

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 grypsine, 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 eleutherodactylines 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 grypsines 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 grypsines 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 grypsines to lie with the eleutherodactylines 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 eleutherodactylines. 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 *Hyllidae* (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.

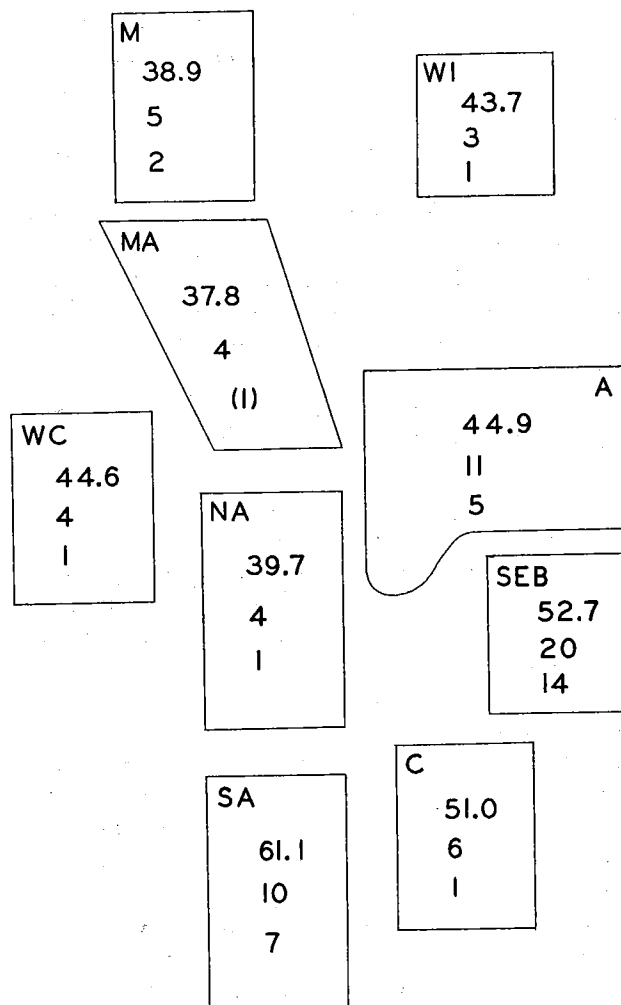


FIGURE 10.—Leptodactylid radiation centers. (M = Mexico, MA = Middle America, WI = West Indies, WC = West coast of South America, NA = northern Andes, SA = southern Andes, A = Amazonia, SEB = Southeastern Brazil, C = Chaco. Within each center, the upper number is the average percentage of primitive states, 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*, *Hydrolaetare*, *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

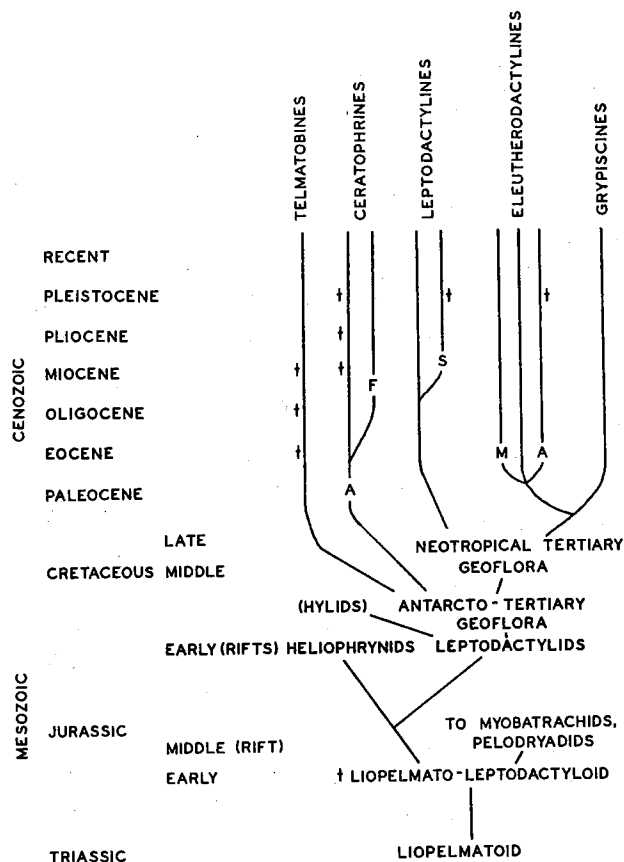


FIGURE 11.—Proposed historical zoogeography of the five leptodactylid groups. (A = arid, F = forest, M = montane, S = savanna; also see text.)

ceratophrines and the leptodactylines. The grypsines represent a forest-stream adaptation that centered in southeastern Brazil, and the eleutherodactylines most likely had their origin as an early grypsine 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

feeding, (4) smaller branchial chambers, and (5) forelimbs that develop close to branchial chambers. There is little doubt that both kinds of tadpoles had an ancestral condition in which food was eaten that was already in suspension in the water column. The two tadpole types differ in that the lemmanuran tadpoles (Ascaphidae, Discoglossidae) have separate branchial chambers with median external openings, have forelimbs that develop close to the branchial chambers, and have one more jaw muscle than the acosmanuran larvae (Pelobatidae, Leptodactylids, Bufonids, Ranoids), which have a single branchial chamber with a sinistral external opening and forelimbs that develop within branchial chambers. Starrett (1973) indicated and Savage (1973) followed that the acosmanuran type of tadpole is monophyletic. If it arose only once from an ancestor with a lemmanuran type of tadpole, then all Southern Hemisphere acosmanuran families had to have an ultimate origin in the Northern Hemisphere. Obviously, Savage (1973) was convinced that the acosmanuran tadpole is monophyletic. One reason for suggesting the leiopelmatid-leptodactylid relationship is to suggest a reason to expect the acosmanuran type of tadpole to have originated twice.

As Savage (1973) points out, during the Jurassic, the families of frogs had a distinctive distribution pattern with respect to tadpole types. The North and South Temperate zones were populated by families with lemmanuran or acosmanuran types of tadpoles, while all northern and southern tropical families had beakless larval types (Xenopus and Scaphiophrynus of Starrett, 1973). The development of denticles and beaks and associated structures for scraping food into suspension doubtless represents a considerable expenditure of energy. This extra energy needed for a specialized feeding apparatus is reflected in a longer metamorphic time for denticled and beaked tadpoles as opposed to beakless tadpoles (Heyer, 1973). If extra energy is required for the specialized feeding apparatus of the lemmanuran and acosmanuran tadpoles, then there must be certain kinds of environments where this kind of feeding apparatus has a distinct selective advantage. There appear to be two kinds of habitats in which a scraping and chewing apparatus is required to exploit aquatic primary productivity. The first is stream environments, in which the algae must be scraped off rocky substrates. The

second is temperate temporary or permanent ponds. The water in such ponds is often clear; the primary productivity is in the form of periphyton. In contrast, temporary tropical ponds in seasonal environments are usually turbid; there is much primary productivity suspended in the water column. The acosmanuran tadpole probably arose in temporary temperate ponds, judging by the distribution of larval types in the Jurassic. If this was the case, it would make sense that similar selective forces, operating on similar sorts of beakless tadpoles continents apart, would result in similar adaptive kinds of tadpoles. In other words, the acosmanuran tadpole may have arisen twice; once in the Pelobatids in the temperate Northern Hemisphere, and a second time in the leiopelmatids in the temperate Southern Hemisphere. Unfortunately, living *Liolopelma* are no help; all three living species have a derived life history pattern of direct development and no fossil leiopelmatid larvae have been found. The crux of the argument hinges, then, on whether the pelobatid acosmanuran tadpole is really the same as the leptodactylid (bufonid, and ranoid) acosmanuran tadpole. Starrett (1973) in her review gives no indication with respect to resolution of this question. I think that given the specialized organism represented by a beakless xenopus type of tadpole, there are an extremely limited number of ways one can functionally mold such a midwater suspension feeder into a scraping and chewing feeder. If this is true, then one might not expect to find great morphological differences among acosmanuran types of tadpoles that had been independently derived from xenopus sorts of larvae. In comparing lemmanuran and acosmanuran types of larvae, it is obvious that there are greater similarities that unite them and lesser kinds of differences that differentiate them. I think the characteristics that unite both kinds of larvae and set them apart from other types are the minimum functional adaptations required for a scraping and chewing existence. Further, the lemmanuran type of tadpole might well be diphyletic, arising once in the stream environment (Ascaphidae) and once in the temperate pond environment (Discoglossidae). In summary, I would not expect there to be great differences in functional morphology between pelobatid tadpoles and leptodactylid tadpoles if they are diphyletic, given there are such a limited number of ways, perhaps one, to

be a really efficient scraping and chewing feeder based on a beakless, xenoanuran sort of tadpole type. Rather, if there are consistent small differences in the way the single branchial chamber is constructed or in how the forelimbs develop within the branchial chambers of pelobatid tadpoles vs. leptodactyloid, bufonid, and ranoid tadpoles, I would argue for a separate origin of the larvae. To my knowledge, such data is not available at present, or if available, certainly not summarized.

Savage (pers. comm.) indicates that even if the lemmanuran tadpole is monophyletic, a southern origin of the Pelobatidae is not unreasonable.

The proposed events depicted diagrammatically on Figure 11 during Middle and Late Jurassic and Early Cretaceous assume that with the advent of continental rifting, the evolutionary stocks diverged as units on each of the continents. This is a reasonable assumption for those leptodactyloid groups not presently associated with beech forests. Evidence is accumulating that the beech forests of Antarctica, South America, and Australia were contiguous up until Paleocene and/or Eocene (Frakes and Kemp, 1972; Foster, 1974). Once the relationships among the Australian and South American leptodactyloids are better understood, it is possible that beech forest faunal components in Australia and South America will be found to be more closely related to each other than either are to other Leptodactyloid groups.

WITHIN-GROUP PATTERNS

TELMATOBINES (Figure 12).—The telmatobines represent an ancient radiation that was essentially confined to the south Andean radiation center. Only one genus occurs in the north Andean radiation center. The radiation has been moderate resulting in 8 genera and about 46 species. By far the most successful genus in terms of numbers of species is *Telmatobius*, with about 30.

CERATOPHRINES (Figure 13).—The primary radiation of the ceratophrines was in the Chaco type of habitat with a secondary radiation in southeastern Brazil. The genus *Ceratophrys* has spread to the Amazon region and there is one species in the west coast lowlands of South America. The presence of *Ceratophrys* on the west coast of South America is most likely due to its presence there prior to the uplifting of the north Andes, rather than an in-

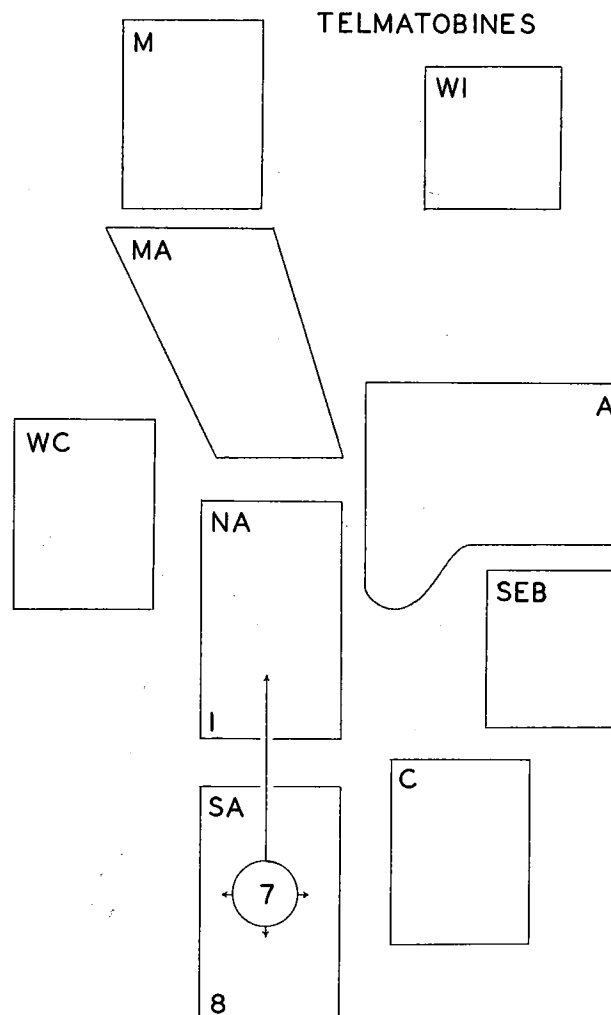


FIGURE 12.—Proposed telmatobine radiation. (Number in circle is number of endemic genera; numbers at bottom are total number of genera; abbreviations as in legend for Figure 10.)

vasion after the Andes had been uplifted. The ceratophrine radiation has been rather small, resulting in about 5 genera and 22 species.

GRYPISCINES (Figure 14).—The grypiscine radiation took place in southeastern Brazil where all members are endemic. The overall adaptation of the group is to the forest stream habitat. Within this general adaptation framework, the most noticeable evolutionary trends are toward terrestriality (direct development) (e.g., *Zachaeus*) and arbo-reality (*Crossodactylodes*). The grypiscine radiation is an old and moderate radiation, which resulted in about 10 genera and 37 species.

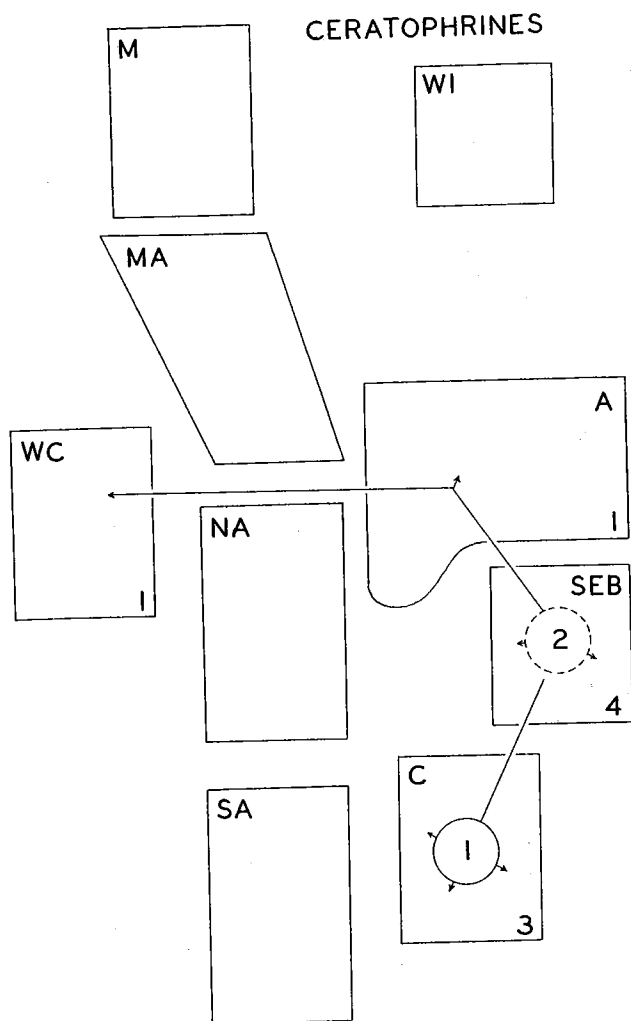


FIGURE 13.—Proposed ceratophrine radiation. (Numbers in circles are numbers of endemic genera; numbers at bottom are total number of genera; solid circle = primary radiation; dashed circle = secondary radiation; abbreviations as in legend for Figure 10.)

LEPTODACTYLINES (Figure 15).—The primary adaptation of the leptodactylines was to the Neotropical Tertiary Geoflora. The remnants of that radiation are found in the derived forests of Amazonia and southeastern Brazil. The size of this primary radiation has been small, resulting in 6 genera and 11 species. The secondary radiation of savanna adapted forms was much more successful and recent, reflected in the fact that the four savanna genera are widespread, none are endemic to a single radiation center, and they are represented by about 85 species. Representatives of the

FIGURE 14.—Proposed grypsine radiation. (Number in circle is number of endemic genera; number at bottom is total number of genera; abbreviations as in legend for Figure 10.)

savanna genera were able to island hop to the West Indies, but have not radiated there. Three species of *Leptodactylus* are represented on the Greater and Lesser West Indian islands, which are more closely related to other South American species than to each other. This would indicate that the leptodactylines were the last leptodactylids to arrive in the West Indies. All of the leptodactyline species found in Mexico (2 *Leptodactylus* and 1 *Physalaemus*) and Middle America (5 *Leptodactylus* and 1 *Physalaemus*) are also found in South America. This indicates that the leptodactylines arrived in Middle America and Mexico relatively recently. This agrees with Savage's (1966) scheme in which

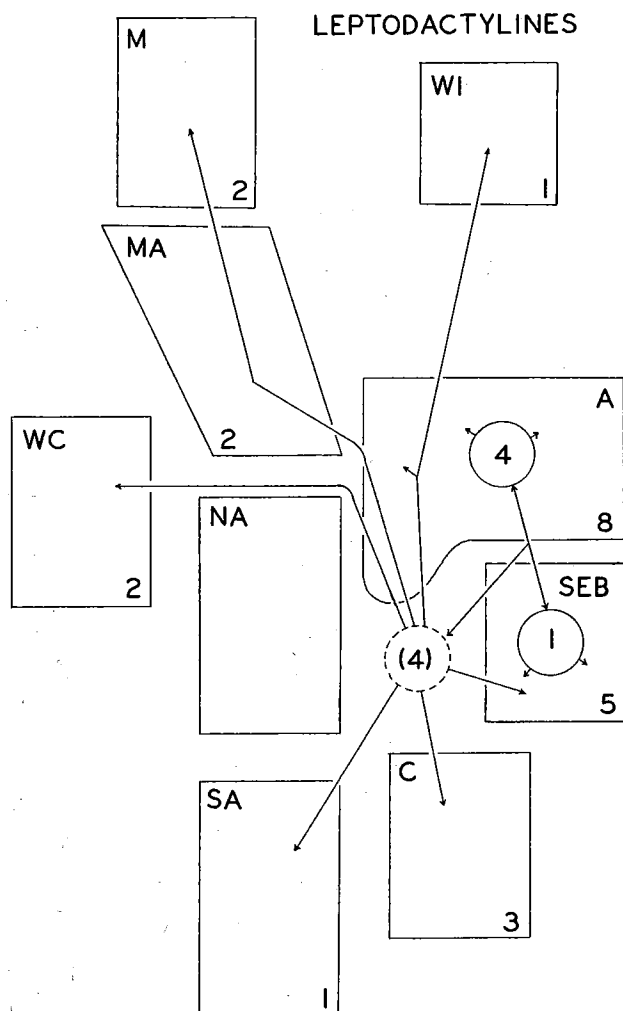


FIGURE 15.—Proposed leptodactyline radiation. (Numbers in circle are numbers of endemic genera; numbers at bottom are total number of genera; solid circles = primary radiations, dashed circle = secondary radiation; abbreviations as in legend for Figure 10; also see text.)

a South American element penetrated Middle America when the land bridge between Middle and South America became reconnected in the Pliocene.

Closely tied in with the success of the savanna adapted leptodactylines is the foam nest. Lynch (1971:220) suggested that the leptodactyline foam nest evolved in response to decreasing equabilities during the Cretaceous. He indicated that the presence of the foam nest allowed the leptodactylines to breed in more xeric environments. I have suggested that the foam nest in *Leptodactylus* was an adaptive response to aridity (1969b, 1974a), but

that the foam nest in *Adenomera* could not be accounted for as an adaptation to arid environments, as the genus is primarily distributed in wet forest (Heyer, 1974a). For *Adenomera*, I suggested that the foam nest was part of an adaptive complex leading to direct development. The results of the present analysis indicate that the foam nest had its evolutionary origin in wet forests and that its original adaptive value was in response to the wet forest environment, such as is demonstrated by the genus *Adenomera* (Heyer, 1974a). This type of foam nest was a preadaptation, then, for the group of frogs which adapted to the drying environments during late Paleocene and Miocene. In other words, the key feature which allowed the savanna leptodactylines such success in adapting to the arid environment, as opposed to members of the other major generic groupings, was the presence of the foam nest, which was preadaptive to the savanna environment.

ELEUTHERODACTYLINES (Figure 16).—The eleutherodactylines have undergone an explosive radiation, some of which may well be continuing at the species level. The history of the eleutherodactylines begins as a grypsine stock in the forests of southeastern Brazil. The key feature which allowed the explosive radiation was clearly the early evolution of direct development. The remnants of this primary radiation remain in southeastern Brazil as two endemic genera containing three species. Not indicated on the diagram of Figure 16 is the diversity represented by *Eleutherodactylus*. The composite genus is found almost wherever eleutherodactylines are found. There is a secondary center of radiation in Amazonia, most probably indicated by at least one endemic genus. The minor radiation of the northern Andes is clearly derived from an Amazonian ancestral stock, and one of the northern Andean genera has penetrated the northern end of the southern Andes. A minor radiation also took place on the west coast of South America. As in the ceratophrynes, the presence of eleutherodactylines on the west coast of South America is most likely because they were there prior to the uplifting of the Andes. There appear to be at least two radiations of the eleutherodactylines in Mexico and Middle America. The first is represented by *Hy-lactophryne* and appears to be the earliest radiation. The second radiation is represented by endemic Mexican and Middle American *Eleutherodactylus*,

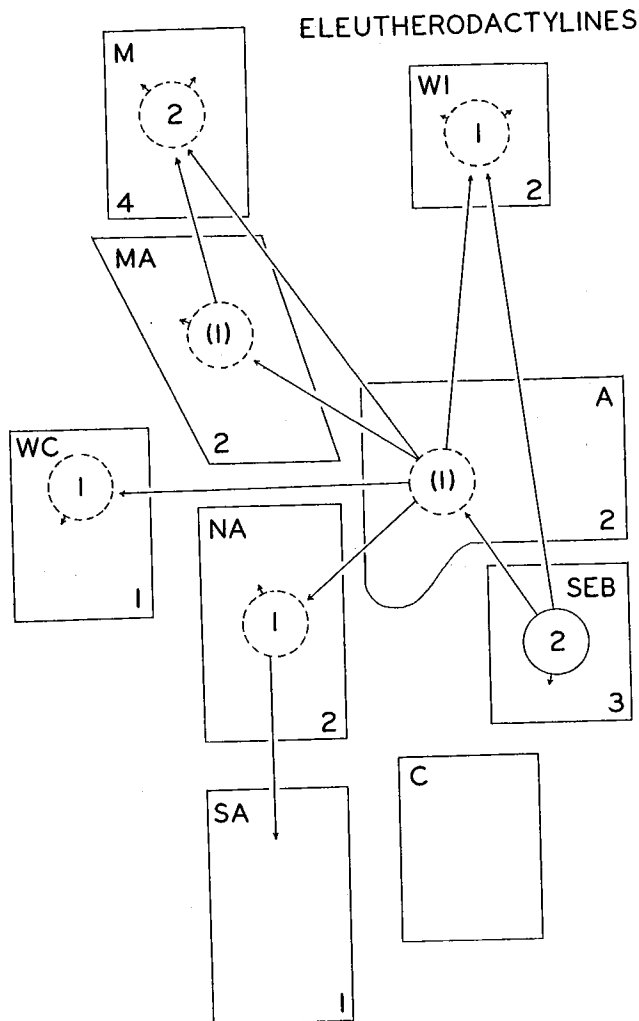


FIGURE 16.—Proposed eleutherodactyline radiation. (Numbers in circles are numbers of endemic genera; numbers at bottom are total number of genera; solid circle = primary radiation; dashed circles = secondary radiations; abbreviations as in legend for Figure 10; also see text.)

Syrrophus, and *Tomodactylus*. Middle and South America were isolated from each other from Paleocene through Miocene and were not connected until Pliocene. The Pliocene is too late for the beginning of the kinds of radiation found. This indicates that the eleutherodactyline stock that gave rise to the two radiations island hopped while Middle and South America were isolated. This is not unreasonable, as eleutherodactylines are good island hoppers as evidenced by their occurrence on almost all West Indian islands. The West Indian eleutherodactyline fauna appears to be the result

of two invasions, an early one, represented by the monotypic *Sminthillus* in Cuba. *Sminthillus* is quite specialized; it may be that the ancestral stock was also specialized, which prevented it from an explosive radiation as in *Eleutherodactylus*. The second, more recent invasion was by an *Eleutherodactylus*-complex member. Further study may indicate at least two invasions by *Eleutherodactylus*-complex members. The explosive radiation of the eleutherodactylines is with the *Eleutherodactylus*-complex, which has about 350 species, most of which are in the West Indies, Middle America, and the slopes of the northern Andes.

ORIGIN AND EVOLUTION OF TERRESTRIALITY

The key to the spectacular success of the *Eleutherodactylus*-complex lies in the evolution of direct development, giving the frogs a completely terrestrial life history. Only the broadest features of this radiation can be outlined at this time due to the poor understanding of the composition of the *Eleutherodactylus*-complex.

In order to trace the origin of direct development, it is necessary to comment on the adaptive significance of the complex life cycle in frogs. The following argument is heavily influenced by the work of Richard Wassersug, who has discussed these points with me. The basic adaptive significance of the frog larvae is to exploit bursts of primary productivity that occur in temporary ponds. This is especially adaptive in seasonal tropical environments, and it appears that the origin of frogs was in seasonal tropical situations. In a seasonal tropical environment, there are predictable physical signals which frogs can interpret that will insure reproductive success. For instance if a frog is buried a certain distance under the soil surface during the dry season, it takes a considerable rainstorm for water to reach the underground point where the frog is buried. Once water reaches the frog, the frog can then burrow out of the soil and reproduce, and the chances are very good that the same rainfall that was sufficient to initiate activity of the frog will form ponds that will last long enough for the larvae to metamorphose. Thus, in seasonal tropical environments the complex life cycle is adaptive, both from an energy utilization viewpoint and a predictive aspect that will insure reproductive success.

The wet forests pose two kinds of problems to the complex life cycle. The first is that there is generally no primary productivity bloom in temporary wet forest ponds, because the release of organic matter by the vegetation is rather continual, not seasonal. The second is that there are no real signals coming from the physical environment that will insure reproductive success. For instance, Inger (1969) has shown that large thundershowers in Borneo are random events. Thus, rainfall pattern does not give any information which would indicate that breeding at one particular rainfall would have a greater likelihood of raising larvae through metamorphosis than any other rainfall. Thus the complex life cycle, as adapted for tropical seasonal environments, is not well adapted for the wet forest environment. I would think that a wet forest environment in these terms could be defined as an environment with a drier season lasting no more than two or three months. Thus, any adaptation toward a terrestrial life cycle would have a selective advantage in the wet forest environment.

This trend toward terrestriality is seen in the present-day grypsines, such as *Zachaenus*. It is interesting to note that in the case of the grypsines, terrestriality has come out of a basic forest-stream adaptational complex. The crux of my argument for proposing that the eleutherodactylines are an early grypsine derivative that attained direct development is based on the supposition that terrestriality originated in a wet forest habitat, and the grypsines, in such an environment, demonstrate repeated trends toward terrestriality. The eleutherodactylines, once they had attained direct development, were able to radiate into a wide variety of ecological zones.

The development of terrestriality in the family Leptodactylidae contains two major features. The first is that the eleutherodactylines, with direct development, have been able to invade ecological adaptive zones unavailable to the other leptodac-

tylid groups. The second point is that terrestriality has been essentially reached within each of the major groups at least once, with the exception of ceratophrines. It is interesting to speculate why the development of terrestriality only led to a radiation in the case of the eleutherodactylines. The telmatobine that approaches terrestriality is *Batrachyla*. Apparently it lacked the genetic flexibility to move out of the beech forests, and terrestrial possibilities within a beech forest are limited. The grypsine forms that are essentially terrestrial are such things as *Cycloramphus* and *Zachaenus*. These are results of continued selective advantages for wet forest frogs, and terrestriality has been approached in this group after the eleutherodactyline radiation occurred; thus there was no ecological access for the terrestrial grypsines. The same appears to be true for *Adenomera*, the terrestrial leptodactyline genus. Its development of terrestriality as a wet forest inhabitant was preceded by the eleutherodactyline radiation. An alternative explanation is that the key feature to the success of eleutherodactylines was the encapsulated egg, which is a more successful mode of terrestriality than the modes seen in *Batrachyla*, *Cycloramphus*, *Zachaenus*, and *Adenomera*, which do not have encapsulated eggs. This alternative explanation could allow the evolution of terrestriality in the eleutherodactylines to have occurred after the origin of terrestriality in the other groups.

Only with the eleutherodactylines did direct development arise in conjunction with a group which had genetic plasticity and ecological and evolutionary access to form a spectacular adaptive radiation. Perhaps it is more than coincidental that the eleutherodactylines form a parallel example to the terrestrial plethodontids which, from a stream adapted ancestor which evolved direct development, underwent an explosive adaptive radiation, much of which was centered in the New World tropics (Wake, 1966).

Appendix: Supplementary Data

SPECIMENS EXAMINED.—The following specimens supplement the data given by Lynch (1971) and Heyer (1974).

LEPTODACTYLIDAE

- Batrachophryne macrostomus*, USNM (in National Museum of National History, Smithsonian Institution, under catalog numbers of former United States National Museum) 118172 muscle dissection (M), KU (University of Kansas, Museum of Natural History) 9817 dry skeleton (S).
Batrachophryne patagonicus, USNM 154170 (M).
Batrachyla leptopus, USNM 196279 (M).
Batrachyla taeniata, USNM 196282 (M).
Caudiverbera caudiverbera, USNM 139788 (M).
Ceratophrys calcarata, USNM 146952 (M).
Crossodactylus gaudichaudii, USNM 164105 (M).
Crossodactylus dispar, USNM 129376 (M).
Cycloramphus fuliginosus, USNM 164121 (M).
Cycloramphus dubius, USNM 129376 (M).
Eleutherodactylus coqui, USNM 86565 (M), USNM 192321 cleared and stained skeleton (CS).
Eleutherodactylus fleischmanni, USNM 67333 (M), KU 68158 (S).
Eleutherodactylus nigrovittatus, USNM-JAP 9140 (M), USNM-GOV 8108 (CS).
Euparkerella brasiliensis, USNM 196288 (M), KU 93192 (CS).
Eupsophus grayi, USNM 139791 (M).
Eupsophus nodosus, USNM 154203 (M).
Holoaden bradei, USNM 196287 (M), KU 107088 (CS).
Hylactophryne augusti, USNM 116420 (M), KU 56187 (CS).
Hylodes aspera, USNM 129155 (M).
Hylodes nasus, USNM 164114 (M).
Ischnocnema quixensis, USNM 194793 (M), KU 104388 (S).
Lepidobatrachus llanensis, USNM-WRH 1360 (M), KU 129706 (S).
Megaelosia goeldi, USNM 96763 (M).
Niceforonia festae, USNM 160957 (M).

- Odontophryne americanus*, USNM 123400 (M).
Odontophryne cultripes, USNM 81138 (M).
Paratelmatobius lutzii, KU 107089 (CS).
Proceratophrys appendiculatus, USNM 12814 (M).
Sminthillus limbatus, USNM 136090 (M), KU 68684 (CS).
Syrrophus campi, USNM 52373 (M).
Syrrophus leprus, USNM 114087 (M).
Telmatobius hauthali, USNM 93208 (M).
Telmatobius jelski, USNM 61162 (M).
Thoropa miliaris, USNM 97765 (M).
Thoropa petropolitana, USNM 164135 (M).
Tomodactylus angustidigitorum, LACM (Natural History Museum, Los Angeles County) 25520 (M).
Tomodactylus nitidus, USNM 114098 (M).
Zachaeus parvulus, USNM 164154 (M).
Zachaeus stejnegeri, USNM 164116 (M).

HELIOPHYRNIDAE

- Heliophryne natalensis*, KU 105925 (CS).
Heliophryne purcelli, USNM 162428 (M).

MYOBATRACHIDAE

- Adelotus brevis*, AMNH (American Museum of Natural History) 59096 (M), KU 147213 (S).
Crinia signifera, USNM 167710 (M), KU 56245 (CS).
Cyclorana australis, USNM 128237 (M).
Glauertia orientalis, AMNH 67394 (M), AMNH 128276 (M).
Heleioporus albopunctatus, USNM 84127 (M).
Kyarranus sphagnicola, AMNH 60707 (M), KU 110331 (CS).
Lechriodus melanopyga, USNM 195572 (M).
Limnodynastes dorsalis, USNM 118774 (M).
Limnodynastes peroni, USNM 167709 (M).
Mixophyes fasciolatus, KU 147227 (S).
Myobatrachus gouldi, AMNH 46052 (M), KU 110333 (CS).
Neobatrachus pictus, AMNH 59114 (M).
Notaden nichollsi, AMNH 67178 (M), KU 93582 (CS).
Philoria frosti, AMNH 67357 (M), KU 50699 (CS).
Pseudophryne bibroni, USNM 167712 (M), KU 83588 (CS).
Taudactylus acutirostris, KU 124233 (CS).
Uperoleia marmorata, AMNH 60643 (M).
Uperoleia rugosa, KU 109861 (CS).

TABLE A.—*Ecological and geographical categories for the study sample*

Table A. -- Ecological and geographical categories for the study sample

Genera	Fossorial	Terrestrial	Aquatic	Arboreal	Africa	Australia	Mexico	Middle America	West Coast S. America	Northern Andes	Southern Andes	Guiana Shield	Amazonia	Chaco	S.E. Brasil	West Indies
LEPTODACTYLIDAE																
Adenomera.....	-	x	-	-	-	-	-	-	-	-	-	-	x	-	x	-
Amblyphrynus.....	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Barycholos.....	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Batrachophrynus.....	-	-	x	-	-	-	-	-	-	-	x	-	-	-	-	-
Batrachyla.....	-	x	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Caudiverbera.....	-	-	x	-	-	-	-	-	-	-	x	-	-	-	-	-
Ceratophrys.....	x	-	-	-	-	-	-	-	x	-	-	-	x	x	-	-
Crossodactylodes.....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Crossodactylus.....	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Cycloramphus.....	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Edalorhina.....	-	x	-	-	-	-	-	-	-	-	-	-	x	-	-	-
E. coqui.....	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x
E. fleischmanni.....	-	x	-	-	-	-	-	x	-	-	-	-	-	-	-	-
E. nigrovittatus.....	-	x	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Euparkerella.....	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Eusophus.....	-	x	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Holoaden.....	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Hydrolaetare.....	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Hylactophryne.....	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-
Hylodes.....	-	x	-	-	-	-	-	-	-	-	-	(x)	-	-	x	-
Hylorina.....	-	x	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Insuetophrynus.....	-	x	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Ischnocnema.....	-	x	-	-	-	-	-	-	-	-	-	-	x	-	x	-
Lepidobatrachus.....	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
Leptodactylus.....	-	x	-	-	-	-	x	x	x	-	-	x	x	x	x	x
Limnomedusa.....	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Lithodytes.....	-	x	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Megaelosia.....	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Niceforonia.....	-	x	-	-	-	-	-	-	-	x	x	-	-	-	-	-
Odontophrynus.....	x	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-
Paratelmatobius.....	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-
Phyllsalsemus.....	x	x	-	-	-	-	x	x	x	x	-	-	x	x	-	-

TABLE B.—Generic character states (arranged by character number) used in character analysis

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Adenomera	A	A	A	A	C	B	B	A	C	A/C/F	B	B	B	B	C	E	D	A	A	A
Amblyphrynus	A	A	A	A	A	B	B	A	C											
Barycholos	A	A	A	A	D	A	C	B	A	B/C	B	A	C	A	B	C	D	A	G	B
Batrachophrynus	A	D	C	A	A	B	B	A	A	A/C									D	D
Batrachyla	A	A	B	A	B	A	A	B	A	A/D	A	A	A	A	A	A	C	B	A	A
Caudiverbera	B	A	B	A	A	A	B	B	A										D	B
Ceratophrys	A	E	B	A	A	E	B	B	A											
Crossodactylodes	A	D	D	A	B	B	A	A	C	A/C	B	B	A	A	A	D	B	A	D	A
Crossodactylus	A	A	D	A	E	F	B	A	D	A/E										
Cycloramphus	A	D	E	D	A	B	A	B	C	A/C	B	B	A	A	A	B	A	A	G	B
Edalorhina	A	A	B	D	A	D	B	A	C	H									H	A
E. coqui	A	A	A	A	D	A	B	A	C	H									F	G
E. fleischmanni	A	A	A	A	D	B	B	A	C	H									F	G
E. nigrovittatus	A	A	A	A	D	A	B	A	C	H									D	D
Euparkerella	A	D	A	A	A	A	B	A	C	A/C	B	B	A	C	A	B	C	C	C	D
Eupsophus	A	E	B	A	A	B	B	A	C	H									B	B
Holoaden	A	D	A	A	A	B	B	A	C										D	A
Hydrolaetare	B	A	A	A	A	B	A	A	C	H									A	G
Hylactophryne	A	A	A	A	A	B	B	A	C	B/C	B	B	A	A	A	B	B	A	D	C
Hylodes	A	A	B	A	E	F	B	A	C	A/E										
Hylorina	B	A	B	G	A	B	B	A	C											
Insuetophrynus	A	B	D	A	A	A	B	A	C											
Ischnocnema	A	A	A	A	A	A	B	A	C	A/E	B	A	A	A	A	I	B	F	G	B
Lepidobatrachus	B	A	B	A	A	B	B	A	E	A/C/F	B	B	A	A	A	A	B	A	A	D
Leptodactylus	A	A	E	H	A	B	B	A	D										G	B
Limnomedusa	B	A	B	A	A	B	B	A	C										B	A
Lithodytes	A	A	A	G	E	F	B	A	C	B/C	B	B	A	A	A	B	B	D	A	B
Megaelosia	A	A	A	A	E	A	B	A	C										D	B
Niceforonia	A	E	A	A	A	B	B	B	F	B/C	B	B	A	A	A	B	I	D	F	D
Odontophrynus	A	D	B	C	A	A	B	A	C	H	B	B	A	C	A	B	A	B	A	C
Paratelmatobius	A	B	B	F	A	E	B	C	C	B/C/F	B	B	B	B	E	A	E	B	E	F
Physalaemus	A	C	C	B	E	A	B	B	C	A/C/G	B	C	B	A	A	H	B	A	D	A
Pleurodema	A	D	B	A	A	B	B	C	A	A/C	B	A	A	A	A	A	C	D	A	B
Proceratophrys	A	D	A	A	A	D	B	A	C	B/C	B	B	A	C	B	A	C	D	A	G
Pseudopaludicola	A	A	A	A	A	B	B	A	C	H	B	B	C	A	B	A	C	D	F	D
Sminthillus	A	C	A	D	D	A	B	A	E	H	B	B	C	C	A	A	G	D	F	B
Syrrophus	A	E	F	A	A	B	B	A	A	B/C	B	B	A	A	A	B	E	C	B	E
Telmatobius	B	D	C	B	A	A	A	A	A	A/C										
Telmatobufo	A	A	B	A	B	A	B	A	D	A/C	B	B	A	A	A	B	B	A	B	B
Thoropa	A	A	A	E	D	A	B	A	C	H									D	A
Tomodactylus	A	A	A	A	F	B	B	A	D										A	A
Vanzolinius	A	A	A	A	A	A	B	A	C	A/E	B	B	A	A	A	A	H	B	A	D
Z. parvulus	A	D	A	A	A	A	B	A	C										A	D
Z. stejnegeri	A	D	A	A	A	A	B	A	C	A/E	B	B	A	A	A	A			A	A

Genus	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Adenomera	A	A	A	A	A	A	B	A	C	C	F	D	A	C	B	B	C
Amblyphrynus	A	A	B	A	A	A	C	A	C								
Barycholos	A	A	B	A	D	A	A	A	C	A	B	C	A	C	A	B	
Batrachophrynus	C	C	A	A	A	C	A	A	B	C	A	A	A	A	A	B	B
Batrachyla	C	C	A	B	A	A	A	A	C	C	D	A	B	A	A	A	A
Caudiverbera	A	A	D	A	C	A	C	A	B	C	C	A	A	A	A	A	
Ceratophrys	A	A	B	A	A	C	A	A	C								
Crossodactylodes	C	C	A	A	A	C	A	B	C	C	A	C	A	C	B	B	B
Crossodactylus	C	C	A	A	A	C	A	A	C	C	A	B	B	A	A	B	B
Cycloramphus	A	A	B	A	A	A	C	A	C	C	A	A	A	C	B	B	B
Edalorhina	A	A	A	A	A	A	A	A	C	A	A	C	A	C	C	B	B
E. coqui	A	A	A	A	A	A	A	B	C	A	A	C	A	C	C	B	B
E. fleischmanni	A	A	B	A	A	A	A	A	C	A	A	C	A	C	C	B	B
E. nigrovittatus	A	A	B	A	G	A	A	A	C	A	A	C	A	C	C	B	B
Euparkerella	A	A	B	A	A	C	A	B	C	A	C	A	A	C	C	B	B
Eupsophus	A	A	A	B	A	B	A	A	B	A	A	C	A	B	A	A	C
Holoaden	A	C	A	B	A	A	A	A	C	A	C	A	A	C	C	A	B
Hydrolaetare	A	A	B	A	D	A	C	A	C	C	E	D	A	A	A	A	B
Hylactophryne	A	A	A	A	B	A	C	A	C	A	A	B	C	C	C	A	B
Hylodes	A	C	A	A	A	A	A	B	C	C	A	C	A	C	C	A	B
Hylorina	C	A	A	B	A	A	C	A	B								B
Insuetophrynus																	B
Ischnocnema	A	A	A	A	B	A	C	A	C	A	A	A	A	C	A	A	B
Lepidobatrachus	A	A	D	A	C	A	C	A	B	D	C	A	B	A	A	A	B
Leptodactylus	A	B	C	A	A	A	C	A	C	A	C	A	D	A	C	A	B
Limnomedusa	A	C	A	B	A	A	A	A	C	C	C	A	D	A	C	B	B
Lithodytes	A	A	A	A	A	A	A	A	C	A	A	A	C	C	C	B	B
Megaelosia	A	A	A	A	E	A	A	A	B	C	A	A	B	A	C	A	B
Niceforonia	A	A	A	A	A	B	A	A	A	C	A	B	A	B	A	A	F
Odontophrynus	A	A	A	A	A	A	C	A	A	C	A	C	B	A	A	A	B
Paratelmatobius	A	A	A	B	A	A	A	A	A	A	E	D	A	B	A	A	G
Physalaemus	A	A	A	A	B	A	A	A	C	C	C	D	A	A	A	A	G
Pleurodema	C	A	A	B	A	A	C	A	A	C	A	A	B	A	A	A	G
Proceratophrys	A	A	B	A	C	A	C	A	C	B	A	E	A	A	A	A	H
Pseudopaludicola	C	C	A	A	A	C	A	A	C	A	A	E	A	C	C	B	B
Sminthillus	A	A	A	A	G	C	A	B	C	A	B	C	A	C	A	B	A
Syrrophus	A	A	A	B	G	B	C	A	B	C							E
Telmatobius	D	C	A	B	D	B	C	A	B								
Telmatobufo	A	A	A	B	D	A	A	A	A	C	A	E	A	A	A	B	B
Thoropa	A	C	A	B	A	A	A	A	B	C	A	C	A	A	C	B	G
Tomodactylus	A	A	A	A	G	A	C	A	B	C	A	C	D	A	C	B	G
Vanzolinius	A	A	B	A	F	A	A	A	C	C	A	C	A	A	C	A	B
Z. parvulus	A	A	B	A	F	A	A	A	C	C	A	C	A	A	C	A	B
Z. stejnegeri	A	A	B	A	F	A	A	A	C	A	B	A	A	A	C	A	B

TABLE B.—*Generic character states (arranged by character number) used in character analysis*
(continued)

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Adelotus	A	D	A	A	A	A	B	A	A	B/C/F	B	A	C	A	C	A	A	A	B	A
Cyclorana	A	A	B	A	A	B	A/B	B	A	A/B/C	B	B	A	A	A	B	B	A	B	B
Helioportus	B	A	E	B/D	A	B	A	B	A/D	A/B/C/D/F	B	A	A	A	A	A	A	B	D	B
Kyarranus	A	D	B	A	A	A	A	A	C	A/F	B	B	C	B	C	A	B	B	B	A
Lechriodus	A	A	B	A	A	A	A	A	C	B/C/F	B	A	A	A	A	A	B	B	A	B
Limnodynastes	A	E	C	A	A	A	A/B	C	B	A/D/F	B	A	A	A	A	A	C	E	B	C
Mixophyes	B	A	B	A	A	A	A	A	A	B/D										
Neobatrachus	B	B	B	A	A	A	A	B	A	A/B/D	B	A	A	A	A	A	A	D	B	A
Notaden	A	D	B	A	A	A	A	B	A	A/D	B	A	A	A	C	A	A	A	B	A
Philoria	A	D	A	B	A	A	A	A	C	A/F	B	F	A	B	C	A	A	D	B	A
Assa	A				A								A	A	C	A				
Crinia	A	E	B	A	A	B	A/B	A	E	B/C	B	A/D	C	B	C	A	D	A	H	A
Glauertia	A	D	A	A	A	A	A	C	A	A/F	B	A/F	C	B	C	A	B	A	B	A
Metacrinia	A	D	A	A	A	A	A	A	C											
Myobatrachus	A	D	A	A	A	A	A	A	C		B	B	C	B	C	A	B	A	A	A
Pseudophryne	A	D	A	F	A	A	A	A	C	B/C	B	D	C	B	C	A	D	A	H	A
Taudactylus	A	D	B	A			B	A	D											
Uperolia	B	D	A	B/D	A	A	A	C	D	B/E	B	B	C	B	C	A	D	A	B	A
Helioportus	B	C	A	A	B	B	B	A	A	A/D	B	B	A	A	A	C	B	A	B	D
Genus	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37			
Adelotus	A	A	A	A	B	A	A	A	B	C	A	A	B	A	A	B				
Cyclorana	A	A	C	A	D/E/F	A	A	A	B	A	A	A	B	A	A	A				
Helioportus	A	A	A	B	B	A	C	A	B	A	A	A	B	A	A	A				
Kyarranus	A	A	A	B	B	A	A	A	B	C	E	A	C	A	A	A				
Lechriodus	A	A	A	A	A	A	A	A	B	C	A	A	A	A	A	A				
Limnodynastes	A	A	A	B	A	A	C	A	B	A	A	A	A	A	A	A			D	
Mixophyes	A	A	B	A	B	A	A	A	B		B		A	A	A	A			D	
Neobatrachus	A	A	A	B	A	A	C	A	B	A	A	A	B	A	A	A				
Notaden	B	C	A	B	A	A	A	A	B	C	A	A	B	A	A	A				
Philoria	A	A	B	B	B	A	C	A	B	C		A	B	A	A	A				
Assa	A			B		C	A		C					A	A					
Crinia	A	C	A	B	H	B	A	A	C	A	E	A	B	A	A	A			D	
Glauertia	A	C	A	B	H	C	A	A	C	C	E	A		A	A	A				
Metacrinia	A	C	A	B	H	C	A	A	C	C			B	A	A	A				
Myobatrachus	A	A	B	B	H	C	A	A	C	C	E	A	B	A	A	A				
Pseudophryne	A	C	A	B	H	C	A	A	C	C	E	A	B	A	A	A			D	
Taudactylus	A	B	B	C	A/H	C	A	A	C	C			B	A	A	A				
Uperolia	A	A	B	A	H	C	A	A	C	C	E	A	B	A	A	A			D	
Helioportus	A	A	A	B	A	A	A	A	B	A	A	A	B	C	B	A			B	

TABLE C.—Generic character states (arranged by character number) used in computer analysis

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Adenomera	0	0	2	0	1	0	1	0	1	0	1	1	1	1	1	1	3
Amblyphrynus	0	0	2	0	0	0	1	0	1	0	1	1	1	1	1	1	3
Barycholos	0	0	2	0	2	1	1	0	1	0	1	0	0	0	0	0	2
Batrachophrynus	0	2	1	0	0	0	1	0	0	0	1	2	0	0	1	0	3
Batrachyla	0	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	2
Caudiverbera	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
Ceratophrys	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1
Crossodactylodes	0	2	0	0	1	0	1	0	1	0	0	0	0	0	0	2	1
Crossodactylus	0	0	0	0	3	2	1	0	2	0	1	1	0	0	0	0	1
Cycloramphus	0	2	1	2	0	0	1	0	1	0	1	1	0	0	0	0	1
Edalorhina	0	0	0	2	0	1	1	0	1	0	1	0	2	0	0	2	1
E. coqui	0	0	2	0	2	0	1	0	1	1	1	0	0	0	1	0	3
E. fleischmanni	0	0	2	0	2	0	1	0	1	1	1	0	0	0	0	0	3
E. nigrovittatus	0	0	2	0	2	0	1	0	1	1	1	0	2	0	1	0	3
Euparkerella	0	2	2	0	0	0	1	0	1	1	1	2	2	0	1	0	1
Eusophus	0	2	0	0	0	0	1	0	1	0	1	1	0	0	0	1	2
Holoaden	0	2	2	0	0	0	1	0	1	1	1	1	2	0	1	0	1
Hydrolaetare	1	0	2	0	0	0	1	0	0	1	1	1	0	0	1	0	3
Hylactophryne	0	0	2	0	0	0	1	0	1	1	1	0	0	0	0	0	3
Hylodes	0	0	0	0	3	2	1	0	2	0	1	1	0	0	0	0	1
Hylorina	1	0	0	3	0	0	1	0	1	0	0	0	0	0	0	0	1
Insuetophrynus	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Ischnocnema	0	0	2	0	0	0	1	0	1	0	1	0	0	0	0	0	1
Lepidobatrachus	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	2	0

Genus	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Adenomera	0	2	0	0	0	0	0	0	0	1	0	1	1	3	3	0	1	1	1	2
Amblyphrynus	0	0	0	0	0	1	0	2	0	1	0	1	1	0	0	0	1	0	0	0
Barycholos	0	3	1	0	0	1	0	3	0	0	0	1	0	1	2	0	0	1	1	1
Batrachophrynus	0	0	1	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	1	0
Batrachyla	0	0	2	1	1	0	1	0	0	0	0	1	1	0	1	0	0	1	0	0
Caudiverbera	1	2	0	0	0	2	0	1	0	0	0	1	3	0	1	0	0	0	1	0
Ceratophrys	1	0	1	0	0	2	0	1	0	1	1	0	1	2	0	1	0	0	0	1
Crossodactylodes	0	0	0	1	0	1	0	0	2	0	0	1	1	0	0	0	1	1	1	0
Crossodactylus	0	0	0	0	1	0	0	0	2	0	1	1	1	0	2	0	1	1	1	0
Cycloramphus	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	1	1	0	1	0
Edalorhina	0	3	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	3
E. coqui	0	3	0	0	0	0	0	0	0	0	1	1	0	0	2	0	1	1	1	0
E. fleischmanni	3	3	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1	4
E. nigrovittatus	3	3	1	0	0	1	0	3	0	0	0	1	0	0	1	0	1	1	1	0
Euparkerella	0	0	2	0	0	1	0	2	0	1	1	0	2	0	0	1	1	1	1	0
Eusophus	1	0	1	0	0	0	1	0	1	0	0	1	0	2	2	1	0	0	0	2
Holoaden	1	1	0	0	1	0	1	0	0	0	1	0	2	0	0	1	0	0	1	1
Hydrolaetare	2	2	0	0	0	1	0	2	0	1	0	1	3	3	0	1	0	1	1	0
Hylactophryne	0	3	1	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	1	3
Hylodes	0	0	1	0	1	0	0	0	0	0	1	1	0	2	0	1	1	1	1	0
Hylorina	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Insuetophrynus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ischnocnema	3	3	1	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	3
Lepidobatrachus	0	1	2	0	0	2	0	1	0	1	1	0	1	2	0	1	0	0	0	0

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Leptodactylus	0	0	1	3	0	0	1	0	2	0	1	1	0	0	0	0	3
Limnomedusa	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0
Lithodytes	0	0	2	3	3	0	1	0	1	0	1	1	0	0	1	0	3
Megaelosia	0	0	2	0	0	0	1	0	2	0	1	1	0	0	0	0	1
Niceforonia	0	2	2	0	0	0	1	0	1	2	1	1	0	0	0	1	3
Odontophrynus	0	2	0	1	0	0	1	0	1	2	0	1	0	0	0	1	1
Paratelmatobius	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1
Physalaemus	0	1	0	1	0	1	1	2	1	0	1	1	1	1	1	1	1
Pleurodema	0	1	0	2	0	0	1	2	2	0	1	1	1	1	0	0	1
Proceratophrys	0	2	2	0	0	0	1	2	0	0	1	0	0	0	0	0	1
Pseudopaludicola	0	1	2	0	0	1	1	0	1	0	1	0	2	1	0	0	3
Sminthillus	0	0	2	0	1	0	1	0	1	1	1	1	2	0	1	2	3
Syrrophus	0	1	2	2	2	0	1	0	2	1	1	1	2	0	0	1	3
Telmatobius	0	2	0	0	0	0	1	0	0	0	1	1	0	0	1	0	2
Telmatobufo	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Thoropa	0	0	0	0	1	0	1	0	2	0	1	1	0	0	0	0	1
Tomodactylus	0	0	2	2	2	0	1	0	1	1	0	0	2	0	0	0	3
Vanzolinius	0	0	2	0	1	0	1	0	2	0	1	1	0	0	0	0	3
Z. parvulus	0	2	2	0	0	0	1	0	1	0	1	1	0	0	0	0	1
Z. stejnegeri	0	2	2	0	0	0	1	0	1	0	1	1	0	0	0	0	1

Genus	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Leptodactylus	0	2	0	0	1	1	0	0	0	1	0	1	1	0	3	0	1	0	1	3
Limnomedusa	2	3	1	0	1	0	1	0	0	0	0	0	1	2	3	0	1	0	1	2
Lithodytes	0	1	0	0	0	0	1	0	0	0	1	0	1	0	3	0	1	1	1	4
Megaelosia	0	1	0	0	0	0	0	2	0	0	0	0	1	0	2	0	1	1	1	0
Niceforonia	3	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0
Odontophrynus	0	2	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	2
Paratelmatobius	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	1	0	0	1	0
Physalaemus	2	2	2	0	0	0	0	0	1	0	0	1	1	3	3	0	1	0	1	3
Pleurodema	0	0	0	1	0	0	1	0	0	1	0	1	1	0	3	0	0	0	0	3
Proceratophrys	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	3
Pseudopaludicola	0	3	0	1	1	0	0	0	2	0	0	1	0	3	4	0	1	0	1	4
Sminthillus	3	0	1	0	0	0	0	3	2	0	1	1	0	0	0	0	1	1	1	1
Syrrophus	3	1	0	0	0	0	1	3	1	0	1	1	0	1	2	0	1	1	1	1
Telmatobius	1	1	1	1	1	0	1	2	1	1	0	0	1	0	2	0	0	0	1	2
Telmatobufo	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Thoropa	0	1	1	0	1	0	1	0	0	0	1	1	0	0	4	0	0	1	1	0
Tomodactylus	3	0	1	0	0	0	0	3	2	0	1	1	0	0	2	0	1	1	1	3
Vanzolinius	0	2	0	0	0	1	0	0	0	0	1	1	0	3	0	1	1	1	1	3
Zachaeus parvulus	0	0	0	0	0	1	0	2	0	1	0	1	1	0	2	0	1	0	1	0
Z. stejnegeri	0	0	0	0	0	1	0	2	0	1	0	0	1	0	0	0	1	0	1	0

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