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

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

*W. Ronald Heyer*

## 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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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 leptodactylids (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 *Eleuthero-*

*dactylus* is very large and the limits of variation are not known. For purposes of this study, three species of *Eleuthero-*  
*dactylus* 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 ter-

restrial (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 ap-

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 Cyclorhines 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
Cyclorhines	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

pendix (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 *Zachaeus* should be split for further analysis; the character analysis for bones alone reflects this division. Both subgroups of *Zachaeus* (sensu Lynch, 1971) have the same external morphology and myological character states as coded for computer analysis.

### Character Analysis

I. 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
Cyclorhines	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, Pelodyadidae, 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:

$$0 \leftarrow 1$$

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 leptodactylids, 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

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
Cyclorhines	2	6	1	0	1	0
Heliophrynids	1	0	0	0	0	0
Fossorial	2	6	1	0	1	0
Terrestrial	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
Amazonia	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

states B and C, genera with the tympanum partially 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:

$$0 \rightarrow 1 \rightarrow 2$$

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 asperities 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,

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
Myobatrachines	5	1	0	1	0	1	0	0
Cyclorhines	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
Myobatrachines	7	0	0	0	0	0
Cyclorhines	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

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.

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:

$$1 \leftarrow 0 \rightarrow 2$$



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 re-coded 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,

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
Cyclorranines	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
Cyclorranines	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

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:

$$0 \rightarrow 1 \rightarrow 2$$

$$\quad \searrow$$

$$\quad \quad 3$$

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

