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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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Contents

	<i>Page</i>
Introduction	1
Methods and Materials	2
Character Selection	2
Study Group	2
Directional Criteria	2
Character Analysis	3
Analysis of Relationships	21
25 Operational Taxonomic Units	21
38 Operational Taxonomic Units	27
Additions, Modifications, and Comments on the Preferred Phylogeny	32
Systematic Conclusions	34
The Preferred Phylogeny and Hennig's Sister-Group Concept	35
Comparisons with Other Schemes	35
Phylogenetic Content of the Characters Analyzed	36
Evolutionary Zoogeography	39
Historical Zoogeography	40
Within-Group Patterns	43
Origin and Evolution of Terrestriality	46
Appendix: Supplementary Data	48
Literature Cited	54

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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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