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RELATIONSHIPS OF THE *MARMORATUS*
SPECIES GROUP (AMPHIBIA, LEPTODACTYLIDAE)
WITHIN THE SUBFAMILY LEPTODACTYLINAE

By W. RONALD HEYER

25

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RELATIONSHIPS OF THE *MARMORATUS*
SPECIES GROUP (AMPHIBIA, LEPTODACTYLIDAE) WITHIN
THE SUBFAMILY LEPTODACTYLINAE¹

By W. RONALD HEYER²

ABSTRACT: The relationships of the *marmoratus* group (subfamily Leptodactylinae) are analyzed. Primitive and derived states for 50 morphological characters are categorized and directions of change of character states are hypothesized for each character. The study sample of 29 taxa includes the five currently recognized species of the *marmoratus* group of the genus *Leptodactylus* and representatives of the other genera comprising the subfamily Leptodactylinae as defined by Lynch (1971). Relationships among the 29 taxa are analyzed by computer on the basis of clusterings of shared advanced character states. The results indicate that the relationships of the *marmoratus* group are best expressed by placing the group in a distinct genus, for which the name *Adenomera* is available. An additional systematic change resulting from the study is the placement of *Leptodactylus discodactylus* Boulenger in the genus *Lithodytes*. The genera *Adenomera*, *Leptodactylus*, and *Lithodytes* are redefined.

INTRODUCTION

The composition of the *marmoratus* species group of the genus *Leptodactylus* has recently been reviewed (Heyer, 1973). The purpose of this paper is to examine the relationships of the *marmoratus* species group to the other species groups within the genus and to other genera within the subfamily Leptodactylinae.

METHODS AND MATERIALS

One aim of this analysis is to utilize suites of different types of characters to infer relationships. My working hypothesis is that the total information gathered from the external morphology of adults and larvae, musculature and osteology of adults, egg morphology, and life history patterns, will more closely approximate relationships than could be inferred by using any one character suite by itself. Two overlapping levels of difference of kinds of information are involved in the hypothesis. Both assume that closeness of relationships are re-

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flected by similarities of genotypes. The first level of difference can be explained by comparing possible information content from characters of external morphology and life history patterns. Both are samplings, albeit indirect, of the genotype. If one of the taxa being compared is a forest floor frog and the other is a burrowing frog, but they have identical reproductive patterns of aquatic eggs and larvae, then different inferences regarding relationships may be deduced depending on the character suite examined. Based upon external morphology, the taxa would be considered quite different, due to differences in body proportions, metatarsal tubercle development, etc. Based on reproductive patterns, the taxa would be considered quite similar. Only by using both subset samples of the genotype would the relationships be best approximated. The second level of difference can be explained by comparing information content of external morphology and skeletal morphology. Here, the respective samples of the genotype may well be overlapping to a greater degree than in the previous example. The information content of the two character suites may thus be more similar and, indeed, one would expect parallel changes in both systems corresponding with a given functional shift. I assume that the two character sets do sample different parts of the genotype, at least in part, and for the same reasons as stated above, the relationships would best be approximated by using the information from both morphological systems. The two aspects of the hypothesis as described here are examined further in a separate paper.

The study organisms were chosen to represent as fully as possible the range of variation within the subfamily. Lynch's (1971) classification is used. Briefly, Lynch recognized four Neotropical subfamilies; the Ceratophryinae, Elosiinae, Leptodactylinae, and Telmatobiinae. Within the subfamily Leptodactylinae, he recognized the following genera: *Barycholos*, *Edalorhina*, *Hydrolaetare*, *Leptodactylus*, *Limnomedusa*, *Lithodytes*, *Paratelmatoobius*, *Physalaemus*, *Pleurodema*, *Pseudopaludicola*. In this study, data were gathered from examination of specimens (Table 1), from the data presented in Lynch (1971), and a few life history character states were provided by the individuals mentioned in the acknowledgments. Information from all five species of the *marmoratus* group is compared with 10 other species of *Leptodactylus*, one species of *Edalorhina*, one *Limnomedusa*, one *Paratelmatoobius*, five *Physalaemus*, two *Pleurodema*, one *Pseudopaludicola*, and the monotypic genera *Barycholos*, *Lithodytes* and *Hydrolaetare*. The ten species of *Leptodactylus* and five *Physalaemus* were chosen to represent the range of variation within the genera. The study specimens were considered to be representative of their respective species; for this analysis, the species is used as the unit of study.

Analysis of the data to infer relationships is done in two stages. The first stage is to analyze the characters, determining primitive and derived states. When more than two states are recognized, direction of change of state is inferred. The second stage of analysis is to use the combinatorial method to produce alternative phylogenies from information based on the direction of ad-

vanced character states. The combinatorial method is described in the relationships section. The determination of primitive and derived character states requires further discussion at this point.

The reasoning of Marx and Rabb (1970) is followed. They recognized ten criteria to determine directional change of character states. Certain of their criteria are not applicable in this study. Those that are, are combined in part and rephrased in terms of the present study sample.

I. Outgroup comparisons—Character state uniform in the outgroup. In order to use this criterion, information is needed from a group of organisms outside the study sample. Ideally, the outgroup would be the ancestral stock to the Subfamily Leptodactylinae. As the ancestral group is not known, generalized leptodactylids which would be expected to contain many of the ancestral states are used. Lynch (1971) has been the only recent author to review the leptodactylids at the family level. He indicated that evolution of the leptodactylids occurred independently through much of their total evolutionary history on the three continents where they are presently distributed. For this reason, the outgroup is limited to the Neotropics for the present paper. On the basis of osteology, life history, and some myology, Lynch (1971) postulated that the following taxa are relatively unspecialized with respect to the Leptodactylinae and are therefore used as the main outgroup for the present analysis: subfamily Ceratophryinae; *Ceratophrys* and *Lepidobatrachus*, and the following tribes of the subfamily Telmatobiinae; Telmatobiini; *Batrachophrynus*, *Caudiverbera*, *Telmatobufo*, *Odontophrynini*; *Odontophrynus*, *Proceratophrys*, and *Alsodini*; *Batrachyla*, *Eupsophus*, *Hylorina*, *Thoropa*. When the character states are not known for this outgroup, or when the evidence is unclear, other outgroups are or could be used. When the unmodified term outgroup appears in this paper from here on, it refers to the above assemblage of genera, however.

A character state is presumed to be primitive if it is found throughout the outgroup and derived if unique or nearly so in the leptodactylines. Marx and Rabb provide the reasoning for this, but one exception is possible. The outgroup may collectively share a character state that represents a specialization with respect to the actual ancestral stock of the Leptodactylines. As the evolutionary process is not always logical, this exception is expected to be a rare, but real, possibility. The sample size of the characters examined must be large enough so the exceptions do not distort the results significantly.

II. Outgroup comparisons—Character state polymorphism in the outgroup. This criterion differs from the first. A character state is presumed to be primitive if it is widespread in the outgroup and derived if unique or nearly so in the Leptodactylines. Marx and Rabb (1970) effectively argue the reasoning for this, but further comment is required here. In criterion I, if the methodology as outlined is followed, there is only one logical determination of whether a given state is primitive or derived. This is not true of criterion II. I nevertheless think that this criterion is useful as long as two conditions are

met. First, most of the outgroup must share a state for it to be considered primitive. Second, a large sample size of characters must be used so that the infrequent misinterpretation of states does not invalidate the results.

III. Morphological and/or ecological specialization. A character state is assumed to be derived if it is predominant in some adaptive specialization. The function of the morphological specialization does not necessarily need to be fully understood. One such adaptive specialization in the subfamily Leptodactylinae involves a shift towards terrestriality.

IV. Correlation of derived states. A concordance of derived states is assumed to be the result of a common genetic history of the taxa.

TABLE 1
List of Specimens Examined

(M indicates muscles examined, C indicates cleared and stained specimen examined, D indicates dry skeleton examined)

- Adenomera andreae*—Personal collection of W. R. Heyer (WRH) 16, C; University of Kansas, Museum of Natural History (KU) 119331, M.
A. bokermanni—Personal collection of W. C. A. Bokermann (WCAB) 34470, C, M; WCAB 14650, M.
A. hylaedactyla—Natural History Museum, Los Angeles County (LACM) 44338, C; LACM 44373, M.
A. marmorata—WCAB 30563, C; WCAB 30567, M.
A. martinezi—Museum of Zoology, University of São Paulo (DZ) 25321, C, M.
Barycholos pulcher—United States National Museum (USNM-GOV) 6475, M; USNM-GOV 8015, C.
Edalorhina perezii—University of Southern California (USC-PERU) 250, M.
Hydrolaetare schmidti—DZ 1455, M; KU 110613, D.
Leptodactylus bolivianus—USC-CRE 178, M; USC-CRE 8256, C.
L. bufonius—WRH 17, C; WRH 35, C; WRH 41, D; WRH 1589, M.
L. chaquensis—Field Museum of Natural History (FM) 69196, M; WRH 36, D; WRH 1587, M.
L. fuscus—WRH 20, C, M; WRH 1387, M.
L. latinasus—WRH 22, C, M; WRH 1434, M.
L. melanonotus—WRH muscle #1, M; WRH 1-12, C; USC-JMS 766, D.
L. mystaceus—WCAB 30850, M; WRH 19, M, C; WRH 34, C; WRH 159, M.
L. ocellatus—FM 80393, M; FM 80396, M; FM 80398, M; FM 80400, M; FM 80402, M; FM 80404, M; FM 80412, M; FM 80415, M; FM 80422, M; FM 80427, M.
L. pentadactylus—USC-CRE 505, M; USC-JMS 277, D; USC-JMS 435, D.
L. wagneri—USC-JMS 881, D; USC-PERU 701, M; WRH 33, C; WRH 42, D; WRH 924, M.
Limnomedusa macroglossa—FM 10252, M; KU 92960, C; KU 92961, D.
Lithodytes discodactylus—USNM-JAP 6156, C; WRH 1138, M.
L. lineatus—KU 104340, C; KU 125941, D; USNM-JAP 2183, C; WRH 1199, M.
Paratelmatobius luzii—KU 92981, C; 107089, C; Museu Nacional, Rio de Janeiro, no number, M.
Physalaemus albonotatus—LACM 73443, M; KU 92987, C.
P. biligonigerus—LACM 74018, M; KU 84768-775, D.
P. fuscocomaculatus—LACM 37697, M; KU 80811, C; KU 84776, D; KU 93010, C.

- P. nattereri*—KU 92845, D; WCAB 39209, M.
P. signiferus—FM 134305, M; KU 93033, C.
Pleurodema brachyops—KU 96159, D; 104318, C.
P. thaul—FM 44205, M.
P. tucumana—LACM 73426, M.
Pseudopaludicola falcipes—FM 9748, M; KU 93056, C.

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The following persons and institutions loaned material for myological and osteological examination: Antenor Leitao de Carvalho, Museu Nacional, Rio de Janeiro; William E. Duellman and J. T. Collins, Museum of Natural History, University of Kansas; Hymen Marx, Field Museum of Natural History; Paulo E. Vanzolini, Museo de Zoologia da Universidade de São Paulo; John W. Wright, Natural History Museum of Los Angeles County.

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Joseph Felsenstein, University of Washington, patiently ran the computer program on the computer facilities at the University of Washington.

Without the kind assistance of all these people or without the support of a grant from the National Science Foundation, GB 27280, administered by Pacific Lutheran University, this report would not have been possible.

ANALYSIS OF CHARACTERS Adult External Morphology

Character 1—Pupil shape. Two states are recognized: 0) pupil horizontal, 1) pupil vertical.

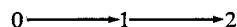
Lynch (1971) recorded state 1 as being rare among leptodactylids. He records 4 out of 11 living genera of the outgroup as having vertical pupils. State I is polymorphic within the tribes and subfamilies of the outgroup and therefore does not allow criterion II to be used. If the neotropical portion of the family Leptodactylidae is taken as the outgroup, then criterion II can be invoked in assuming that State I is the derived state. The direction of change of character states is:

0 → 1

Character 2—Tympanum visibility. Three states are recognized: 0) tympanum distinct externally, 1) tympanum somewhat covered by skin, but still barely visible externally, 2) tympanum completely hidden and not visible externally.

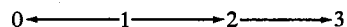
All three states are relatively common in the outgroup (Lynch, 1971). The covering of the tympanum is part of the trend leading to earlessness, a

well documented morphological specialization among frogs. State 2 is assumed to be derived on the basis of criterion III. The direction of change of character states is:



Character 3—External vocal sacs. The states are determined from preserved males. Four states are recognized: 0) a large, expanded, single vocal sac, 1) no vocal sac visible externally, although present internally, 2) indications of lateral vocal folds, 3) paired lateral vocal sacs well developed.

Within the genus *Leptodactylus*, there has been a trend towards terrestriality. One character correlating with the trend is the vocal sac. In the more aquatic members, state 1 is the rule. In the more terrestrial members, states 2 and 3 are common. Based on criterion III, state 3 is assumed to be advanced over state 1 with state 2 being intermediate. The outgroup does not provide any clear cut clue as both states 0 and 1 are represented. Morphologically it is simplest to assume that state 0 is an independent advancement over state 1. The directions of change of character states are:



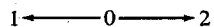
Character 4—Male thumb. Three states are recognized: 0) male thumb lacking any modifications, 1) thumb with brown or black nuptial adspersities, resembling sandpaper, 2) thumb with one or two horny spines.

State 1 is the commonest state in the outgroup, uniform in the Ceratophryinae and Alsodini (Lynch, 1971) and assumed to be the primitive state based on criterion II. State 2 is a rare state in leptodactylid frogs and is assumed to be derived on the basis of criterion II. State 0 has seemingly been derived via two routes. In the case of members of the *fuscus* species group of *Leptodactylus*, state 0 is derived from state 2 (Heyer, 1969b). This route is indicated as state 3. There is no evidence that state 0, as found in other leptodactylines, has gone through state 1. Morphologically the simplest assumption is that these other cases of state 0, here indicated 0, have been derived directly from state 1. The directions of change of character states are:



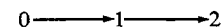
Character 5—Glands. The extent, type, and shape of body glands varies considerably in the Leptodactylinae. Only three extreme states are recognized: 0) no well defined glands of states 1 and 2, 1) glandular dorsolateral folds, 2) distinct inguinal gland.

State 0 is the commonest state in the outgroup with only *Hylorina* having state 1 (Lynch, 1971) and is assumed to be the primitive state on the basis of criterion II. Morphologically it is easiest to assume that states 1 and 2 are independent derivations of state 0. The directions of change of character states are:



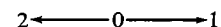
Character 6—Toe disks. Three states are recognized: 0) tips of the toes not expanded into disks, 1) tips of the toes expanded into distinct disks but the dorsal surfaces of the disks not divided, 2) dorsal surfaces of the disked toes divided longitudinally. Only *Leptodactylus bokermanni* and *hylaedactylus* show intraspecific variation in some specimens having state 0, others state 1. For the present purposes, both species are coded as having state 1.

State 0 is common in the outgroup, only some Alsodini have state 1 (Lynch, 1971) and is assumed to be the primitive state on the basis of criterion II. In the present analysis, state 2 is rarer than state 1, and as state 2 is the rarest state in leptodactylids as a group (Lynch, 1971), it is assumed to be the most derived state. The direction of change of character states is:



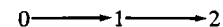
Character 7—Tarsus. Three states are recognized: 0) tarsus with at least some indication of a fold extending from the inner metatarsal tubercle to from one half to the full length of the tarsus, 1) tarsal fold short, ending in a tubercle about mid-tarsus, 2) tarsus smooth, lacking tubercles or folds. In some species categorized as exhibiting state 1, the fold is extremely weakly developed and in *Barycholos pulcher* the fold is absent, leaving only the tubercle.

State 0 is the common state for all frogs, including the outgroup, and is assumed to be the primitive state on the basis of criterion I. The directions of change of character states are:



Character 8—Metatarsal tubercles. Three states are recognized: 0) metatarsal tubercles not pronounced or cornified, 1) tubercles pronounced and pointed, 2) tubercles enlarged and heavily cornified.

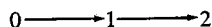
State 0 is the commonest state in the outgroup, although state 2 is reasonably represented (Lynch, 1971). The spadelike tubercles of state 2 are adaptations for burrowing. The members of the outgroup are either fossorial or aquatic frogs. It is impossible to tell *a priori* whether the leptodactylines had a more fossorial or aquatic ancestor. Therefore, it is difficult to determine which state is primitive. The spade of the outgroup is a single spade, the modified inner tubercle, while state 2 of the leptodactylines is composed of double spades, both tubercles being enlarged. The evidence suggests that state 0 is primitive. The direction of change of character states is:



Character 9—Toe webbing. Three states are recognized: 0) toes webbed, at least basally, 1) toes with lateral fringes but not distinctly webbed, 2) toes without webs or fringes. I interpret state 2 narrowly, state 1 broadly.

State 0 is the most common in the outgroup; state 1 found only in some Odontophrynini and Alsodini, state 2 found only in some Alsodini (Lynch, 1971). There is a general trend in leptodactylids from aquatic to terrestrial

life histories which correlates with webbing for aquatic members, free toes in terrestrial species. State 0 is assumed to be primitive on the basis of criteria II and III. The direction of change of character states is:



Egg and Larval External Morphology

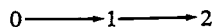
Character 10—Larval vent. Two states are recognized: 0) vent median, 1) vent dextral.

State 0 is most common in the outgroup, state 1 is confined to the *Telmatobiini* (Lynch, 1971) and is assumed to be the primitive state on the basis of criterion II. The direction of change of character states is:



Character 11—Larval denticle rows. Three states are recognized: 0) larval denticle rows $\frac{2}{3}$, well developed, 1) denticle rows $\frac{2}{3}$, weakly developed, 2) denticle rows absent.

State 0 is most common in the outgroup, the exceptions being the *Ceratophryinae* and *Caudiverbera* (Lynch, 1971) and assumed to be the primitive state based on criterion II. State 2 appears to be a morphological derivative of state 1. The direction of change of character states is:



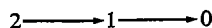
Character 12—Egg pigment. Two states are recognized: 0) eggs with melanin, 1) eggs lacking melanin.

State 0 eggs are typically aquatic pond eggs, state 1 eggs are usually hidden in some fashion. State 1 is assumed the derived state on the basis of criterion III. The direction of change of character states is:



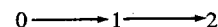
Character 13—Clutch size. Three states are recognized: 0) small clutch size (<50 eggs/clutch), 1) moderate clutch size (50-1000 eggs/clutch), 2) large clutch size (>1000 eggs/clutch). There is an inverse relationship of clutch size and size of individual egg.

Large clutches are associated with more aquatic breeding habits, small clutches are associated with more terrestrial life histories. Large clutches are assumed to be primitive on the basis of criterion III. The direction of change of character states is:



Character 14—Egg deposition. Three states are recognized: 0) eggs deposited in a gelatinous mass on top of the water, 1) eggs deposited in a foam nest on top of the water, 2) eggs deposited in a foam nest in burrows away from the water.

State 0 is found in the outgroup (Lynch, 1971) and assumed to be the primitive state on the basis of criterion I. State 2 is an ecological specialization leading towards terrestriality and assumed to be the most derived state on the basis of criterion III. The direction of change of character states is:



Adult Musculature

Three muscle complexes were examined to attempt to sample different functional units: 1) jaw musculature. The depressor mandibulae and adductor mandibulae open and close the jaws, 2) hyoid musculature. Although both the jaw muscles and hyoid muscles are involved in feeding, there may be different strategies involved. For example, the jaws may act as the sole means of food capture or the hyoid and tongue may act as the means of capturing food. 3) hindlimb musculature associated with the femur. These muscles control locomotion in part.

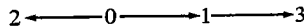
Jaw Muscles

Starrett's (1968) terminology is followed. No variation was found in the adductor muscles studied: all specimens lacked the adductor mandibulae externus superficialis, all specimens had the adductor mandibulae posterior subexternus.

Character 15—Depressor mandibulae. Four states are recognized. State 0 consists of three sites of origin: on the dorsal fascia, on the squamosal bone or the crista parotica, and on the annulus tympanicus. There may be distinct slips (DFSQAT in Starrett's (1968) terminology) or fibers to the annulus tympanicus may not be clearly demarcated from the fibers to the squamosal or the crista parotica. In all cases, the extent of origin from the three areas is roughly equivalent. State 1 consists of two equal sites of origin, the dorsal fascia and the squamosal bone or the crista parotica. There is intraspecific variation in whether or not a few fibers originate from the annulus tympanicus. State 2 is similar to state 1, except the two slips are not in the same plane. The slip from the squamosal region originates deeper than the slip originating from the dorsal fascia (DFSQd in Starrett's (1968) terminology). State 3 is characterized by the mass of the muscle originating from the dorsal fascia with a smaller slip originating from the squamosal region (DFSq in Starrett's (1968) terminology). There is intraspecific variation in whether or not a few fibers originate from the annulus tympanicus.

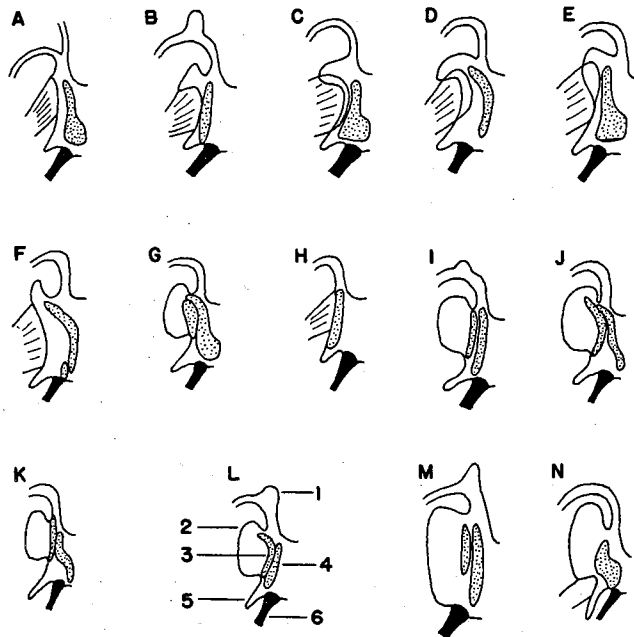
Starrett (1968) thought that a double origin of the depressor mandibulae from the dorsal fascia and squamosal region was primitive to a single origin from the squamosal region. Her reasoning was that the double origin is widespread in frogs, reptiles, and other amphibians. In the frogs Starrett examined representative of the *Ceratophryinae* and *Odontophryni*, all had character

state 0. This state is assumed to be primitive using criterion I. A shift to more or less equal origin from the dorsal fascia and squamosal region is assumed to be derived; there are two patterns, states 1 and 2 which are assumed to be independently derived. A major origin from the dorsal fascia with a small slip originating from the squamosal region, state 3, is assumed to be secondarily derived from state 1. The directions of change of states are summarized as:



Hyoid Musculature

Trewavas (1933) examined the hyolaryngeal apparatus in a broad spectrum of frogs. Her terminology is followed here. Lynch (1971) used certain characteristics from the hyoid complex in his classification. The following muscles were examined in this study: geniohyoideus medialis, geniohyoideus lateralis, anterior petrohyoideus, sternohyoideus, omohyoideus, and hyoglossus. There is considerable variation in the hyoid apparatus and associated musculature (Fig. 1). The only muscle examined which did not vary was the hyoglossus.



Before describing the variation found, a comment on the function of the apparatus is warranted. DeJongh and Gans (1969) and Martin and Gans (1972) have shown that with the exception of the hyoglossus, all the muscles examined function in both respiration and calling. It is reasonable to assume that the hyoglossus is involved in tongue movement associated with feeding. There appear to be two ends of a continuum involving hyoid shape and insertion of the anterior petrohyoideus and sternohyoideus muscles in particular. Based on the little comparative work that has been done, one can not determine *a priori* which pattern might lead to a more efficient adaptive type when any one of the three functions in which the apparatus is involved is being most strongly selected for.

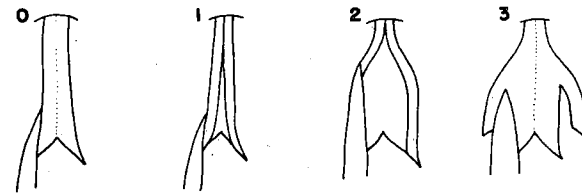


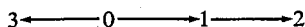
FIGURE 2. Character states of geniohyoideus medialis muscle. Sternohyoideus muscle present on left of diagrams, removed on right of diagrams. See text.

Character 16—Geniohyoideus medialis. Four states are recognized (Fig. 2). In state 0, the muscle is continuous medially, dividing posteriorly where the posteromedial processes of the hyoid articulate with the body of the hyoid. The hyoglossus muscle is completely covered ventrally by the geniohyoideus medialis. In state 1, the muscle is divided medially, exposing part of the hyoglossus. The sternohyoideus covers little of the geniohyoideus medialis. In state 2, the muscle is divided ventrally. The posterior half of the geniohyoideus muscle is covered by the sternohyoideus. An external slip is present in state 3

FIGURE 1. Diagrammatic representations of hyoid apparatus and attachments of anterior petrohyoideus and sternohyoideus muscles from ventral view for selected leptodactylines. Insertion of anterior petrohyoideus on edge of hyoid plate only indicated by muscle outline (A), insertion on edge and ventral body of hyoid indicated by muscle outline extending onto hyoid (C), insertion on ventral body of hyoid only indicated by outline of insertion area (L, 3). 1—Anterior process of hyale, 2—alary process, 3—area of insertion of anterior petrohyoideus muscle, 4—area of insertion of sternohyoideus muscle, 5—posterolateral process, 6—posteromedial process. A—*Barycholos pulcher*, B—*Edalorhina perezii*, C—*Leptodactylus bokermanni*, D—*Leptodactylus hylaedactylus*, E—*Leptodactylus andreae*, F—*Leptodactylus marmoratus*, G—*Leptodactylus martinezi*, H—*Limnomedusa macroglossa*, I—*Physalaemus biligonigerus*, J—*Physalaemus fuscomaculatus*, K—*Physalaemus signiferus*, L—*Physalaemus albonotatus*, M—*Pseudopaludicola falcipes*, N—*Hydrotaetare schmidti*.

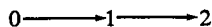
which is lacking in the other three states. The additional slip attaches to the posteromedial process of the hyoid apparatus. The internal slip is the same as the entire muscle of state 0. Character state 2 is confined to those species having broad winglike alary processes of the hyoid.

As Lynch (1971) points out, winglike processes of the alary are rare in leptodactylids and represent a derived condition. As only taxa with winglike alary processes have state 2, I used criterion IV in determining state 2 as a derived state. State 1 is intermediate between states 0 and 2. State 3 is unique as far as I know to *Limnomedusa macroglossa* and is assumed to be derived on the basis of criterion I. The directions of change in character states are:



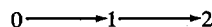
Character 17—Geniohyoideus lateralis. Three states are recognized. In state 0, the geniohyoideus lateralis originates on the anterior lower jaw and separates into two slips posteriorly. The internal slip inserts on the posteromedial process of the hyoid, the external slip inserts on the posterolateral process of the hyoid or on the body of the hyoid in the region where the posterolateral process would be, were it present. In some specimens, there appeared to be an attachment of the muscle to the hyale, but may have been due to method of preservation. State 1 is similar to state 0 except that there is a definite attachment of the muscle to the hyale, which is indicated by a lateral flaring of the muscle to attach to the hyale anterolaterally. State 2 is similar to state 1 and differs in that a distinct muscle slip attaches to the hyale anterolaterally.

State 2 occurs rarely among frogs in general (Trewavas, 1933) and in the study sample and is assumed to be derived on the basis of criterion II. State 1 appears to be an intermediate condition. The direction of change in character states is:



Character 18—Anterior petrohyoideus. The patterns of insertion of this muscle are quite variable (Fig. 1). Three states appear to encompass the variation noted. In state 0, the anterior petrohyoideus inserts entirely on the edge of the hyoid apparatus (Fig. 1, A, B, F, H, N). In state 1, the muscle inserts in part on the edge of the hyoid and on the ventral body of the hyoid in part (Fig. 1, C, D, E). In state 2, the muscle inserts entirely on the ventral surface of the hyoid body (Fig. 1, G, I, J, K, L, M).

Lynch (1971) indicated that the outgroup has state 0 and that state 2 is a rare state in leptodactylid frogs. State 2 is assumed to be advanced on the basis of criterion I. State 1 appears to be intermediate between states 0 and 2. The direction of change in character states is:



Character 19—Sternohyoideus origin. All specimens have a lateral or external slip that is continuous with the rectus abdominis muscle. The varia-

tion occurs where the sternohyoideus originates from the posterior sternal apparatus. Three states are recognized. In state 0, a single medial slip originates from the meso- and xiphisterna. The actual attachment may vary from the condition figured (Fig. 3, 0) to attachment on the anterior portion of the mesosternum (only) and the xiphisternum, but in all cases a single muscle slip is involved. In state 1, a distinct slip originates from the anterior portion of the mesosternum, another slip originates from the posterior meso- and/or the xiphisternum (Fig. 3, 1). In state 2, a single medial slip originates from the anterior mesosternum only (Fig. 3, 2).

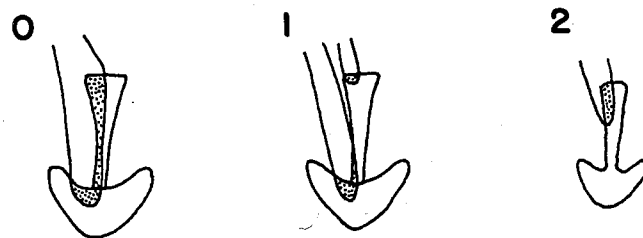
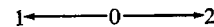


FIGURE 3. Character states of sternohyoideus origin. Stippling indicates area of attachment. See text.

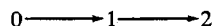
State 2 is unique in the sample and is assumed to be derived on the basis of criterion I. The situation for the outgroup is not known. All members of the outgroup have a cartilaginous plate for the meso- and xiphisternum and probably have a single medial slip originating from the sternal plate. As Lynch (1971) suggests, the sternal conditions of the Leptodactylinae are derived for the family; state 1 of the sternohyoid origin is only found with the derived sternal apparatus, hence state 1 is assumed derived on the basis of criterion IV. The simplest explanation for direction of character states is that the two derived states are independent derivations of state 0:



Character 20—Sternohyoideus insertion. The variation in patterns of insertion on the hyoid body is great (Fig. 1). Three states appear to encompass the variation. In state 0, the sternohyoideus inserts in a narrow band near the lateral edges of the hyoid (Fig. 1, B, H, I, L, M). In state 1, the muscle has some fibers inserting near the lateral edges of the hyoid and some fibers also attaching near the midline of the hyoid posteriorly (Fig. 1, C, E, G). In state 2, the sternohyoideus inserts in a narrow band with the fibers attached near the midline posteriorly (Fig. 1, D, F, J, K).

Lynch (1971) indicates the pattern in the outgroup corresponds to state

0 and that state 2 is rare in leptodactylid frogs. State 2 is assumed to be derived over state 0 based on criterion I. State 1 appears to be an intermediate condition between states 0 and 2. The direction of change in character states is:



Character 21—Omohyoideus. Four states are recognized. In state 0 the muscle is lacking. In state 1, the muscle inserts partly on the hyoid plate and partly on the fascia between the posterolateral and posteromedial processes of the hyoid (Fig. 4, 1). In state 2, the muscle inserts entirely on the body of the hyoid plate ventrally (Fig. 4, 2). In state 3, the muscle inserts on the edge of the hyoid plate anterolaterad to the posteromedial process of the hyoid (Fig. 4, 3). A certain amount of intraspecific variation was noted. In the individual of *Edalorhina perezii* I examined, the omohyoideus was absent (state 0), while Trewavas (1933) indicated the specimen she examined had state 1 of the omohyoideus. In two individual *L. bokermanni* I examined, one had state 0, the other state 2, but the muscle was composed of few fibers.

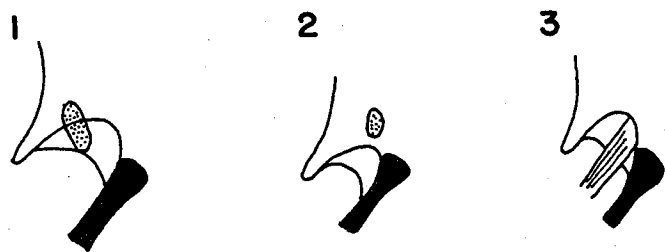
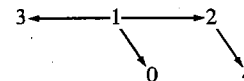


FIGURE 4. Character states of omohyoideus insertion. Insertion indicated by stippling (1, 2) or muscle outline (3). See text.

No information is available from the outgroup. State 2 is almost always associated with derived states of the anterior petrohyoideus and sternohyoideus muscles and is assumed to be derived over state 1 on the basis of criterion IV. The loss of the muscle has occurred from both states 1 and 2 and is assumed to be a derived state over the presence of the muscle. For directional purposes, where intraspecific variation occurs, the state 0 is treated as a derived state of the state the muscle shows when present. For *P. signiferus*, the only state noted was state 0, but as all other *Physalaemus* examined showed state 2, *P. signiferus* state 0 is assumed to be a derived state of state 2 and is indicated as state 4. State 3 is unique in this study to *Pleurodema thaul* and assumed to be a derived

state of state 1 on the basis of criterion I. The directions of change of character states are:



Thigh Muscles

In general, the methods of Limeses (1964) were followed so that the present observations would be consistent with hers. Intraspecific variation was handled in the following three ways: 1) More than one individual of a species was examined during the present analysis, 2) A series of 10 *Leptodactylus ocellatus* were examined five years ago as a part of another study (Heyer, 1968b). This species is not one included in the study, but does serve as one source of character variability within a species, 3) Observations were made on different individual specimens of the same species five years ago and for the present study. In some cases, differences of judgment are involved rather than an actual difference in character state. These differences were included as intraspecific variation as the differences would probably occur if other workers categorized the variation. The following complexes and muscles were examined: Complex of distal tendons, iliacus externus, iliacus internus, tensor fasciae latae, gracilis minor, semitendinosus, sartorius, accessory head of the adductor magnus, adductor longus, gluteus. I was unable to categorize the minimal variation encountered in the development of the iliacus internus muscle. Limeses (1964) provides data on representatives of Lynch's subfamily Ceratophryinae and tribe Odontophrynini. This information is used for comparative purposes as the outgroup to the Leptodactylinae.

Character 22—Complex of distal thigh muscle tendons. Limeses (1964) recognized three states which are followed here. In state 3, the tendon of the semitendinosus attaches on the knee below the insertion of the sartorius and the tendons of the gracilis minor and major pass dorsad to the tendon of the semitendinosus (Limeses, 1964, case A, Fig. 1). In state 0, the tendon of the semitendinosus is confluent with the posterior portion of the sartorius insertion on the knee and the tendons of the gracilis minor and major pass dorsad to the tendon of the semitendinosus (Limeses, 1964, case B, Fig. 1). In state 1, the tendon of the semitendinosus pierces the tendon of the gracilis minor and major (Limeses, 1964, case C, Fig. 1). Recent careful examination indicates that my previous interpretation of the distal tendon complex in *L. marmoratus* is wrong (Heyer, 1968b, 1969a). Previously I stated the tendons involved were fused into a single plane. Examination of muscle stained specimens indicates that all members of the *marmoratus* group have state 0. Intraspecific variation exists with states 0 and 1 occurring in a single species. These cases are recognized as state 2.

Limeses (1964) states that case 3 is primitive as it is found in bufonids,

the presumed ancestral stock of the Ceratophryniids. She also demonstrated that state 3 is by far the commonest state among the Ceratophryinae and Odontophrynini she examined. State 3 is assumed to be primitive on the basis of criterion II. State 0 is the commonest state in this study sample; state 1 is the rarest, with state 2 intermediate between states 0 and 1. State 1 is assumed to be the most derived on the basis of criterion II. The direction of change of character states is:

3 → 0 → 2 → 1

Character 23—*Iliacus externus*. Three states are recognized. In state 0, the *iliacus externus* muscle extends no more than half the distance anteriorly on the iliac bone from where the leg muscles join the iliac to the anterior extremity of the iliac (medium and short states of Limeses, 1964, Fig. 2). In state 1, the *iliacus externus* extends from over one half to not more than three quarters the distance of the iliac (Long A state of Limeses, 1964, Fig. 2). In state 2, the *iliacus externus* extends from three quarters to the full length of the iliac (Long B state of Limeses, 1964, Fig. 2). The states are categorized so that all intraspecific variation observed occurs within a single state.

State 0 is by far the commonest state of Ceratophryinae and Odontophrynini, the exception occurring in some *Ceratophrys* (Limeses, 1964) and thus assumed to be primitive on the basis of criterion II. The direction of change of character states is as follows:

0 → 1 → 2

Character 24—*Tensor Fasciae Latae*. Three states are recognized. In state 0, the *tensor fasciae latae* inserts posterior to the *iliacus externus* muscle on the iliac bone (States C-1 and C-2 of Limeses, 1964, Fig. 4). There is intraspecific variation on the relative sizes of the origin and insertion portions of the muscle. In state 1, the *tensor fasciae latae* inserts at the same level on the iliac bone as the *iliacus externus* muscle (State D of Limeses, 1964, Fig. 4). In state 2, the *tensor fasciae latae* inserts anterior to the *iliacus externus* muscle on the iliac bone.

State 0 is the commonest state found in the ceratophrynes and odontophrynins, the exception occurring in some *Lepidobatrachus* and is assumed to be primitive on the basis of criterion II. State 1 is morphologically intermediate between states 0 and 2. The direction of change of character states is:

0 → 1 → 2

Character 25—*Gracilis Minor*. The variation observed was very difficult to categorize. The muscle varies in its breadth and thickness. It is particularly difficult to determine the state of a very broad but thin muscle. Only two extreme states are recognized. In state 0, the muscle is broad, covering the *gracilis major* entirely. The muscle may also cover part of the *adductor magnus* and may be either relatively thick or thin (voluminous and well-developed states of Limeses, 1964). In state 1, the muscle covers only part of the *gracilis*

major and is composed of a few weak fibers (rudimentary state of Limeses, 1964).

State 1 is rare in the present sample as well as the outgroup, being found only in some *Ceratophrys* (Limeses, 1964) and is assumed to be derived on the basis of criterion II. The direction of change of character states is:

0 → 1

Character 26—*Semitendinosus*. Four states are recognized. In state 0, the interior (with respect to the femur) and exterior portions of the *semitendinosus* unite in a common tendon distally. There is no distinct tendon of the exterior portion. The two portions may be equal in development, or the exterior portion is larger than the interior (Fig. 5, 0, also Limeses, 1964, Fig. 5, A, B-1, B-2). The reason for combining all of Limeses' states is that six species demonstrate intraspecific variation between her states A, B-1, one species has states B-1 and B-2, and one species has states A, B-1, and B-2). In state 1, the exterior portion has a distinct distal tendon which attaches to the bulk of the interior portion. The exterior portion is well developed, but smaller than the interior portion (Fig. 5, 1). State 2 is similar to state 1 except the exterior portion is much reduced (Fig. 5, 2). In state 3, the exterior portion has a distinct tendon which attaches to the bulk of the interior portion. The two portions are about equally developed, but they are displaced so the bulk of the exterior portion is proximal, the bulk of the interior portion is distal (Fig. 5, 3).

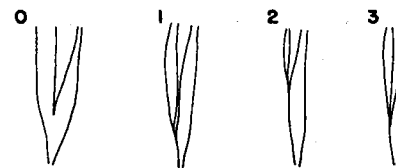


FIGURE 5. Character states of *semitendinosus* muscle. See text.

The outgroup uniformly has state 0 (Limeses, 1964) and is assumed to be the primitive state on the basis of criterion I. There appear to be two morphological specializations of state 0; one leading to state 3, the other leading to state 2 with state 1 as an intermediate. The directions of change of character states are:

3 ← 0 → 1 → 2

Character 27—*Sartorius*. Three states are recognized. In state 0, the *sartorius* is moderately developed (Narrow type of Limeses, 1964). In state 1, the *sartorius* is a broad muscle, completely covering the *adductor longus* and

almost all of the adductor magnus (wide type of Limeses, 1964, Fig. 6 B). In state 2, the sartorius is a very narrow muscle, exposing much of the adductor longus and adductor magnus muscles (very narrow type of Limeses, Fig. 6 A).

As Limeses (1964) points out, state 0 is the commonest condition found in any grouping of frogs and is assumed to be primitive on the basis of criterion II. The directions of change of character states are:

2 ← 0 → 1

Character 28—Accessory head of the adductor magnus. Three states are recognized. In state 0, there is no distinct tendon of the accessory head of the adductor magnus. Either the fibers of the accessory head join the tendon of the interior portion of the semitendinosus or the fibers of the accessory head of the adductor magnus and interior portion of the semitendinosus join together to form a common tendon (Fig. 7, A-1, A-2, B of Limeses, 1964). The reason for combining all her types into a single state is that one species has types A-1 and A-2, three species have states A-1 and B, and two species have states A-2 and B). In state 1, the accessory head of the adductor magnus ends proximally in a tendon which attaches to the muscle fibers of the interior portion of the semitendinosus. In state 2, the accessory head of the adductor magnus is absent.

The commonest condition of the outgroup is state 0, state 2 is found in *Lepidobatrachus* and one *Ceratophrys* (Limeses, 1964) and is assumed to be the primitive state on the basis of criterion II. The directions of change of character states are:

2 ← 0 → 1

Character 29—Adductor longus. Three states are recognized. In state 0 the adductor longus is well developed and inserts either entirely on the knee, on the knee and on the adductor magnus muscle, or on the adductor magnus muscle only but near the knee. Except in specimens which have state 1 of the sartorius muscle, the adductor longus is visible without dissection. In state 1, the adductor longus is reduced, the insertion is entirely on the adductor magnus muscle, not next to the knee region and always covered by the sartorius muscle completely. In state 2, the adductor longus is absent.

Based on Limeses' Figures (1964, Plates I, II, III), the state of the outgroup is 1 and is thus assumed to be the primitive state based on criterion I. The directions of change of character states are:

0 ← 1 → 2

Character 30—Gluteus. Two states are recognized. In state 0, the gluteus is well developed, but smaller than the cruralis. The muscle inserts both on the cruralis muscle and on the knee. In state 1, the gluteus is smaller than in state 0 and inserts entirely on the cruralis muscle.

Based on Limeses' figures (1964, Plates I, II, III) the state of the out-

group is for the gluteus to be equal to or greater in bulk than the cruralis and the insertion is entirely on the knee. Assuming this state is primitive on the basis of criterion I, state 1 is morphologically the most advanced with state 0 being intermediate. The direction of change of character states is:

0 → 1

Adult Skeleton

Character 31—Quadratojugal. Two states are recognized: 0) quadratojugal well developed, contacting maxilla, 1) quadratojugal reduced or absent, not contacting maxilla.

State 0 is the common state of the outgroup, state 1 occurring in two genera of the Alsodini (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:

0 → 1

Character 32—Maxillary teeth. Two states are recognized: 0) maxillary teeth present, 1) maxillary teeth absent. Rudimentary maxillary teeth are categorized as state 0.

The commonest state in the outgroup is state 0, state 1 occurring in two genera of Telmatobiini (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:

0 → 1

Character 33—Nasals. Two states are recognized: 0) nasals fused or just separated from each other, 1) nasals widely separated.

State 0 is the commonest state in the outgroup, state 1 being found in the Alsodini (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:

0 → 1

Character 34—Frontoparietal fontanelle. Three states are recognized: 0) no frontoparietal fontanelle, 1) frontoparietal fontanelle present, small, 2) frontoparietal fontanelle present, extensive. State one includes species showing intraspecific variation with either a small fontanelle present or absent.

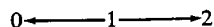
All three states are about equally represented in the outgroup (Lynch, 1971). States 1 and 2 are probably paedomorphic states of state 0 and thus are derived. The direction of change of character states is:

0 → 1 → 2

Character 35—Squamosal. Three states are recognized: 0) the zygomatic ramus is much longer than the otic ramus, the otic ramus is rudimentary, 1) the zygomatic ramus is just longer than, just shorter than, or equal to the otic

ramus, 2) the zygomatic ramus is much shorter than the otic ramus, the zygomatic ramus is rudimentary.

State 2 is rare in the outgroup, being found only in *Thoropa* (Lynch, 1971) and is assumed to be derived based on criterion II. States 0 and 1 are both well represented in the outgroup (Lynch, 1971). If state 2 is derived, then morphologically it is simplest to assume that state 0 is independently derived from state 1. The directions of change of character states are:



Character 36—Vomerine teeth. Two states are recognized: 0) vomerine teeth present, 1) vomerine teeth absent. Rudimentary vomerine teeth are included in state 0.

State 0 is the commonest in the outgroup, state 1 found only in *Batrachophrynus* (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:



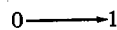
Character 37—Median contact of vomers. Two states are recognized: 0) vomers not in contact medially, 1) vomers in broad median contact.

State 0 is the commonest state in the outgroup (Lynch, 1971) and is assumed to be primitive on the basis of criterion II. The direction of change of character states is:



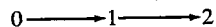
Character 38—Anterior articulation of vomer. Two states are recognized: 0) the vomer does not articulate with either the premaxilla or maxilla, 1) the vomer articulates with either the premaxilla or maxilla.

Both states are reasonably represented in the outgroup (Lynch, 1971). State 1 strengthens the snout region and correlates with a fossorial habitat. State 1 is assumed derived on the basis of criterion III. The direction of change of character states is:



Character 39—Relationship of sphenethmoid with the optic foramen. Three states are recognized: 0) the posterior extent of the sphenethmoid is widely separated from the optic foramen, 1) the posterior extent of the sphenethmoid closely approximates the optic foramen, 2) the posterior extent of the sphenethmoid borders the optic foramen.

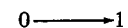
State 2 gives greater strength to the central skull region and correlates with a fossorial habitat within *Leptodactylus* (Heyer, 1969b). State 2 is assumed derived on the basis of criterion III. The direction of change of character states is:



Character 40—Anterior extent of sphenethmoid. Two states are recog-

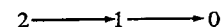
nized: 0) sphenethmoid extending anteriorly no more than the middle of the vomerine bones, 1) sphenethmoid extending anteriorly beyond the middle of the vomerine bones. State 1 includes calcification of the ethmoid region which is fused with the sphenethmoid bone.

The state 1 condition gives a stronger snout. This is correlated with a fossorial habitat within the genus *Leptodactylus* (Heyer, 1969b) and is assumed to be the derived state based on criterion III. The direction of change of character states is:



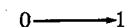
Character 41—Pterygoid-parasphenoid overlap. Three states are recognized: 0) no pterygoid-parasphenoid overlap in an anterior-posterior plane, 1) the pterygoid overlaps the parasphenoid in an anterior-posterior plane, but the elements are not in contact, 2) the pterygoid and parasphenoid overlap and are in contact. I find the condition in *Pleurodema* and *Pseudopaludicola* to be state 0, which agrees with Lynch on pages 173 and 185 but disagrees with Lynch on page 51.

State 2 is the common condition in the outgroup, state 0 found in some *Telmatobiini* and one genus of *Alsodini* (Lynch, 1971) and is considered the primitive condition based on criterion II. Morphologically, state 1 is intermediate between states 0 and 2. The direction of change of character is:



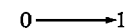
Character 42—Occipital condyles. Two states are recognized: 0) occipital condyles closely juxtaposed, 1) occipital condyles moderately or widely separated.

State 0 is the common state within the outgroup, state 1 found only in two genera of *Alsodini* (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:



Character 43—Anterior processes of the hyale. Two states are recognized: 0) anterior processes of the hyale are present, 1) there are no anterior processes of the hyale. Figure 2F in Heyer (1969a) is incorrect as the process of the hyale indicated is actually a nerve. I disagree with Lynch (1971:35) who stated that anterior processes of the hyale are present in *Lithodytes*.

Anterior processes of the hyale represent parts of the hyoid skeletal arches that are lost in frogs lacking the processes. State 0 is thus assumed to be the primitive state. The direction of change of character states is:



Character 44—Alary process of hyoid. The variation in configuration of the alary process is considerable (Fig. 1). Three states are arbitrarily defined. In state 0 the process is extremely reduced or absent (Fig. 1, A, H). In state 1, the alary process is somewhat narrow and often stalked (Fig. 1, B, C, D, E,

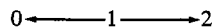
TABLE 2

Character states of 29 species of frogs. No information is indicated by a 9

	CHARACTERS AND STATES																																																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50					
<i>Barycholos pulcher</i>	0	0	0	0	0	1	1	0	2	9	9	1	0	9	0	2	0	0	1	1	2	0	2	0	0	1	1	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	0	0	0	1	2	0	1	2				
<i>Edalorhina perezii</i>	0	0	1	1	2	0	1	0	1	0	0	9	9	9	0	1	1	0	1	0	0	0	1	0	0	0	1	0	0	2	2	1	1	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1		
<i>Hydrolaetare schmidti</i>	1	0	1	0	0	0	0	0	0	9	9	9	9	9	3	0	0	0	1	1	2	0	2	0	0	1	1	2	0	0	0	0	1	0	0	1	0	0	1	1	1	1	2	0	1	1	1	1	0	1	1	0	2	0	
<i>Leptodactylus bokermanni</i>	0	0	2	0	0	1	0	0	2	0	1	1	0	2	3	0	0	1	0	1	4	0	2	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	2	0	1	1	1	1	0	1	1	0	1	0	2	0			
<i>L. bolivianus</i>	0	0	1	2	1	0	0	0	1	0	0	0	2	1	3	0	0	0	1	0	1	2	2	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0	2	0					
<i>L. bufonius</i>	0	0	3	3	0	0	0	0	2	0	0	1	1	2	3	0	2	0	0	0	1	0	2	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	2	1	1	1	1	1	0	1	0	0	2	0			
<i>L. chaquensis</i>	0	0	2	2	1	0	0	0	1	0	0	0	2	1	3	0	0	0	0	0	1	2	2	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	2	1	1	1	0	1	0	0	2	0				
<i>L. discodactylus</i>	0	0	1	3	0	2	0	0	1	9	9	1	2	9	3	0	0	0	1	0	1	0	2	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	1	2	0	2	0				
<i>L. fuscus</i>	0	0	3	3	1	0	0	0	2	0	0	1	1	2	3	0	1	0	1	0	1	0	2	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	2	1	2	1	1	1	0	1	0	0	2	0					
<i>L. hylaedactylus</i>	0	0	2	0	0	1	0	0	2	0	2	1	0	2	3	2	1	1	0	2	2	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	0	1	0	0	1	1	1	1	0	1	1	0	2	0				
<i>L. latinasus</i>	0	0	2	3	0	0	0	0	2	0	0	1	1	2	3	0	2	0	0	0	1	0	2	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	2	1	1	1	1	1	0	1	0	0	2	0			
<i>L. andreae</i>	0	0	2	0	0	1	0	0	2	9	9	1	0	9	3	0	0	1	1	1	2	0	2	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	2	0				
<i>L. marmoratus</i>	0	0	2	0	0	1	0	0	2	9	9	1	0	2	3	2	2	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	1	1	1	1	1	0	1	2	0	2	0				
<i>L. martinezi</i>	0	0	1	0	0	0	0	0	2	9	9	1	0	9	3	2	0	2	0	1	2	0	2	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	0	0	2	0		
<i>L. melanotus</i>	0	0	1	2	0	0	0	0	1	0	0	0	2	1	3	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	1	1	1	1	0	1	0	0	2	0			
<i>L. mystaceus</i>	0	0	2	3	1	0	0	0	2	0	0	1	1	2	3	0	1	0	0	0	1	0	2	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	2	1	1	1	1	1	1	0	1	0	0	2	0		
<i>L. pentadactylus</i>	0	0	1	2	1	0	0	0	2	0	0	9	9	1	3	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	1	0	1	0	0	2	0			
<i>L. wagneri</i>	0	0	1	2	0	0	0	0	1	0	0	0	2	1	3	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	2			
<i>Limnomedusa macroglossa</i>	1	0	1	1	0	0	0	0	1	9	9	9	9	3	3	0	0	1	0	1	0	1	0	2	0	0	0	1	1	0	0	0	1	0	0	1	2	1	0	0	0	0	0	1	0	1	0	0	0	0	1	2			
<i>Lithodytes lineatus</i>	0	0	9	0	0	2	0	0	2	9	9	1	9	9	3	0	0	0	1	1	1	0	2	0	0	1	1	1	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	1	2	0	2	0			
<i>Physalaemus albonotatus</i>	0	1	0	1	0	0	1	1	1	1	0	1	9	1	1	1	0	2	1	0	2	0	1	0	2	0	0	1	0	1	3	0	1	0	1	0	2	1	0	0	0	0	0	0	0	1	0	2	0	0	0	1	2		
<i>P. biligonigerus</i>	0	2	0	1	0	0	1	2	1	1	0	1	9	1	3	0	0	2	1	0	2	0	1	0	2	0	0	0	1	2	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	1	0	2	0	0	0	1	2		
<i>P. fuscomaculatus</i>	0	2	0	1	2	0	1	2	1	1	0	1	2	1	1	0	0	2	0	2	2	0	2	0	2	2	0	0	1	0	0	0	0	0	0	1	0	2	1	0	1	0	0	0	0	1	1	2	0	0	0	1	2		
<i>P. nattereri</i>	0	2	0	1	2	0	1	2	2	1	0	1	9	1	1	2	0	2	0	2	2	0	2	0	2	2	0	0	1	0	1	0	1	0	1	1	0	2	1	0	0	0	0	0	1	1	2	0	0	0	1	1	2		
<i>P. signiferus</i>	0	1	0	1	2	0	0	1	2	1	0	1	9	1	1	2	0	2	0	2	4	0	1	0	0	3	0	1	2	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	1	1	2	0	0	0	0	1	0		
<i>Pleurodema thaul</i>	0	1	0	1	2	0	0	1	1	0	0	0	9	0	1	1	0	0	0	0	3	0	1	0	0	0	1	0	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	2	1			
<i>P. lucumana</i>	0	0	0	1	0	0	0	2	1	0	0	9	9	1	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	0	0	3	2	1	0	0	1	0	1	2	2	0	0	0	0	0	0	1	0	1	0	0	0	2	1
<i>Pseudopaludicola falcipes</i>	0	2	0	0	0	0	1	1	1	1	0	0	9	0	2	1	0	2	2	0	2	0	2	0	2	0	0	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	0	2	1	0	0	1	0	0			
<i>Paratelmatobius lutzi</i>	0	2	1	1	0	0	2	0	0	9	9	0	9	9	0	2	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	1	0	0	0	3	0		

F). In state 2, the alary process is broad and winglike (Fig. 1, G, I, J, K, L, M).

Two conditions are found in the outgroup, state 0 and state 1 (Lynch, 1971). In the evolutionary process, it is easier to lose a structure than gain it. State 1 is thus assumed to be primitive. States 0 and 2 are both rare in leptodactylid frogs (Lynch, 1971), and are assumed to be independently derived from state 1. The directions of change of character states are:



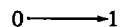
Character 45—Posterolateral process of hyoid. Two states are recognized: 0) the process is present, 1) it is absent.

State 1 is unique to *Pseudopaludicola falcipes* in this study and is very rare among leptodactylids (Lynch, 1971). State 1 is thus assumed to be derived on the basis of criterion I. The direction of change of character state is:



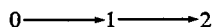
Character 46—Dorsal crest of ilium. Two states are recognized: 0) ilium without dorsal crest, or a dorsal crest weakly developed, 1) ilium with a well-developed dorsal crest.

State 0 is the common condition in the outgroup, the exception being *Caudiverbera* (Lynch, 1971) and is assumed to be primitive on the basis of criterion II. The direction of change of character states is:



Character 47—Terminal phalanges. Three states are recognized: 0) terminal phalanges knobbed, either single or slightly bifurcate, 1) terminal phalanges definitely T-shaped, but not expanded, 2) terminal phalanges T-shaped, expanded.

State 0 is the commonest condition in the outgroup, the exceptions are two genera of Alsodini (Lynch, 1971) and is assumed to be the primitive state based on criterion II. The direction of change of character states is:



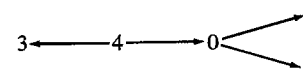
Character 48—Omosternum. Two states are recognized: 0) omosternum present, expanded, 1) omosternum absent, the entire anterior sternum a slender rod.

State 0 is the common condition in frogs and is assumed to be primitive on the basis of criterion I. The direction of change of character states is:



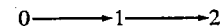
Character 49—Mesosternum. Four states are recognized: 0) mesosternum a broad bony element, single posteriorly (Lynch, 1971, Fig. 35A), 1) mesosternum a broad bony element, bifurcate posteriorly (Lynch, 1971, Fig. 35C), 2) mesosternum a bony style (Lynch, 1971, Fig. 35B), 3) mesosternum an amorphous broad bony element (Lynch, 1971, Fig. 35D).

The outgroup members all have large cartilagenous plates (Lynch, 1971), designated here as state 4. Lynch argued that state 0 is a morphological advancement over the cartilage plate and that states 1 and 2 are derived from state 0. State 3 appears to be an independent specialization of a cartilagenous plate, with deposition of bone salts to strengthen the mesosternal region. Apparently this same phenomenon has occurred in the genus *Eleutherodactylus* (Lynch, 1971, Fig. 34C). The directions of change of character states are:



Character 50—Xiphisternum. Three states are recognized: 0) xiphisternum entire, single, 1) xiphisternum single, bifurcate posteriorly, 2) xiphisternum double.

State 2 is rare in leptodactylid frogs and is assumed to be derived on the basis of criterion I. The direction of change of character states is:



The listing of character states by species is presented in Table 2.

RELATIONSHIPS

The combinatorial method of Sharrock and Felsenstein (personal communication) was used to organize the preceding data into clusters of species sharing derived character states. Phylogenies were then constructed with the clustering information. The combinatorial method utilizes the computer to scan the data, producing all subsets of the data which share character states. The method assumes that the direction of change of character states within a character is not reversible. Several options are available with the combinatorial method. I chose to ignore the primitive states and form the clusters of shared character states on the basis of derived character states only. The reasoning is that primitive states indicate that the organism has not changed from the ancestral condition and tell nothing of the evolutionary history of the organism. This is basically the Hennig approach which is currently the focus of much discussion; any recent copy of Systematic Zoology will introduce the interested reader to this literature.

A large number of phylogenies can be constructed from the combinatorial information. To build the phylogeny of Figure 6, two guidelines were followed. First, the data were examined for presence of sister-groups consisting of two taxa. The top branches of the tree were chosen as the pairs of species that share the most characters in a derived state. In this study, the two species sharing the most derived character states are *Physalaemus fuscomaculatus* and *P. nattereri*. The next largest assemblage of species containing both *P. fuscomaculatus* and *P. nattereri* is a group of three, adding *P. biligonigerus*,

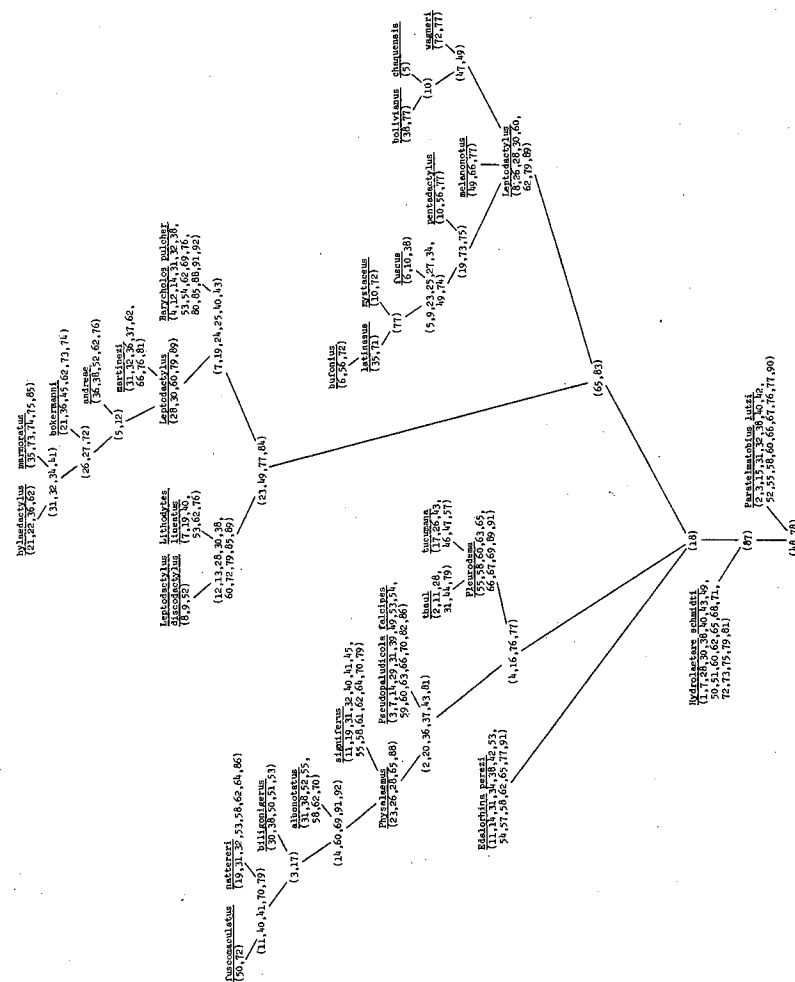


FIGURE 6. Proposed phylogenetic relationships among the 29 taxa of this study with *Barycholos* nearest the *marmoratus* group. Generic names are used as recognized by Lynch (1971) and are placed at character state cluster points so that all taxa above that point will be included within the genus. Also see text.

etc. A second sister group is *Leptodactylus hylaedactylus* and *L. marmoratus*, etc. In other words, the phylogeny was constructed so that the number of shared character states was maximized. Second, where certain alternative routes were possible, I chose the alternative consistent with one of the following three clusterings. The compositions of these clusterings were chosen to reduce the total number of alternative phylogenies. The three clusterings are: 1) *Pleurodema thaul* and *P. tucumana*; 2) the *marmoratus* group—*L. andreae*, *bokermanni*, *hylaedactylus*, *marmoratus*, *martinezi*; 3) the following *Leptodactylus*—*L. bufonius*, *fuscus*, *latinasus*, *mystaceus*.

The reasoning behind using this operational guideline is as follows. Suppose *Pleurodema thaul* shares 5 advanced character states with *P. tucumana* and species A. According to the first operational guideline, alternative phylogenies could be constructed, the first uniting *P. thaul* and *P. tucumana*, the second uniting *P. thaul* and sp. A. By using the second guideline, the choice is made for *P. thaul* and *P. tucumana*. This implies that the several characters shared by *P. thaul* and sp. A represent convergent adaptations. In essence, by recognizing the three clusters a known element is being added to the phylogeny construction process, but only where the first operational guideline allows it. The danger in using this guideline is, of course, that if the clusterings recognized in this guideline are not natural, then the resultant phylogeny will not be the best phylogeny possible. Extreme care must be used in recognizing the clusterings used in the second operational guideline. I feel that the available evidence is strong that these groupings are natural (i.e. that the included species are more closely related to one another than to species of other groups) and that they can be considered as operational knowns. Although it would be more satisfying intellectually to utilize only the first guideline and then discuss the relative merits of all possible phylogenies so constructed, the maintenance of these groupings would be the major criterion by which the phylogenies would be judged. By having these few known elements to aid in making choices when choices are possible by the first guideline, the number of phylogenies is reduced from a rather high number to a much more reasonable number. The time saved in actual phylogeny construction and in manuscript space explaining the relative merits of the phylogenies constructed using only guideline one are considerable.

The combinatorial method of data organization does not produce a phylogeny, but organizes the data so that phylogenies can be constructed from large amounts of data. The value of the method is that all combinations are available, so that the phylogeny builder knows exactly where each choice was made, what taxa are involved in the choices, and what character states are involved in the choices.

As indicated, the phylogeny of Figure 6 is not the only phylogeny possible; the possible changes are now examined.

First, using the guidelines as described above, there are minor branching sequence possibilities within four lines. In each case, all variations in branch-

ing sequence have a common ancestral condition. The five species of *Physalae-mus* can be reordered, but the five species, regardless of the branching sequence among them, always have a common ancestral condition which separates them from any other taxa. Similarly, *Leptodactylus bolivianus*, *chaquensis*, *melanonotus*, and *wagneri* could be reordered among themselves; *Leptodactylus bufonius*, *fuscus*, *latinasus*, and *mystaceus* could be reordered among themselves; and *L. andreae*, *bokermanni*, *hylaedactylus*, *marmoratus*, and *martinezi* could be reordered among themselves. All these changes are minor; what stands out is that the groupings are distinctive.

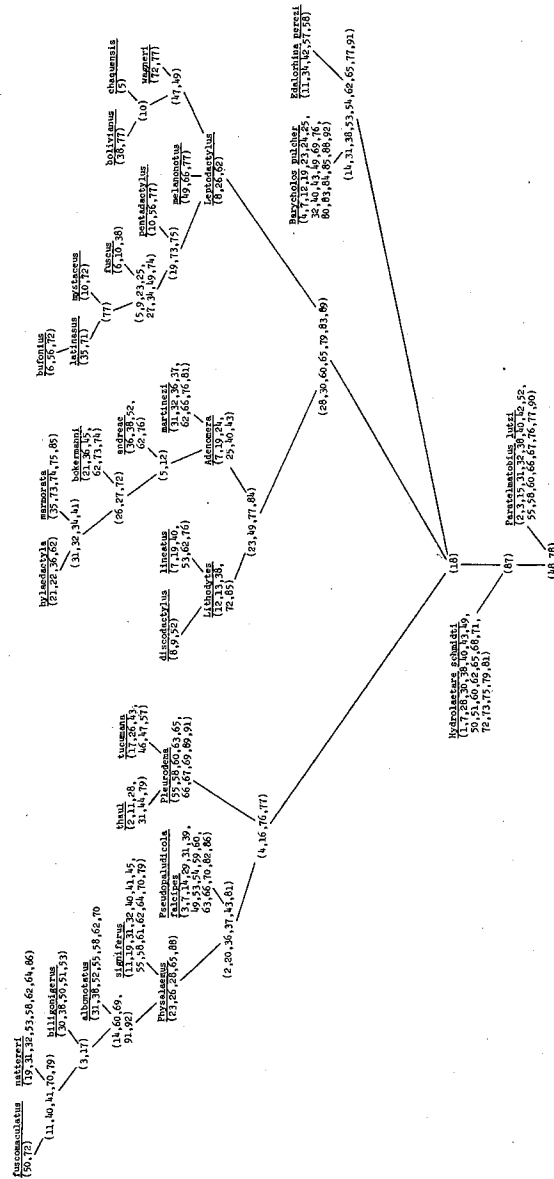
The alternative locations of *Barycholos* in the phylogeny presents a different kind of problem. The most characters it shares with any given taxon is 21 and the taxon is *Physalae-mus nattereri*. But *P. nattereri* shares 31 advanced character states with *P. fuscomaculatus*, so that relationship is chosen. *Barycholos* shares 20 advanced character states (not all the same) with each of the following taxa individually: *L. andreae*, *hylaedactylus*, *marmoratus*, and *martinezi*. *Leptodactylus hylaedactylus* and *marmoratus* share 30 advanced character states between them, however, so that arrangement is preferred. The highest number of shared advanced character states that *Barycholos* shares with any group of taxa is 16 with members of the *marmoratus* group. The character states shared are 7, 18, 19, 23, 24, 25, 40, 43, 48, 49, 65, 77, 78, 83, 84, 87. Four of these are shared by all taxa under consideration: 18, 48, 78, 87. The remaining are states of the following characters: male thumb, toe webbing, egg pigmentation, clutch size, sternohyoideus insertion, omohyoideus, iliacus externus muscle, nasal bone, pterygoid-parasphenoid relationship, ilium, and terminal phalanges. (See Table 3 for correlation of the character state numbers used in the phylogeny with the character and state numbers used in the analysis of characters section.) The phylogeny of Figure 6 represents this position. *Barycholos* shares 11 advanced states with the five species of *Physalae-mus* including the four states shared by all taxa under consideration. The remaining 7 are 4, 23, 43, 65, 76, 77, 88, and are states of the following characters: vocal sac, egg pigmentation, omohyoideus, nasal bones, pterygoid-parasphenoid relationship, and mesosternum. At the same level, however, *Pseudopaludicola* shares 14 advanced states with the five *Physalae-mus* species. To fit *Barycholos* at a lower branching sequence would put it sharing 7 advanced character states with a combination of *Physalae-mus*, *Pleurodema*, and *Pseudopaludicola*. A better alternative is 13 character states shared with *Edalorhina*. The 9 character states (excluding the same 4 as above) are 14, 31, 38, 53, 54, 62, 65, 77, 91 and are states of the following characters: tarsal element structures, geniohyoideus medialis, sternohyoideus origin, semitendinosus, gluteus, nasal bones. What is involved, then, is an attempt to determine the best fit among the following taxa: *marmoratus* group, *Barycholos*, *Physalae-mus*, *Pseudopaludicola*, and *Edalorhina*. The 10 advanced states shared by *Physalae-mus* and *Pseudopaludicola* (excluding the same 4 as above) are 2, 4, 16, 20, 36, 37, 43, 76, 77, 81, which are states of the follow-

TABLE 3
Character State Directory

A. Character state number as used in Phylogenies, B. Character number used in Character Analysis, C. Character state number used in Character Analysis.

A.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
B.	1	2	2	3	3	3	4	4	4	5	5	6	6	7	7	8	8	9	9
C.	1	1	2	0	2	3	0	2	3	1	2	1	2	1	2	1	2	1	2
A.	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
B.	10	11	11	12	13	13	14	14	15	15	15	16	16	16	17	17	18	18	19
C.	1	1	2	1	0	1	1	2	1	2	3	1	2	3	1	2	1	2	1
A.	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
B.	19	20	20	21	21	21	21	22	22	23	23	24	24	25	26	26	26	27	27
C.	2	1	2	0	2	3	4	1	2	1	2	1	2	1	1	2	3	1	2
A.	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
B.	28	28	29	29	30	31	32	33	34	34	35	35	36	37	38	39	39	40	41
C.	1	2	0	2	1	1	1	1	1	2	0	2	1	1	1	1	2	1	0
A.	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92			
B.	41	42	43	44	44	45	46	47	47	48	49	49	49	49	50	50			
C.	1	1	1	0	2	1	1	1	2	1	0	1	2	3	1	2			

ing characters: tympanum visibility, vocal sac, metatarsal tubercles, tadpole vent, anterior petrohyoideus, omohyoideus, pterygoid-parasphenoid relationship, and alary process of the hyale. I subjectively evaluate the shared character state combinations of the *Barycholos-Edalorhina* combination being the weakest because it is the only combination which lacks a distinctive skeletal feature (the nasal bone state is involved several times in this clustering). There does not appear to be any clear cut reason for choosing any pair among the other possibilities as better, based on the character states involved. This includes choosing between *Barycholos-Physalae-mus* and *Pseudopaludicola-Physalae-mus*. Thus, on the basis of number of shared states, it seems best to choose the *Pseudopaludicola-Physalae-mus* pair. The next best choice (aside from with the *marmoratus* group) of alternate placement of *Barycholos* would be to pair it with *Edalorhina*, even though the character state combinations appear weakest among all possible groupings. The resultant phylogeny (Fig. 7) has certain advantages to compensate the apparent worse fit of *Barycholos*. The new phylogeny has nine fewer character state convergences than the old phylogeny and the relationships among *Lithodytes*, the *marmoratus* group, and the remaining *Leptodactylus* are tightened up. This is consistent with all three groups being recognized as part of the same genus from time to time. For these reasons, I prefer the phylogeny represented in Figure 7 as best representing the probable phylogeny of the taxa under consideration.



The placement of two taxa, *Pseudopaludicola* and *Leptodactylus discodactylus* requires further comment. The position of *Pseudopaludicola* is further substantiated by the fact that it shares the most advanced states (21) with *Physalaemus nattereri* and the cluster that it shares the most number of advanced states with is *Physalaemus*, as represented in the phylogeny. The close relationship of *Lithodytes lineatus* and *Leptodactylus discodactylus* was not anticipated but apparently is warranted. The species with which *Lithodytes lineatus* shares the most characters (22) is *L. andreae*. *Leptodactylus andreae* shares 23 states with the cluster of *L. bokermanni*, *L. hylaedactylus*, and *L. marmoratus*. Further, this breaks up members of the *marmoratus* group which is not warranted on the basis of current systematic consensus. *Lithodytes* shares 20 or 21 characters with several combinations of species from the *marmoratus* group. *Lithodytes* also shares 20 characters with *L. discodactylus*. The highest number of shared states that *L. discodactylus* shares with any taxon is 20 with *Lithodytes*.

TAXONOMIC CONCLUSIONS

The study set out to analyze the relationships of the *marmoratus* group within the subfamily and the study sample was chosen to accomplish this purpose. The way in which the study sample was chosen places limitations on speculations beyond how the *marmoratus* group relates to the other taxa.

Within the limits of this study, I think the following conclusions are justifiable:

- 1) Within the subfamily, two major clusters of taxa are evident, what had been termed *Lithodytes* and *Leptodactylus* on the one hand, and *Physalaemus*, *Pleurodema*, and *Pseudopaludicola* on the other.
- 2) Within the *Lithodytes-Leptodactylus* cluster, three groups are evident corresponding to A) *Lithodytes lineatus* and *L. discodactylus*, B) The *marmoratus* group, and C) Remaining *Leptodactylus*.

My concept of the genus is that it: 1) is a taxon of convenience, 2) should represent a single line of ancestry, and 3) should represent a unique adaptational complex if at all possible. With respect to point one, the size of the genus should be manageable. In my opinion, the genus *Eleutherodactylus* should be divided on this basis. In the present instance, convenience does not apply as the maximum number of species involved in the genus *Leptodactylus* (broad sense) is under 50. With respect to point two, three alternatives are possible to reflect lines of ancestry depending on the level preferred:

FIGURE 7. Preferred phylogenetic relationships among the 29 taxa of this study with *Barycholos* nearest *Edalorhina*. Generic names are used as recognized in this study and are placed at character state cluster points so that all taxa above that point will be included within the genus. Also see text.

A) a single genus, which would be indicated at the state cluster (28, 30, 60, 65, 79, 83, 89) of Fig. 7; B) two genera, the genus *Leptodactylus* represented as it is in Fig. 7, the second genus would be indicated at state cluster (23, 49, 77, 84) of Fig. 7; C) three genera, as indicated in Fig. 7. I use the third point in choosing among these alternatives. As developed elsewhere, members of the *marmoratus* group are forest frogs and their adaptations are in response to the forest environment (Heyer, 1973) while members of the genus *Leptodactylus* (narrow sense, as in Fig. 7) are savanna frogs and their adaptations are in response to the savanna environment (Heyer, 1969b, 1973). Thus, the relationships between these two assemblages are best represented at the generic level. The two species included in *Lithodytes* in Fig. 7 are not as well understood as some members of the other two groups. The two species do share a number of advanced states in common, one of which, dorsally divided toe disks, is unique in the study sample. As a genus name is already available for this unit, I prefer to recognize these two species as a genus distinct from *Leptodactylus* and *Adenomera*.

Leptodactylus is thus restricted to include members of the *melanonotus*, *ocellatus*, *pentadactylus*, and *fuscus* species groups with the exception of *L. discodactylus*. *Adenomera* includes members of the *marmoratus* group. *Lithodytes* consists of *L. lineatus* and *L. discodactylus*. This arrangement of *Lithodytes* may be subject to further evaluation as almost nothing is known of the life histories of the two included species and the karyotypes have not been compared. The only further change would be recognition of *L. discodactylus* as a distinct genus as it is clearly not closely related to either *Adenomera* or *Leptodactylus*.

3) The relationships of *Barycholos*, *Edalorhina*, *Hydrolaetare*, *Limnomedusa*, (which does not appear on Figs. 6 or 7) and *Paratelmatobius* are removed from the two major clusters within the subfamily. This can be explained in two different ways; 1) either these taxa represent early, specialized divergences from a common ancestor or, 2) closer relatives may be found in the subfamily Telmatobiinae as defined by Lynch (1971). The comparison of these taxa with members of the subfamily Telmatobiinae (fide Lynch) is not only recommended but necessary if formal names are to be applied to suprageneric taxonomic groupings.

COMPARISON WITH PREVIOUSLY PROPOSED PHYLOGENIES

Lynch (1971) provides a summary of previous phylogenetic schemes for the taxa under consideration, so that comparison with his conclusions will suffice. The similarities and differences between his analysis and this one should be pointed out. We both use many of the same characters and character states, with some exceptions. The major difference is in the treatment of the character states. Lynch apparently used a combination of primitive and

derived states in determining the relationships and he gave some characters greater weight than others. In this study, only derived character states were used in determining relationships and the only weighting of the characters was in choosing which characters and states would be included in the study.

Lynch (1971) was more concerned with relationships among the subfamilies he recognized than relationships with the subfamilies. He did comment on certain intergeneric relationships, however, which can be compared with the relationships proposed herein. He synonymized a group of previously recognized genera into the genus *Physalaemus*. The results of this study are consistent with his action, but it should be pointed out that in the present study, representatives of *Physalaemus* were not chosen to elucidate relationships among themselves. Lynch did not recognize the subgeneric category in his work, but did recognize it informally within the genus *Leptodactylus* to separate the *marmoratus* group from the other species. Here the distinction is raised to the generic level.

Lynch (1971:182) considered *Physalaemus* and *Pseudopaludicola* to be closely related; this is supported in the present study. The interpretation of the placement of *Barycholos*, *Pleurodema*, *Paratelmatobius*, *Edalorhina*, and *Hydrolaetare* differ. Lynch (1971:192) indicates that *Barycholos* is most closely related to the subgenus *Adenomera* and *Lithodytes*; that *Pleurodema* is the most primitive genus (p. 207); that *Paratelmatobius* has its nearest relationship to *Physalaemus* although the relationship is not close (p. 184); that *Edalorhina* is an intermediate between *Lithodytes* and *Physalaemus* (p. 178); and infers that the closest relationship of *Hydrolaetare* within the subfamily is with *Leptodactylus*. The results of this study indicate that if the genera *Barycholos*, *Edalorhina*, *Hydrolaetare*, and *Paratelmatobius* do in fact have their closest relationship with the other members of the subfamily, then they are earlier offshoots of the leptodactyline stock and hence more primitive than *Pleurodema*.

CHARACTER STATE EVALUATIONS

The character states can be evaluated in two different ways. Blocks of character states representing different functional systems can be compared to see if the components yield the same results as the total data set. This aspect is examined elsewhere. The aspect examined here is the evaluation of how the individual character states relate within the preferred phylogenetic diagram. In the following subjective classification, all character states are assumed to be adaptive. The only criterion that is used to determine whether the character state is of value in determining the proposed phylogenetic relationships is where the particular state appears in the tree. For example, if a state appears once in the phylogeny in a cluster leading to *Adenomera* and *Lithodytes*, that character state is considered very useful in determining relationships. Alternatively, a character state that appears 11 times, each time at a different end

point of the phylogeny is not considered useful in elucidating relationships.

The following character states are considered the best states in determining relationships: 8, 13, 16, 18, 20, 23, 37, 48, 78, 83, 87. States 13, 16, 18, 20, 48, 78, 87 are represented by a single appearance in the phylogeny. States 8, 37, and 83 are represented twice, state 23 is represented three times.

The following character states are useful in determining relationships but not to the degree as the previous states: 2, 4, 7, 9, 19, 24, 25, 26, 30, 36, 54, 67, 73, 74, 75, 81, 84, 88, 89. These states are represented on the diagram (Fig. 7) from 2 to 6 times and do not define clusters as neatly as the previous character states. In the character analysis, *Lithodytes discodactylus* was coded as state 9, meaning that the lack of thumb spines had gone through an ancestral state to thumb spines present. This was based on the false assumption that the species was related to members of the *melanotus* species group of the genus *Leptodactylus*. The results of this study indicate that the state in question should have been coded as a 7, which would then place state 7 as an ancestral condition to both *Adenomera* and *Lithodytes*.

The following states are neutral in their usefulness in determining relationships: 1, 5, 6, 10, 12, 15, 17, 21, 22, 27, 28, 29, 34, 39, 41, 43, 44, 46, 59, 61, 65, 79. Of these, 1, 15, 22, 29, 39, 44, 46, 59, 61, are unique to individual end-point taxa and are of no use in determining relationships. The remainder are represented from two to five times in the phylogeny (Fig. 7) and do not appear to either add or detract in determining relationships.

The following states, if used to cluster groups of species, would yield a very different phylogeny, and are thus of negative value in determining relationships within the context of the preferred phylogeny (Fig. 7): 3, 11, 14, 31, 32, 33, 35, 38, 40, 42, 45, 46, 47, 49, 50, 51, 52, 53, 55, 56, 57, 58, 60, 62, 66, 69, 70, 71, 72, 76, 77, 80, 85, 86, 91. The states are represented from 2 to 11 times in the phylogeny. Three alternatives are possible to account for this category: 1) the character states did in fact arise independently in limited clusters of taxa several times; 2) the character states within characters need to be redefined; or 3) the assumed direction of change of character states within characters is incorrect. These possibilities are explored further after the following section which accounts for alternative one in part.

Character State Clusters—Two types of character state clusters are examined: 1) those clusters of character states shared by related taxa; and 2) certain clusters of character states shared by taxa not closely related.

The clusters of shared character states leading to and including the generic clusters are characterized by having at least one state from the first two categories listed above, that is, at least one of the states in each cluster is relatively diagnostic of only that cluster. Examination of the states involved in the clusters indicates a scattering of states from all sorts of systems which do not appear to represent a single functional adaptation with two exceptions. The combination of a male thumb lacking nuptial adspersities, toes lacking fringe or web, and less than 50 eggs/clutch defining *Adenomera* in part sug-

gests a basic adaptation towards terrestriality. Advanced states of the semitendinosus, accessory head of the adductor magnus, and adductor longus muscles of the thigh in the two *Pleurodema* examined suggest a functional change in the leg musculature. Further species within the genus would need to be examined to see if this in fact represents a basic functional generic adaptation.

Adenomera and members of the *fuscus* species group share several states, listed in order of degree of sharing, beginning with the states shared by all species of both groups: (19) toes free, (23) eggs lacking melanophores, (25) 50-1000 eggs/clutch, (49) iliacus externus muscle extends from $\frac{3}{4}$ to full length of the iliac bone anteriorly, (5) indications of paired lateral vocal sacs, (77) pterygoid and parasphenoid bones overlap but are not in contact, (26, 27) the foam nest is placed away from water, (72) vomer bones articulate with the premaxilla and/or maxilla, (34) geniohyoideus lateralis muscle has a lateral flare, (73, 74) the sphenethmoid bone borders the optic foramen, (75) the sphenethmoid bone extends anteriorly beyond the vomers. Character states 19, 23, 25, 5, 27, 72, 73, 74, and 75 appear to be related to the same general functional complex. Both groups are more terrestrial than other closely related groups and a key feature to achieving a greater degree of terrestriality is placement of the foam nest out of the water into an incubating chamber which is constructed by the frogs. The anterior portion of the skull is strengthened in these forms as they apparently use the snout and the hind limbs in forming the incubating chamber. With males calling from isolated locations away from the water, a different type of call is more appropriate (Heyer and Bellin, 1973, Heyer and Straughan, Ms.), which is reflected morphologically by the indications of paired lateral vocal sacs to radiate the call. Since the eggs are out of direct sunlight, the melanophores have been lost.

Adenomera and *Physalaemus* share several states, listed in order of degree of sharing, beginning with the states shared by all the species of both groups: (28) depressor mandibulae with two sites of equal origin on the dorsal fascia and the squamosal bone or the crista parotica, (65) the nasal bones are separated, (23) eggs lack melanophores, (77) the pterygoid and parasphenoid bones overlap without contact, (43) the omohyoideus is on the ventral surface of the body of the hyoid plate, (60) the adductor longus muscle is well developed, (26) the foam nest is placed on the water, (40) the sternohyoideus inserts near the edge and the midline of the hyoid body, (79) the anterior process of the hyale is absent, (36) the anterior petrohyoideus inserts on the edge and body of the hyoid plate, (62) gluteus small, (38) the sternohyoideus originates as two slips, (76) the pterygoid and parasphenoid elements do not overlap, (31, 32) the geniohyoideus medialis is divided ventrally, (37) the anterior petrohyoideus inserts on the hyoid body only, (81) the alary process of the hyoid is broad and winglike. Character states 43, 40, 79, 36, 38, 31, 32, 37, 81 are all involved with the hyoid apparatus and asso-

ciated musculature. Basically, the difference is broad and winglike or narrow and stalked alary processes with associated muscle attachment patterns.

Limnomedusa shares the most character states with the following four taxa: *Physalaemus biliginigerus*, 18, 28, 30, 38, 50, 51, 53, 65, 77, 87, 88, 91, 92; *Barycholos pulcher*, 18, 38, 53, 54, 62, 65, 77, 80, 87, 88, 91, 92; *Physalaemus nattereri*, 18, 28, 53, 62, 65, 77, 79, 87, 88, 91, 92; *Hydrolaetare schmidti*, 1, 28, 30, 38, 50, 51, 62, 65, 79, 87. Derived states of the mesosternum are shared by all combinations, and *Limnomedusa* also shares derived states of the xiphisternum with all but *Hydrolaetare*. *Limnomedusa* and *Barycholos* are unique in sharing reduced or absent alary processes of the hyoid, *Limnomedusa* and *Hydrolaetare* are unique in having vertical pupils. Beyond these observations, examination of the states does not indicate any possible groupings of significance.

Possible Errors in Character State Evaluations—The direction of character state changes were evaluated using a certain set of guidelines. As the guidelines were logical, some character state determinations may be incorrect as organisms do not always follow logical evolutionary pathways. The purpose of this section is not to improve the phylogeny or the data on which it is based but rather to point out those characters which appear to have been incorrectly evaluated. Once pointed out, applications of more data or different analytic procedures can determine the best arrangement of the characters. One of the advantages of the combinational method of analysis is that possible errors can be located.

The approach is 1) to identify the character states that correlate poorly with the phylogeny, 2) to try different character state interpretations, and if the 3) new interpretations are much more consistent with the phylogeny, then 4) one may conclude that the original interpretations might be incorrect and should be examined further. One of the main criteria used to determine whether a change in states is an improvement is whether the total number of convergences in the phylogeny is reduced by the change. This method thus allows for a somewhat independent evaluation of character states. Again, to make the point clear, the purpose of this section is to point out possible errors, not to reevaluate them.

As documented above, *Lithodytes discodactylus* has character state 7 rather than 9.

Certain character states that were assigned a negative value in predicting relationships have been accounted for. States 31, 32, 38, 40, 72 have been shown to be linked to a hyoid unit change which has probable functional significance and has been derived independently several times. Character state 33 is unique to *Limnomedusa* and state 80 is shared with *Barycholos* only. Examination of the remaining states having negative value in determining relationships allows three groupings. The first is comprised of states which appear to have independently arisen more than once. In other words, there is no strong evidence to suspect otherwise. The states are 3, 11, 14, 35, 42, 45, 47,

50, 51, 52, 53, 55, 56, 57, 58, 66, 69, 70, 71, 85, 86, 91 which each appear from 2 to 6 times on the phylogenetic diagram (Fig. 7). The second category is comprised of states 76 and 77 in which an apparent redefinition of states is called for. Both 76 and 77 are states of the same character involving the relationship of pterygoid and the parasphenoid bones. The best adjustment that could be made with the information as coded would be to combine states 76 and 77 into one primitive state. That would make the previous primitive state the derived state which would then combine *Hydrolaetare*, *Leptodactylus chaquensis*, and *L. fuscus*. This arrangement is not predictive in determining relationships either. If there is useful information in the pterygoid-parasphenoid bone relationship, the variation might be categorized into different states than I recognized. The third grouping consists of character states in which the direction of change of states was probably incorrectly inferred. Three states are involved, 49, 60, 62. State 49 is the length of the iliacus externus muscle along the iliac bone and was assumed to be the most derived state of the three states recognized of the character. The previous ordering was character 23, state 0 \longrightarrow state 1 (now state 48) \longrightarrow state 2 (now state 49). Reversing the direction of change to 2 \longrightarrow 1 \longrightarrow 0 would result in the following clusters: state 1, *Edalorhina*, *Leptodactylus pentadactylus*, all *Physalaemus*, *Pleurodema*, and *Paratelmatobius*; state 0, *Limnomedusa*. This would improve the phylogeny considerably by removing seven convergences that are accounted for by state 49 from the phylogeny. A reversal of direction involving state 60 would improve the phylogeny by removing six convergences and adding only two. The previous state change directions of character 29 (adductor longus muscle) were 0 (now state 60) \longleftarrow 1 \longrightarrow 2 (now state 61). The new directions of change for character 29 would be 1 \longleftarrow 0 \longrightarrow 2. The taxa sharing state 1 are *Barycholos*, *Edalorhina*, and *Limnomedusa*. The result would add to the relationship of *Barycholos* and *Edalorhina* in the phylogeny. State 62 is a state of the gluteus muscle. Reversing the direction of change of states would improve the phylogeny slightly by substituting seven convergences for 11 represented by state 62. The previous direction of change was for character 30, state 0 \longrightarrow state 1 (now 62). The new direction would be 1 \longrightarrow 0, which groups the following taxa: *Lithodytes discodactylus*, *Adenomera marmorata*, *Physalaemus biliginigerus* and *fuscomaculatus*, both *Pleurodema*, *Pseudopaludicola*, and *Paratelmatobius*. This clustering would be rather neutral in its usefulness in defining the relationships presented in Figure 7. The high number of convergences (7) still remaining after the change suggests that the variation present in the character might be profitably redescribed. The criteria used in determining the direction of change of states in all three cases were I and II, which would indicate that most or all of the outgroup might have advanced states for these three characters. It is interesting to note that if incorrect inferences were made in these three characters, they were not sufficient to drastically alter the relationships. In other words, the data sample is large enough to allow for a few errors.

Character State Predictions—The phylogenetic diagram (Fig. 7) allows character state predictions where information was not available in some cases. This was most true for life history data in the present case. According to the diagram (Fig. 7) a foam nest is not required for *Lithodytes*, *Barycholos*, *Edalorhina*, *Hydrolaetare*, or *Paratelmatobius* for which no breeding behavior is known. With the known information, a foam nest has apparently been independently derived four times. As this is a key adaptation towards terrestriality at least in *Adenomera* and *Leptodactylus* (Heyer, 1969b, 1973), it is interesting to note that true independence of the pond for all of the life cycle has only been attained once among these genera, in the genus *Adenomera*.

GENERIC REDEFINITIONS

The results of this study require the redefinition of three genera. These follow. Full generic synonymies may be found in Lynch (1971).

Adenomera Fitzinger in Steindachner, 1867

Type species: *Adenomera marmorata* Fitzinger in Steindachner, 1867, by monotypy.

Diagnosis: The only leptodactylid genera in the New World having a bony style for the mesosternum are *Adenomera*, *Leptodactylus*, *Lithodytes*, and *Pleurodema*. *Adenomera* differs from *Pleurodema* is not having a well developed frontoparietal fontanelle (well developed in *Pleurodema*), the quadratojugal contacts the maxilla (incomplete maxillary arch), and smaller size, less than 31 mm snout-vent length (35-65 mm S-VL). *Adenomera* differs from *Leptodactylus* in having T-shaped terminal phalanges (knobbed in *Leptodactylus*). *Adenomera* differs from *Lithodytes* in not having the dorsal toe disk surfaces divided.

Definition: Pupil horizontal; tympanum distinct; male vocal sac internal, indications of lateral vocal folds present or absent; male thumb lacking nuptial adspersities; body lacking distinct glands; toe tips expanded into disks or not, if disked, dorsal surfaces not divided; tarsal fold present or weakly developed; metatarsal tubercles neither pronounced or cornified; toes without web or fringe, free; larval vent median; larval denticle rows $\frac{2}{3}$, weakly developed or absent; eggs lacking melanophores; few eggs per clutch (<50/clutch); eggs in foam nest deposited away from standing water; depressor mandibulae condition DFsq; geniohyoideus medialis continuous medially or divided ventrally; geniohyoideus lateralis with or without distinct slip to hyale; anterior petrohyoideus insertion on edge, edge and body, or body of hyoid; sternohyoideus origin from one or two slips on meso- and xiphisternum; sternohyoideus insertion near lateral edge and midline of hyoid or midline of hyoid only; omohyoideus insertion on body of hyoid or absent; tendon of semitendinosus confluent with posterior portion of sartorius insertion on knee and tendons of gracilis minor and major passing dorsad to tendon of semitendinosus; iliacus

externus extending from $\frac{3}{4}$ to full length of iliac bone; tensor fasciae latae insertion posterior to iliacus externus on iliac bone; gracilis minor broad or narrow; interior and exterior portions of semitendinosus united in common distal tendon, two portions equal in bulk or exterior larger; sartorius moderately developed; accessory head of adductor magnus without distinct tendon; adductor longus well developed; gluteus insertion on cruralis and knee or cruralis only; quadratojugal well developed, contacting maxilla; maxillary teeth present; nasal bones widely separated; small frontoparietal fontanelle or absent; zygomatic ramus of squamosal just longer than, just shorter than, or equal to otic ramus; vomerine teeth present; vomers not contacting medially; vomer articulation with premaxilla and/or maxilla present or absent; posterior extent of sphenethmoid widely separated from or bordering optic foramen; sphenethmoid extending anteriorly to middle of vomers or beyond; occipital condyles moderately or widely separated; no anterior processes of hyale; alary process of hyoid somewhat narrow and often stalked or broad and winglike; posterolateral process of hyoid present; ilium with well-developed dorsal crest; terminal phalanges T-shaped, expanded or not; omosternum present, expanded; mesosternum a bony style; xiphisternum single, entire; diploid chromosome number 24 or 26 (Bogart, personal communication).

Content: Five species are recognized in the most recent revision (Heyer, 1973, and Table 4). One and possibly two more species are being described by other workers.

Leptodactylus Fitzinger, 1826

Type species: *Rana fusca* Schneider, 1799. Lynch (1971:187) stated, "*Rana typhonia* Daudin is *R. sibilatrix* Wied, 1824, which Heyer (1968[a]) considered identical with *Rana fusca* Schneider, 1799, for which he designated a neotype. However, at least some of the syntypes of *Rana fusca* are extant (W. C. A. Bokermann, personal communication), and study of these must be made before Heyer's action can be accepted." I have subsequently asked W. C. A. Bokermann if he knew Schneider's types are extant. He indicated that Lynch mistranslated his comments. What Bokermann expressed to Lynch was that he preferred to designate type species where the collecting locality was known with some precision. As this is truer for *Rana typhonia* than either *Rana fusca* or *Rana sibilatrix* his preference would be to designate *Rana typhonia* as the type species of the genus. Bokermann did not think Schneider's types were still extant and in subsequent inquiries to individuals and institutions not contacted previously I have been unable to locate anyone who thinks Schneider's types are extant. Based on the rules of priority and due to the confusion regarding use of the names *sibilatrix*, *sibilator*, and *typhonius* for the same taxon, I still think the best solution consistent with the available evidence is to regard *Rana fusca* Schneider as the appropriate name for the taxon in question.

Diagnosis: The only leptodactylid genera in the New World having a

bony style for the mesosternum are *Adenomera*, *Leptodactylus*, *Lithodytes*, and *Pleurodema*. *Leptodactylus* differs from *Pleurodema* in not having a well developed frontoparietal fontanelle (well developed in *Pleurodema*), and the quadratojugal contacts the maxilla (incomplete maxillary arch). *Leptodactylus* differs from *Adenomera* and *Lithodytes* in having knobbed shaped terminal phalanges (T-shaped in *Adenomera* and *Lithodytes*).

Definition: Pupil horizontal; tympanum distinct; vocal sac internal, paired external vocal sacs present, weakly developed, or absent; male thumb with horny spines or not; glandular dorsolateral folds present or absent; toe tips usually not expanded into disks; tarsal fold present; metatarsal tubercles neither pronounced nor cornified; toes with lateral fringes or not; larval vent median; larval denticle rows $\frac{2}{3}$, well developed; eggs with or without melanophores; moderate (50-1000 eggs) or large (>1000 eggs) clutch size; eggs deposited in foam nest on top of water or in burrows away from water; depressor mandibulae condition DFsq; geniohyoideus medialis continuous medially; geniohyoideus lateralis not attaching to hyale or attaching with or without a definite slip; anterior petrohyoideus inserts on edge of hyoid body; sternohyoideus origin with single or double slips from meso- and xiphisternum; sternohyoideus insertion on narrow band near lateral edge of hyoid body; omohyoideus insertion on hyoid plate and fascia between posterolateral and posteromedial processes of the hyoid; tendon of semitendinosus confluent with posterior portion of sartorius insertion on knee and tendons of gracilis minor and major passing dorsad to tendon of semitendinosus or tendon of semitendinosus piercing tendon of gracilis minor and major; iliacus externus extending from $\frac{1}{2}$ to full length of ilium; tensor fasciae latae inserting posterior to iliacus muscle on iliac bone; gracilis minor broad; interior and exterior portions of semitendinosus uniting in common tendon distally, two portions equal in development or exterior portion larger; sartorius moderate or broad; no distinct tendon of accessory head of adductor magnus; adductor longus well developed; gluteus inserting entirely on cruralis; quadratojugal well developed, contacting maxilla; maxillary teeth present; nasals widely separated; frontoparietal fontanelle small or absent; zygomatic ramus of squamosal just longer than, just shorter than, or equal to otic ramus; vomerine teeth present; vomers in broad median contact or not; vomer articulating with premaxilla and/or maxilla or not; posterior extent of sphenethmoid widely separated from optic foramen to bordering optic foramen; sphenethmoid extending anteriorly to middle of vomers or beyond; occipital condyles moderately or widely separated; no anterior process of hyale; alary process somewhat narrow and stalked; posterolateral process of hyoid present; ilium with well developed dorsal crest; terminal phalanges knobbed; omosternum present, expanded; mesosternum a bony style; xiphisternum entire, single; diploid chromosome number 22.

Content: Approximately 35 species tentatively arranged in four species groups (Table 4).

Lithodytes Fitzinger, 1843

Type species: *Rana lineata* Schneider, 1799, by original designation.

Diagnosis: The only leptodactylid genera in the New World having a bony style for the mesosternum are *Adenomera*, *Leptodactylus*, *Lithodytes*, and *Pleurodema*. Among these, *Lithodytes* is the only genus to have large toe disks with divided dorsal surfaces.

Definition: Pupil horizontal; tympanum distinct; vocal sac internal; male thumb without nuptial adspersities; body without well-defined glands; toes disked with dorsal surfaces divided longitudinally; tarsal fold present; metatarsal tubercles neither pronounced nor cornified; toes with lateral fringes or free; eggs lacking melanophores; large clutch size (>1000 eggs); depressor mandibulae condition DFsq; geniohyoideus medialis continuous medially; geniohyoideus lateralis without lateral flare or slip; anterior petrohyoideus insertion on edge of hyoid; sternohyoideus origin with distinct slips from anterior mesosternum and another from posterior meso- and/or xiphisternum; sternohyoideus insertion near lateral edge of hyoid; omohyoideus insertion on hyoid plate and fascia between posterolateral and posteromedial process of hyoid; tendon of semitendinosus confluent with posterior portion of sartorius insertion on knee and tendons of gracilis minor and major passing dorsad to tendon of semitendinosus or tendon of semitendinosus piercing tendon of gracilis minor and major; iliacus externus extending from $\frac{3}{4}$ to full length of iliac bone; tensor fasciae latae insertion posterior to iliacus externus on iliac bone; gracilis minor narrow to broad; interior and exterior portions of the semitendinosus uniting in common tendon distally, exterior portion larger or equal to interior (smaller) portion with distinct distal tendon attaching to bulk of interior portion; sartorius moderately developed; accessory head of adductor magnus without distinct tendon; adductor longus well developed; gluteus insertion on cruralis only or cruralis and knee; quadratojugal well developed, contacting maxilla; maxillary teeth present; nasals widely separated; no frontoparietal fontanelle; zygomatic ramus of squamosal just longer than, just shorter than, or equal to otic ramus; vomerine teeth present; vomers not in medial contact; vomer articulation with premaxilla and/or maxilla; posterior extent of sphenethmoid widely separated from optic foramen; sphenethmoid extending anteriorly to middle of vomers; occipital condyles moderately or widely separated; no anterior processes of hyale; alary process of hyoid somewhat narrow and stalked; posterolateral process of hyoid present; ilium with well-developed dorsal crest; terminal phalanges T-shaped, expanded; mesosternum a bony style; xiphisternum entire, single; diploid chromosome number 18 (for *L. lineatus*).

Content: Two species are now recognized (Table 4). *Plectomantis rhodostima* Cope, 1874 may also be referable to this genus. E. Malnate (personal communication) has not been able to locate the type at this time, but the type may be identified at a later time in the Philadelphia collections.

TABLE 4

Species proposed or commonly associated with the genus *Leptodactylus*. For the genus *Leptodactylus*, provisional assignments into species groups are indicated by F (Fuscus group), M (Melanonotus group), O (Ocellatus group), and P (Pentadactylus group). Allocations immediately following a question mark are uncertain

Name Proposed	Present Allocation
<i>Cystignathus albilabris</i> Gunther, 1859	<i>Leptodactylus albilabris</i> F
<i>Leptodactylus anceps</i> Gallardo, 1964	<i>Leptodactylus latinasus</i> F
<i>Leptodactylus andicola</i> Boettger, 1891	<i>Leptodactylus ? andicola</i> F
<i>Leptodactylus andreae</i> Muller, 1923	<i>Adenomera andreae</i> , new combination
<i>Leptodactylus bokermanni</i> Heyer, 1973	<i>Adenomera bokermanni</i> , new combination
<i>Leptodactylus bolivianus</i> Boulenger, 1898	<i>Leptodactylus bolivianus</i> O
<i>Leptodactylus brevipes</i> Cope, 1887	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus bufo</i> Andersson, 1911	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus bufonius</i> Boulenger, 1894	<i>Leptodactylus bufonius</i> F
<i>Leptodactylus caliginosus</i> Girard, 1853	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus chaquensis</i> Cei, 1950	<i>Leptodactylus chaquensis</i> O
<i>Leptodactylus curtus</i> Barbour and Noble, 1920	<i>Leptodactylus labrosus</i> F
<i>Leptodactylus dantasi</i> Bokermann, 1959	<i>Leptodactylus dantasi</i> M
<i>Leptodactylus darlingtoni</i> Cochran, 1935	<i>Eleutherodactylus jugans</i>
<i>Leptodactylus diptychus</i> Boulenger, 1918	<i>Leptodactylus ? poecilochilus</i> F
<i>Leptodactylus diptyx</i> Boettger, 1885	<i>Adenomera hylaedactyla</i>
<i>Leptodactylus discodactylus</i> Boulenger, 1883	<i>Lithodytes discodactylus</i> , new combination
<i>Cystignathus discolor</i> Reinhardt and Lutken, 1861	<i>Eupsophus miliaris</i>
<i>Leptodactylus dominicensis</i> Cochran, 1923	<i>Leptodactylus ? albilabris</i> F
<i>Leptodactylus dominicensis</i> Muller, 1923	<i>Leptodactylus ? pentadactylus</i> P
<i>Cystignathus echinatus</i> Brocchi, 1877	<i>Leptodactylus melanonotus</i> M
<i>Leptodactylus fallax</i> Müller, 1926	<i>Leptodactylus ? pentadactylus</i> P
<i>Leptodactylus flavopictus</i> Lutz, 1926	<i>Leptodactylus pentadactylus</i> P
<i>Cystignathus fragilis</i> Brocchi, 1877	<i>Leptodactylus labialis</i> F
<i>Rana fusca</i> Schneider, 1799	<i>Leptodactylus fuscus</i> F
<i>Leptodactylus gaigae</i> Cochran, 1938	<i>Paratelmatobius gaigae</i>
<i>Rana giga</i> Spix, 1824	<i>Leptodactylus ? pentadactylus</i> P
<i>Leptodactylus glandulosus</i> Cope, 1887	<i>Adenomera hylaedactyla</i>
<i>Leptodactylus goliath</i> Jimenez de la Espada, 1875	<i>Leptodactylus pentadactylus</i> P
<i>Cystignathus gracilis</i> Dumeril and Bibron, 1841	<i>Leptodactylus gracilis</i> F
<i>Leptodactylus gualambensis</i> Gallardo, 1964	<i>Leptodactylus fuscus</i> F
<i>Hylodes hallowellii</i> Cope, 1862	<i>? Leptodactylus hallowellii</i>
<i>Leptodactylus hemidactyloides</i> Andersson, 1945	<i>Lithodytes lineatus</i>

TABLE 4 (continued)

Name Proposed	Present Allocation
<i>Leptodactylus hololius</i> Boulenger, 1918	<i>Adenomera hylaedactyla</i>
<i>Cystignathus hylaedactylus</i> Cope, 1868	<i>Adenomera hylaedactyla</i> , new combination
<i>Cystignathus hylodes</i> Reinhardt and Lutken, 1861	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus inoptatus</i> Barbour, 1914	<i>Eleutherodactylus inoptatus</i>
<i>Leptodactylus insularum</i> Barbour, 1906	<i>Leptodactylus ? bolivianus</i> O
<i>Leptodactylus intermedius</i> Lutz, 1930	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus knudseni</i> Heyer, 1972	<i>Leptodactylus knudseni</i> P
<i>Leptodactylus kreffti</i> Werner, 1904	<i>? Eupsophus</i>
<i>Cystignathus labialis</i> Cope, 1877	<i>Leptodactylus labialis</i> F
<i>Leptodactylus labrosus</i> Jimenez de la Espada, 1875	<i>Leptodactylus labrosus</i> F
<i>Rana labyrinthica</i> Spix, 1824	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus laticeps</i> Boulenger, 1918	<i>Leptodactylus laticeps</i> P
<i>Leptodactylus latinasus</i> Jimenez de la Espada, 1875	<i>Leptodactylus latinasus</i> F
<i>Rana latrans</i> Steffen, 1815	<i>Leptodactylus ocellatus</i> O
<i>Eleutherodactylus leptodactyloides</i> Andersson, 1945	<i>Leptodactylus wagneri</i> M
<i>Rana lineata</i> Schneider, 1799	<i>Lithodytes lineatus</i>
<i>Leptodactylus longirostris</i> Boulenger, 1882	<i>Leptodactylus ? longirostris</i> F
<i>Rana luctator</i> Hudson, 1892	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus macroblepharus</i> Miranda-Ribeiro, 1926	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus maculilabris</i> Boulenger, 1896	<i>Leptodactylus poecilochilus</i> F
<i>Leptodactylus mantipus</i> Boulenger, 1908	<i>? Eleutherodactylus</i>
<i>Adenomera marmorata</i> Fitzinger in Steindachner, 1867	<i>Adenomera marmorata</i>
<i>Leptodactylus martinezi</i> Bokermann, 1956	<i>Adenomera martinezi</i> , new combination
<i>Cystignathus melanonotus</i> Hallowell, 1860	<i>Leptodactylus melanonotus</i> M
<i>Leptodactylus melini</i> Lutz and Kloss, 1952	<i>Adenomera hylaedactyla</i>
<i>Cystignathus microtis</i> Cope, 1879	<i>Leptodactylus melanonotus</i> M
<i>Leptodactylus minutus</i> Nobel, 1923	<i>Adenomera hylaedactyla</i>
<i>Rana mystacea</i> Spix, 1824	<i>Leptodactylus mystaceus</i> F
<i>Cystignathus mystacinus</i> Burmeister, 1861	<i>Leptodactylus mystacinus</i> F
<i>Leptodactylus nanus</i> Muller, 1922	<i>Adenomera marmorata</i>
<i>Leptodactylus natalensis</i> Lutz, 1930	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus nattereri</i> Lutz, 1926	<i>Leptodactylus podicipinus</i> M
<i>Cystignathus nebulosus</i> Girard, 1853	<i>? Eupsophus</i>
<i>Leptodactylus nigrescens</i> Andersson, 1945	<i>Lithodytes discodactylus</i>
<i>Leptodactylus novaeutoniae</i> Ahl, 1936	<i>Limnomedusa macroglossa</i>
<i>Leptodactylus occidentalis</i> Taylor, 1937	<i>Leptodactylus melanonotus</i> M

TABLE 4 (continued)

Name Proposed	Present Allocation
<i>Rana ocellata</i> Linnaeus, 1758	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus ocellatus macrosternum</i> Miranda-Ribeiro, 1926	<i>Leptodactylus ? macrosternum</i> O
<i>Leptodactylus ocellatus reticulata</i> Cei, 1949	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus ochraceus</i> Lutz, 1930	? <i>Eleutherodactylus</i>
<i>Rana octoplicata</i> Werner, 1893	<i>Leptodactylus ocellatus</i> O
<i>Leptodactylus pachyderma</i> Miranda-Ribeiro, 1926	<i>Leptodactylus pentadactylus</i> P
<i>Rana pachypus</i> Spix, 1824	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus pallidirostris</i> Lutz, 1930	<i>Leptodactylus wagneri</i> M
<i>Cystignathus parvulus</i> Girard, 1853	<i>Zachaeus parvulus</i>
<i>Rana pentadactyla</i> Laurenti, 1768	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus pentadactylus dengleri</i> Melin, 1941	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus pentadactylus mattogrossensis</i> Schmidt and Inger, 1951	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus pentadactylus rubidoides</i> Andersson, 1945	<i>Leptodactylus pentadactylus</i> P
<i>Cystignathus perlaevis</i> Cope, 1879	<i>Leptodactylus melanonotus</i> M
<i>Platymantis petersii</i> Steindachner, 1864	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus plaumanni</i> Ahl, 1936	<i>Leptodactylus fuscus</i> F
<i>Cystignathus podicipinus</i> Cope, 1862	<i>Leptodactylus podicipinus</i> M
<i>Cystignathus poecilochilus</i> Cope, 1862	<i>Leptodactylus poecilochilus</i> F
<i>Leptodactylus poeppigi</i> Melin, 1941	<i>Adenomera hylaedactyla</i>
<i>Leptodactylus prognathus</i> Boulenger, 1888	<i>Leptodactylus latinasus</i> F
<i>Leptodactylus pulcher</i> Boulenger, 1898	<i>Barycholos pulcher</i>
<i>Leptodactylus pumilio</i> Boulenger, 1920	<i>Eleutherodactylus parvus</i>
<i>Entomoglossus pustulatus</i> Peters, 1870	<i>Leptodactylus pustulatus</i> M
<i>Rana pygmaea</i> Spix, 1824	<i>Leptodactylus ? ocellatus</i> O
<i>Leptodactylus quadrivittatus</i> Cope, 1893	<i>Leptodactylus poecilochilus</i> F
<i>Leptodactylus raniformis</i> Werner, 1899	<i>Leptodactylus ? raniformis</i> F
<i>Leptodactylus rhodomystax</i> Boulenger, 1883	<i>Leptodactylus rhodomystax</i> P
<i>Lepodactylus rhodonotus</i> Gunther, 1868	<i>Leptodactylus rhodonotus</i> P
<i>Plectomantis rhodostima</i> Cope, 1874	? <i>Lithodytes rhodostima</i>
<i>Leptodactylus romani</i> Melin, 1941	<i>Leptodactylus bolivianus</i> O
<i>Gnathophysa rubido</i> Cope, 1874	<i>Leptodactylus rhodonotus</i> P
<i>Leptodactylus rugosus</i> Nobel, 1923	<i>Leptodactylus rugosus</i> P
<i>Leptodactylus rugosus</i> Melin, 1941	<i>Adenomera hylaedactyla</i>
<i>Cystignathus schomburgkii</i> Troschel, 1848	<i>Leptodactylus fuscus</i> F
<i>Leptodactylus serialis</i> Girard, 1853	<i>Leptodactylus ocellatus</i> O
<i>Rana sibilatrix</i> Wied-Neuwied, 1825	<i>Leptodactylus fuscus</i> F
<i>Leptodactylus stenodema</i> Jimenez de la Espada, 1875	<i>Leptodactylus stenodema</i> P
<i>Leptodactylus stictigularis</i> Noble, 1923	<i>Leptodactylus rhodomystax</i> P
<i>Leptodactylus syphax</i> Bokermann, 1969	<i>Leptodactylus syphax</i> P
<i>Leptodactylus trivittatus</i> Lutz, 1926	<i>Adenomera marmorata</i>

TABLE 4 (continued)

Name Proposed	Present Allocation
<i>Leptodactylus troglodytes</i> Lutz, 1926	<i>Leptodactylus bufonius</i> F
<i>Leptodactylus tuberculosus</i> Andersson, 1945	<i>Ischnocnema quixensis</i>
<i>Rana typhonia</i> Daudin, 1803	<i>Leptodactylus fuscus</i> F
<i>Cystignathus typhonius</i> Dumeril and Bibron, 1841	<i>Leptodactylus fuscus</i> F
<i>Leptodactylus validus</i> Garman, 1887	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus vastus</i> Lutz, 1930	<i>Leptodactylus pentadactylus</i> P
<i>Leptodactylus ventrilineatus</i> Shreve, 1936	<i>Eleutherodactylus ventrilineatus</i>
<i>Leptodactylus ventrimaculatus</i> Boulenger, 1902	<i>Leptodactylus ventrimaculatus</i> F
<i>Leptodactylus vilarsi</i> Melin, 1941	<i>Leptodactylus ? rhodomystax</i> P
<i>Plectromantis wagneri</i> Peters, 1862	<i>Leptodactylus wagneri</i> M
<i>Leptodactylus wuchereri</i> Jimenez de la Espada, 1875	<i>Leptodactylus pentadactylus</i> P

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