A Preliminary Analysis of the Intergeneric Relationships of the Frog Family Leptodactylidae

W. RONALD HEYER

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ABSTRACT

Heyer, W. Ronald. A Preliminary Analysis of the Intergeneric Relationships of the Frog Family Leptodactylidae. *Smithsonian Contributions to Zoology,* number 199, 55 pages, appendix, 16 figures, 38 tables, 1975.—Thirty-seven characters of external morphology, myology, osteology, life history, and chromosome morphology are studied. For each character, the evolutionary directions of changes of states are inferred. This information is used to construct a phylogenetic hypothesis of the intergeneric relationships of the New World frog family Leptodactylidae. Five major groupings of leptodactylids are proposed: the telmatobines, ceratophrines, leptodactylines, grypiscines, and eleutherodactylines. Formal recognition of these groupings is delayed until more information becomes available which will likely modify the intra- and intergroup relationships. The phylogenetic analysis demonstrates that the five groups are robust units, however.

Recognition of the five groups allows a reinterpretation of the historical zoogeography of the family. The family Leptodactylidae had its origins in the temperate beech forests of South America. The telmatobines represent a remnant of the original leptodactylid stock, which has remained in the beech forests. Two groups became adapted to drying conditions, the ceratophrines and leptodactylines. The grypiscines represent a forest-stream adaptational complex that centered in southeastern Brazil. The eleutherodactylines were probably derived from a grypiscine ancestor. Early attainment of direct development in the eleutherodactylines was a preadaptation which resulted in an explosive radiation of the *Eleutherodactylus*-complex, which is now represented by about 350 species which occupy diverse environmental situations.

A leptodactylid-liopelmatid relationship is suggested, which has the advantages of an in situ evolution of the leptodactylids rather than a migration from North Temperate regions as previously proposed. An alternate leptodactylid-discoglossid relationship argument which was based in large part on tadpole evidence is countered by a consideration of the major functional adaptations of tadpoles.

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Contents

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Introduction

Until recently, the family Leptodactylidae has been an unstable category in frog classification. For example, Noble (1931) placed the genera currently considered to form the family into two families, the Bufonidae and Brachycephalidae. Within the family Bufonidae, Noble recognized seven subfamilies, of which three contained various genera recognized in this paper. Subsequent taxonomic accounts have been based either on a small set of specific characters, a limited number of genera, or both. The single exception is the work of Lynch (1971, 1973a). The most significant change since Noble has been the recognition of the family Leptodactylidae as a group distinct from the Bufonidae. The inclusion or exclusion in the family Leptodactylidae of the Australian and African genera, and of such New World genera as *Allophryne, Geobatrachus, Pseudis, Rhinoderma,* and *Sminthillus* has been in large part a matter of preference, for, until recently, no comprehensive review of the situation has been available. The concept of the genus within the family has also changed considerably from Boulenger's (1882) recognition of 34 genera to the 63 genera recognized by Gorham (1966). Lynch (1971, 1973a) has made a significant contribution to the systematics of the Leptodactylidae with his recent review of the family at the genus level.

The present work is an attempt to interpret and extend data presented by Lynch (1971, 1973a), and to use the analytical methodology of Hennig (1966) to produce a phylogenetic hypothesis.

This phylogenetic approach has been applied to one segment of the family, Lynch's (1971) subfamily Leptodactylinae (Heyer, 1974a). In that study (Heyer, 1974a), certain differences with Lynch's (1971) scheme were found with respect to systematic conclusions. Specifically, the question was raised whether some genera Lynch assigned to the subfamily Leptodactylinae did not in fact have closer relationships to genera in Lynch's subfamily Telmatobiinae. This study was initiated to answer that question. It soon became apparent that a preliminary analysis of the relationships among the New World leptodactylid genera would be the best approach. The present study must be preliminary because total information is not available for some rare, monotypic genera, and the range of variation for certain large genera is not available at this time. It is hoped that the character analysis section will provide a base upon which additional data can be added and analyzed as it becomes available.

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Harold K. Voris, Field Museum of Natural History.

I have liberally stolen ideas from the following individuals who discussed various aspects of the paper with me: Ronald I. Crombie, Smithsonian Institution; Richard F. McGinnis, Pacific Lutheran University; Jay M. Savage, University of Southern California; Beryl Simpson, Smithsonian Institution; Richard Wassersug, University of Chicago; David B. Wake, University of California, Berkeley; and George R. Zug, Smithsonian Institution.

David B. Wake and George R. Zug carefully read the manuscript and offered many helpful suggestions.

Methods and Materials

Briefly, character states are categorized for a suite of characters from the study sample. The directionality of states is analyzed and the information from derived states is used to generate possible phylogenetic trees.

CHARACTER SELECTION

Characters of myology, osteology, adult and larval external morphology, and life history are sampled. Samplings from a variety of systems produce a more robust phylogeny than sampling of a single system in leptodactylid frogs (Heyer, in prep.). Basically, characters that have been used in previous systematic treatments are used. Information on character states is taken from the literature (Lynch, 1971, and sources cited therein. Heyer, 1974a) and from examination of specimens (Appendix).

STUDY GROUP

The family Leptodactylidae is used in the restricted sense, limited to New World leptodactyloids (Lynch, 1973a). The genus is the unit of study. As many genera as possible are included. Inclusion of a genus depends on having complete morphological information from at least one species. Some rare, monotypic genera were not included due to lack of material at this time.

The genera recognized by Lynch (1971) are used with the exceptions of the addition of the genera *Adenomera* (see Heyer, 1974a) and *Vanzolinius* (Heyer, 1974b). The genus *Eleutherodactylus* is very large and the limits of variation are not known. For purposes of this study, three species of *Eleutherodactylus* are analyzed individually, one species each from the West Indies, Middle America, and South America.

DIRECTIONAL CRITERIA

The reasoning of Marx and Rabb (1970) as used previously (Heyer, 1974a) is followed. As the sample for this study differs from the previous samples, the criteria need to be restated.

I. OUTGROUP COMPARISONS (character state uniform in the outgroup).—To use this criterion, information is needed from a group of organisms outside the study sample. The ideal outgroup would be the ancestral stock to the Leptodactylidae. Two closely related families are used as the major outgroup to the Leptodactylidae, the Australian family Myobatrachidae, and the African family Heliophrynidae. If the distribution of states in these outgroups does not allow directionality to be assumed, other familial outgroups are used as appropriate.

A character state is presumed to be primitive if it is found throughout the outgroup and derived if unique or nearly so in the study sample.

II. OUTGROUP COMPARISONS (character state polymorphism in the outgroup).—A character state is presumed to be primitive if it is widespread in the outgroup and derived if unique or nearly so in the study sample. As indicated previously, a large sample size of characters is needed to swamp the effect of those possible rare instances where evolution has not operated in a logical manner (Heyer, 1974a).

III. MORPHOLOGICAL SPECIALIZATION.—A character state is assumed to be derived if it is predominant in some adaptive specialization.

IV. ECOLOGICAL SPECIALIZATION.—A state is considered to be derived when it is relatively much more abundant in taxa with a particular mode of life than in all taxa. A state is considered primitive if it has differential relative abundance among taxa classified by adaptive zone.

At this time, only extreme adaptive categories can be recognized due to the lack of information on many genera. The following ecological categories are considered: aquatic, fossorial, arboreal, and terrestrial (broad sense). Ecological categories for the genera are presented in the appendix (Table A).

V. Geographic Restriction.—A state is assumed to be derived if it is predominant in taxa from a particular geographic area. The following geographic areas appear to be important in leptodactylid frogs: Mexico; Middle America; west coast lowlands of South America; northern Andes; southern Andes; Guyana Shield; Amazonia; southeastern Brazil; Gran Chaco; West Indies. Geographic categories for the genera are presented in the appendix (Table A). After the analysis was completed, R. Crombie informed me that *Telmatobius* was also found in the northern Andes. Its omission in the character analysis section does not change any decisions. The corrected distribution was included for the analysis which led to Figure 12.

The mechanics of sorting out the occurrence of character states by genera among the outgroup, ecological, and distributional categories was done with E–Z sort cards. Data were gathered serially, external morphology first, myology and life history second, and osteology and karyotype last. Characters were analyzed when all available data for each character grouping had been gathered. The appendix (Table B) reflects the data on which the character analysis was based. In some cases, more information became available at a later time; this information was included in the computer analysis section. During the osteological analysis, I felt *Zachaenus* should be split for further analysis; the character analysis for bones alone reflects this division. Both subgroups of *Zachaenus* (sensu Lynch, 1971) have the same external morphology and myological character states as coded for computer analysis.

Table 1.—*Character 1: Pupil shape* (N = The total number of genera which exhibit a given state. N may be less than the sum of the numbers in the columns because a genus may exhibit more than one ecological or geographic category for a given state. The outgroup is comprised of the Australian Myobatrachines and Cycloranines of the family Myobatrachidae and the African family Heliophrynidae. The ecological categories are fossorial, terrestrial, aquatic, and arboreal. The remaining categories are geographic categories for the New World.)

State	A	B
N	51	11
Myobatrachines	7	1
Cycloranines	7	3
Heliophrynids	0	1
Fossorial	7	3
Terrestrial	37	5
Aquatic	3	1
Arboreal	3	0
Mexico	5	0
Middle America	4	0
West Coast South America	3	0
North Andes	3	0
South Andes	7	3
Guiana Shield	3	0
Amazonia	9	1
Chaco	4	1
Southeast Brasil	17	1
West Indies	3	0

Character Analysis

1. Pupil Shape.—State A: pupil round. State B: pupil horizontal.

The distribution of states by genera among outgroup, ecological, and geographic categories is presented in Table 1.

State A is more widespread than state B in terms of ecological and geographic categories. Except for *Hydrolaetare,* all New World genera are from southern South America. This could be interpreted in two ways. First, because state B is relatively restricted to southern South America it could be derived because it is a rather localized phenomenon. Second, it could be argued to be primitive because (1) state B is also found in Australian and African genera, (2) the earliest leptodactylids occurred in southern South America, therefore (3)

Table 2.—*Character 2: Tympanum visibility* (see Table 1 and text for explanation)

State	A	B	C	D	E
N	28	4	4	19	6
Myobatrachines	0	0	0	6	1
Cycloranines	4	1	0	4	1
Heliophrynids	0	0	1	0	0
Fossorial	3	1	1	4	2
Terrestrial	20	2	3	11	4
Aquatic	1	1	0	1	1
Arboreal	2	0	1	0	0
Mexico	3	0	2	0	0
Middle America	2	0	2	0	0
West Coast South America	2	0	1	0	1
North Andes	0	0	1	0	1
South Andes	3	1	1	2	3
Guiana Shield	2	0	1	0	0
Amazonia	8	1	1	0	1
Chaco	2	1	1	1	1
Southeast Brasil	8	2	1	7	0
West Indies	2	0	0	0	0

state B is a primitive state that is still found in the ancestral region of South America.

The application of criteria so far does not lead to a clear-cut choice. In expanding the outgroup to include other related families, vertical pupils (state B) are found in the Pelobatidae, Pelodryadidae, and some Hylidae. Thus, applying criterion II to this larger outgroup, state B is assumed to be the primitive state. Lynch (1973a) also argued that vertical pupils are primitive. For purposes of coding for computer analysis, numerical categorization of the states is preferable. Thus, state A=state 0, state B=state 1. The direction of change of character states is:

0 ← 1

2. Tympanum Visibility.—State A: tympanum well developed, easily seen externally. State B: tympanum partially concealed, but still visible externally. State C: intrageneric variability, some species with state A, others with state B. State D: tympanum completely hidden, may be absent. State E: intrageneric variability, some species with state C, others with state D.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 2. State A is broadly distributed among ecological categories and geographic areas in the New World. States B and C are found in few genera with no real patterns of distribution. State D is widespread among the Australian leptodactyloids, with a slight trend of occurrence in fossorial genera and a distinct trend of occurrence only in southern South America. State E is similar in its distribution to state D.

State D might be considered primitive on the basis of criteria I and II. States B–E might be considered derived on the basis of criterion III, with the hidden ear correlated with a fossorial ecological adaptation. States B, D, and E are derived according to criterion V, as the states are relatively restricted in geographic occurrence. I choose criteria III and IV in this case, as the trend toward earlessness has been shown to correlate with higher altitudes (e.g., McDiarmid, 1971, for bufonids) and is apparent in other burrowing frogs (e.g., Microhylidae). As states B, C, and E are represented by few genera and represent intrageneric variation in part, the states are combined for purposes of further analysis. New state 0=old state A; new state 1=old states B and C, genera with the tympanum paritally concealed at least in some member species; new state 2=old states D and E, tympanum hidden, at least in some member species. The direction of change of character states is:

0 → 1 → 2

Table 3.—*Character 3: Male thumb* (see Table 1 and text for explanation)

State	A	B	C	D	E	F
N	29	22	3	3	3	1
Myobatrachines	5	2	0	0	0	0
Cycloranines	2	6	1	0	1	0
Heliophrynida	1	0	0	0	0	0
Fossorial	2	6	1	0	1	0
Terrestrisl	21	14	1	2	2	0
Aquatic	0	2	1	0	0	1
Arboreal	3	0	0	0	0	0
Mexico	3	1	0	0	1	0
Middle America	2	1	0	0	1	0
West Coast South America	1	2	0	0	1	0
North Andes	2	1	0	0	0	0
South Andes	1	5	2	1	0	1
Guiana Shield	0	2	0	0	1	0
Amazonis	7	3	0	0	1	0
Chaco	1	4	0	0	1	0
Southeast Brasil	8	6	0	2	2	0
West Indies	2	0	0	0	1	0

3. Male Thumb.—State A: male thumb lacking either a nuptial pad or spines. State B: nuptial pad present. State C: intrageneric variation, some species with state A, others with state B. State D: spines present. State E: intrageneric variation, some species with state A, others with state D. State F: intrageneric variation, some species with state B, others with state D.

The distribution of states among outgroup, ecological, and geographic categories is presented in Table 3. State A has the most general distribution. Criteria I and II are not applicable, as the outgroup is well represented with both states B and C. Criterion IV appears to be applicable to state B, as several fossorial and one-half of the aquatic genera have this state. Criterion V does not seem to apply. Morphological specialization, criterion III, suggests that state A is derived because some sort of nuptial asperity is commonly found in forms that breed in water. The nuptial asperity aids the male to hold onto the female during amplexus. Application of the criteria so far does not yield consistent results. Part of the problem may be due to the amount of intrageneric variation which led to the recognition of states C, E, and F, each of which is represented by few genera. The situation is resolved by enlarging the outgroup. Members of the families Bufonidae and Hylidae often have nuptial asperities. Therefore I consider the presence of nuptial asperities to be the primitive state. The amount and type of intrageneric variation observed (Table 3) necessitates recognition of only three states: state 0 = old states B, D, and F, some sort of nuptial asperities uniformly presented; state 1 = old states C, E, nuptial asperities absent in some member species; state 2 = old state A, no nuptial asperities in any member species. Two trends are apparent: (1) spines are probably a derived condition over a pad; (2) development of spines and loss of nuptial aspersities have occurred several times in the leptodactyloid frogs. Because of this, the data must be reduced to the new states recognized if the same directional criteria are to apply equally for the entire study sample. The direction of change of character states is:

$$0 \rightarrow 1 \rightarrow 2$$

4. **Body Glands** (eight extreme states are recognized).—State A: no well-defined parotoid, inguinal, or dorsolateral folds. State B: well-defined parotoid glands present. State C: intrageneric variation, some species with state A, others with state B. State D: well-defined inguinal glands present. State E: intrageneric variation, some species with state A, others with state D. State F: intrageneric variation, some species with state C, others with state D. State G: well-defined dorsolateral folds. State H: intrageneric variation, some species with state A, others with state G.

TABLE 4.—*Character 4: Body glands* (see Table 1 and text for explanation)

State	A	B	C	D	E	F	G	H
N	46	4	1	3	2	2	2	1
Myobstrschines	5	1	0	1	0	1	0	0
Cycloranines	8	2	0	1	0	0	0	0
Heliophrynids	1	0	0	0	0	0	0	0
Fossorial	8	1	1	1	0	1	0	0
Terrestrial	30	2	0	3	1	1	2	1
Aquatic	4	0	0	0	0	0	0	0
Arboreal	1	0	0	1	1	0	0	0
Mexico	1	0	0	1	1	1	0	1
Middle America	1	0	0	1	0	1	0	1
West Coast South America	2	0	0	0	0	1	0	1
North Andes	2	0	0	0	0	1	0	0
South Andes	7	1	0	0	1	0	1	0
Guiana Shield	1	0	0	0	1	0	0	1
Amazonia	7	0	0	1	0	1	1	1
Chaco	3	0	1	0	0	1	0	1
Southeast Brasil	14	0	1	1	1	0	0	1
West Indies	2	0	0	0	0	0	0	1

TABLE 5.—*Character 5: Toe disks* (see Table 1 and text for explanation)

State	A	B	C	D	E	F
N	44	5	1	6	4	1
Myobstrachines	7	0	0	0	0	0
Cycloranines	9	0	0	0	0	0
Heliophrynids	0	1	0	0	0	0
Fossorial	11	0	0	0	0	0
Terrestrial	26	4	1	3	4	1
Aquatic	4	0	0	0	0	0
Arboreal	0	0	0	3	0	0
Mexico	3	0	0	2	0	0
Middle America	2	0	0	2	0	0
West Coast South America	3	0	0	1	0	0
North Andes	3	0	0	0	0	0
South Andes	9	1	0	0	0	0
Guiana Shield	2	0	0	0	1	0
Amazonia	6	0	1	1	1	1
Chaco	6	0	0	0	0	0
Southeast Brasil	12	2	1	0	3	0
West Indies	0	1	0	1	0	0

The distribution of states by genera among outgroup, ecological, and geographic categories is presented in Table 4. On the basis of criteria II, IV, and V, state A is assumed to be the primitive state and states B–H are assumed derived. Because so few genera are represented among states B–H, the states should be combined in part. The following states can be combined with no loss of information: B with C, D with E, and G with H. A problem arises with state F. Clearly, state F could be derived from two routes, either from states B and C or from states D and E. For coding purposes, it seems best to double code those genera having state F so they could be derived from either route. Each of the types of body glands appears to be an independent derivation. The recombined states are: new state 0 = old state A; new state 1 = old states B, C, and F, parotoid glands present in some or all member species; new state 2 = old states D, E, and F, inguinal glands present in some or all member species; new state 3 = old states G and H, dorsolateral folds present in some or all member species. The directions of change of character states are:

$$\begin{tikzcd} 1 & 0 \arrow[l] \arrow[r] \arrow[dr] & 2 \\ & & 3 \end{tikzcd}$$

5. TOE DISKS.—State A: no well-defined disks. State B: disks on toes. State C: intrageneric variation, some species with state A, others with state B. State D: toes disked with circumferential groove. State E: toes disked with dorsal scutes. State F: toes disked with 3–5 dorsal longitudinal grooves. *Leptodactylus wagneri* is the only species in the genus that demonstrates intraspecific variation in having states 0 or 1; the genus is coded as state 0.

The distribution of states by genera among outgroup, ecological, and geographical categories is presented in Table 5.

Application of criterion I using the Australian leptodactyloids as the outgroup indicates state A to be primitive. Criteria IV and V also support state A as primitive because the state is broadly distributed among fossorial, terrestrial, and aquatic zones and among most geographic areas in the New World. Also, all arboreal genera have toe disks with circumferential grooves, indicating that state D is derived. Because both states C and F are represented by single genera, the states should be recoded for further analysis. States B and C can be combined without loss of information. State F is a morphologically unique and distinctive state among the study sample. As such, it does not yield information on common ancestries. If state A is primitive, then states B and C are derived and states D and E are independent derivations of a combination of states B and C. Into this scheme, state F would have to be coded along with states B and C into a single state.

The new coding is: new state 0 = old state A, no toe disks; new state 1 = old states B, C, and E, toes disked in all or some of the member species, not with circumferential grooves or dorsal scutes; new state 2 = old state D, toe disks with circumferential grooves; new state 3 = old state E, toe disks with dorsal scutes. The directions of change of character states are:

$$\begin{tikzcd} 0 \arrow[r] & 1 \arrow[r] \arrow[dr] & 2 \\ & & 3 \end{tikzcd}$$

TABLE 6.—*Character 6: Tarsal decoration* (see Table 1 and text for explanation)

State	A	B	C	D	E	F
N	29	19	1	2	1	3
Myobatrachines	4	1	0	0	0	0
Cycloranines	8	2	0	0	0	0
Heliophrynids	0	1	0	0	0	0
Fossorial	4	6	0	0	1	0
Terrestrial	19	10	1	2	1	3
Aquatic	2	2	0	0	0	0
Arboreal	3	0	0	0	0	0
Mexico	3	1	0	0	1	0
Middle America	1	2	0	0	1	0
West Coast South America	0	2	1	0	1	0
North Andes	2	0	0	0	1	0
South Andes	3	4	0	0	0	0
Guiana Shield	0	2	0	0	0	1
Amazonia	2	6	0	2	1	0
Chaco	0	4	0	1	1	0
Southeast Brasil	8	6	0	1	0	3
West Indies	2	1	0	0	0	0

TABLE 7.—*Character 7: Outer metatarsal tubercle* (see Table 1 and text for explanation)

State	A	B
N	20	44
Myobatrachines	8	1
Cycloranines	10	1
Heliophrynids	0	1
Fossorial	9	4
Terrestrial	12	30
Aquatic	1	3
Arboreal	0	3
Mexico	0	4
Middle America	0	4
West Coast South America	0	4
North Andes	0	3
South Andes	2	8
Guiana Shield	0	3
Amazonia	0	11
Chaco	1	5
Southeast Brasil	0	18
West Indies	0	3

6. TARSAL DECORATION.—State A: no folds, flaps, or tubercles. State B: tarsal fold. State C: tarsal tubercle. State D: tarsal fold and tubercle. State E: intrageneric variation, some species with state B, others with state C, others with state D. State F: extensive tarsal flap.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 6. Criterion I clearly indicates that states C–F are derived. Criterion V further suggests that state F is derived. Criteria I and V do not distinguish between states A and B. Criterion IV suggests in part that state A is specialized, as all arboreal genera lack any tarsal modifications. States A and B are both found in bufonids, hylids, and discoglossids; state A characterizes the pelobatids. Thus there does not appear to be any logical way of determining whether state A or B is primitive. The character is treated in a conservative manner, combining both states A and B as primitive. The redescribed character states, combining states A and B, and states C, D, and E because of unique taxa are: state 0: tarsus with fold or without modifications; state 1: tarsus with tubercle, at least in some species; state 2: tarsus with extensive flap. The directions of change of character states are:

1 ← 0 → 2

7. Outer Metatarsal Tubercle.—State A: absent. State B: present.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 7. Criterion II suggests that state A is primitive; criterion IV suggests that state B is derived, as all arboreal taxa have state B; criterion V suggests that state A is derived, as it is restricted to southern South America. The restricted area is in the presumed ancestral home of the leptodactylids; therefore, criterion II is not negated and state A is assumed the primitive state. For further coding purposes, A=0, B=1. The direction of change of character states is:

0 → 1

8. Inner Metatarsal Tubercle.—State A: normal or pointed. State B: a cornified spade. State C: intrageneric variation, some species with state A, others with state B.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 8. Criteria I and II do not appear to apply to this character; the development of a spade is a morphological specialization, thus criterion III indicates that state B is derived; criterion IV also indicates that states B and C are derived, as the states are found in fossorial genera. State C is intermediate between states A and B. For further coding purposes, A=0, B=1, C=2. The direction of change of states is:

Table 8.—*Character 8: Inner metatarsal tubercle* (see Table 1 and text for explanation)

State	A	B	C
N	48	7	6
Myobatrachines	5	0	2
Cycloranines	5	3	1
Heliophrynids	1	0	0
Fossorial	0	7	4
Terrestrial	36	0	2
Aquatic	4	0	0
Arboreal	3	0	0
Mexico	4	0	1
Middle America	3	0	1
West Coast South America	2	1	1
North Andes	2	0	1
South Andes	9	0	1
Guiana Shield	2	0	1
Amazonia	9	1	1
Chaco	2	3	1
Southeast Brasil	15	1	2
West Indies	3	0	0

0 → 2 → 1

Table 9.—*Character 9: Toe webbing* (see Table 1 and text for explanation)

State	A	B	C	D	E	F
N	17	4	26	9	4	1
Myobatrachines	1	0	3	2	1	0
Cycloranines	6	1	3	1	0	0
Heliophrynids	1	0	0	0	0	0
Fossorial	8	1	1	1	0	1
Terrestrial	3	4	21	8	3	0
Aquatic	4	0	0	0	0	0
Arboreal	0	0	2	0	1	0
Mexico	0	0	3	0	2	0
Middle America	0	1	1	0	2	0
West Coast South America	1	0	2	0	1	0
North Andes	0	0	3	0	0	0
South Andes	4	1	3	0	1	0
Guiana Shield	0	0	0	1	2	0
Amazonia	2	0	7	1	1	0
Chaco	2	0	2	0	1	1
Southeast Brasil	2	1	7	5	2	1
West Indies	0	0	2	0	1	0

9. Toe Webbing.—State A: webbing present. State B: webbing present or absent. State C: no web. State D: lateral toe fringe present. State E: intrageneric variation, some species with state C, others with state D. State F: intrageneric variation, some species with state A, others with state E.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 9. Criteria I and II are not applicable; criterion IV suggests that state C is derived, as the arboreal genera have state C; criterion V indicates that state D is derived, as the state is predominant in southeastern Brazil. Members of the bufonids, hylids, ascaphids, discoglossids, and pelobatids commonly have webbing; therefore, state A is assumed the primitive state. The number of states can be reduced without loss of information as follows: state 0: toes webbed; state 1: toes free in some or all species; state 2: toes fringed in some or all species. State 2 is morphologically intermediate between

TABLE 10.—*Character 10: Life history* (see Table 1 and text for explanation)

State	A	B	C	D	E	F	G	H
N	23	17	23	8	5	9	1	10
Myobatrachines	0	3	2	0	1	0	0	0
Cycloranines	7	6	4	5	0	6	0	0
Heliophrynids	1	0	0	1	0	0	0	0
Fossorial	8	5	5	5	1	3	0	0
Terrestrial	15	9	16	3	4	8	1	5
Aquatic	0	3	2	1	0	0	0	1
Arboreal	0	0	0	0	0	0	0	3
Mexico	1	1	2	0	0	2	0	3
Middle America	1	1	2	0	0	2	0	2
West Coast South America	2	1	2	1	0	2	0	0
North Andes	0	1	1	0	0	1	0	0
South Andes	5	3	6	1	1	0	1	0
Guiana Shield	2	1	2	0	0	1	1	0
Amazonia	3	2	5	1	0	3	0	1
Chaco	3	3	3	1	1	2	0	0
Southeast Brasil	8	4	10	0	2	2	1	3
West Indies	1	0	0	0	0	1	0	2

states 0 and 1 and is assumed to be phylogenetically intermediate. The direction of change of character states is:

0 → 2 → 1

10. LIFE HISTORY.—The coding of life history categories poses certain problems. Several distinct states are evident that are part of the same complex in part and mutually exclusive in part. One could therefore recognize one character with extreme states or break up the information into two or more characters. The danger with this latter course is that certain information would be overemphasized as it would appear in two or more characters. The best course appears to be to recognize the maximum number of discrete states, such that certain genera will have more than one state, then upon analysis of distribution of states, recategorize the states.

Eight states are recognized. State A: tadpole present, median vent. State B: tadpole present, dextral vent. (Lynch, 1971, states on page 26 that *Caudiverbera* and *Odontophrynus* have dextral vents; in the generic accounts, both are listed as median on pages 115, 131. Examination of the only *Odontrophrynus* tadpole at hand (USNM 121324, *O. cultripes*) indicates a dextral vent. For purposes of coding, I assume *Caudiverbera* also has a dextral vent.) State C: tadpole present, mouthparts with a dentical row formula of 2/3. State D: tadpole present, mouthparts with a dentical row formula greater than 2/3. State E: tadpole present, mouthparts with a dentical row formula less than 2/3. State F: larvae present, eggs placed in foam nest. State G: larvae present, eggs placed in foam nest in some species, not in others. State H: no tadpole, direct development from encapsulated egg. For present purposes, state H is interpreted narrowly and does not include cases where eggs hatch into larvae which in turn metamorphose without feeding.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 10. Criteria I and IV support the generally accepted hypothesis that direct development is derived with respect to presence of a tadpole. The only criterion that allows a distinction between whether a median or dextral vent is primitive is criterion IV; all the aquatic genera have state B indicating it is derived. Similarly there are no strong indications as to which type of denticle formula is primitive or whether a foam nest is derived. Foam nests are not found in ascaphids, pelobatids, bufonids, dendrobatids, centrolenids, or most hylids. Thus, a foam nest is probably derived. There is no evidence to suggest whether a foam nest was an intermediate stage in the evolution of direct development. The safest assumption to make for present purposes is to recognize only two states: state 0: tadpole present; state 1: direct develop-

TABLE 11.—*Character 11: Adductor mandibularis muscle* (see Table 1 and text for explanation)

State	A	B
N	5	48
Myobatrachines	0	5
Cycloranines	0	9
Heliophrynids	0	1
Fossorial	2	9
Terrestrial	1	34
Aquatic	1	3
Arboreal	1	2
Mexico	1	4
Middle America	1	3
West Coast South America	1	3
North Andes	0	2
South Andes	1	6
Guiana Shield	0	3
Amazonia	1	10
Chaco	2	3
Southeast Brasil	0	16
West Indies	0	3

ment. The direction of change of character states is:

0 → 1

11. Adductor Mandibularis Muscle.—State A: both adductor mandibulae posterior subexternus and adductor mandibulae externus superficialis present ("s+e" in Starrett's 1968 terminology). State B: adductor mandibulae posterior subexternus only present ("s" in Starrett's 1968 terminology). Starrett (1968) listed *Elosia* (=*Hylodes*) *lateristrigata* as having condition s + e. In examining two other species of *Elosia* (Appendix 1), I found the condition to be s; I then examined *H. lateristrigata* (USNM 101720) and also find it to have the s only condition. Starrett probably examined an incorrectly identified specimen. I find the condition of *Sminthillus* to be state B, contrary to Starrett (1968).

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 11. Criterion I indicates that state B is derived; none of the other criteria appear useful in determining which state is primitive. Starrett (1968) argued that the s + e condition is primitive to the s condition as a loss of a muscle slip is involved. As evolutionary trends often involve simplification of parts, her reasoning is followed. For further coding purposes, A=0, B=1. The direction of change of states is:

0 → 1

12. Depressor Mandibulae Muscle.—State A: muscle originates from the dorsal fascia, squamosal and otic region, and annulus tympanicus; the relative bulk of fibers may vary, but all three regions are clearly involved. State B: muscle origin from dorsal fascia and squamosal and otic region only, as in state A, the relative bulk of the two slips may vary. State C: intrageneric variation, some species with state A, some species with state B. State D: muscle origin from squamosal and otic region only. State E: intrageneric variation, some species with state B and some with state D. State F: origin from squamosal and otic region and annulus tympanicus.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 12. Clearly the primitive state is either A or B. Application of criteria I, II, IV, and V do not indicate which state is the primitive one. Starrett (1968) indicated that an origin from both the dorsal fascia and the squamosal region was primitive to an origin from the squamosal region only. She did not comment on the annulus tympanicus. Morphologically, state A is a more generalized state than B. In a previous study in which state A was considered primitive, there was no evidence that indicated otherwise (Heyer, 1974a). Therefore, I consider state A to be primitive. As states D, E, and F are unique to single genera of New World leptodactylids, the states are redescribed for further

Table 12.—*Character 12: Depressor mandibulae muscle* (see Table 1 and text for explanation)

State	A	B	C	D	E	F
N	22	24	2	3	1	3
Myobatrachines	2	2	0	2	0	1
Cycloranines	6	2	0	0	0	1
Heliophrynids	0	1	0	0	0	0
Fossorial	9	2	0	0	0	1
Terrestrial	10	20	1	3	0	2
Aquatic	2	1	0	0	1	0
Arboreal	2	0	1	0	0	0
Mexico	1	2	1	0	0	1
Middle America	0	3	1	0	0	0
West Coast South America	2	2	0	0	0	0
North Andes	1	1	0	0	0	0
South Andes	2	3	1	0	1	0
Guiana Shield	0	2	1	0	0	0
Amazonia	5	6	0	0	0	0
Chaco	4	2	0	0	0	0
Southeast Brasil	5	10	1	1	0	0
West Indies	1	2	0	0	0	0

Table 13.—*Character 13: Geniohyoideus medialis muscle* (see Table 1 and text for explanation)

State	A	B	C
N	33	3	18
Myobatrachines	1	0	5
Cycloranines	7	0	2
Heliophrynids	1	0	0
Fossorial	8	1	2
Terrestrial	21	3	12
Aquatic	3	0	1
Arboreal	1	0	2
Mexico	2	1	2
Middle America	2	1	1
West Coast South America	2	1	1
North Andes	1	1	0
South Andes	6	1	0
Guiana Shield	2	1	0
Amazonia	6	2	3
Chaco	3	1	2
Southeast Brasil	11	2	4
West Indies	2	0	1

purposes as follows: state 0: origin from dorsal fascia, squamosal and otic region, and annulus tympanicus or squamosal, otic region and annulus tympanicus only; state 1: origin from dorsal fascia and squamosal and otic region in some or all species; state 2: origin from squamosal and otic region in some or all species. The direction of change of character states is:

$$0 \rightarrow 1 \rightarrow 2$$

13. Geniohyoideus Medialis Muscle.—State A: muscle contiguous medially (Heyer, 1974a, fig. 2, 0). State B: muscle contiguous medially in some species, separated medially in others. State C: muscle separated medially (Heyer, 1974a, fig. 2, 2).

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 13. Since state B is intermediate between states A and C, the question is the direction of change involved. Application of the criteria does not give clear-cut indications of the direction of change. Because the ecological and geographic categories of state A are more broadly represented, state A is assumed the primitive state. For further coding purposes, A=0, B=1, C=2. The direction of change of character states is:

$$0 \rightarrow 1 \rightarrow 2$$

14. Anterior Petrohyoideus Muscle.—State A: the muscle inserts on the lateral edge of the hyoid plate. State B: the muscle inserts on the ventral body of the hyoid in some or all species.

Table 14.—*Character 14: Anterior petrohyoideus muscle* (see Table 1 and text for explanation)

State	A	B
N	44	10
Myobatrachines	1	5
Cycloranines	7	2
Heliophrynids	1	0
Fossorial	8	2
Terrestrial	27	9
Aquatic	4	0
Arboreal	3	0
Mexico	4	1
Middle America	3	1
West Coast South America	3	1
North Andes	1	1
South Andes	7	0
Guiana Shield	3	0
Amazonia	8	3
Chaco	4	2
Southeast Brasil	15	2
West Indies	2	0

Table 15.—*Character 15: Sternohyoideus muscle* (see Table 1 and text for explanation)

State	A	B	C	D	E
N	31	11	10	1	1
Myobatrachines	0	0	6	0	0
Cycloranines	5	0	4	0	0
Heliophrynids	1	0	0	0	0
Fossorial	7	0	2	0	1
Terrestrial	20	6	8	1	1
Aquatic	2	2	0	0	0
Arboreal	2	1	0	0	0
Mexico	4	0	0	0	1
Middle America	3	0	0	0	1
West Coast South America	2	1	0	0	1
North Andes	0	1	0	0	1
South Andes	5	2	0	0	0
Guiana Shield	3	0	0	0	0
Amazonia	5	3	0	1	1
Chaco	5	0	0	0	1
Southeast Brasil	13	3	0	1	0
West Indies	1	0	0	0	0

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 14. Criteria IV and V indicate that state A is primitive. State A is found in bufonids, hylids, dendrobatids, and pelobatids, also indicating that the state is primitive. For further coding purposes, A=0, B=1. The direction of change of states is:

$$0 \rightarrow 1$$

15. Sternohyoideus Muscle Insertion.—State A: muscle insertion entirely near lateral edge of hyoid body (Heyer, 1974a, fig. 1). State B: insertion with some fibers near lateral edge of hyoid body, some fibers near midline of hyoid body (Heyer, 1974a, fig. 1). State C: muscle insertion of narrow band of fibers extending to midline of hyoid body (Heyer, 1974a, fig. 1). State D: intrageneric variation, some species with state A, others with state C. State E: intrageneric variation, some species with state A, others with state D. *Lepidobatrachus* has a unique insertion pattern with two distinct slips, one inserting near where the alary process normally is, the other inserting near the posterolateral process. Because both slips insert on the lateral border, *Lepidobatrachus* is coded as state A.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 15. State C is confined to the Australian outgroups. State B is not represented in any of the

FIGURE 1.—Omohyoideus character states.

outgroups and is considered derived on the basis of criterion I. State A is generally found among hylids, pelobatids, and dendrobatids (Trewavas, 1933), and is considered the primitive stage. As states D and E are only found in single taxa, the states are combined and redefined for further analysis as follows: state 0: muscle insertion near lateral edge of hyoid body in all species or some species with insertion near midline; state 1: muscle insertion with some fibers near midline and some fibers near lateral edge in all species or some species with insertion near midline. The direction of change of states is:

$$0 \rightarrow 1$$

16. OMOHYOIDEUS MUSCLE.—State A: muscle absent. State B: muscle insertion on hyoid body and fascia between posteromedial and posterolateral processes (Figure 1B). State C: muscle insertion on hyoid body only (Figure 1C). State D: intrageneric variation, some species with state B, some with state C. State E: intrageneric variation, some species with state A, others with state C. State F: muscle insertion on edge of hyoid plate adjacent the posteromedial process (Figure 1F). State G: intrageneric variation, some species with state A, others with state F. State H: intrageneric variation, some species with state C, others with state F. State I: muscle inserts on edge of posterolateral process (Figure 1I).

TABLE 16.—*Character 16: Omohyoideus muscle* (see Table 1 and text for explanation)

State	A	B	C	D	E	F	G	H	I
N	20	12	9	2	3	1	2	2	3
Myobatrachines	6	0	0	0	0	0	0	0	0
Cycloranines	7	0	0	0	0	0	0	0	0
Heliophrynids	0	0	1	0	0	0	0	0	0
Fossorial	7	1	1	0	2	0	0	0	0
Terrestrial	12	11	4	1	2	0	1	2	3
Aquatic	2	0	1	1	0	0	0	0	0
Arboreal	0	0	1	0	0	1	1	0	0
Mexico	1	0	0	0	1	1	1	0	1
Middle America	1	1	0	0	1	0	1	0	0
West Coast South America	2	0	1	0	1	0	0	0	0
North Andes	0	0	0	0	1	0	0	0	1
South Andes	1	1	1	1	0	0	1	1	1
Guiana Shield	1	1	0	0	0	0	0	1	0
Amazonia	3	3	2	0	2	0	0	0	1
Chaco	3	0	1	0	2	0	0	0	0
Southeast Brasil	2	5	4	1	2	0	0	2	1
West Indies	2	0	1	0	0	0	0	0	0

TABLE 17.—*Character 17: Iliacus externus muscle* (see Table 1 and text for explanation)

State	A	B	C	D	E
N	7	23	5	16	2
Myobatrachines	0	2	0	3	0
Cycloranines	5	3	1	0	0
Heliophrynids	0	1	0	0	0
Fossorial	5	6	1	0	0
Terrestrial	3	15	3	13	1
Aquatic	0	2	2	0	0
Arboreal	0	0	0	2	1
Mexico	0	1	0	2	2
Middle America	0	1	0	1	2
West Coast South America	0	2	0	1	1
North Andes	0	1	0	1	0
South Andes	0	2	4	1	0
Guiana Shield	0	2	0	0	1
Amazonia	0	4	0	6	1
Chaco	1	3	0	1	1
Southeast Brasil	1	13	0	2	1
West Indies	0	0	0	2	1

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 16. All Australian leptodactyloids examined have state A, but the other outgroup member, *Heliophryne*, has state C. The absence of the muscle appears to be a morphological specialization; on the basis of criterion III, together with the consensus that evolution often involves a simplification of parts, state A is considered derived. The criteria allow no further distinctions to be made. The states are combined and redescribed for purposes of further analysis as follows: state 0: muscle present in all species; state 1: muscle present in some species, absent in others; state 2: muscle absent in all species. The direction of change of states is:

$$0 \rightarrow 1 \rightarrow 2$$

17. ILIACUS EXTERNUS MUSCLE.—State A: muscle extends less than one-half anteriad on ilium. State B: muscle extends from one-half to three-fourths anteriad on ilium. State C: intrageneric variation,

some species with state A, others with state B. State D: muscle extends from three-fourths to full length anteriad on ilium. State E: intrageneric variation, some species with state B, others with state D.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 17. Criteria I and II are not applicable as the various states are spread throughout the outgroup. Criterion IV indicates that state D is derived as arboreal genera have that state. Criterion IV appears to apply also to state A as several fossorial genera have that state. Criterion V also indicates that state A is derived as the state is restricted to southern South America. State B is morphologically intermediate between states A and D. As state E represents intrageneric variation and is represented by two genera, it is combined with state D. For further coding purposes, A=0, B=1, C=2, D=3. The directions of change of character states are:

0 ← 2 ← 1 → 3

18. **Tensor Fasciae Latae Muscle.**—State A: the muscle inserts posterior to the anterior extent of the iliacus externus on the ilium (Figure 2A). State B: muscle inserts at same level as anterior extent of iliacus externus on the ilium (Figure 2B). State C: intrageneric variation, some species with state A, others with state B. State D: muscle inserts anterior to forward extent of iliacus externus on the ilium (Figure 2D). State E: intrageneric variation, some species with states A, B, or D. State F: muscle inserts on anterior end of ilium immediately anterior to iliacus externus and the tensor fasciae latae and the iliacus externus are contiguous for a considerable length (Figure 2F).

Table 18.—*Character 18: Tensor fasciae latae* (see Table 1 and text for explanation)

State	A	B	C	D	E	F
N	33	6	1	4	2	7
Myobatrachines	5	0	0	0	0	0
Cycloranines	4	2	0	2	1	0
Heliophrynids	1	0	0	0	0	0
Fossorial	6	2	0	1	2	0
Terrestrial	24	1	1	2	2	5
Aquatic	2	2	0	0	0	0
Arboreal	1	0	0	0	0	2
Mexico	2	0	0	0	1	2
Middle America	1	0	0	0	1	2
West Coast South America	2	1	0	0	1	0
North Andes	0	0	0	0	1	1
South Andes	3	2	1	0	0	1
Guiana Shield	3	0	0	0	0	0
Amazonia	6	1	0	1	1	2
Chaco	4	1	0	0	1	0
Southeast Brasil	14	1	0	1	0	1
West Indies	2	0	0	0	0	1

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 18. The broad distribution of state A among the outgroup, ecological, and geographic categories indicates that state A is the primitive state. Because states C and E represent intrageneric variation and are represented by single New World genera, they are combined with states B and D, respectively. State F is distinctive morphologically, but could be derived from state D. However, I think it is best to be conservative at this point and not to assume that state F was derived from state D. For coding purposes, a conservative interpretation is that state F is independently derived from state A. For ease of further analysis, the states are recoded as: state 0=old state A; state 1=old states B and C; state 2=old states D and E; state 3=old state F. The directions of changes of states are:

3 ← 0 → 1 → 2

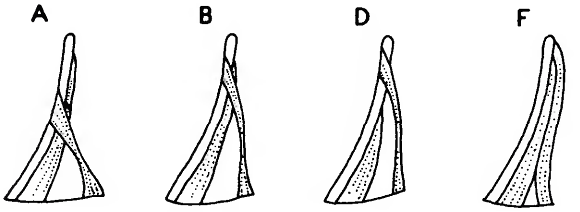


Figure 2.—Tensor fasciae latae character states.

19. **Semitendinosus Muscle.**—State A: interior and exterior heads about equal bulk, or exterior

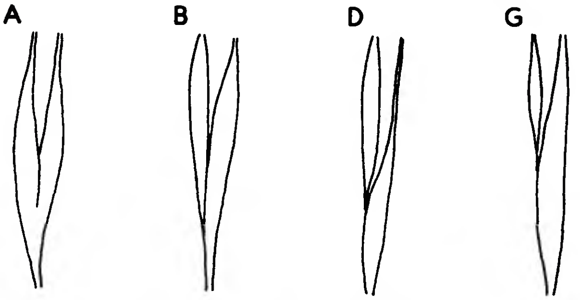


Figure 3.—Semitendinosus character states.

Table 19.—*Character 19: Semitendinosus*
(see Table 1 and text for explanation)

State	A	B	C	D	E	F	G	H
N	6	17	1	16	1	1	8	3
Myobatrachines	1	2	0	0	0	0	0	2
Cycloranines	0	8	0	1	0	0	0	0
Heliophrynids	0	1	0	0	0	0	0	0
Fossorial	0	6	1	3	0	1	0	0
Terrestrial	4	10	0	10	0	1	8	2
Aquatic	1	0	0	2	1	0	0	0
Arboreal	0	1	0	1	0	0	0	1
Mexico	1	1	0	1	0	1	1	0
Middle America	1	1	0	0	0	1	1	0
West Coast South America	1	0	0	1	0	1	1	0
North Andes	0	0	0	1	0	1	0	0
South Andes	1	0	0	5	1	0	0	0
Guiana Shield	1	0	0	2	0	0	0	0
Amazonia	4	1	0	1	0	1	4	0
Chaco	1	1	1	1	0	1	1	0
Southeast Brasil	2	3	1	8	0	0	3	0
West Indies	1	0	0	0	0	0	0	1

head bulkier (Figure 3A). State B: exterior head smaller than and attached by a tendon to interior head (Figure 3B). State C: intrageneric variation, some species with state A, others state B. State D: interior and exterior portions about equal, exterior portion attached by tendon to interior portion, bulks of two portions displaced (Figure 3D). State E; intrageneric variation, some species state B, others state D. State F: intrageneric variation, some species with states A, B, or D. State G: exterior head rudimentary, attached by tendon to interior portion (Figure 3G). State H: exterior head absent.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 19. Criterion II indicates that state B is the primitive state. Criterion V indicates that state D is primitive. In a previous study in which state A was considered the primitive state (Heyer, 1974a), character state D of the semitendinosus did not predict the relationships as accepted. Therefore, in this case, criterion V is followed and state D is considered the primitive state. All the states make a morphological series which are assumed to correlate with evolutionary directions of change. As states C, E, and F represent intrageneric variation and are represented by single genera, the states are recoded as follows: new state 0=old state D; new state 1=old states B and E; new state 2=old states A, C, and F; new state 3=old states G and H. The directions of change of character states are:

$$3 \leftarrow 0 \rightarrow 1 \rightarrow 2$$

20. Adductor Longus Muscle.—State A: muscle well developed, insertion is on or near the knee, usually visible superficially. State B: muscle poorly developed, inserts entirely on adductor magnus muscle, covered entirely by sartorius muscle. State C: intrageneric variation, some species with state A, others with state B. State D: muscle absent. State E: intrageneric variation, some species with state A, others state D.

The distribution of states among the outgroup, ecological, and geographic categories is presented in Table 20. Criterion II suggests that state A is primitive. State A is also commonly found in bufonids, hylids, centrolenids, and dendrobatids (Dunlap, 1960) and is assumed the primitive state. As states C and E represent intrageneric variation and are found in few genera, the states are combined and renumbered as follows: state 0=old state A; state 1=states B and C; state 2=states D and E. The direction of change of character states is:

$$0 \rightarrow 1 \rightarrow 2$$

21. Quadratojugal.—State A: quadratojugal present, contacting maxilla. State B: quadratojugal present, not contacting maxilla. State C: quadratojugal absent. State D: intrageneric variation, some

Table 20.—*Character 20: Adductor longus muscle*
(see Table 1 and text for explanation)

State	A	B	C	D	E
N	27	17	4	4	1
Myobatrachines	5	0	0	0	0
Cycloranines	5	3	1	0	0
Heliophrynids	0	0	0	1	0
Fossorial	4	4	1	1	1
Terrestrial	17	12	2	3	1
Aquatic	2	0	2	0	0
Arboreal	2	1	0	0	0
Mexico	2	2	0	0	1
Middle America	2	1	0	0	1
West Coast South America	1	2	0	0	1
North Andes	0	1	0	0	1
South Andes	2	2	2	1	0
Guiana Shield	2	0	1	0	0
Amazonia	6	4	0	0	1
Chaco	3	1	0	1	1
Southeast Brasil	11	4	1	1	0
West Indies	2	1	0	0	0

TABLE 21.—*Character 21: Quadratojugal* (see Table 1 and text for explanation)

State	A	B	C	D
N	56	1	5	1
Myobatrachines	8	0	0	0
Cycloranines	9	1	0	0
Heliophrynids	1	0	0	0
Fossorial	9	1	0	0
Terrestrial	36	0	5	0
Aquatic	3	0	0	1
Arboreal	3	0	0	0
Mexico	5	0	0	0
Middle America	4	0	0	0
West Coast South America	4	0	0	0
North Andes	3	0	0	0
South Andes	5	0	3	1
Guiana Shield	2	0	1	0
Amazonia	10	0	1	0
Chaco	5	0	1	0
Southeast Brasil	16	0	3	0
West Indies	3	0	0	0

species with state A, others with state C. Lynch (1971) incorrectly lists *Notaden* as having no quadratojugals (p. 38); the generic account correctly gives the character state as state B as used here (p. 82 and fig. 57).

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 21. Criteria II, IV, and V all indicate that the primitive state is state A. As state B is not found in a Neotropical genus, and state D is represented by a single genus, the states can be redescribed as follows: state 0: quadratojugal present, contacting maxilla; state 1: quadratojugal uniformly absent or absent in some species. The direction of change of states is:

0 → 1

22. NASAL CONTACT WITH MAXILLA.—State A: the nasal either contacts the maxilla or the two elements are in proximity to each other; I used this state broadly, interpreting any nasal configuration which appears to give strength to the nasal-maxillary region as state A. State B: intrageneric variation, some species with state A, others with state C. State C: nasal widely separated from maxilla.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 22. Criteria II, IV, and V indicate that state A is primitive. As only a single Neotropical genus has state B, it is combined with state C for further analysis. For further coding purposes, A = 0, B and C = 1. The direction of change of character states is:

TABLE 22.—*Character 22: Nasal contact with maxilla* (see Table 1 and text for explanation)

State	A	B	C
N	45	2	13
Myobatrachines	2	1	4
Cycloranines	9	0	1
Heliophrynids	1	0	0
Fossorial	9	0	2
Terrestrial	29	2	9
Aquatic	3	0	1
Arboreal	3	0	0
Mexico	4	1	0
Middle America	3	1	0
West Coast South America	3	1	0
North Andes	3	0	0
South Andes	6	0	2
Guiana Shield	1	1	1
Amazonia	9	1	1
Chaco	4	1	1
Southeast Brasil	12	1	6
West Indies	2	1	0

0 → 1

23. NASAL CONTACT WITH FRONTOPARIETAL.—State A: nasals not in contact with frontoparietal. State B: nasals in contact with frontoparietal. State C: intrageneric variation, some species with state A, others with state B. State D: nasals fused with frontoparietal.

TABLE 23.—*Character 23: Nasal contact with frontoparietal* (see Table 1 and text for explanation)

State	A	B	C	D
N	38	17	2	3
Myobatrachines	4	3	0	0
Cycloranines	7	2	1	0
Heliophrynids	1	0	0	0
Fossorial	7	1	1	2
Terrestrial	26	13	1	0
Aquatic	3	0	0	1
Arboreal	3	0	0	0
Mexico	4	0	1	0
Middle America	2	1	1	0
West Coast South America	1	1	1	1
North Andes	2	1	0	0
South Andes	7	0	0	1
Guiana Shield	2	0	1	0
Amazonia	6	3	1	1
Chaco	3	0	1	2
Southeast Brasil	12	6	1	0
West Indies	2	0	1	0

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 23. Criterion I indicates that state D is derived; criteria IV and V indicate state A is primitive. As only one neotropical genus has state C, states B and C are combined for further analysis. For further coding purposes, A=0, B+C=1, D=2. The direction of change of character states is:

$$0 \rightarrow 1 \rightarrow 2$$

24. **EXTENT OF COVERING OF FONTANELLE BY THE FRONTOPARIETALS.**—State A: frontoparietals meet medially, not exposing fontanelle; questionable states are included in state A. State B: frontoparietals separated medially, exposing fontanelle. State C: intrageneric variation, some species with state A, others with state B.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 24. Criterion II suggests that state B is primitive. As no Neotropical genus has state C, it is not analyzed further. For further coding purposes, A=0, B=1. The direction of change of character states is:

$$0 \leftarrow 1$$

25. **SQUAMOSAL.**—State A: zygomatic ramus slightly longer than, slightly shorter than, or equal to otic ramus, neither ramus modified. State B: as in state A with a definitely expanded otic plate. State C: as in state B with the zygomatic ramus articulating with the maxilla. State D: zygomatic ramus much longer than otic ramus, neither modified. State E: as in state D with the zygomatic ramus articulating with the maxilla. State F: as in state D with an otic plate. State G: otic ramus much longer than zygomatic ramus. Only extreme and obvious modifications are recognized in states B–G; for example, a small otic plate is coded as state A if the two rami are about equal in length.

TABLE 24.—*Character 24: Fontanelle* (see Table 1 and text for explanation)

State	A	B	C
N	37	24	1
Myobatrachines	1	6	1
Cycloranines	4	6	0
Heliophrynids	0	1	0
Fossorial	6	5	0
Terrestrial	25	15	1
Aquatic	2	2	0
Arboreal	2	1	0
Mexico	4	1	0
Middle America	3	1	0
West Coast South America	4	0	0
North Andes	3	0	0
South Andes	3	6	0
Guiana Shield	2	1	0
Amazonia	11	0	0
Chaco	6	0	0
Southeast Brasil	14	5	0
West Indies	3	0	0

TABLE 25.—*Character 25: Squamosal* (see Table 1 and text for explanation)

State	A	B	C	D	E	F	G
N	31	7	4	5	2	3	12
Myobatrachines	1	0	0	0	0	0	2
Cycloranines	4	5	0	1	1	1	7
Heliophrynids	1	0	0	0	0	0	0
Fossorial	5	1	3	1	1	1	1
Terrestrial	23	6	0	0	1	2	9
Aquatic	2	0	1	1	0	0	0
Arboreal	1	0	0	0	0	0	2
Mexico	2	1	0	0	0	0	2
Middle America	3	0	0	0	0	0	1
West Coast South America	2	0	1	0	0	0	1
North Andes	2	0	0	1	0	0	0
South Andes	6	0	1	2	0	0	0
Guiana Shield	3	0	0	0	0	0	0
Amazonia	7	1	1	1	0	0	1
Chaco	4	0	2	0	0	0	0
Southeast Brasil	14	1	1	0	1	2	0
West Indies	2	0	0	0	0	0	1

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 25. Criteria IV and V indicate that state A is primitive. A problem arises in attempting to determine the polarities of the states with respect to state F. That is, state F could either be derived through state B or state D. As few genera are involved, it appears that the best present solution is to combine several of the states, thereby bypassing the problem. The new character states are: new state 0=old states A and B; new state 1=old state C; new state 2=old states D, E, and F; new state 3=old state G. The directions of changes of character states are:

$$\begin{tikzcd} 1 & 0 \arrow[l] \arrow[r] \arrow[dr] & 2 \\ & & 3 \end{tikzcd}$$

26. **VOMERINE TEETH.**—State A: teeth present. State B: intrageneric variation, teeth present or absent. State C: teeth absent.

TABLE 26.—*Character 26: Vomerine teeth* (see Table 1 and text for explanation)

State	A	B	C
N	43	6	14
Myobatrachines	0	1	7
Cycloranines	10	0	0
Heliophrynids	1	0	0
Fossorial	9	1	1
Terrestrial	28	4	10
Aquatic	2	1	1
Arboreal	1	1	1
Mexico	2	2	1
Middle America	2	2	0
West Coast South America	3	1	0
North Andes	1	2	0
South Andes	6	3	1
Guiana Shield	3	0	0
Amazonia	9	1	1
Chaco	4	1	1
Southeast Brasil	15	0	4
West Indies	2	0	1

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 26. Application of the criteria does not indicate clearly which state is primitive, although the more general distribution of state A would suggest that this is primitive. This is also supported by the fact that most frogs have vomerine teeth. For further coding purposes, A=0, B=1, C=2. The direction of change of states is:

$$0 \rightarrow 1 \rightarrow 2$$

TABLE 27.—*Character 27: Median contact of vomers* (see Table 1 and text for explanation)

State	A	B	C
N	40	1	21
Myobatrachines	8	0	0
Cycloranines	5	0	5
Heliophrynids	1	0	0
Fossorial	3	0	8
Terrestrial	29	1	11
Aquatic	3	0	1
Arboreal	3	0	0
Mexico	3	0	2
Middle America	3	0	1
West Coast South America	2	0	2
North Andes	2	0	1
South Andes	6	0	3
Guiana Shield	1	0	2
Amazonia	5	1	5
Chaco	2	0	4
Southeast Brasil	10	1	8
West Indies	2	0	1

27. MEDIAN CONTACT OF VOMERS.—State A: vomers not in medial contact. State B: intrageneric variation, some species with contact, others without. State C: vomers in medial contact.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 27. Criteria II and IV indicate that state A is primitive. As only one genus has state B, it is combined with state C for further analysis. For further coding purposes, A=0, B+C =1. The direction of change of character states is:

$$0 \rightarrow 1$$

28. PROOTIC FUSION WITH FRONTOPARIETAL.—State A: elements not fused. State B: elements fused.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 28. Criteria I, IV, and V indicate that state A is primitive. For further coding purposes, A=0, B=1. The direction of change of character states is:

$$0 \rightarrow 1$$

29. OCCIPITAL CONDYLES.—State A: condyles confluent. State B: condyles close to each other. State C: condyles widely separated. State D: intrageneric variation, some species with state B, others with state C. Lynch (1971) states that the Grypiscini is characterized in part in having the occipital condyles widely separated medially (p. 135). His figure of *Zachaenus parvulus* substantiates this (p. 140, fig. 91); however, his figure of *Z. stejnegeri* shows

TABLE 28.—*Character 28: Prootic fused with frontoparietal* (see Table 1 and text for explanation)

State	A	B
N	51	9
Myobatrachines	7	0
Cycloranines	10	0
Heliophrynids	1	0
Fossorial	9	2
Terrestrial	36	4
Aquatic	4	0
Arboreal	0	3
Mexico	3	2
Middle America	3	1
West Coast South America	3	1
North Andes	2	0
South Andes	9	0
Guiana Shield	2	1
Amazonia	9	1
Chaco	4	2
Southeast Brasil	16	3
West Indies	1	2

TABLE 29.—*Character 29: Occipital condyles* (see Table 1 and text for explanation)

States	A	B	C	D
N	1	22	37	1
Myobatrachines	0	0	8	0
Cycloranines	0	10	0	0
Heliophrynids	0	1	0	0
Fossorial	1	8	2	0
Terrestrial	0	12	28	1
Aquatic	0	3	1	0
Arboreal	0	0	3	0
Mexico	0	0	4	1
Middle America	0	0	3	1
West Coast South America	1	0	2	1
North Andes	0	0	3	0
South Andes	0	5	3	0
Guiana Shield	0	0	2	1
Amazonia	1	0	9	1
Chaco	1	2	2	1
Southeast Brasil	0	5	13	1
West Indies	0	0	2	1

TABLE 30.—*Character 30: Anterior process of the hyale* (see Table 1 and text for explanation)

State	A	B	C
N	21	1	32
Myobatrachines	1	0	4
Cycloranines	4	0	5
Heliophrynids	1	0	0
Fossorial	4	0	7
Terrestrial	13	1	22
Aquatic	1	0	3
Arboreal	3	0	0
Mexico	3	0	2
Middle America	2	0	2
West Coast South America	1	0	3
North Andes	1	0	1
South Andes	1	1	5
Guiana Shield	0	0	3
Amazonia	4	0	7
Chaco	1	0	5
Southeast Brasil	5	0	13
West Indies	2	0	1

the occipital condyles in medial proximity (p. 140, fig. 92). I assume the figures are correct.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 29. Criterion II suggests that state B is primitive; criterion V suggests that state C is primitive. Lynch (1971, p. 53) indicated that the primitive frog families, bufonids, and *Rhinoderma* have state B. State B is considered the primitive state. As few genera have either states A or D, the states are combined for further analysis as: new state 0 = old states A and B; new state 1 = old states C and D. The direction of change of character states is:

0 → 1

30. ANTERIOR PROCESS OF THE HYALE.—State A: anterior process present; only well-defined processes are included; anterior bumps or swellings of the hyales are not considered as state A. State B: intrageneric variation, some species with state A, others with state C. State C: anterior process absent.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 30. Application of the criteria do not clearly indicate whether state A or C is the primitive state. The anterior process of the hyale represents a part of the hyoid arch that is lost in frogs lacking the processes. State A is thus assumed to be the primitive state. As only one genus has state B, it can be combined with state C as a single state. For further coding purposes, A = 0, B + C = 1. The direction of change of states is:

0 → 1

31. ALARY PROCESS OF THE HYOID.—State A: alary process narrow, stalked. State B: alary process rudimentary. State C: no alary process. State D: alary process short, not distinctly stalked. State E: alary process broad and winglike. State F: intrageneric variation, some species with state D, others with

TABLE 31.—*Character 31: Alary process of the hyoid* (see Table 1 and text for explanation)

State	A	B	C	D	E	F
N	35	3	5	1	9	1
Myobatrachines	0	0	0	0	5	0
Cycloranines	7	1	0	0	1	0
Heliophrynids	1	0	0	0	0	0
Fossorial	7	0	2	0	2	0
Terrestrial	24	2	2	0	7	1
Aquatic	3	0	0	1	0	0
Arboreal	2	1	0	0	0	0
Mexico	3	1	0	0	1	0
Middle America	2	1	0	0	1	0
West Coast South America	1	1	1	0	1	0
North Andes	1	0	0	0	1	0
South Andes	6	0	0	1	0	0
Guiana Shield	3	0	0	0	0	0
Amazonia	6	0	1	0	3	1
Chaco	2	0	2	0	2	0
Southeast Brasil	13	0	3	0	1	1
West Indies	3	0	0	0	0	0

state E. Lynch (1971) gives as a character state for the Cycloraninae that the alary process has a narrow stalk (p. 75). Trewavas (1933) figures the process of *Mixophyes,* a cycloranine, as being rudimentary (p. 438, fig. 28). I follow her figure.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 31. Criterion I indicates that state C is derived. There is a morphological series among the states, but knowing that state C is derived does not determine whether state A or state E is primitive. Criteria IV and V indicate that state A is primitive because of the general distribution among categories. If state A is primitive, there have been two morphological trends starting with a narrow, stalked alary process. As states D and F are represented by single genera, they are combined with other states and redescribed as: state 0: alary process narrow, stalked; state 1: alary process rudimentary; state 2: no alary process; state 3: alary process not stalked, usually broad and winglike. The directions of change of states are:

$$3 \leftarrow 0 \rightarrow 1 \rightarrow 2$$

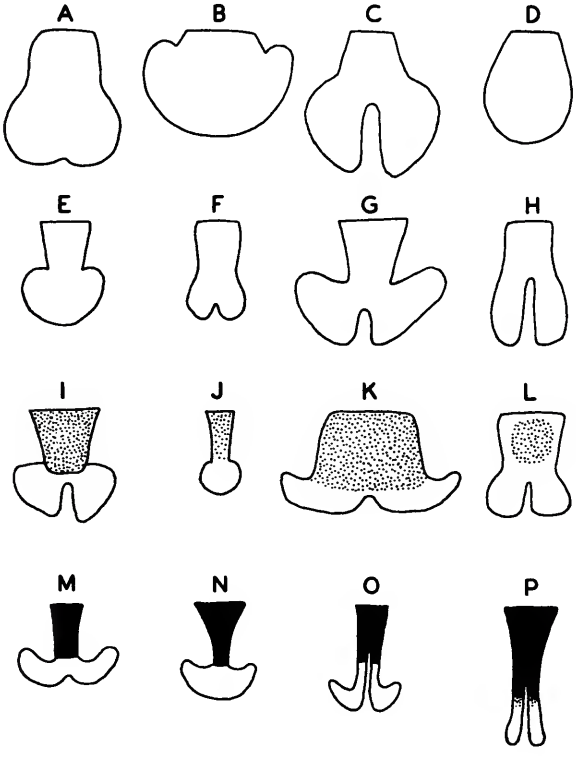


FIGURE 4.—Representative sternal apparati (diagrammatic). (A-D, state A; E-H, state B; I-L, state C; M-P, state D. A = *Odontophrynus,* B = *Notaden,* C = *Lepidobatrachus,* D = *Helioporus,* E = *Batrachyla,* F = *Cycloramphus,* G = *Eleutherodactylus fleischmanni,* H = *Thoropa petropolitana,* I = *Eleutherodactylus coqui,* J = *Syrrophus,* K = *Telmatobius,* L = *Zachaenus parvulus,* M = *Edalorhina,* N = *Hydrolaetare,* O = *Limnomedusa,* P = *Thoropa miliaris.*)

TABLE 32.—*Character 32: Posterior sternum*
(see Table 1 and text for explanation)

State	A	B	C	D	E
N	25	6	13	9	2
Myobatrachines	5	0	0	0	0
Cycloranines	8	0	1	0	0
Heliophrynida	1	0	0	0	0
Fossorial	10	0	0	1	0
Terrestrial	13	6	8	8	2
Aquatic	2	0	2	0	0
Arboreal	0	0	3	0	0
Mexico	0	1	2	2	0
Middle America	0	1	1	2	0
West Coast South America	1	0	1	2	0
North Andes	0	1	0	1	0
South Andes	3	2	2	1	0
Guiana Shield	0	0	1	2	0
Amazonia	1	1	1	7	1
Chaco	3	0	0	2	1
Southeast Brasil	5	2	5	4	2
West Indies	1	0	1	1	0

32. POSTERIOR STERNUM.—The posterior sternum has traditionally been given great taxonomic weight in classification schemes of the leptodactylid genera. Previously, I considered the variation encountered to have more phylogenetic meaning than the recognition of only two states, that is, a cartilagenous plate versus a bony style (1974a). In order to more objectively categorize the variation encountered, diagrams of each of the sternal apparati were drawn on 6½- × 7½-cm cards. At least one card was prepared for each genus. If the posterior sternum showed variation within a genus, more cards were prepared. The name of each genus was written on the back of each card. The cards were arranged alphabetically and numbered consecutively on the side with the diagram. I then sorted the cards into similar piles, using only the numbers as identifications for which card was represented in which pile. After I had determined four basic states, I gave the cards to my coworkers to sort. They arrived at three states. They agreed that it

was reasonable to split one of their states into the two I recognized.

Five states are recognized (Figure 4): State A: the posterior sternum a simple cartilagenous plate; the sides of the plate broaden posteriorly to the attachment to the pectoral girdle; a posterior bifurcation may be present or absent. State B: the posterior sternum is cartilagenous; the sides of the sternum are either parallel or they narrow posterior to the attachment to the pectoral girdle; a xiphisternum is often developed, which may or may not have a posterior bifurcation. State C: similar to state B with deposition of mineral in the mesosternal area; a xiphisternum is always differentiated. State D: posterior sternum differentiated into a bony style for the mesosternum and a cartilagenous xiphisternum. State E: intrageneric variation, some species with state B, others with state D. The recognition of four major states differs from Lynch (1971), most notably in that some of the genera exhibiting state C as defined here were included either in Lynch's cartilagenous state or in Lynch's bony style state.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 32. Criteria I and II clearly indicate that state A is primitive. Criterion IV further indicates that state C is derived, as all arboreal genera have that state. One could make a morphological series starting with state A→B→C→D. However, the intrageneric variation represented by state E indicates that state D has been directly derived from state B. For further coding purposes, A=0, B=1, C=2, D=3, E=4. The directions of changes of states are:

$$\begin{tikzcd}
0 \arrow[r] & 1 \arrow[r] \arrow[dr] & 4 \arrow[r] & 3 \\
& & 2 &
\end{tikzcd}$$

33. **Relationship of Transverse Process of Last Presacral Vertebra to Sacral Vertebra.**—State A: last presacral vertebra about same width as sacrum. State B: last presacral vertebra much shorter than sacrum.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 33. Criterion II suggests that state B is primitive, whereas criterion V suggests that state A is primitive. Trueb (1973), on the basis of the distribution of state B among the more primitive families of frogs, considered the state primitive. State B is considered primitive. For further coding purposes, A=0, B=1. The change of direction of character states is:

$$0 \leftarrow 1$$

34. **Sacral Diapophyses.**—State A: sacral diapophyses expanded. State B: intrageneric variation, some species with state A, others with state C. State C: sacral diapophyses rounded.

The distribution of states by genera among the

Table 33.—*Character 33: Last presacral vertebral width* (see Table 1 and text for explanation)

States	A	B
N	38	21
Myobatrachinea	0	6
Cycloranines	3	6
Heliophrynids	0	1
Fossorial	2	8
Terreatrial	28	11
Aquatic	2	1
Arboreal	3	0
Mexico	5	0
Middle America	4	0
West Coast South America	3	1
North Andes	2	0
South Andes	7	2
Guiana Shield	3	0
Amazonia	10	1
Chaco	3	3
Southeast Brasil	15	4
West Indies	3	0

Table 34.—*Character 34: Sacral diapophyses* (see Table 1 and text for explanation)

State	A	B	C
N	34	2	27
Myobatrachines	8	0	0
Cycloranines	10	0	0
Heliophrynids	0	0	1
Fosaorial	10	1	0
Terrestrial	14	2	20
Aquatic	3	0	1
Arboreal	0	0	3
Mexico	0	1	4
Middle America	0	1	3
West Coast South America	2	1	1
North Andes	0	1	2
South Andes	7	0	3
Guiana Shield	1	0	2
Amazonia	3	1	8
Chaco	3	1	2
Southeast Brasil	6	1	12
West Indies	0	0	3

outgroup, ecological, and geographic categories is represented in Table 34. State B is intermediate between states A and C; the question is whether state A or C is primitive. Criterion II indicates that state A is primitive; criterion IV suggests state C is derived, as all arboreal genera have state C, while state A has a broader ecological representation. The bufonids, hylids, and centrolenids have state A, indicating the state is primitive. As only two genera demonstrate state B, old states B and C are combined into a single state. For further coding purposes, A=0, B+C=1. The direction of change of states is:

0→1

35. **Terminal Phalanges.**—State A: terminal phalanges simple, knobbed, or claw-shaped. State B: terminal phalanges T-shaped.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 35. Criteria II, IV, and V indicate that state A is primitive. For further coding purposes, A=0, B=1. The direction of change of states is:

0→1

36. **Dorsal Crest of the Ilium.**—State A: no dorsal crest. State B: well-defined dorsal crest present.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 36. Criterion II suggests that state A is primitive, whereas criterion V suggests that state B is primitive. Trueb (1973, p. 100) indicates that primitive frog families have state A. State A is considered the primitive state. For further coding purposes, A=0, B=1. The direction of change of character states is:

0→1

TABLE 35.—*Character 35: Terminal phalanges* (see Table 1 and text for explanation)

State	A	B
N	44	19
Myobatrachines	7	1
Cycloranines	10	0
Heliophrynids	0	1
Fossorial	11	0
Terrestrial	27	15
Aquatic	4	0
Arboreal	0	3
Mexico	3	2
Middle America	2	2
West Coast South America	3	1
North Andes	3	0
South Andes	9	1
Guiana Shield	2	1
Amazonia	7	4
Chaco	6	0
Southeast Brasil	12	7
West Indies	1	2

TABLE 36.—*Character 36: Dorsal crest of the ilium* (see Table 1 and text for explanation)

State	A	B
N	20	36
Myobatrachines	6	0
Cycloranines	6	4
Heliophrynids	1	0
Fossorial	9	1
Terrestrial	12	27
Aquatic	0	4
Arboreal	0	3
Mexico	0	5
Middle America	0	4
West Coast South America	1	3
North Andes	0	2
South Andes	3	4
Guiana Shield	1	2
Amazonia	1	10
Chaco	3	3
Southeast Brasil	3	15
West Indies	0	3

37. **Diploid Chromosome Number.**—State A: intrageneric variation of 26 and more than 26. State B: 26. State C: intrageneric variation of 24 or 26.

TABLE 37.—*Character 37: Diploid chromosome number* (see Table 1 and text for explanation)

State	A	B	C	D	E	F	G	H	I
N	2	13	3	5	1	1	9	1	2
Myobatrachines	0	0	0	3	0	0	0	0	0
Cycloranines	0	0	0	2	0	0	0	0	0
Heliophrynids	0	1	0	0	0	0	0	0	0
Fossorial	1	1	0	1	0	1	2	0	0
Terrestrial	0	10	3	5	0	0	7	1	2
Aquatic	0	1	0	0	1	0	0	0	0
Arboreal	1	1	0	0	0	0	1	0	0
Mexico	1	0	0	0	0	0	4	0	0
Middle America	1	0	0	0	0	0	2	0	1
West Coast South America	1	0	0	0	0	0	2	0	0
North Andes	0	0	0	0	0	0	1	0	0
South Andes	0	4	1	0	1	0	1	0	0
Guiana Shield	0	1	0	0	0	0	2	0	0
Amazonia	1	0	1	0	0	0	5	1	1
Chaco	1	1	0	0	0	1	2	1	0
Southeast Brasil	0	6	2	0	0	1	4	1	0
West Indies	0	1	0	0	0	0	1	0	0

State D: 24. State E: intrageneric variation of 26 (or more) or 22. State F: intrageneric variation of 24 or 22. State G: 22. State H: intrageneric variation of 22 or less. State I: less than 22.

The distribution of states by genera among the outgroup, ecological, and geographic categories is presented in Table 37. The criteria indicate that either state B or state G is the primitive state. Criterion II indicates that between states B and G, B is primitive. As this corresponds with the consensus of opinion among chromosome workers, state B is considered to be the primitive state. As one state occurs only in the outgroup, and three states are represented by single genera, the states are redefined: state 0: 26; state 1: intrageneric variation of 26 and more than 26; state 2: intrageneric variation of some combination of 26 (or more), 24, 22; state 3: 22; State 4: less than 22, at least in some species. The directions of change of character states are:

1 ← 0 → 2 → 3 → 4

Analysis of Relationships

25 Operational Taxonomic Units

Complete data are available for 25 genera (Appendix: Table C). The relationships among these genera are analyzed first, with two purposes in mind. The first is to compare different analytic methods so that a choice, when made, will be based on a full data set. The second is that once an analytic method is chosen as best, the results based on the full data set can act more or less as a standard for analysis of the larger data set in which some data observations are not known at this time.

Relationships Based on Primitive and Derived States.—On philosophical grounds, I am opposed to deducing phylogenies based in part on primitive character states (see next section). The results of an analysis based on primitive and derived states is included for two reasons: (1) to compare with results based only on derived states to see how the results differ, and (2) for interest, as this method resembles the way one mentally deduces relationships, that is, one mentally compares overall similarity.

The results of an unweighted pair-group method of clustering using simple matching coefficients is presented in Figure 5.

Relationships Based on Derived States.—One of the principles Hennig (1966) outlined is proposing relationships based only upon derived states. The reasoning for this is straightforward. Primitive states merely indicate that an ancestral character has not changed and a taxon with a primitive state has not diverged from the ancestor with respect to that state. Taxa sharing clusters of derived states, on the other hand, indicate common derivations from an ancestral condition and are indicative of relationships. As taxa represent collections of primitive and derived character states, it is logical to base relationships only upon the derived states. Apparently, some workers equate the practice of using only derived states to analyze relationships with the practice of considering primitive states to be useless and discarding them altogether. Such is not the case. Primitive states are important in the process of analyzing characters; after all, one needs to know what a primitive state is in order to know what a derived state is for any character. Also, it may be very informative to know which taxa have changed the least from the presumed ancestral stock, which means looking at those taxa that have the greatest number of primitive states (for an external example, see Rabb and Marx, 1973).

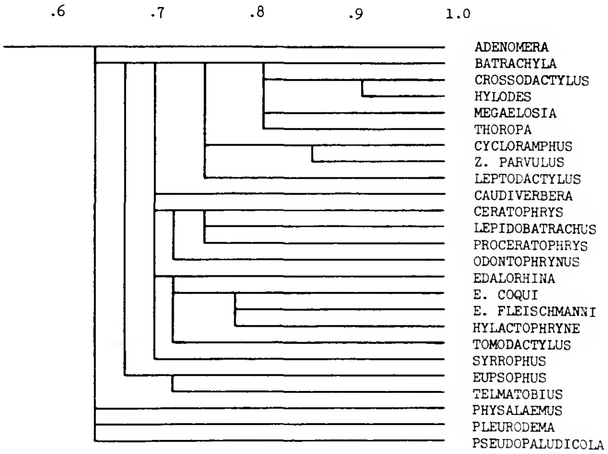


Figure 5.—Predicted phylogenetic relationships of 25 OTUs using an unweighted pair-group method of clustering using simple matching coefficients. (Both primitive and derived states are included in the analysis.)

Using the data matrix (Appendix: Table C), two different analytic assumptions may be made. The first is to base the relationships only upon the derived states exhibited by the taxa, ignoring possible ancestral but derived states. This assumes that the state exhibited was derived directly from the primitive state. As one does not know for certain the ancestral states of a given character due to the incompleteness of the fossil record, this may appear to be a reasonable assumption. A result of an unweighted, single linkage method using a simple matching coefficient of only derived states is presented in Figure 6.

A second analytic assumption is the inclusion of possible ancestral but derived states. In other words, where there is more than one derived state for a given character, the information from the character state trees (as analyzed in the character analysis section) is included. This assumes that there was some organism ancestral to the taxon that had the ancestral but derived state. The analytic method used was the combinatorial method developed by Felsenstein and Sharrock. One of the options of the combinatorial method is to include the information from the character state trees. The combinatorial method locates all nonredundant monothetic character and taxa subsets and prints them out. A monothetic cluster possesses a unique set of states which is both sufficient and necessary for membership in the cluster. It is termed monothetic because the defining set of character states is unique. A redundant combination is one completely contained within a larger combination sharing the same character states. A number of phylogenies can then be constructed from the clusters. The phylogeny of Figure 7 was constructed by maximizing the number of states at each cluster point. This was done by finding the two taxa that shared the most derived states and then finding the taxon or taxa which shared the most derived states with the initial two, etc. This is essentially sister-group formation in terms of Hennigian terminology (see later section for an explanation of sister-groups). The combinatorial program recodes the derived states in numerical sequence (Table 38).

As the phylogenies of Figures 6 and 7 differ, a choice needs to be made as to which has the greater probability of being correct.

First, it is interesting to note that the following clusters appear in all three phylogenies: (1) the two *Eleutherodactylus*, *Hylactophryne*, *Syrrophus*, and *Tomodactylus*; (2) *Crossodactylus*, *Hylodes*, and *Megaelosia*; (3) *Eupsophus* and *Telmatobius*; (4) *Ceratophrys* and *Lepidobatrachus*, and (5) *Odontophrynus* and *Proceratophrys*. These are robust clusters, independent of the three analytic methods used. The reason for this is that each of these clusters share such a large number of derived

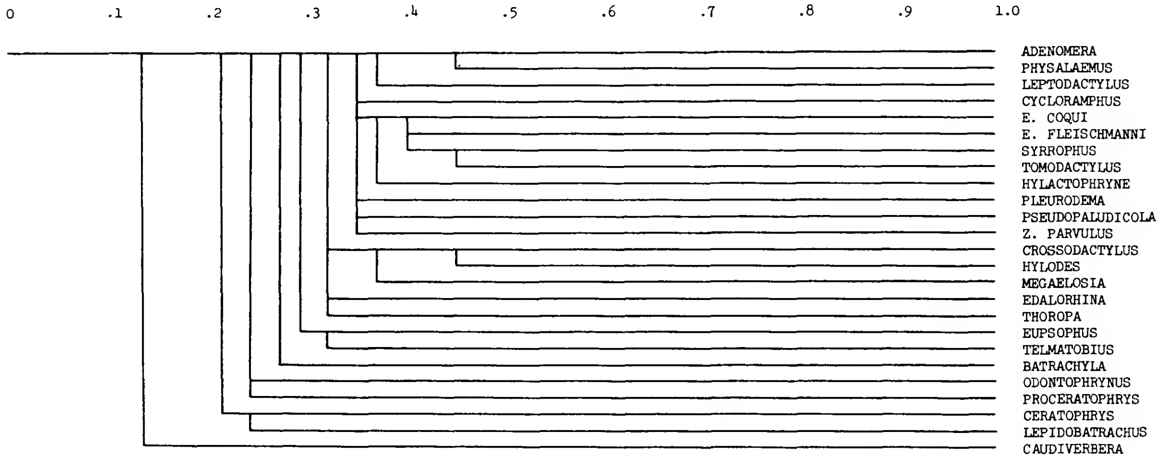


FIGURE 6.—Predicted phylogenetic relationships of 25 OTUs using an unweighted, single linkage method using a simple matching coefficient. (Derived states only are included in the analysis.)

TABLE 38.—*Character/state directory*

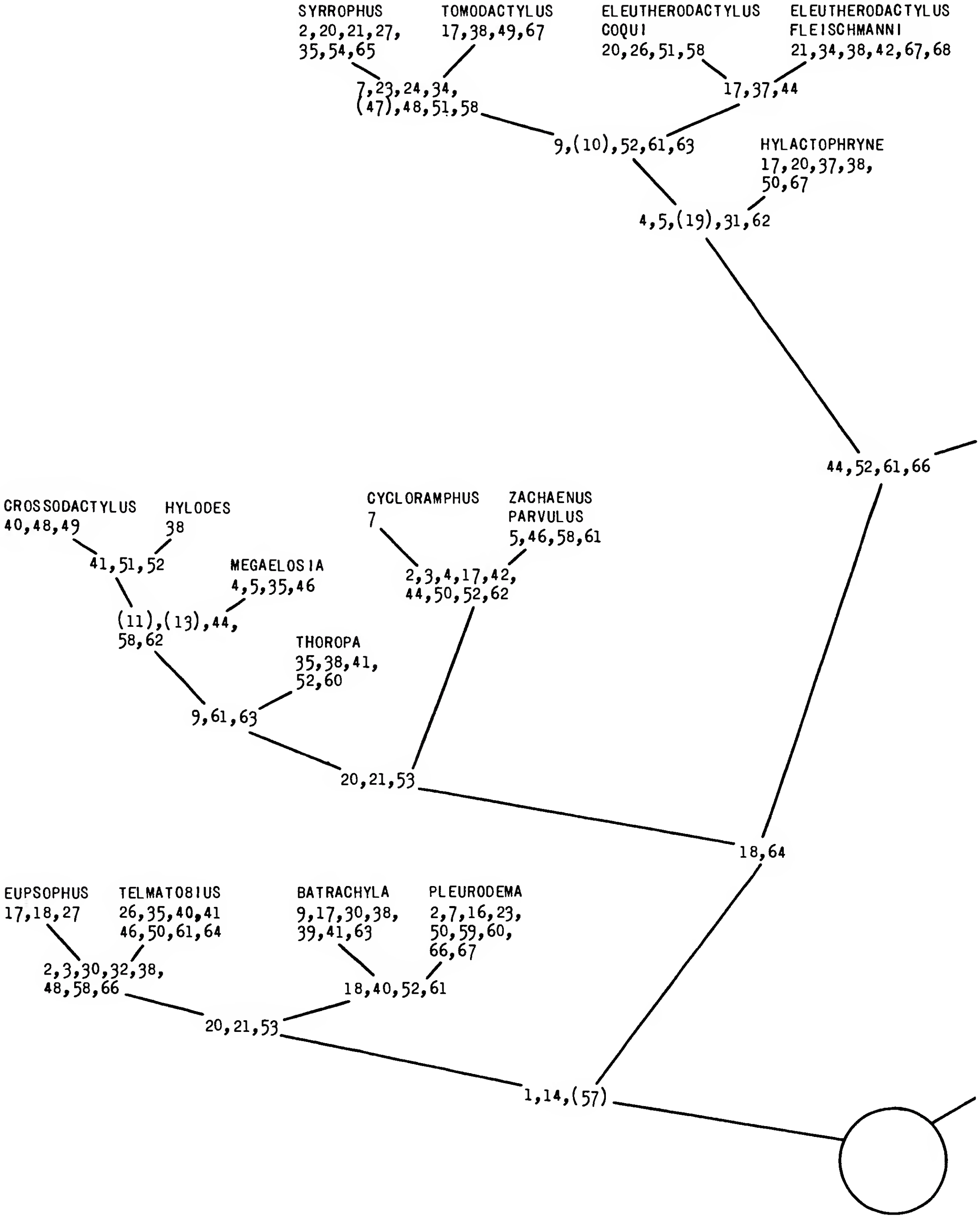
Character Number	1	2	3	4	5	6	7	8	9	10
Character State Number	1	2	2	3	3	4	4	4	5	5
Transition to State	0	1	2	1	2	1	2	3	1	2
Character Number	11	12	13	14	15	16	17	18	19	20
Character State Number	5	6	6	7	8	8	9	9	10	11
Transition to State	3	1	2	1	1	2	1	2	1	1
Character Number	21	22	23	24	25	26	27	28	29	30
Character State Number	12	12	13	13	14	15	16	16	17	17
Transition to State	1	2	1	2	1	1	1	2	0	2
Character Number	31	32	33	34	35	36	37	38	39	40
Character State Number	17	18	18	18	19	19	19	20	20	21
Transition to State	3	1	2	3	1	2	3	1	2	1
Character Number	41	42	43	44	45	46	47	48	49	50
Character State Number	22	23	23	24	25	25	25	26	26	27
Transition to State	1	1	2	0	1	2	3	1	2	1
Character Number	51	52	53	54	55	56	57	58	59	60
Character State Number	28	29	30	31	31	31	32	32	32	32
Transition to State	1	1	1	1	2	3	1	2	3	4
Character Number	61	62	63	64	65	66	67	68		
Character State Number	33	34	35	36	37	37	37	37		
Transition to State	0	1	1	1	1	2	3	4		

states that they still cluster when primitive states are included.

Certain character states that were not included in the analysis can be used to determine whether the phylogeny represented in Figure 6 or 7 is the more probable. The placement of *Cycloramphus* and *Zachaenus parvulus* differ in Figures 6 and 7. Lynch (1971) indicates that these two taxa share the derived state of a ventral phlange on the body of the hyoid. Only *Hydrolaetare* also has this state. Further, *Cycloramphus* and *Zachaenus parvulus* share a common, derived life history pattern of having large eggs which hatch as late larvae and live in wet leaves. The additional evidence strongly suggests that *Cycloramphus* and *Zachaenus parvulus* are closely related. This close relationship is best expressed in the phylogeny of Figure 7. For that reason, the methodology used to arrive at the phylogeny represented in Figure 7 is chosen over the methodology used to arrive at the phylogeny represented in Figure 6.

As mentioned, a number of phylogenies can be constructed from the cluster information that was used to construct the phylogeny of Figure 7. Some of the possible alternatives should be mentioned, but first a general limitation of the method should be pointed out. The end point clusters, which are based upon clusters of many character states, are robust. The basal clusters are not robust because they are based upon very few character states. For taxa which branch out basally, such as *Caudiverbera*, which has the fewest derived character states of the genera analyzed, the proposed relationships may well be due to convergence because so few states are involved. Character analysis may indicate whether the clusters appear to be reflective of relationships or convergence, but the very method itself cannot clearly discern basal relationships when the clusters are based on few characters.

There are three other alternative clusterings of *Adenomera, Edalorhina, Leptodactylus, Physalaemus,* and *Pseudopaludicola*. Each of the four patterns has certain advantages, which will not be detailed, but the important point is that the closest relationships of each of these taxa appears to be in the cluster of all five taxa. The reason for not detailing the alternative clusters is that the addition of certain genera in the next stage of analysis may modify and clarify the clustering pattern. The only other arrangement that gives a significantly different pattern from the figured phylogeny (Figure 7) is with the placement of the genus *Pleurodema*. At the level shown in Figure 7, *Pleurodema* shares 10 states with *Batrachyla*. *Pleurodema* shares 17 states with *Physalaemus*. *Physalaemus* shares 22 states with *Adenomera*, 20 states with *Pseudopaludicola*, 19 states with *Edalorhina*, and 18 states with *Leptodactylus*. *Pleurodema* shares 14 states with *Adenomera* and *Leptodactylus*, 13 states with *Pseudopaludicola* and *Edalorhina*. The best cluster which fits *Pleurodema*, together with any combination of the other four genera, is a cluster of 10 states including *Pleurodema, Adenomera, Edalorhina, Physalaemus,* and *Pseudopaludicola*. This leaves out *Leptodactylus*, which makes a better fitting unit with *Adenomera, Edalorhina, Physalaemus,* and *Pseudopaludicola* than does *Pleurodema*. At a cluster of 10 states, *Pleurodema* fits in with *Batrachyla*, as figured (Figure 7). *Pleurodema* clusters with *Adenomera, Edalorhina, Leptodactylus, Physalaemus,* and *Pseudopaludicola* at a level of 9 shared states. This is the same number of states that the cluster of *Adenomera, Edalorhina, Leptodactylus, Physalaemus,* and *Pseudopaludicola* shares with the cluster of the two species of *Eleutherodactylus, Hylactophryne, Syrrophus,* and *To-*


SYRROPHUS
2,20,21,27,
35,54,65
TOMODACTYLUS
17,38,49,67
ELEUTHERODACTYLUS
COQUI
20,26,51,58
ELEUTHERODACTYLUS
FLEISCHMANNI
21,34,38,42,67,68
7,23,24,34,
(47),48,51,58
17,37,44
9,(10),52,61,63
HYLACTOPHRYNE
17,20,37,38,
50,67
4,5,(19),31,62
44,52,61,66
CROSSODACTYLUS
40,48,49
HYLODES
38
41,51,52
MEGAELOSIA
4,5,35,46
(11),(13),44,
58,62
THOROPA
35,38,41,
52,60
9,61,63
CYCLORAMPHUS
7
ZACHAENUS
PARVULUS
5,46,58,61
2,3,4,17,42,
44,50,52,62
20,21,53
18,64
EUPSOPHUS
17,18,27
TELMATOBIUS
26,35,40,41
46,50,61,64
2,3,30,32,38,
48,58,66
BATRACHYLA
9,17,30,38,
39,41,63
PLEURODEMA
2,7,16,23,
50,59,60,
66,67
18,40,52,61
20,21,53
1,14,(57)

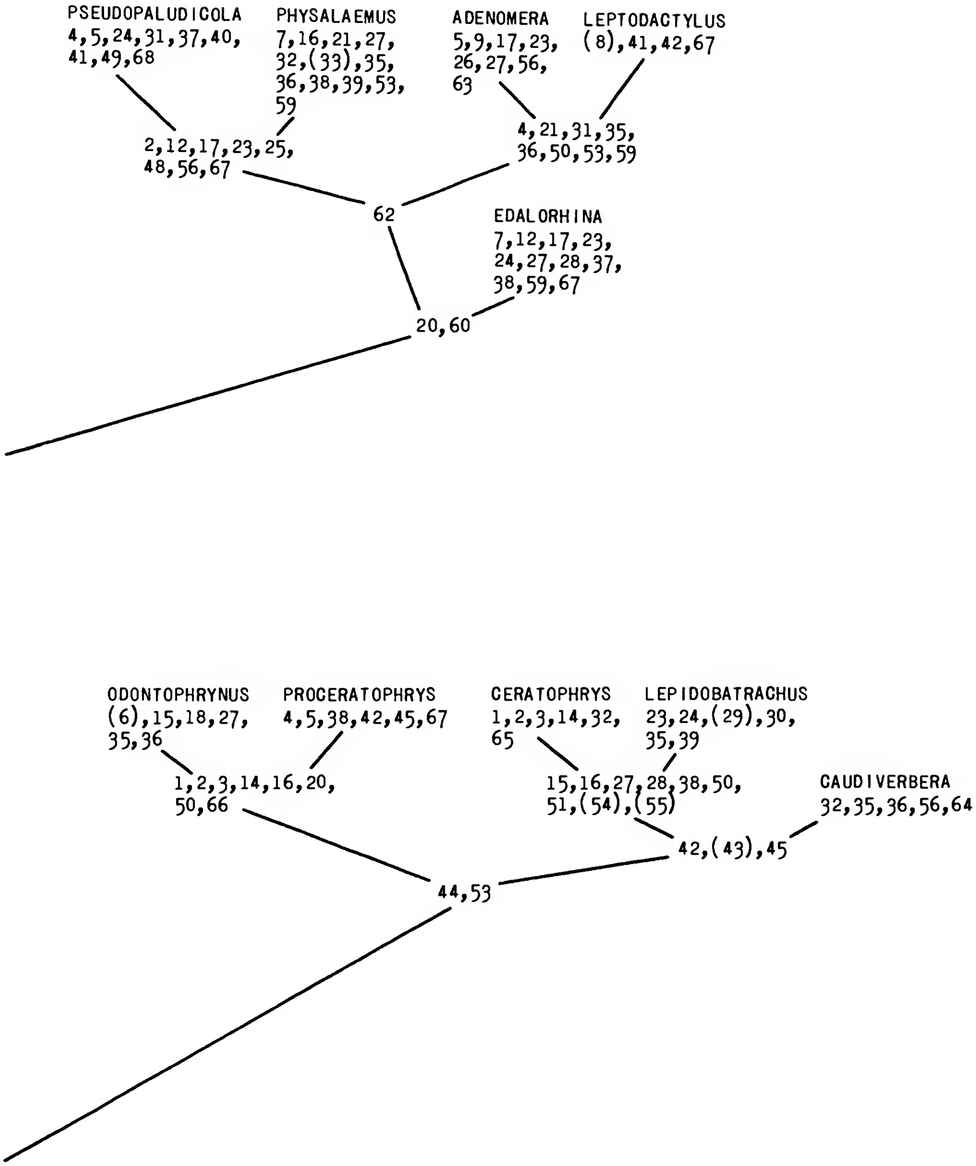
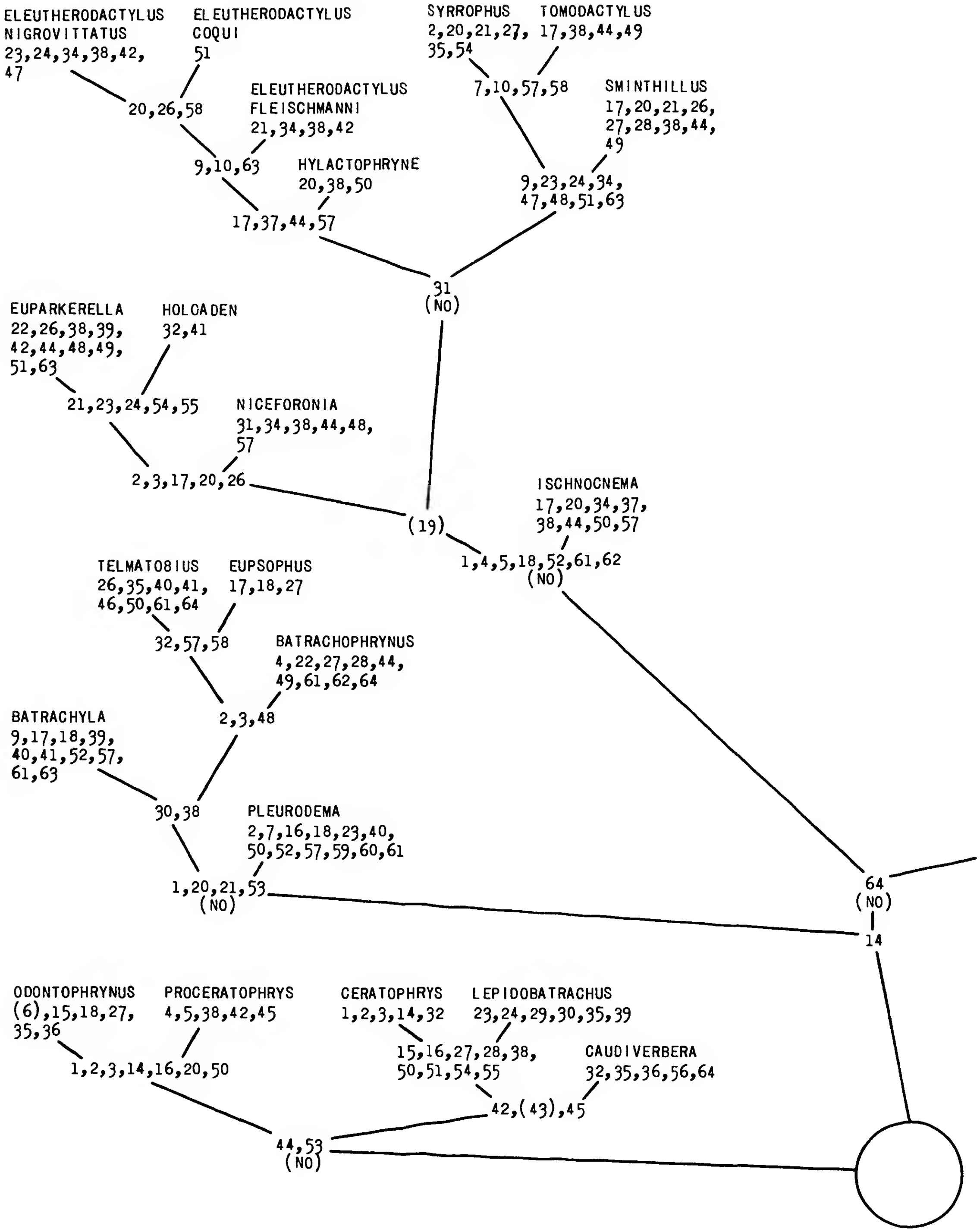


FIGURE 7.—Predicted phylogenetic relationships of 25 OTUs using the combinatorial method. (Derived states only are included in the analysis; numbers in parentheses are unique state appearances in the phylogeny.)


ELEUTHERODACTYLUS
NIGROVITTATUS
23,24,34,38,42,
47
ELEUTHERODACTYLUS
COQUI
51
20,26,58
ELEUTHERODACTYLUS
FLEISCHMANNI
21,34,38,42
9,10,63
HYLACTOPHRYNE
20,38,50
17,37,44,57
SYRROPHUS
2,20,21,27,
35,54
TOMODACTYLUS
17,38,44,49
7,10,57,58
SMINTHILLUS
17,20,21,26,
27,28,38,44,
49
9,23,24,34,
47,48,51,63
31
(NO)
EUPARKERELLA
22,26,38,39,
42,44,48,49,
51,63
HOLOADEN
32,41
21,23,24,54,55
NICEFORONIA
31,34,38,44,48,
57
2,3,17,20,26
(19)
ISCHNOCNEMA
17,20,34,37,
38,44,50,57
1,4,5,18,52,61,62
(NO)
TELMATOBIUS
26,35,40,41,
46,50,61,64
EUPSOPHUS
17,18,27
32,57,58
BATRACHOPHRYNUS
4,22,27,28,44,
49,61,62,64
2,3,48
BATRACHYLA
9,17,18,39,
40,41,52,57,
61,63
30,38
PLEURODEMA
2,7,16,18,23,40,
50,52,57,59,60,61
1,20,21,53
(NO)
64
(NO)
14
ODONTOPHRYNUS
(6),15,18,27,
35,36
PROCERATOPHRYS
4,5,38,42,45
1,2,3,14,16,20,50
CERATOPHRYS
1,2,3,14,32
LEPIDOBATRACHUS
23,24,29,30,35,39
15,16,27,28,38,
50,51,54,55
CAUDIVERBERA
32,35,36,56,64
42,(43),45
44,53
(NO)

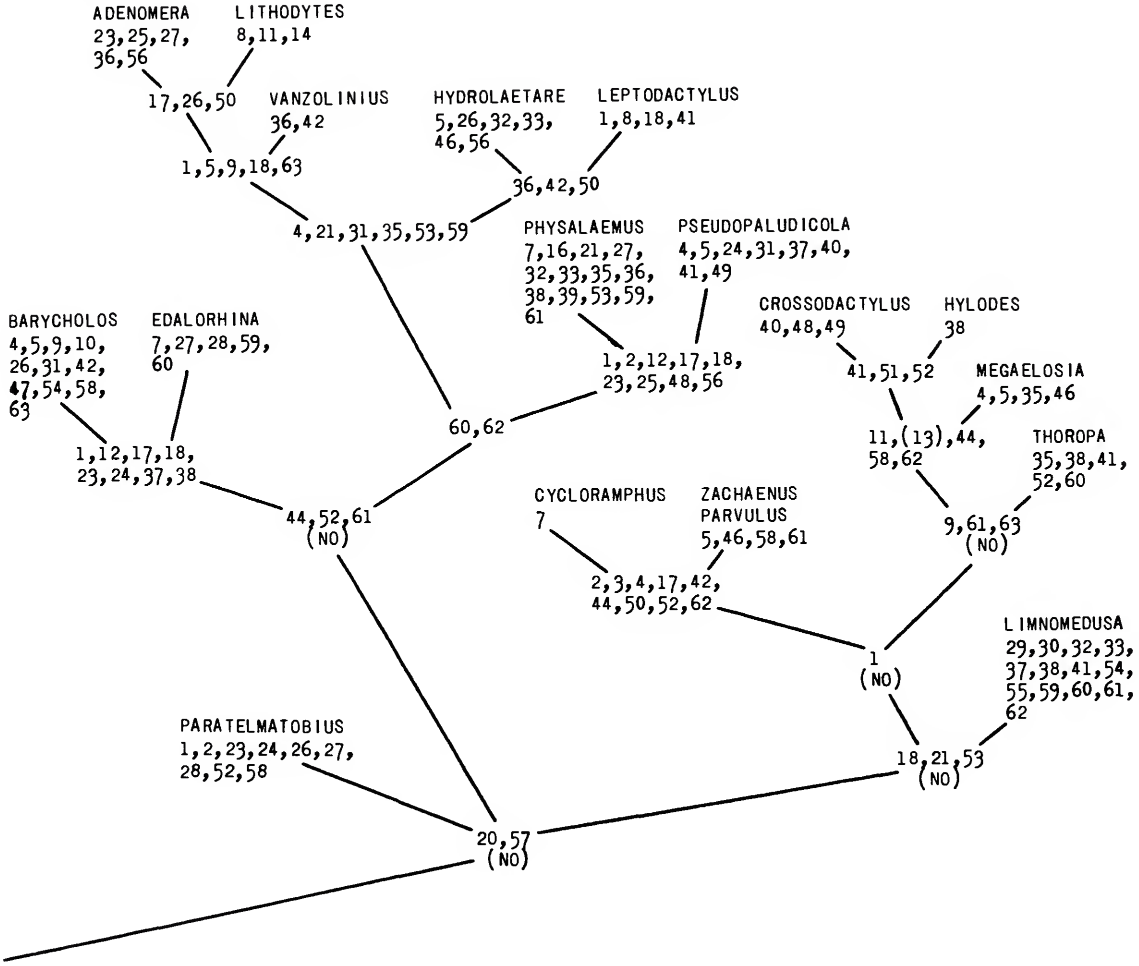


FIGURE 8.—Predicted phylogenetic relationships of 38 OTUs using the combinatorial method. (Derived states only are included in the analysis; numbers in parentheses are unique state appearances in the phylogeny; "NO" in parentheses indicates a nonmonothetic cluster; see text.)

modactylus. Thus, there does not appear to be any reason for preferring the placement of *Pleurodema* in either of the two possible places in the phylogeny. Analysis of the character states involved in the alternative clusterings might give support for choosing one location over the other, but that is deferred until the additional genera have been analyzed.

38 OPERATIONAL TAXONOMIC UNITS

A computer run of the combinatorial method was attempted using 39 taxa and 37 characters. The 39 taxa represent those for which a full set of morphological information was available. The additional 14 taxa lack either information on life history, karyotype, or both (Appendix: Table C). The program had a preset limit of 2000 clusters, which was exceeded. After two attempts at sufficiently reducing the data matrix to accommodate the program, it ran with 28 OTUs and 35 characters. The limit of the program was then increased to 3000 clusters. The full data set of 39 OTUs and 37 characters exceeded this new limit. When the matrix was reduced to 33 OTUs and 36 characters, the program ran. In this last run, the taxa and character that were deleted were done so for the following reasons. The taxa removed were *Caudiverbera, Ceratophrys, Lepidobatrachus, Odontophrynus,* and *Proceratophrys.* In the intermediate run of 28 OTUs and 35 characters, all generic units that had not been included in the initial run of 25 OTUs and 37 characters were represented. Also included in the intermediate run were *Caudiverbera, Ceratophrys,* and *Odontophrynus* (*Lepidobatrachus* and *Proceratophrys* were deleted). *Ceratophrys* and *Odontophrynus* came out closely related to each other and not related with the other taxa; *Caudiverbera* was isolated at the base of the phylogeny; the other taxa were all related with the remaining taxa. In other words, the new OTUs being analyzed all had closer relationships with taxa other than with *Ceratophrys, Odontophrynus,* and *Caudiverbera.* As the cluster of the five genera *Caudiverbera, Ceratophrys, Lepidobatrachus, Odontophrynus,* and *Proceratophrys* remained unchanged from the initial run, these genera were removed from the data matrix of the final run. The character removed was character 37, the karyotype, as several of the taxa lacked information on this character. The only other character for which information was missing for some taxa was character 10, life history. For purposes of analysis, no information for character 10 was entered as a 9 in the data matrix and the program treated that character as having the primitive state.

A new phylogeny was constructed which included all 38 taxa. The phylogeny of Figure 8 represents the initial maximization of clusters combining the information for *Caudiverbera, Ceratophrys, Lepidobatrachus, Odontophrynus,* and *Proceratophrys* from the initial run and all other taxa from the last run. Two kinds of clustering information are indicated, in addition to the numbers and kinds of characters represented by each cluster. Character states that appear but once in the phylogeny are indicated, as well as clusters that are not monothetic.

Several changes are possible in the phylogeny figured (Figure 8). In choosing the phylogeny which has the greater probability of reflecting relationships, the following criteria were used: (1) a decrease in the number of convergent states, (2) an increase in the number of monothetic clusters, (3) an increase in the number of unique state appearances within the tree, (4) maximizing the number of derived states in any clusters.

The cluster of *Ceratophrys* and *Lepidobatrachus* can be joined with the cluster of *Odontophrynus* and *Proceratophrys* at a level of four shared states. At the lower level of two shared states, *Caudiverbera* is linked in. This change results in the addition of one convergence of states, the loss of a unique appearance of a state, and no change in the number of monothetic clusters. The changes appear to weaken the phylogeny.

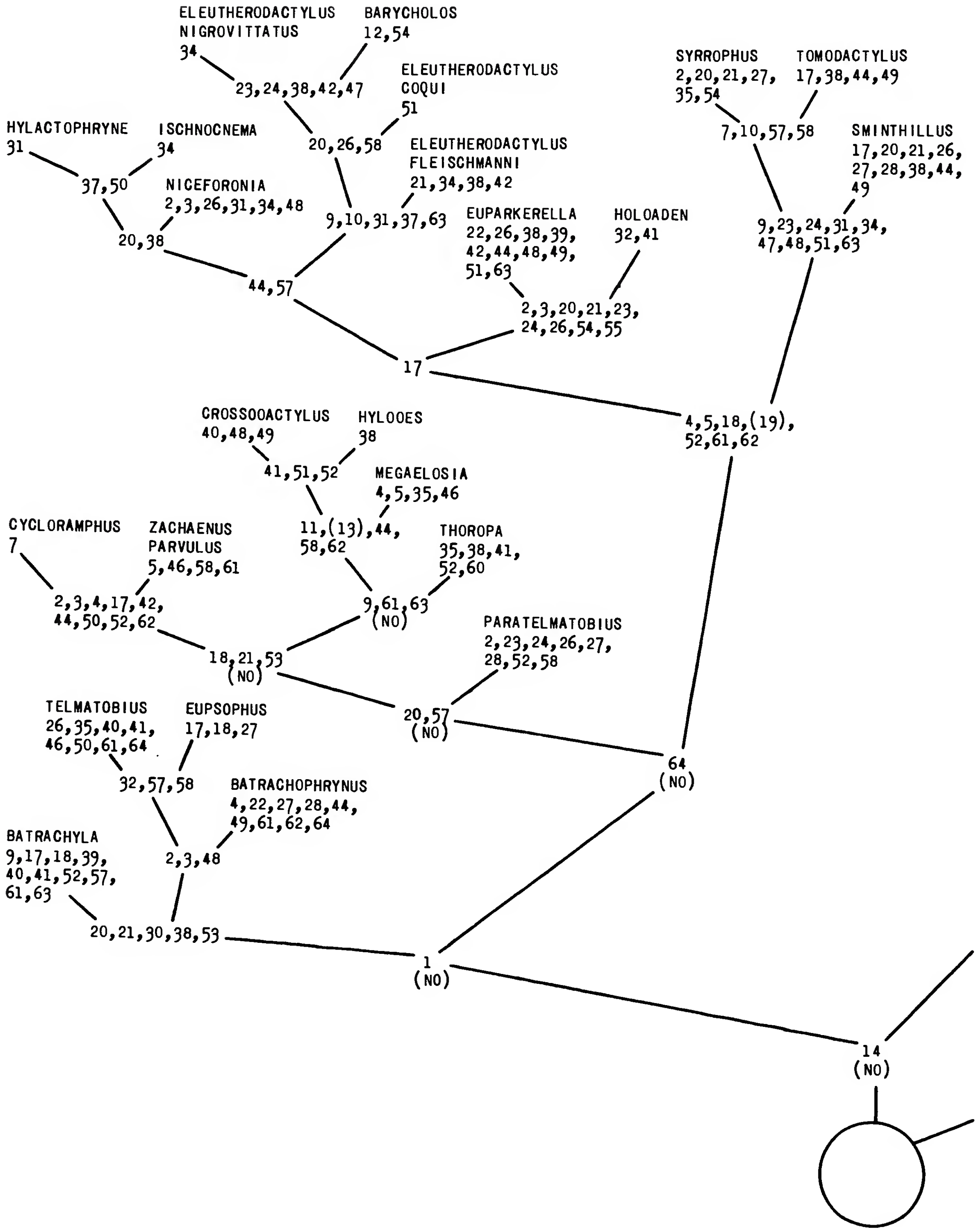
In the sample *Hylactophryne* and *Ischnocnema* share more states with each other than with any other taxa. The reason that they are separated in the phylogeny of Figure 8 is that *Ischnocnema* is excluded from intermediate clusters as it does not have state 19. State 19 is a terrestrial life history. The information for this state is not known for *Ischnocnema* with certainty, although it is reasonable to assume that it might have a terrestrial life history. If a terrestrial life history is assumed for *Ischnocnema* and it is placed next to *Hylactophryne* in the phylogeny, and that is the only change made, the phylogeny of Figure 8 is improved by the loss of six convergent states; the number of unique state appearances is unchanged; and as a change in the data is being assumed, the printout cannot be used to determine whether a change in monothetic clusters results. Due to the expense of the computer runs, having the information for monothetic clusters is not worth the cost. As the purpose of this entire analysis is to deduce the probable relationships based on available data, the best fit of data assumes *Ischnocnema* to have a terrestrial life history. This assumption is made, and the resultant changes incorporated into the phylogeny of Figure 9.

Niceforonia can be moved from the cluster shown on Figure 8 to a cluster of states shared with the cluster of *Hylactophryne* and *Ischnocnema.* This relocation improves the phylogeny by reducing three convergences; no changes in the appearance of unique states, and because of the presumed change in coding for *Ischnocnema,* the situation for monothetic cluster changes is not known. As the relocation represents improvement, the changes are incorporated into the phylogeny of Figure 9.

The two taxa that share the most derived states with each other in the total data set are *Barycholos* and *Eleutherodactylus nigrovittatus.* The reason that they do not appear together in the phylogeny of Figure 8 is that *Barycholos* will not cluster with any combination of other taxa that combine with *E. nigrovittatus* because *Barycholos* lacks states 19 and 62. Character State 19 is a terrestrial life history and the reproductive pattern is not known for certainty for *Barycholos;* the program treated no information as a primitive state. *Barycholos* is suspected of having direct development, due to the large size of the few nonpigmented eggs found in females (Heyer, 1969a). Character state 62 is rounded sacral diapophyses. Other than states 19 and 62, *Barycholos* shares every character state with *E. nigrovittatus* represented by all ancestral clusters. As state 62 appears to be the only real state excluding *Barycholos* from the eleutherodactylines, I reexamined the state in a cleared and stained skeleton of *Barycholos* (USNM–GOV 8015). The tips of the diapophyses are more heavily stained, giving an illusion of distal expansion, but the diapophyses are rounded, not expanded as previously coded. To check this new reassessment of coding objectively, I laid out a number of leptodactylid skeletal preparations showing expanded and rounded conditions, including *Barycholos,* and asked my colleagues to group them into the two states. *Barycholos* was consistently grouped with those other skeleta having rounded sacral diapophyses. When character state 62 is corrected for in *Barycholos,* and character state 19 is assumed, the transfer of *Barycholos* next to *E. nigrovittatus* results in the following changes. The phylogeny is improved by the removal of 11 convergences. No changes are made in the appearance of unique states. The monothetic cluster situation for the eleutherodactylines cannot be determined because of changes of data assumptions, but the removal of *Barycholos* from *Edalorhina* results in the addition of the monothetic cluster joining *Edalorhina* with *Physalaemus, Pseudopaludicola,* etc. The evidence clearly suggests that *Barycholos* is most closely related to *E. nigrovittatus* of those taxa included in the analysis. This relationship is depicted in the phylogeny of Figure 9.

The placement of *Pleurodema* in the phylogeny of Figure 8 has been discussed previously. As in Figure 8, *Pleurodema* can be placed with another assemblage of genera. *Pleurodema* shares the most states with *Physalaemus.* If this pair is chosen, a monothetic cluster of 11 states joins *Adenomera, Leptodactylus, Lithodytes, Physalaemus, Pleurodema, and Vanzolinius* (as in Figure 9). Another monothetic cluster of six states includes *Edalorhina, Limnomedusa, Pseudopaludicola* and *Thoropa* with the above six genera. *Edalorhina* shares a monothetic cluster of 15 states with *Pseudopaludicola,* and *Limnomedusa* shares a monothetic cluster of 11 states with *Thoropa.* With these changes, the best fit basally is for *Hydrolaetare* to join with the cluster at five states and *Paratelmatobius* to come in at three shared states. The results of these changes are a loss of one convergence, the addition of the appearance of one unique state, and the addition of three monothetic clusters. As this change involves the movement of *Thoropa,* further evaluation is needed before a decision can be reached. If *Thoropa* is taken from this new clustering and returned to the cluster of *Crossodactylus, Hylodes,* and *Megaelosia,* but within the framework of the new placement of *Pleurodema,* the following result: an improvement by the loss of five convergences; no change in the number of appearances of unique states; but a loss of three monothetic clusters ensues. *Thoropa* fits in both places at 11 shared states. With both changes, it would appear that there is an overall loss of six convergences with no changes in number of appearances of unique states or monothetic clusters. The monothetic cluster situation is improved, however, because a nonmonothetic cluster is added to a region of the phylogeny already characterized by nonmonothetic clusters, while two other lineages are improved with the addition of monothetic clusters. In addition, all genera which are known to have a foam nest are united with the new placement of *Pleurodema.* The replacement of *Thoropa* would be improved if it had state 62, rounded sacral diapophyses. As I had already made an error with this character in *Barycholos,* I rechecked the condition in *Thoropa*: the sacral diapophyses are definitely expanded in *Thoropa miliaris* (USNM 97765). The overall evidence suggests that the relationships of *Pleurodema* and *Thoropa* are best expressed as shown in the phylogeny of Figure 9.

Within the framework of the above changes as shown in Figure 9, *Edalorhina* can be paired with *Limnomedusa* at 10 shared states and *Hydrolaetare* can be paired with *Pseudopaludicola* at 13 states. This has the disadvantage of adding four


ELEUTHERODACTYLUS NIGROVITTATUS 34
BARYCHOLOS 12,54
23,24,38,42,47
ELEUTHERODACTYLUS COQUI 51
SYRROPHUS 2,20,21,27, 35,54
TOMODACTYLUS 17,38,44,49
HYLACTOPHRYNE 31
ISCHNOCNEMA 34
20,26,58
ELEUTHERODACTYLUS FLEISCHMANNI 21,34,38,42
7,10,57,58
SMINTHILLUS 17,20,21,26, 27,28,38,44, 49
37,50
NICEFORONIA 2,3,26,31,34,48
9,10,31,37,63
EUPARKERELLA 22,26,38,39, 42,44,48,49, 51,63
HOLOADEN 32,41
9,23,24,31,34, 47,48,51,63
20,38
44,57
2,3,20,21,23, 24,26,54,55
17
4,5,18,(19), 52,61,62
CROSSODACTYLUS 40,48,49
HYLODES 38
41,51,52
MEGAELOSIA 4,5,35,46
CYCLORAMPHUS 7
ZACHAENUS PARVULUS 5,46,58,61
11,(13),44, 58,62
THOROPA 35,38,41, 52,60
2,3,4,17,42, 44,50,52,62
9,61,63 (NO)
PARATELMATOBIUS 2,23,24,26,27, 28,52,58
18,21,53 (NO)
20,57 (NO)
TELMATOBIUS 26,35,40,41, 46,50,61,64
EUPSOPHUS 17,18,27
64 (NO)
32,57,58
BATRACHOPHRYNUS 4,22,27,28,44, 49,61,62,64
BATRACHYLA 9,17,18,39, 40,41,52,57, 61,63
2,3,48
20,21,30,38,53
1 (NO)
14 (NO)

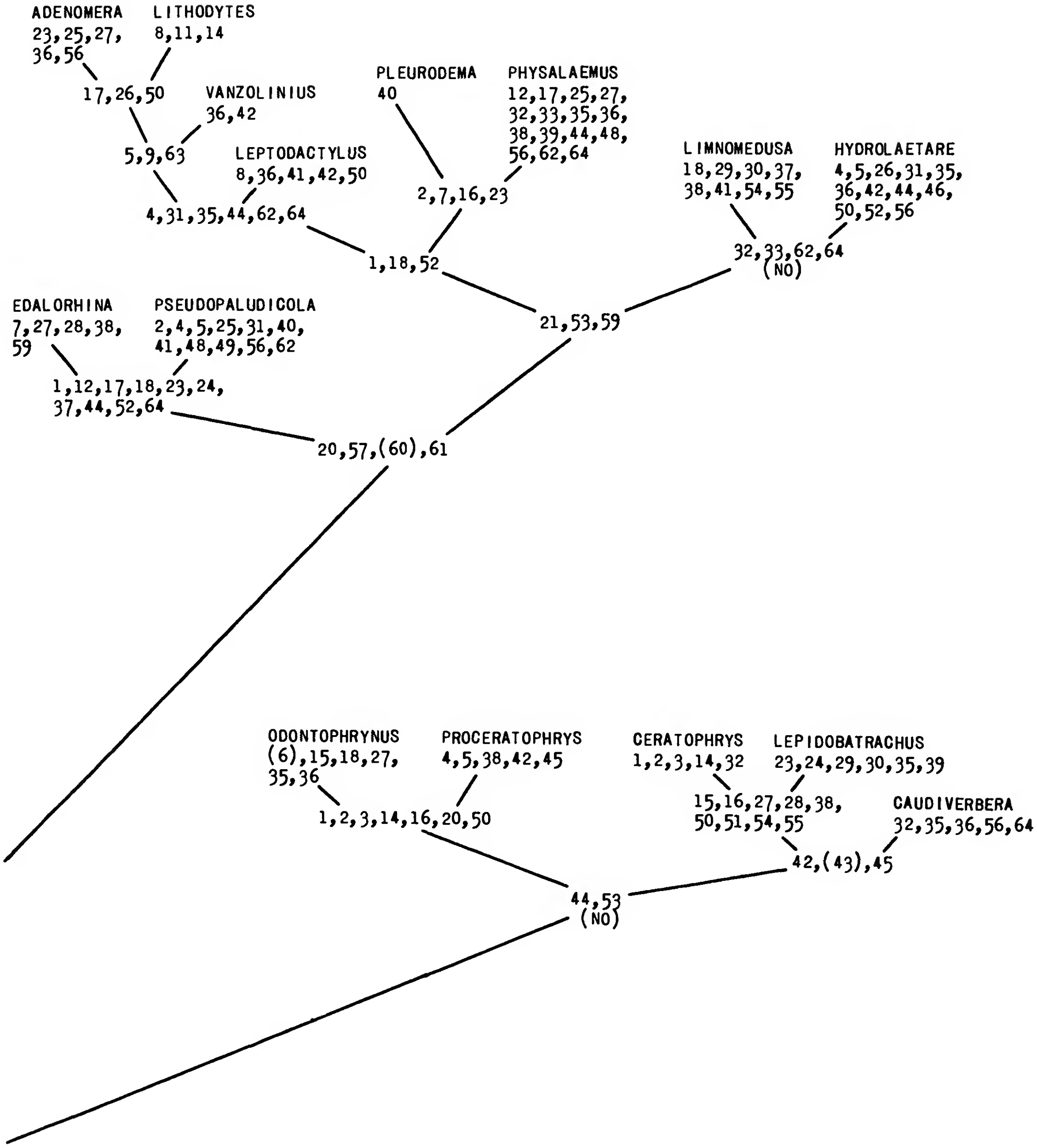


FIGURE 9.—Preferred predicted phylogenetic relationships of 38 OTUs using the combinatorial method. (Derived states only are included in the analysis; numbers in parentheses are unique state appearances in the phylogeny; "NO" in parentheses indicates a nonmonothetic cluster; see text.)

convergences, but the advantage of adding one monothetic cluster. It is difficult to choose among these conflicting indications, so the relationships are left as shown in the phylogeny of Figure 9.

With all of the above changes that have been incorporated into the phylogeny of Figure 9, *Paratelmatobius* now fits best with the line leading to *Crossodactylus*, etc., as it shares five states in this assemblage rather than three states with the other lineage. No other changes result from this relocation.

The relationships shown in Figure 9 represent what I believe are the best fit of the data with the probable relationships among those taxa included in the analysis.

Additions, Modifications, and Comments on the Preferred Phylogeny

Considerable data were missing for certain genera, and intrageneric samples were small for some genera analyzed. The reasons data are missing are essentially two: (1) some genera are known from one or a very few specimens; in such cases, there is not enough material available to make muscle dissections or skeletal preparations; (2) several genera have not been systematically reviewed recently and the species content of the genera is not known. To undertake reviews of these genera would take many years; for example, I have been systematically reviewing the genus *Leptodactylus* since 1965 and am about halfway completed. Possible modifications of the phylogeny with the inclusion of more genera or more samples of some genera are now discussed alphabetically by genus.

Amblyphrynus: The known derived states for *Amblyphrynus* are (derived states for which no information is known for the character in parentheses): 1, 4, 5, 14, 17, 18, (19–39), 42, 44, 46, 50, (51), 52 (53–60), 61, 62, (64). Of these states known, *Amblyphrynus* shares most with the eleutherodactyline genera and certainly fits well into the basal cluster of characters shared by all eleutherodactyline genera. See *"Eleutherodactylus"* for futher comments.

Barycholos: Lynch (1973b) suggested that *Leptodactylus mantipus* Boulenger, known only from the holotype, should be included in the genus *Barycholos*. The single most important character state linking these two taxa, according to Lynch, was the presence of a sternal style which was bifurcate posteriorly. I had examined the holotype in 1969, at which time the pectoral girdle region had not been dissected. Since I use different character states for the sternum than those Lynch recognizes in part, I asked Alice G. C. Grandison to examine the sternum of the holotype and to compare it against my four categories. She kindly responded with a drawing which clearly indicates that according to shape, it is either state 1 or 2 of character 32. Grandison further stated (pers. comm.) that "there is no ossification. It is a broad plate, bifurcated posteriorly and I'd have thought cartilagenous." Thus *mantipus* has state 1 of character 32 (character state 57 as it appears in the phylogenies). Combining my observations with these provided by Lynch (1973b), the known derived states for *mantipus* are: 1, (4–5), 10, 14, 17, 18, (19–47), (50–56), 57 (61–64). For the known characters, *mantipus* seems to fall well within the eleutherodactylines, near the cluster including *Barycholos, Eleutherodactylus, Hylactophryne, Ischnocema,* and *Niceforonia.* The differences between *mantipus* and *Barycholos pulcher* listed by Lynch (1973b) in combination with a different sternal apparatus suggest that the two taxa belong to separate genera. For the present, the relationships would best be expressed by considering *mantipus* an *Eleutherodactylus,* rather than belonging to either *Barycholos* or *Leptodactylus.*

Batrachophrynus: Lynch (1971, p. 123) was of the opinion that the relationships between *Batrachophrynus* and *Telmatobius* were very close but that the relationships were difficult to assess because so few species have been studied. This study was also based on limited species samplings of these two genera.

Crossodactylodes: The known (and unknown) derived states for *Crossodactylodes* are: 1, 3, 9, 14, 17, 18 (19–39), 42, 44, 48, 49, 52 (53–60), 61, 63 (64). These states indicate relationships with *Cycloramphus, Thoropa,* and *Zachaenus.* Also see *"Zachaenus."*

Eleutherodactylus: The sample of *Eleutherodactylus* used in this analysis comprises less than 1 percent of the known species. How much of the variation within *Eleutherodactylus* was included in this study is unknown. Within the limits of this study, two alternate conclusions may be drawn with respect to *Eleutherodactylus:* (1) *Barycholos* should be included in *Eleutherodactylus, Eleutherodactylus* would then be monophyletic, or; (2) *Eleutherodactylus* as presently understood is polyphyletic. I think the latter conclusion is the correct one. Once the species groups of *Eleutherodactylus* are reasonably well defined and their relationships analyzed within the eleutherodactyline complex, the relationships as represented within the phylogeny of Figure 9 may be considerably altered. For example, I think it likely that there are some Middle American species groups of *Eleutherodactylus* that are more closely related to *Syrrophus* and *Tomodactylus* than other *Eleutherodactylus*. This would then bring *Syrrophus* and *Tomodactylus* closer with the species of *Eleutherodactylus* analyzed in this study and bring *Sminthillus* in at a much lower branching level. When the relationships of the *Eleutherodactylus* species groups are analyzed, the relationships of *Amblyphrynus* and *Eleutherodactylus mantipus* will also be clarified. One thing is clear: while there may be considerable reshuffling within the eleutherodactylines as more units are added for analysis, the integrity of the eleutherodactylines as a unit will remain. From the limited character sampling of *Eleutherodactylus* that I have done, together with what is reported in the literature, there is little doubt that the relationships of *Eleutherodactylus* as presently understood would be much better expressed if *Eleutherodactylus* were partitioned into several genera.

Hylorina: The known (and unknown) derived states for *Hylorina* are: 8, (12–13), 14, 17, 18, (20–39), 40, 50, (53–60), 61, (64). None of the known derived states fit any of the basal clusters of the phylogeny of Figure 9. For the few known derived characters, *Hylorina* shares most with *Batrachyla*. Such a relationship would bring the cluster of genera including *Batrachyla* at a lower level to the presumed common ancestor than indicated in Figure 9, as *Hylorina* does not have State 1.

Insuetophrynus: The known (and unknown) derived states for *Insuetophrynus* are: 1, 2, (12–13), 14, (17–47), (50–56), (61), 62, (64). With so few known derived states, the relationships could lie most anywhere on the phylogeny of Figure 9. Based on intuition, I would place *Insuetophrynus* with *Batrachyla, Batrachophrynus,* etc.

Macrogenioglottus: Reig (1972) discussed the relationships of the monotypic *Macrogenioglottus* and proposed a new family for it. Lynch (1971) treated the taxon as a synonym of the genus *Odontophrynus*. I have not examined any specimens, but the data provided by Reig (1972) indicates that *Macrogenioglottus* has the following known (and unknown) derived states: 1, 2, (4–5), 14, 15, 16, 18, (23–24), (26), 29, 30, 35, 36, 42, 44, 51, 53, 54, 55, (64). Two things are clear within the context of the phylogeny of Figure 9. First, the relationships lie with the cluster represented by *Caudiverbera, Ceratophrys, Lepidobatrachus, Odontophrynus,* and *Proceratophrys*. Second, *Macrogenioglottus* and *Odontophrynus* each have a cluster of character states not shared with the other. The differences are great enough that for present analytic purposes, the relationships would be obscured by considering *Macrogenioglottus* and *Odontophrynus* as congeneric. *Macrogenioglottus* shares the following states with the following combinations of taxa: 11 each with *Ceratophrys* and *Lepidobactrachus,* 10 with *Odontophrynus,* 7 with *Proceratophrys,* 5 with *Caudiverbera;* 6 with a cluster including both *Ceratophrys* and *Lepidobatrachus,* 4 with a cluster including *Odontophrynus* and *Proceratophrys,* and 1 with a cluster including *Caudiverbera, Ceratophrys,* and *Lepidobatrachus*. The data indicate that *Macrogenioglottus* has its closest relationships to *Ceratophrys, Lepidobatrachus, Odontophrynus,* and *Proceratophrys,* and that its inclusion tightens up this cluster and excludes *Caudiverbera*. It is pointless to speculate further on the exact relationships of *Macrogenioglottus* until (1) the full data set becomes available for *Macrogenioglottus,* and, more importantly, (2) more species are examined, especially of *Odontophrynus* and *Ceratophrys* including what many authors consider the distinct genus *Chacophrys*.

Physalaemus: The five species of *Physalaemus* used in this analysis were chosen to get a cross section of the genus as defined by Lynch (1971). *Physalaemus* has one of the highest proportions of character state variability within the entire sample. It may be that when additional samples of more species of *Physalaemus* are analyzed, the relationships would be best expressed by partitioning the genus. If partitioned, the relationships expressed within the phylogeny of Figure 9 would probably change little, however, because the *Physalaemus*-complex is likely a monothetic group.

Pleurodema: As with *Physalaemus,* the sample used in this analysis was small. A greater understanding of the variation within the genus as presently conceived may lead to partitioning of the genus, which could have an effect on the phylogeny represented in Figure 9. The discontinuities in geographic distribution and life history, with some species having foam nests and others not, are particularly suggestive that the genus is polyphyletic.

Scythrophrys: Lynch (1971) proposed a new genus for *Zachaenus sawayae* Cochran. So few derived character states are known for the only specimen so far known that its relationships cannot be determined with any assurance. It probably is most related to the *Zachaenus, Thoropa,* and *Paratelmatobius* cluster. See also *"Zachaenus."*

Telmatobufo: The known (and unknown) derived character states for *Telmatobufo* are: 2, 3, 4, 6, (12–13), (20–39), (41–43), 46, (52–60), 61, (64). *Telmatobufo* shares the most states with *Batrachophrynus.* Assuming that *Telmatobufo* has its closest relationships with *Batrachyla, Batrachophrynus,* etc., the inclusion of *Telmatobufo* would result in the entire cluster being independently derived from the presumed ancestral stock, as *Telmatobufo* has neither states 1 nor 14.

Zachaenus: In the middle of the character analysis, I thought it best to separate the data on *Z. parvulus* from the data on *Z. stejnegeri.* As the limits of the combinatorial program were always approached or exceeded with the data samples, the data for *Z. stejnegeri* were never included. The derived states for *stejnegeri* are: 1, 2, 3, 4, 5, 14, 17, 18, 20, 21, 42, 44, 46, 50, 53, 61, 62, 64. The most states are shared with *Z. parvulus,* but the states that are not shared, 52 and 58, would considerably modify the relationships among *Cycloramphus, Crossodactylus, Hylodes, Megaelosia, Thoropa, Paratelmatobius,* and *Zachaenus* as expressed in the phylogeny of Figure 9. Two conclusions may be drawn. First, characters 52 and 58, having to do with the separation of the occipital condyles and the type of sternum are fundamental characters within the total phylogeny. Thus the relationships as presently understood would best be expressed by generically separating *stejnegeri* from *parvulus.* Lynch (1971) was the first author to suggest combining the taxa in the same genus. I think the data presented here warrant removing *Craspedoglossa* from the synonymy of *Zachaenus.* The second conclusion is that the relationships within this total assemblage are unclear, as indicated in part by the several nonmonothetic clusters in the phylogeny of Figure 9 for this group. I think the relationships among this group will be modified considerably as more information is available on the variability and state content of *Craspedoglossa, Crossodactylodes, Scythrophrys, Thoropa,* and *Zachaenus.* The group itself will remain intact as all genera have a number of derived states in common.

Systematic Conclusions

As is clear from the previous section, this study is a preliminary analysis due to the lack of knowledge of states for some genera and intrageneric variability for other genera. The combined information on relationships clearly indicates five major groupings within the family. I think the groupings will remain intact as more information becomes available, but that the relationships within and among groupings will be subject to change with the addition of more information. The limits of this study do not clearly demonstrate that the five groups constitute a monophyletic group. Thus, the relationships among the five groups themselves can only be outlined in broadest terms for the present. See "Historical Zoogeography" for further comment. Due to likely future modifications, the proposal of these five categories as formal taxonomic units is premature. Rather, I prefer to consider these units as informal for the present. The units and their components follow in alphabetical arrangement.

1. Ceratrophrines
   - *Ceratophrys*
   - *Lepidobatrachus*
   - *Macrogenioglottus*
   - *Odontophrynus*
   - *Proceratophrys*
2. Eleutherodactylines
   - *Amblyphrynus*
   - *Barycholos*
   - *Eleutherodactylus*-complex
   - *Euparkerella*
   - *Holoaden*
   - *Hylactophryne*
   - *Ischnocnema*
   - *Niceforonia*
   - *Sminthillus*
   - *Syrrophus*
   - *Tomodactylus*
3. Grypiscines
   - *Craspedoglossa*
   - *Crossodactylodes*
   - *Crossodactylus*
   - *Cycloramphus*
   - *Hylodes*
   - *Megaelosia*
   - *Paratelmatobius*
   - *Scythrophrys*
   - *Thoropa*
   - *Zachaenus*
4. Leptodactylines
   - *Adenomera*
   - *Edalorhina*

Hydrolaetare
Leptodactylus
Limnomedusa
Lithodytes
Physalaemus
Pleurodema
Pseudopaludicola
Vanzolinius

5. Telmatobines
Batrachophrynus
Batrachyla
Caudiverbera
Eupsophus
Hylorina
Insuetophrynus
Telmatobius
Telmatobufo

The Preferred Phylogeny and Hennig's Sister-Group Concept

In addition to the concept of deducing relationships on the basis of shared, derived clusters of states, Hennig (1966) advocated the formation of sister-groups. Sister-groups require involvement of at least two characters, with reciprocal representation of primitive and derived states. Hennig (1966) proposed that this operational definition of sister-groups indicates a common point of evolutionary divergence. The phylogeny of Figure 9 was not constructed with sister-group formation as a criterion. The location of sister-groups within the preferred phylogeny is discussed by group.

For the Telmatobines represented in Figure 9, all clusters represent sister-groups; this is also true for the ceratophrine genera of Figure 9.

Within the grypiscines, *Thoropa* does not form a sister-group with *Crossodactylus, Hylodes* and *Megaelosia*. Otherwise, all other groups are sister-groups.

Within the leptodactylines, *Limnomedusa* and *Hydrolaetare* do not form a sister-group with *Adenomera, Lithodytes, Vanzolinius, Leptodactylus, Pleurodema,* and *Physalaemus.* All other clusters yield sister-groups. With a slight rearrangement, all cluster groups can be sister-groups within the leptodactylines. *Limnomedusa* forms a sister-group with *Adenomera, Lithodytes, Vanzolinius, Leptodactylus, Pleurodema,* and *Physalaemus.* Next, *Hydrolaetare* forms a sister-group with *Adenomera, Lithodytes, Vanzolinius, Leptodactylus, Pleurodema, Physalaemus,* and *Limnomedusa.*

Within the eleutherodactylines, there are several instances of clusters which do not represent sister-groups. The best rearrangement of taxa yields two major groups. Group 1 is represented by *Eleutherodactylus nigrovittatus* and *Barycholos* add *Eleutherodactylus coqui* add *Eleutherodactylus fleischmanni* add *Hylactophryne* and *Ischnocnema* add *Niceforonia.* Group 2 is represented by *Syrrophus* and *Tomodactylus* add *Sminthillus* add *Euparkerella* and *Holoaden.* All clusters within the two groups are sister-groups; groups 1 and 2 are not sister-groups.

Among the five major groups, only the eleutherodactylines and leptodactylines form sister-groups with one another.

The sister-group concept allows an assessment of weaknesses in the phylogeny. In this case, those areas where sister-groups cannot be formed with the available data are within the grypiscines and eleutherodactylines and among the five major groups. These are the weakest parts of the phylogeny in terms of the data. In terms of the grypiscines and eleutherodactylines, the weakness of proposed relationships will be corrected only with gathering more data. Gathering more data may not help to resolve the relationships among the five major groups because of the extreme likelihood of convergent data not allowing sister-group formation at that level. The best test for the validity of the five proposed groupings at present is to see if the five groupings make sense biogeographically.

Comparison with Other Schemes

The only major difference between the phylogenies of Figures 7 and 9 is the placement of *Pleurodema,* which has already been discussed. The similarities mean that the deletion of the karyotype character in the analysis leading to the phylogeny of Figure 9 did not affect the overall analysis of relationships.

Lynch (1971) has been the first since Boulenger (1882) to systematically review the entire family Leptodactylidae. Lynch (1971) provides a historical review of all the suprageneric classifications proposed for various sections of the family. The interested reader is referred to Lynch's review for a more complete comparison with the informal classification proposed herein. My informal groups are generally equivalent to certain of Lynch's subfamilies and tribes with certain exceptions as explained below.

Ceratophrines.—Several South American workers (e.g., Reig, 1972, and sources cited therein) consider the ceratophrines to represent a distinct family. These workers consider the ceratophrines to have the same generic composition as recognized in this study. Lynch (1971) restricted his subfamily Ceratophryinae to include only the recent genera *Ceratophrys* and *Lepidobatrachus.* Lynch (1971) placed the genera *Odontophrynus* and *Proceratophrys* as a tribe into the subfamily Telmatobiinae. The results of this analysis indicate that the relationships of *Odontophrynus* and *Proceratophrys* lie with *Ceratophrys* and *Lepidobatrachus,* not with the genera Lynch placed in the subfamily Telmatobiinae. This study does not provide evidence either for or against recognition of the ceratophrines as a distinct family. Such an analysis would need to compare the five groups recognized here with other family groupings generally recognized to be related to the leptodactylids.

ELEUTHERODACTYLINES.—This grouping is equivalent to Lynch's (1971) tribe Eleutherodactylini of the subfamily Telmatobiinae. The only difference is that this study indicates that the genus *Barycholos* is an eleutherodactyline rather than a member of the subfamily Leptodactylinae as suggested by Heyer (1969a) and Lynch (1971).

Grypiscines.—The grypiscines as recognized herein are composed of members of four different groupings proposed by Lynch (1971). The members of Lynch's subfamily Elosiinae and tribe Grypiscini of the subfamily Telmatobiinae are completely included. In addition, the results of this study indicate that *Paratelmatobius* is a grypiscine, rather than a member of the subfamily Leptodactylinae as proposed by Lynch (1971) and *Thoropa* is a grypiscine, rather than a member of the tribe Alsodini of the subfamily Telmatobiinae.

LEPTODACTYLINES.—This grouping is equivalent to Lynch's (1971) subfamily Leptodactylinae except for Lynch's inclusion of *Barycholos,* an eleutherodactyline, and *Paratelmatobius,* a grypiscine, as discussed previously.

TELMATOBINES.—This group is equivalent to a combination of Lynch's tribes Alsodini and Telmatobiini of the subfamily Telmatobiinae with the exception of *Thoropa,* which Lynch (1971) considered an alsodine, but is here considered a grypiscine as discussed above.

The study was initiated because of uncertain relationships of some genera from a previous analysis (Heyer, 1974a). The previous study concluded that there were two major clusterings of leptodactylines: (1) *Adenomera, Leptodactylus, Lithodytes,* and *Vanzolinius,* and (2) *Physalaemus, Pleurodema,* and *Pseudopaludicola.* The present study agrees with the first cluster completely, but indicates that *Pseudopaludicola* is not as closely related to *Physalaemus* as indicated in the previous study. Examination of additional species of *Pseudopaludicola, Physalaemus,* and *Pleurodema* is needed to clarify the relationships among these genera. The previous analysis could not distinguish whether *Barycholos, Edalorhina, Hydrolaetare, Limnomedusa,* or *Paratelmatobius* were basally related with the other leptodactylines or had closer relationships elsewhere in the family. This study indicates that *Edalorhina, Hydrolaetare,* and *Limnomedusa* are related to the other leptodactylines, but that *Barycholos* is an eleutherodactyline and that *Paratelmatobius* is a grypiscine.

Phylogenetic Content of the Characters Analyzed

Once the best phylogeny is chosen, the behavior of the individual states can be evaluated within the phylogeny. Certain states are better than others in producing any given phylogeny. Those states that form large clusters in the phylogeny contain more phylogenetic information than those that do not, in terms of that given phylogeny. The analysis of characters of a given phylogeny will only have as much meaning as the degree of reflection the phylogeny is to reality. Such an analysis assumes that all states are adaptive, but that some states contain more phylogenetic information than others.

The particular phylogeny analyzed is identical to Figure 9 except that *Caudiverbera* is independently derived from a common ancestor as is the cluster of *Batrachyla, Batrachophrynus, Eupsophus,* and *Telmatobius.* This particular phylogenetic arrangement maximizes monothetic clusters and numbers of states within clusters. To facilitate comparison of characters, each state used in the phylogeny was evaluated with respect to its clustering behavior within the phylogeny as follows. The number of times a particular state actually appears in the phylogeny is divided by the total number of times the state could appear in the phylogeny. The lower the number, the better the state behaves in forming clusters. For example, if a state appears once in a cluster ancestral to five taxa inclusively, the state has a value of 1 (a single appearance in the phylogeny, although the state is shared by all five taxa above the cluster in which the state appears) divided by 5 (the total number of times the state could appear) equals 0.20. Alternatively, if another state appears in a phylogeny five times, but in each case the appearance is in an end point taxon, the state has a value of 5 divided by 5 equals 1. Thus a state with a value of one has no phylogenetic information. All states are analyzed in this fashion. When a given character is represented by more than one state, an average value of the component states is used as the value for that character. The values for each character were plotted on a graph by occurrence. There are no clear groupings, but the following characterizations appear reasonable. The best characters in terms of clustering behavior in the preferred phylogeny have values ranging from 0.08 to 0.21. Good characters range in value from 0.26 to 0.42. Average characters range from 0.49 to 0.72. Poor characters range from 0.77 to 1.00. The adjectives "best, good, average, poor" as used throughout the remainder of this section represent these value ranges. This method of analysis, while having the desirable trait of reproducibility has one minor drawback in terms of describing the phylogenetic value content of characters within a phylogeny—there are two ways of arriving at low numbers. The first is for the state to have a unique appearance in the phylogeny and the cluster in which it appears is ancestral to several taxa. This is the best kind of character with respect to clustering behavior, and is referred to as a Type I character for the best character category. The second is for a given state to appear a low number of times in the phylogeny, but each appearance is ancestral to several taxa. This is referred to as a Type II best character. All good, average, and poor characters are Type II. While the Type II character state is descriptive of large clusters and thus aids in the production of the phylogeny, it is obviously not the same quality of state as the Type I state. This problem is not present at the other end of the spectrum. High values always represent low phylogenetic content.

The overall average clustering value for the 64 characters used to build the phylogeny of Figure 9 is 0.54. The average value for external characters is 0.48, for muscle characters the average value is 0.61, and for skeletal characters the average value is 0.54.

The only best Type I character is character 10, life history.

There are four best Type II characters: pupil shape, outer metatarsal tubercle, anterior process of the hyale, last presacral vertebral width.

There are 11 good characters: male thumb, toe disks, toe webbing, adductor mandibularis muscle, omohyoideus muscle, fontanelle, occipital condyles, posterior sternum, sacral diapophyses, terminal phalanges, dorsal crest of ilium.

There are 13 average characters: tympanum visibility, tarsal decoration, inner tarsal tubercle, depressor mandibulae muscle, geniohyoideus medialis muscle, sternohyoideus muscle, iliacus externus muscle, tensor fasciae latae, semitendinous muscle, nasal contact with frontoparietal, squamosal, median contact of vomers, prootic fused with frontoparietal.

There are 7 poor characters: body glands, anterior petrohyoideus muscle, adductor longus muscle, quadratojugal, nasal contact with maxilla, vomerine teeth, alary process of the hyoid.

The diploid chromosome number was not included in the data set from which the phylogeny of Figure 9 was produced. The clustering index value for the character derived from the phylogeny of Figure 7 is 0.79, indicating that overall, the diploid number has little phylogenetic information. State 66 of the character, variation of the $2N=26$, 24, 22 (which in the tree will also include the derivable states of 67, $2N=22$ and state 68, $2N=$ less than 22) has a value of 0.27. Thus, within the character, one of the states does have good phylogenetic information, although the state appears four times in the tree. It is interesting to note that if the phylogenies of Figures 7 and 9 are reasonably correct, the diploid number of 22 has arisen more than once in the family. Also, it would be much more parsimonious to assume that the diploid numbers of 24 and 26, found in *Adenomera*, represent a secondary reversion to a higher diploid number from an immediately ancestral condition of 22, rather than the retention of the primitive state. Further kinds of data are needed to determine the status of the *Adenomera* karyotype. The conclusion seems warranted that caution must be used in proposing relationships at the generic level based only on the karyotype, reinforcing the same conclusion of a study done at a lower level of analysis (Heyer and Diment, 1974).

The variation of clustering values of individual states is similar to the average of the states for all 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 xiphisternum 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 convinced 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 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 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 diagramatically (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 Hylidae (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.

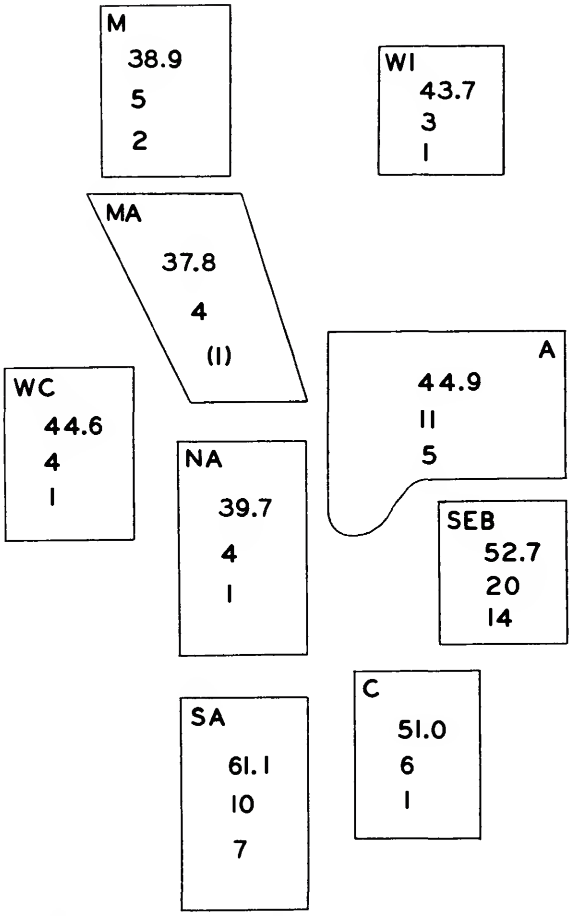


Figure 10.—Leptodactylid radiation centers. (M = Mexico, MA = Middle America, WI = West Indies, WC = West coast of South America, NA = northern Andes, SA = southern Andes, A = Amazonia, SEB = Southeastern Brazil, C = Chaco. Within each center, the upper number is the average percentage of primitive states,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

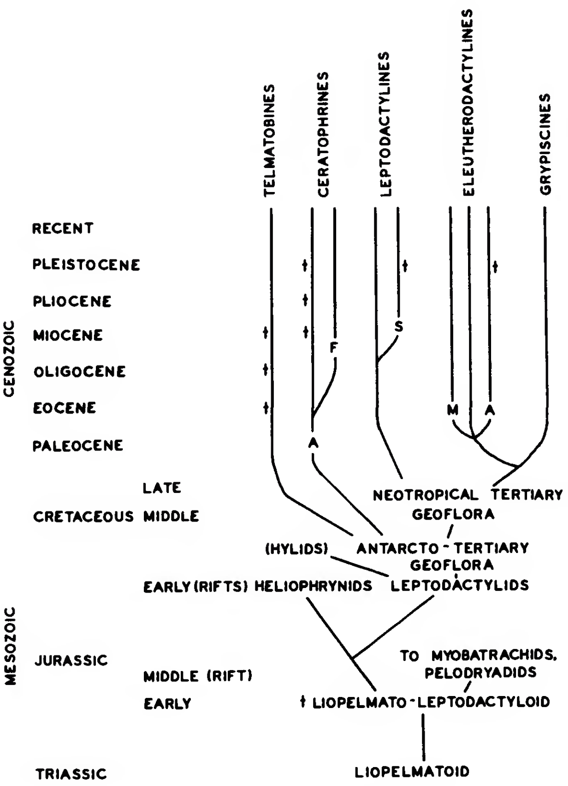


FIGURE 11.—Proposed historical zoogeography of the five leptodactylid groups. (A = arid, F = forest, M = montane, S = savanna; also see text.)

ceratophrines and the leptodactylines. The grypiscines represent a forest-stream adaptation that centered in southeastern Brazil, and the eleutherodactylines most likely had their origin as an early grypiscine 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 leptodactyloids 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 leptodactyloids from a leiopelmatid ancestor also simplifies the zoogeographic origin of the bufonids and ranoids (Savage, pers. comm.). Savage (1973) based a northern leptodactyloid 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, Leptodactyloids, 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-leptodactyloid 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 (Xenoanura and Scoptanura 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 liopelmatids in the temperate Southern Hemisphere. Unfortunately, living *Liopelma* are no help; all three living species have a derived life history pattern of direct development and no fossil liopelmatid larvae have been found. The crux of the argument hinges, then, on whether the pelobatid acosmanuran tadpole is really the same as the leptodactyloid (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 xenoanuran 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 xenoanuran 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 leptodactyloid 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 invasion 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., *Zachaenus*) and arboreality (*Crossodactylodes*). The grypiscine radiation is an old and moderate radiation, which resulted in about 10 genera and 37 species.

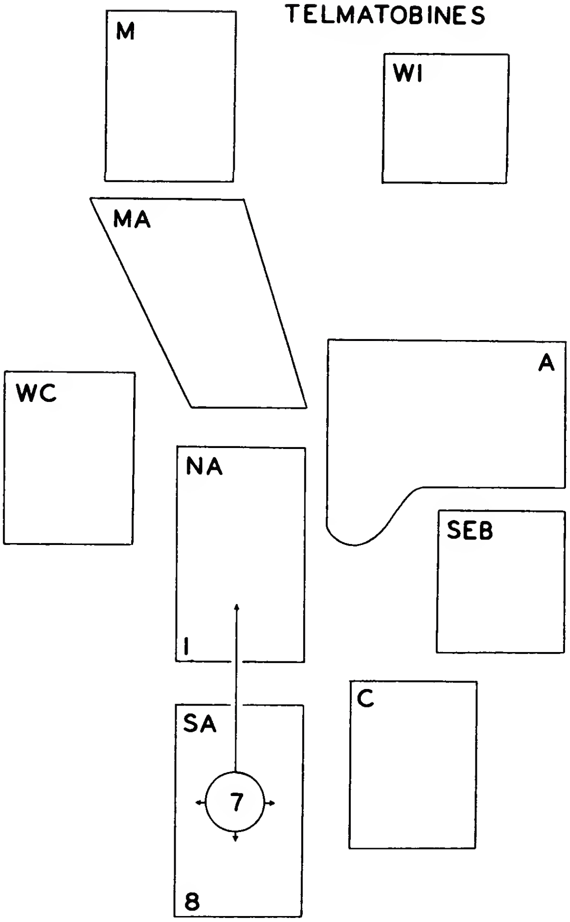


Figure 12.—Proposed telmatobine radiation. (Number in circle is number of endemic genera; numbers at bottom are total number of genera; abbreviations as in legend for Figure 10.)

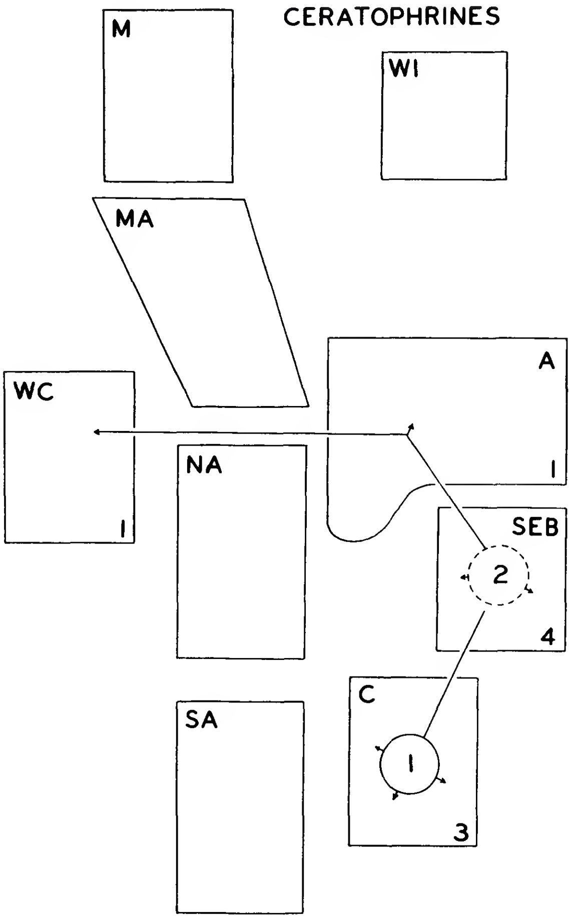


FIGURE 13.—Proposed ceratophrine radiation. (Numbers in circles are numbers of endemic genera; numbers at bottom are total number of genera; solid circle = primary radiation; dashed circle = secondary radiation; abbreviations as in legend for Figure 10.)

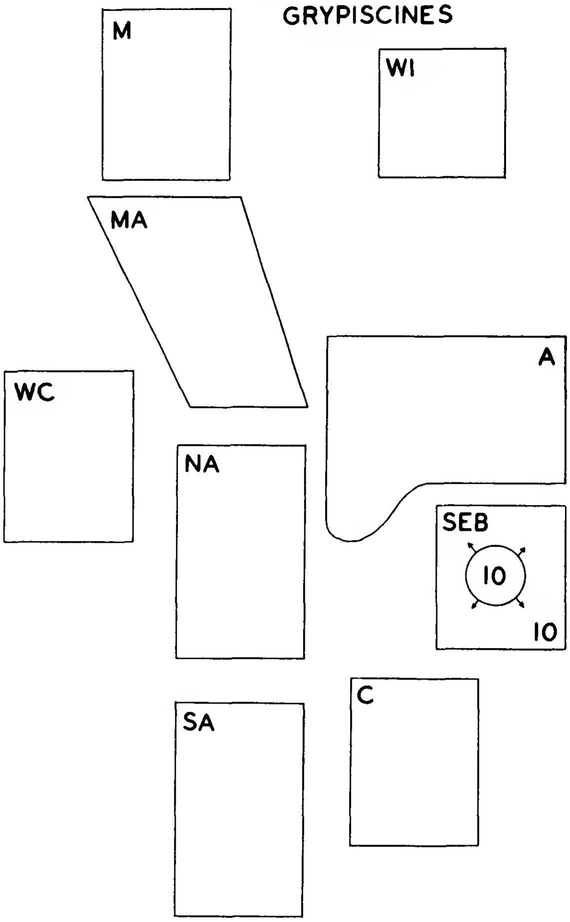


FIGURE 14.—Proposed grypiscine radiation. (Number in circle is number of endemic genera; number at bottom is total number of genera; abbreviations as in legend for Figure 10.)

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 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

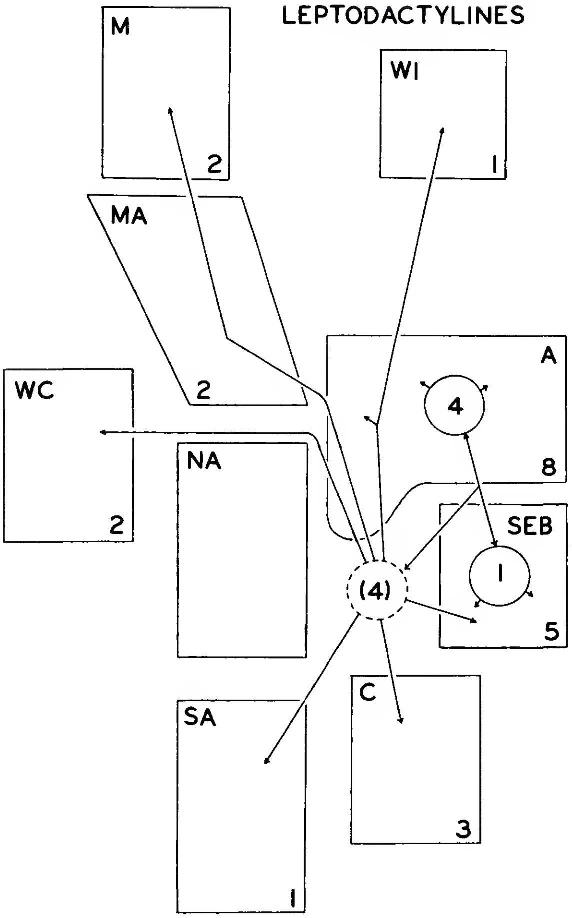


FIGURE 15.—Proposed leptodactyline radiation. (Numbers in circle are numbers of endemic genera; numbers at bottom are total number of genera; solid circles = primary radiations, dashed circle = secondary radiation; abbreviations as in legend for Figure 10; also see text.)

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 grypiscine 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 ceratophrines, 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 *Hylactophryne* and appears to be the earliest radiation. The second radiation is represented by endemic Mexican and Middle American *Eleutherodactylus,*

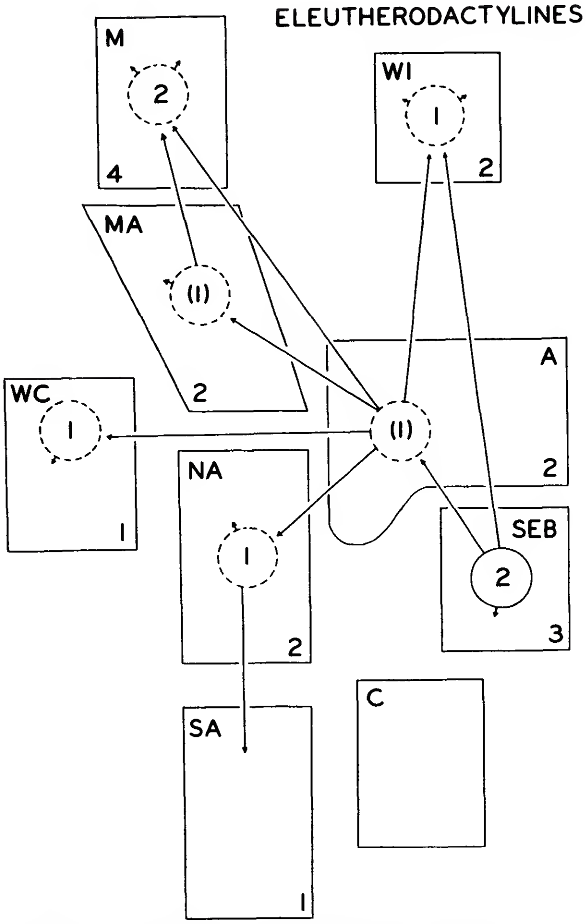


FIGURE 16.—Proposed eleutherodactyline radiation. (Numbers in circles are numbers of endemic genera; numbers at bottom are total number of genera; solid circle = primary radiation; dashed circles = secondary radiations; abbreviations as in legend for Figure 10; also see text.)

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 grypiscines, such as *Zachaenus*. It is interesting to note that in the case of the grypiscines, terrestriality has come out of a basic forest-stream adaptational complex. The crux of my argument for proposing that the eleutherodactylines are an early grypiscine derivative that attained direct development is based on the supposition that terrestriality originated in a wet forest habitat, and the grypiscines, 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 leptodactylid 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 grypiscine 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 grypiscines. 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 ancester 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

Batrachophrynus 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).

Batrachophrynus 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).

Odontophrynus americanus, USNM 123400 (M).

Odontophrynus cultripes, USNM 81138 (M).

Paratelmatobius lutzi, 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).

Zachaenus parvulus, USNM 164154 (M).

Zachaenus stejnegeri, USNM 164116 (M).

HELIOPHRYNIDAE

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	-
Physalaemus.........	x	x	-	-	-	-	x	x	x	x	-	-	x	x	-	-

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

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
Pleurodema..........	-	x	-	-	-	-	-	-	-	-	x	x	-	-	x	-
Proceratophrys......	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Pseudopaludicola....	-	x	-	-	-	-	-	-	-	-	-	-	x	x	x	-
Sminthillus.........	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Syrrophus...........	-	-	-	x	-	-	x	x	-	-	-	-	-	-	-	-
Telmatobius.........	-	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-
Telmatobufo.........	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Thoropa............	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Tomodactylus.......	-	-	-	x	-	-	x	-	-	-	-	-	-	-	-	-
Vanzolinius........	-	x	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Zachaenus..........	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-
CYCLORANINAE																
Adelotus...........	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Cyclorana..........	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Helioporus.........	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Kyarranus..........	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Lechriodus.........	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Limnodynastes......	x	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Mixophyes..........	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Neobatrachus.......	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Notaden............	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Philoria...........	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
MYOBATRACHINAE																
Assa...............	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Crinia.............	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Glauertia..........	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Metacrinia.........	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Myobatrachus.......	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Pseudophryne.......	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Taudactylus........	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Uperolia...........	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
HELIOPHRYNIDAE																
Heliophryne.........	-	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	A	B	A	C											
Barycholos	A	A	A	A	D	C	B	A	C		B	A	C	A	B	C	D	A	G	B
Batrachophrynus	A	D	C	A	A	B	B	A	A	B/C	B	E	A	A	A	A	C	A	D	C
Batrachyla	A	A	B	A	B	A	B	A	C	A/C	B	B	A	A	A	B	C	A	D	D
Caudiverbera	B	A	B	A	A	A	A	A	A	B/D	A	A	A	A	A	C	B	B	A	A
Ceratophrys	A	E	B	A	A	B	B	B	A	A/D	A	A	A	A	A	A	B	B	D	B
Crossodactylodes	A	D	D	A	B	A	B	A	C											
Crossodactylus	A	A	D	A	E	F	B	A	D	A/C	B	B	A	A	A	D	B	A	D	A
Cycloramphus	A	D	E	D	A	A	B	A	B	A/E	B	B	A	A	A	B	B	A	D	A
Edalorhina	A	A	B	D	A	D	B	A	C	A/C	B	A	C	A	A	A	B	A	G	B
E. coqui	A	A	A	A	D	A	B	A	C	B	B	A	A	A	B	C	D	A	H	A
E. fleischmanni	A	A	A	A	D	B	B	A	B	H	A	B	A	A	A	B	D	F	G	B
E. nigrovittatus	A	A	A	A	D	A	B	A	C	B	B	A	C	A	B	B	D	F	G	B
Euparkerella	A	D	A	A	A	A	B	A	C	H	B	D	C	A	B	C	B	A	D	D
Eupsophus	A	E	B	A	A	B	B	A	B	A/C	B	B	A	A	A	G	C	C	D	B
Holoaden	A	D	A	A	A	A	B	A	C	B	B	B	C	A	B	C	B	B	B	A
Hydrolaetare	B	A	A	A	A	B	B	A	A		B	B	A	A	B	C	D	D	A	A
Hylactophryne	A	A	A	A	A	A	B	A	C	H	B	F	A	A	A	I	D	A	G	B
Hylodes	A	A	B	A	E	F	B	A	D	B/C	B	B	A	A	A	B	B	A	D	C
Hylorina	B	A	B	G	A		B	A	C	A/E										
Insuetophrynus	A	B	D	A	A		B	A												
Ischnocnema	A	A	A	A	A	A	B	A	C		B	A	A	A	A	I	B	F	G	B
Lepidobatrachus	B	A	B	A	A	B	A	B	A	A/E	A	A	C	A	A	A	A	A	B	D
Leptodactylus	A	A	E	B	A	B	B	A	E	A/C/F	B	B	A	A	A	B	E	A	A	A
Limnomedusa	B	A	B	A	A	B	B	A	D		B	B	A	A	A	B	A	D	G	B
Lithodytes	A	A	A	G	E	B	B	A	C		B	B	A	A	B	B	D	A	B	A
Megaelosis	A	A	A	A	E	F	B	A	D	B/C	B	B	A	A	A	B	B	A	B	A
Niceforonia	A	E	A	A	A	A	B	A	C		B	A	A	A	B	I	D	F	D	B
Odontophrynus	A	D	B	C	A	B	B	B	F	B/C	B	A	A	A	A	E	B	A	C	A
Paratelmatobius	A	B	B	A	A	A	B	A	A	H	B	A	C	A	B	A	B	A	D	A
Physalaemus	A	C	B	F	A	E	B	C	C	B/C/F	B	B	B	B	E	E	B	E	F	E
Pleurodema	A	C	B	E	A	B	B	C	E	A/C/G	B	C	B	A	A	B	B	A	D	A
Proceratophrys	A	D	A	A	A	B	B	C	A	A/C	B	A	A	A	A	C	B	A	D	B
Pseudopaludicola	A	B	A	A	A	D	B	A	C	B/C	B	A	C	B	A	C	D	A	G	A
Sminthillus	A	A	A	A	B	A	B	A	C	B	B	B	C	A	B	A	D	F	D	B
Syrrophus	A	C	A	D	D	A	B	A	E	B	B	C	C	A	A	G	E	F	B	A
Telmatobius	A	E	F	A	A	B	B	A	A	B/C	B	B	A	A	B	D	C	B	E	C
Telmatobufo	B	D	C	B	A		A	A	A	A/C										
Thoropa	A	A	B	A	B	A	B	A	D	A/C	B	B	A	A	A	B	B	A	B	B
Tomodactylus	A	A	A	E	D	A	B	A	C	H	A	A	C	A	A	F	D	F	D	B
Vanzolinius	A	A	A	A	F	B	B	A	D		B	B	A	A	A	B	D	A	A	A
Z. parvulus	A	D	A	A	A	A	B	A	C	A/E	B	B	A	A	A	B	B	A	D	A
Z. stejnegeri	A	D	A	A	A	A	B	A	C	A/E	B	B	A	A	A		B	A	D	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	D	A	C		C				A	C	A		
Barycholos	A	A	B	A	G	A	A	A	C	A	B	C	A	A	B	B	
Batrachophrynus	A	A	A	A	A	C	A	A	B	C	A	A	A	C	A	B	
Batrachyla	C	C	A	B	A	A	A	A	C	C	A	B	A	A	B	A	B
Caudiverbera	A	A	D	A	C	A	A	A	B	C	D	A	B	A	A	B	B
Ceratophrys	A	A	D	A	C	A	C	B	A	C	C	A	B	A	A	A	A
Crossodactylodes	A	A	B	A	A	C	A	A	C				A	A	B		
Crossodactylus	C	C	A	A	A	C	A	B	C	C	A	C	A	C	B	B	B
Cycloramphus	A	A	B	A	A	A	C	A	C	C	A	B	B	B	A	B	B
Edalorhina	A	A	A	A	A	A	A	A	C	A	A	D	A	A	A	B	G
E. coqui	A	A	A	A	A	A	A	B	C	A	A	C	A	C	B	B	B
E. fleischmanni	A	A	B	A	A	A	A	A	C	A	A	B	A	C	B	B	I
E. nigrovittatus	A	A	B	A	G	A	A	A	C	A	A	C	A	C	B	B	
Euparkerells	A	A	B	A	A	C	A	B	C	A	C	A	A	C	B	B	
Eupsophus	A	A	A	B	A	B	A	A	B	B	A	C	B	A	A	A	C
Boloaden	A	C	A	B	A	A	A	A	C	A	C	A	A	C	A	B	
Hydrolaetare	A	A	B	A	D	A	C	A	C	C	E	D	A	C	A	B	
Hylactophryne	A	A	A	A	B	A	C	A	C	A	A	B	A	C	A	B	G
Hylodes	A	C	A	A	A	A	A	B	C	C	A	C	A	C	B	B	B
Hylorina	C	A	A	B	A	A	C	A	B				A	A	A		B
Insuetophrynus						A						A		C	A		B
Ischnocnema	A	A	A	A	B	A	C	A	C	A	A	B	A	C	A	B	G
Lepidobatrachus	A	A	D	A	C	A	C	B	B	C	C	A	B	A	A	A	B
Leptodactylus	A	B	C	A	A	A	C	A	D	C	A	D	A	C	A	B	G
Limnomedusa	A	C	A	B	A	A	A	A	B	C	C	D	A	C	A	B	C
Lithodytes	A	A	A	A	A	A	C	A	C	C	A	D	A	C	B	B	I
Megaelosia	A	A	A	A	E	A	A	A	B	C	A	C	A	C	B	B	B
Niceforonia	A	A	A	A	A	B	A	A	C	A	A	B	A	C	A	B	
Odontophrynus	A	A	A	A	A	A	C	A	B	C	A	A	B	A	A	A	F
Paratelmatobius	A	A	A	B	A	A	A	A	C	A	A	C	B	A	A	B	
Physalaemus	A	A	A	A	A	B	A	A	C	C	E	D	A	B	A	B	G
Pleurodema	C	A	A	B	A	A	C	A	C	C	A	D	A	A	A	A	G
Proceratophrys	A	A	B	A	C	A	C	A	B	C	A	A	B	A	A	A	G
Pseudopaludicola	C	C	A	A	A	C	A	A	C	A	E	E	A	C	A	B	B
Sminthillus	A	A	A	A	G	C	A	B	C	A	A	A	A	C	B	B	
Syrrophus	A	A	A	B	G	B	A	B	C	A	B	C	A	C	B	B	A
Telmatobius	D	C	A	B	D	B	C	A	B	C	A	C	A	A	A	B	E
Telmatobufo	A			B	D	A	A	A					A	A	A		
Thoropa	A	C	A	B	A	A	A	A	C	C	A	E	A	A	B	B	B
Tomodactylus	A	A	A	A	G	C	A	B	C	A	A	C	A	C	B	B	G
Vanzolinius	A	A	B	A	A	A	A	A	C	C	A	D	A	C	B	B	G
Z. parvulus	A	A	B	A	F	A	C	A	C	C	A	C	A	C	A	B	B
Z. stejnegeri	A	A	B	A	F	A	C	A	B	C	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
Helioporus	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	B	B	A	B	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		B	A/F	C	B	C	A	B	A	B	A
Metacrinia	A	D	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
Heliophryne	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	C	A	B	A	A	A	B	A	A	A	
Helioporus	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		A	A	B	
Lechriodus	A	A	A	A	A	A	A	A	B	C	A	C	A	A	A	B	
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	B	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		
Metacrinia	A	C	A	B	H	C	A	A	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				B	A	B	A	
Uperolia	A	A	B	A	H	C	A	A	C	C	E	A	B	A	A	A	D
Heliophryne	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								
Barycholos	0	0	2	0	2	1	1	0	1		1	0	2	0	1	0	3
Batrachophrynus	0	2	1	0	0	0	1	0	0	0	1	2	0	0	0	2	2
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	0	0	0	0	0	1
Ceratophrys	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	2	1
Crossodactylodes	0	2	0	0	1	0	1	0	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	0	1	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
Eupsophus	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	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		1	0	1	0							
Insuetophrynus	0	1	0	0	0		1	0									
Ischnocnema	0	0	2	0	0	0	1	0	1		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	1	0	2	0	1		1				0	1	0		
Barycholos	0	3	1	0	0	1	0	3	0	0	0	1	0	1	2	0	0	1	1	
Batrachophrynus	0	0	1	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	1	
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	0	1	3	0	1	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	1	0	0	2	0	0	1				0	0	1		
Crossodactylus	0	0	0	1	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	0	0	3	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. fleishmanni	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	2	0	1	1	1	
Euparkerella	0	0	2	0	0	1	0	0	2	0	1	1	0	2	0	0	1	1	1	
Eusophus	1	0	1	0	0	0	1	0	1	0	0	0	1	0	2	1	0	0	0	2
Holoaden	1	1	0	0	1	0	1	0	0	0	0	1	0	2	0	0	1	0	1	
Hydrolaetare	2	2	0	0	0	1	0	2	0	1	0	1	1	3	3	0	1	0	1	
Hylactophryne	0	3	1	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	3
Hylodes	0	0	1	0	1	0	0	0	0	0	1	1	1	0	2	0	1	1	1	0
Hylorina				1	0	0	1	0	0	1	0	0				0	0	0		0
Insuetophrynus									0					0	0		1	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		1	1	0	0	0	0	0
Lithodytes	0	0	2	3	3	0	1	0	1		1	1	0	0	1	0	3
Megaelosia	0	0	2	0	3	2	1	0	2	0	1	1	0	0	0	0	1
Niceforonia	0	2	2	0	0	0	1	0	1	1	1	0	0	0	1	0	3
Odontophrynus	0	2	0	1	0	0	1	1	2	0	1	0	0	0	0	1	1
Paratelmatobius	0	1	0	0	0	0	1	0	0		1	0	2	0	1	2	1
Physalaemus	0	1	0	1	0	1	1	2	1	0	1	1	1	1	0	1	1
Pleurodema	0	1	0	2	0	0	1	2	2	0	1	1	1	0	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							
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		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	0	0	0	1	0	1	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	
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	
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	
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			1	2	0	0	0					0	0	0		
Thoropa	0	1	1	0	1	0	1	0	0	0	0	1	1	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	0	1	1	0	3	0	1	1	1	3
Zachaenus 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	

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Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½" top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 pages, including typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index,* if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys,* number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy,* use the short form (taxon, author, date:page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within an entry, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in, or at the end of, the entry. For *references within the text,* use the author-date system: "(Jones, 1910)" and "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910:122, pl. 20: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of, or in addition to, the English system.

Illustrations (line drawings, maps, photographs, shaded drawings) can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed *Plates,* and individual components should be lettered (Plate 9*b*) but may be numbered (Plate 9: figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork. An instruction booklet for the preparation of illustrations is available from the Press on request.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." For capitalization of titles in foreign languages, follow the national practice of each language. Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

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