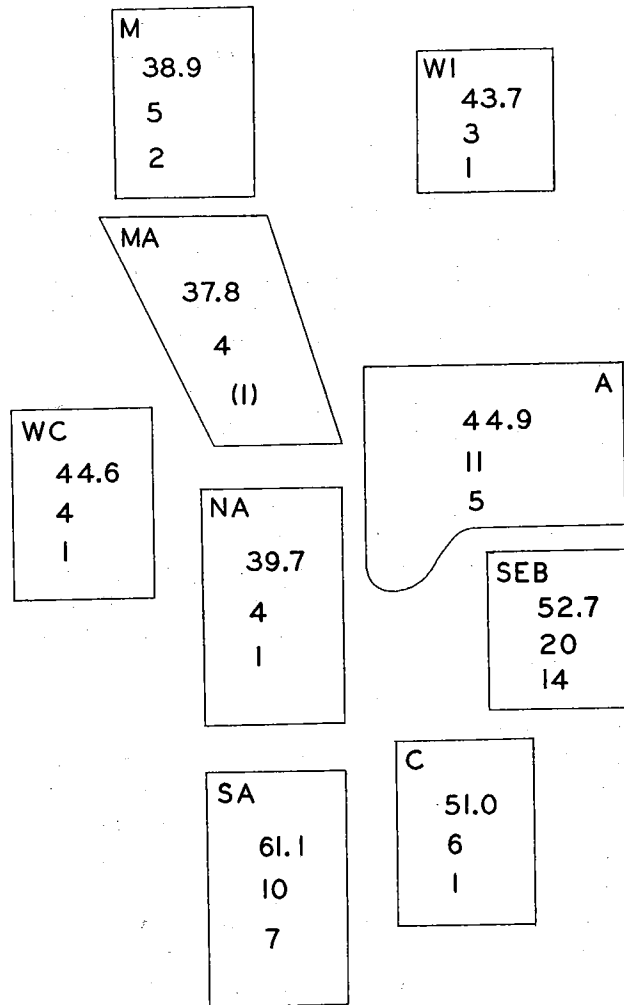


FIGURE 10.—Leptodactylid radiation centers. (M = Mexico, MA = Middle America, WI = West Indies, WC = West coast of South America, NA = northern Andes, SA = southern Andes, A = Amazonia, SEB = Southeastern Brazil, C = Chaco. Within each center, the upper number is the average percentage of primitive states, the middle number is the total number of genera, and the lower number is the number of endemic genera; also see text.)

ECOLOGICAL ADAPTATIONS.—The following broad adaptations appear to be the major ones exhibited by living leptodactylids: (1) adaptations associated with temperate beech forest environments; (2) adaptations associated with tropical and subtropical forests; (3) adaptations to tropical montane environments; (4) arid adaptations, such as to the Gran Chaco environment; and (5) savanna adaptations. The exact ecological adaptations are not

known for several of the genera: the assignments are based on whatever information is available.

Data on radiation centers and ecological adaptations are summarized by groups.

TELMATOBINES.—Seven of the eight genera comprising the telmatobines are restricted to the beech forests of the southern Andes. *Telmatobius* is found in the northern and southern Andes. All adaptations within the group appear to be responses to particular habitats within the beech forest ecosystem. Most notable are the trends toward adult aquatic adaptations (*Batrachophrynus*, *Caudiverbera*, *Telmatobius*), stream adaptations (*Telmatobufo*), and toward terrestriality (*Batrachyla*).

CERATOPHRINES.—All genera are found in either the Chaco and/or southeastern Brazil. In addition, *Ceratophrys* is found in Amazonia and the east coast of South America. The present ecological adaptations are either adaptations to arid environments and/or forest environments. The overall morphology of ceratophrines strongly suggests a basic semifossorial adaptation. The semifossorial adaptations would clearly have a selective advantage in arid environments and it seems most reasonable to assume that the basic adaptation of ceratophrines was to an arid environment and that the semifossorial adaptations allowed secondary access into forested situations.

LEPTODACTYLINES.—The 10 genera comprising the leptodactylines are collectively widely distributed—they occur in every radiation center except the northern Andean center. The genera which demonstrate endemic patterns are found either in Amazonia (*Edalorhina*, *Hydrotaetare*, *Lithodytes*, *Vanzolinius*) or southeastern Brazil (*Limnomedusa*). All genera have ecological adaptations to either forest or savanna environments. In sorting out which adaptation is basic to leptodactylines, forest or savanna, the restricted distribution patterns of the forest genera opposed to the widespread distribution patterns of the savanna genera indicate that the forest adaptation set was primary, the savanna adaptations secondary.

GRYPISCINES.—All 10 genera are limited to the southeastern Brazil radiation center, although *Hylodes* has been reported from the Guianas. Rivero (1968) described *Elosia duidensis* from Mt. Duida, Venezuela, as the only member of the genus *Elosia* to occur outside of southeastern Brazil. Lynch (1971) pointed out that *Hylodes* is the

proper generic name for *Elosia*. Rivero (1968) did not examine the specimens for myological or osteological information. Clearly, he placed his new species in *Hylodes* on the basis of dorsally divided disks and fringed toes. Dorsally divided disks are found in *Hylodes*, *Crossodactylus*, and *Megaelosia* of the grypiscines, and *Lithodytes* of the leptodactylines, and I have observed the state in some *Eleutherodactylus* of southeastern Brazil. Rivero (1968) commented on the *Eleutherodactylus*-like appearance of his new species. The evidence suggests to me that *duidensis* is a member of the *Eleutherodactylus*-complex and not a *Hylodes*. All grypiscines are found in forested habitats and further, eight of the genera are adapted to forest stream life in one way or another. It is this overall forest stream adaptational complex that convinces me that the grypiscines are a natural unit.

ELEUTHERODACTYLINES.—The eleutherodactylines are the most diverse of the groups. Members are found in all radiation centers except the Chaco, and some genera are endemic in five of them. The major ecological adaptive types are to arid, forest, and tropical montane environments. The ancestral home and adaptive type of the eleutherodactylines centers upon the origin of terrestriality. As argued more fully later, I believe the origin to be in the forests of southeastern Brazil.

HISTORICAL ZOOGEOGRAPHY

Savage (1973) summarized the major biogeographic patterns of living frog families, including the family Leptodactylidae. Savage listed the following events as being of prime importance on the diversification of leptodactylid frogs: the splitting up of Gondwanaland, first into east and west portions in middle Jurassic, and a second splitting of continents in the early Cretaceous; and the diversification of climatic and vegetation zones in the Paleocene, including the appearance of xeric climates and vegetations. The most parsimonious blend of radiation centers, ecological adaptive types, continental changes, climatic and vegetational changes, and Savage's (1973) arguments is represented in the diagram of Figure 11. The overall trend is clear: the family had its origin in the beech forests of temperate South America, where a remnant of that original stock still remains. Two stocks became adapted to drying conditions, the

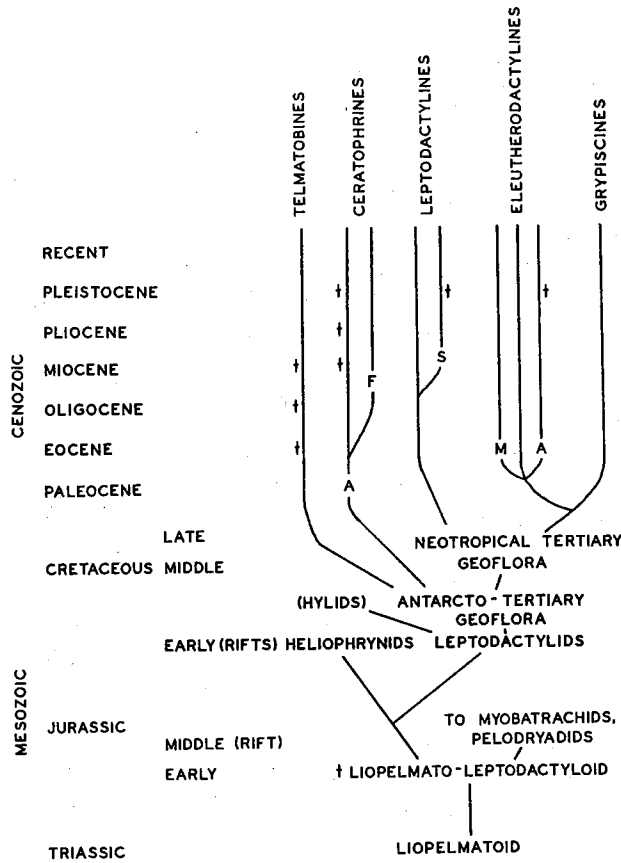


FIGURE 11.—Proposed historical zoogeography of the five leptodactylid groups. (A = arid, F = forest, M = montane, S = savanna; also see text.)

ceratophrynes and the leptodactylines. The grypsicines represent a forest-stream adaptation that centered in southeastern Brazil, and the eleutherodactylines most likely had their origin as an early grypsicine stock. Before discussing each of the group patterns in more detail, it is instructive to compare and contrast the pattern proposed thus far (Figure 11) with previous proposals.

Vuilleumier (1968) was the first to point out that the beech forest frog fauna of South America was neither relictual nor depauperate but rather was a consequence of a long and complex history. Vuilleumier (1968) also suggested the frog fauna of the beech forests was represented by four historical units. Lynch (1973a) contradicted the validity of Vuilleumier's four historical units and stated that his "... analysis must be rejected because his conclusions are in part based upon the erroneous conclusions of other authors" (p. 214).

Actually, Lynch concurred with Vuilleumier's major contention, as Lynch proposed that the origin of the family was in the beech forests of temperate South America.

All recent studies (Vuilleumier, 1968, Lynch, 1971, Savage, 1973) concur that the family originated in temperate South America. There is considerable difference of opinion as to how the ancestral stock to the Leptodactylidae arrived in its ancestral home. Lynch (1971) considered (1) that the leptodactylids were closely related to the pelobatids, (2) that the pelobatids arose in the Northern Hemisphere, and (3) that the leptodactylids represented a southward migration from the Northern Hemisphere through the tropics to the South Temperate Zone. Lynch (1971) based the close pelobatid-leptodactylid relationships on shared primitive states, a concept I philosophically reject. As shown by Savage (1973) the pelobatids and leptodactylids have little relationship in common.

Savage (1973) also proposed a holarctic migration for the leptodactylids, but from a discoglossoid ancestor. As is clear from his diagrams (pp. 400-401), deriving the leptodactylids in situ from a leiopelmatid ancestor is a distinct possibility, in fact, one that Savage has considered (pers. comm.). The proposed leiopelmatid-leptodactylid relationship has a distinct zoogeographical advantage—it does not require the unseemingly long migration of a north temperate group across many thousands of miles of tropics to the southern temperate region, only to expand and differentiate northward again. An in situ origin of leptodactylids from a leiopelmatid ancestor also simplifies the zoogeographic origin of the bufonids and ranoids (Savage, pers. comm.). Savage (1973) based a northern leptodactylid origin on tadpole evidence. Savage (1973) found that Starrett's (1973) proposal of four suborders of frogs based upon larval characteristics makes zoogeographic sense. Only two of Starrett's (1973) tadpole types need be discussed for present purposes. Both larval types have denticles and beaks for scraping food sources from a substrate and placing the foodstuff into temporary suspension. Both types of tadpoles differ from other tadpoles in: (1) feeding actions are more separated from respiration, (2) presence of a long coiled gut for algae feeding, (3) presence of extra jaw cartilages, muscles, and accessory mouth structures for

