

Analysis of the Intergeneric
Relationships of the Australian
Frog Family Myobatrachidae

W. RONALD HEYER
and
DAVID S. LIEM

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ABSTRACT

Heyer, W. Ronald, and David S. Liem. Analysis of the Intergeneric Relationships of the Australian Frog Family Myobatrachidae. *Smithsonian Contributions to Zoology*, number 233, 29 pages, 28 figures, 2 tables, 1976.—Forty-two characters of external morphology, myology, osteology, and life history are studied. For each character, the evolutionary directions of changes of states are inferred. This information is used to construct a phylogenetic hypothesis of the intergeneric relationships of the primarily Australian frog family Myobatrachidae. Three major groupings of myobatrachids are proposed; these are accorded subfamilial status. One of the subfamilies is defined as new. In addition, three genera are proposed as new.

It is proposed that the ancestral myobatrachid stock was associated with the Antarcto-Tertiary Geoflora. Several genera still demonstrate a distribution associated with this beech-podocarp vegetation. Major evolutionary events in the family have been associated with stream adaptations, trends toward and including direct development and fossorial adaptations. Convergence in these events with the leptodactylid frog fauna of southern South America is commented upon.

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*W. Ronald Heyer
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Introduction

The intergeneric relationships of the Australian frog family Myobatrachidae (Leptodactylidae of most authors) have been analyzed recently. Lynch (1971) used a standard systematic approach to the problem while Liem (in press) used a numerical taxonomy approach. Neither author used the phylogenetic approach as outlined by Hennig (1966). The purpose of this paper is to apply the same methods of analysis of relationships to the Australian myobatrachids as have been applied recently to the Neotropical leptodactylids (Heyer, 1975a).

METHODS AND MATERIALS.—Character states are categorized for a number of characters from the study sample. The directionality of states is analyzed and the information from derived states is used to generate possible phylogenetic trees.

The characters used are mostly those described by Liem (in press). Liem's study included members of the family Pelodyadidae. Characters in Liem's study which have uniform states in the Myobatrachidae are not used. Some other of Liem's characters, for which not enough comparable information is known in other frogs to deter-

mine directionality of states, are also deleted.

The taxa used for analysis are those recognized by Liem (in press) with certain exceptions. Blake (1973) and Liem (in press) used similar numerical techniques of analysis on some of the same genera with conflicting systematic results. For purposes of analysis, the smallest generic groupings are used to test the hypotheses of Blake and Liem. In addition to the genera recognized by Liem (in press), the following units are added: (1) *Crinia georgiana*, (2) *Crinia haswelli*, (3) *Ranidella* (as used by Blake, 1973), and (4) *Pseudophryne occidentalis*.

The criteria used for determining directionality of character states are the same as those used previously (Heyer, 1975a). In those cases where the character states of this study are the same as those used in the leptodactylid study (Heyer, 1975a), the arguments for directionality are the same and are not recounted here. This omission is occasioned by the other study's having used the myobatrachids as the major outgroup for determination of state directionality. A primitive state for the leptodactylids can also be assumed to be the primitive state for the myobatrachids if the assumption is made that the myobatrachids and leptodactylids had a common ancestor. The primitive state is always coded as zero in the character analysis section.

Life history and geographic range data were taken from the published literature (most of the

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papers included in "Literature Cited"), Ian R. Straughan's unpublished dissertation (1966), and personal observations (DSL).

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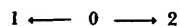
Thanks are due also to Hobart M. Smith, University of Colorado, who originally suggested the collaboration that produced this manuscript.

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Character Analysis

CHARACTER 1, maxillary teeth: *state 0*, maxillary teeth present, pedicellate; *state 1*, maxillary teeth present, fanglike, at least in some species; *state 2*, maxillary teeth uniformly absent or absent in some species.

Trueb (1973:79) indicated that states 1 and 2 are independently derived states from state 0. The directions of change of character states are:

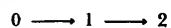


CHARACTER 2, nasal contact with frontoparietal: *state 0*, nasals not in contact with frontoparietal; *state 1*, nasals in contact with frontoparietal.

Heyer (1975a) indicated that state 0 is primitive.

CHARACTER 3, carotid canal: *state 0*, exposed shallow channel or carotid canal absent; *state 1*, exposed shallow canal present, at least in some species; *state 2*, carotid canal present, at least in some species.

Lynch (1971) suggested that the carotid canal is formed by thickening of the frontoparietal posteriorly and/or involving dermal coossification resulting in the enclosure of the carotid artery in a bony canal. Since the vast majority of frogs have state 0, it is considered the primitive state (criterion II of Heyer, 1975a). The direction of change of character states is:



CHARACTER 4, frontoparietal fontanelle: *state 0*, frontoparietals separated medially, exposing fon-

tanelle; *state 1*, frontoparietal fontanelle covered, at least in some species.

Heyer (1975a) showed that state 0 is the primitive state.

CHARACTER 5, sphenethmoid: *state 0*, sphenethmoid entire; *state 1*, sphenethmoid divided, at least in some species.

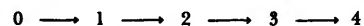
Trueb (1973) thought state 1 reflects reduced ossification. Among the New World and African leptodactyls, only *Euparkerella* and *Tomodactylus* have state 1 (Lynch, 1971). State 1 is considered the derived state (criterion II of Heyer, 1975a).

CHARACTER 6, squamosal: *state 0*, zygomatic and otic rami about equal length, both moderately long; *state 1*, zygomatic ramus shorter than otic ramus, at least in some species.

Heyer (1975a) showed state 0 to be primitive.

CHARACTER 7, vomer and vomerine teeth: *state 0*, vomer and vomerine teeth present uniformly; *state 1*, intrageneric variation, all species with vomer present, at least some species with vomerine teeth absent; *state 2*, vomer present, vomerine teeth absent uniformly; *state 3*, intrageneric variation, at least some species with vomer and vomerine teeth absent; *state 4*, vomer and vomerine teeth uniformly absent.

Heyer (1975a) indicated state 0 to be the primitive state. The direction of change of character states is:



CHARACTER 8, intervertebral disc: *state 0*, intervertebral disc fused to the posterior end of the centrum (procoelous); *state 1*, intervertebral disc free between centra of presacral vertebrae (amphicoelous).

Trueb (1973) considered amphicoely as the probable ancestral frog condition, but thought it likely that amphicoely in modern frogs is a pedomorphic trait, hence derived. The African leptodactylid, *Heleophryne*, is amphicoelous, the New World leptodactylids are uniformly procoelous. Thus, the closest outgroup members do not clearly indicate which state is primitive. Expansion of the outgroup clarifies the situation. Bufonids, hylids, pseudids, dendrobatids, and centrolenids are uniformly procoelous. State 0 is considered the primitive state.

CHARACTER 9, cervical vertebrae: *state 0*, cervical

and second vertebrae free; *state 1*, cervical and second vertebrae fused.

Trueb (1973) stated the fused condition to be derived. Lynch (1971) found state 0 uniformly in the African and Neotropical leptodactyloids. State 0 is considered the primitive state (criterion I of Heyer, 1975a).

CHARACTER 10, cervical cotyles: *state 0*, cervical cotyles narrowly separated; *state 1*, cervical cotyles widely separated.

Heyer (1975a) indicated state 0 to be the primitive state.

CHARACTER 11, relationship of transverse process of last presacral vertebra to sacral vertebra: *state 0*, last presacral vertebra noticeably shorter than sacrum; *state 1*, last presacral vertebra about same width as sacrum.

Heyer (1975a) indicated the primitive state to be 0.

CHARACTER 12, sacral diapophyses: *state 0*, sacral diapophyses expanded; *state 1*, sacral diapophyses rounded uniformly, in at least some species.

Heyer (1975a) indicated the primitive state to be 0.

CHARACTER 13, coccyx: *state 0*, prezygapophyses and transverse processes present; *state 1*, prezygapophyses and transverse processes absent.

Trueb (1973) suggested state 0 to be primitive.

CHARACTER 14, dorsal crest of ilium: *state 0*, no dorsal crest; *state 1*, well defined crest present.

Heyer (1975a) indicated the primitive state to be 0.

CHARACTER 15, carpals: *state 0*, first, second, third carpal and naviculare free; *state 1*, at least one element of state 0 demonstrating fusion.

Geocrinia victoriana is the only member of the genus demonstrating state 1. Since all other species have state 0, *Geocrinia* is coded as state 0. Trueb (1973) and Liem (1970), following Howes and Ridewood (1888), indicated state 0 to be the primitive state.

CHARACTER 16, prehallux: *state 0*, prehallux of 1 to 3 segments with blunt or pointed distal segments; *state 1*, prehallux of one shovel shaped segment, at least in some species.

Heyer (1975a) indicated state 0 to be primitive.

CHARACTER 17, cricoid: *state 0*, cricoid forming a complete ring; *state 1*, cricoid not forming a complete ring.

All Neotropical and African leptodactyloids

have state 0 (Lynch, 1971). State 0 is assumed the primitive state (Criterion I of Heyer, 1975a).

CHARACTER 18, alary process of the hyoid: *state 0*, alary process broad and wing-like; *state 1*, alary process stalked, distally expanded into rounded or oval plates.

Heyer (1975a) considered state 1 to be the primitive state, but found it to be a poor predictor of phylogenetic relationships. In a consideration of the relationships among the species of the genus *Adenomera* (Heyer, 1975b), the better assumption appeared to be that state 0 is the primitive state. State 0 is here considered the primitive state.

CHARACTER 19, anterior process of the hyale: *state 0*, anterior process present; *state 1*, anterior process absent.

Heyer (1975a) indicated state 0 to be primitive.

CHARACTER 20, depressor mandibulae muscle: *state 0*, slip from dorsal fascia present; *state 1*, intrageneric variation, some species with state 0, others with state 2; *state 2*, no dorsal fascia slip.

The condition for *Asa* is not known and assumed to be primitive for purposes of analysis. Heyer (1975a) indicated that state 0 is primitive relative to state 2 as described here. The direction of change of character states is:

$$0 \longrightarrow 1 \longrightarrow 2$$

CHARACTER 21, adductor mandibularis muscle: *state 0*, both adductor mandibulae posterior subexternus and adductor mandibulae externus superficialis present; *state 1*, adductor mandibulae posterior subexternus only present; *state 2*, adductor mandibulae externus superficialis only present.

Heyer (1975a) indicated state 0 is primitive. Directions of change of character states are:

$$1 \longleftarrow 0 \longrightarrow 2$$

CHARACTER 22, supracoracoideus superficialis and profundus muscles: *state 0*, muscles separate; *state 1*, muscles fused, at least in some species.

Jones (1933) demonstrated that state 0 is the general state in frogs. State 0 is assumed the primitive state (Criterion II of Heyer, 1975a).

CHARACTER 23, adductor longus muscle: *state 0*, muscle inserting on knee; *state 1*, muscle inserting on distal $\frac{1}{2}$ to $\frac{1}{3}$ of adductor magnus muscle or absent.

Heyer (1975a) indicated that state 0 is primitive.

CHARACTER 24, semitendinosus muscle distal ten-

don insertion: *state 0*, distal tendon insertion ventral to femoral tendon of gracilis muscle; *state 1*, distal tendon insertion dorsal to femoral tendon of gracilis muscle; *state 2*, distal tendon piercing the gracilis muscle or femoral tendon of the gracilis muscle.

State 0 is the common state among the frogs considered to be related to, or primitive to, the myobatrachids (Dunlap, 1960). State 0 is assumed the primitive state (Criterion II of Heyer, 1975a). The directions of changes of character states are:

$$1 \leftarrow 0 \rightarrow 2$$

Taudactylus species demonstrate both states 1 and 2. As these states are coded as independently derived, the genus is coded as having state 0 for purposes of analysis.

CHARACTER 25, adductor magnus muscle: *state 0*, accessory head absent; *state 1*, accessory head present.

State 0 is found in the Ascaphidae, Discoglossidae, Liopelmatidae, Microhylidae, Pelobatidae, Pipidae, and Rhinophrynidae; *state 1* is the usual state for the remaining families (Dunlap, 1960). State 0 is assumed to be the primitive state (Criterion II of Heyer, 1975a, for expanded outgroup).

CHARACTER 26, extensor cruris brevis muscle: *state 0*, muscle as long as tibio-fibula; *state 1*, muscle from $\frac{1}{3}$ to $\frac{2}{3}$ length of tibio-fibula.

The common condition among frogs is *state 0* (Dunlap, 1960). State 0 is assumed the primitive state (Criterion II of Heyer, 1975a).

CHARACTER 27, abductor brevis plantaris hallucis muscle: *state 0*, muscle absent; *state 1*, muscle present, no accessory slip; *state 2*, muscle and accessory slip present.

The muscle is absent in *Ascaphus*, *Leiopelma*, *Pipa*, and *Rhinophrynus* (Dunlap, 1960), suggesting that this is the primitive state (Criterion II of Heyer, 1975a). Liem (in press) stated that an accessory slip was essentially unique to certain myobatrachids. The direction of change of character states is:

$$0 \rightarrow 1 \rightarrow 2$$

CHARACTER 28, Omohyoideus: *state 0*, muscle present in all species; *state 1*, muscle present in some species, absent in others; *state 2*, muscle absent in all species.

Heyer (1975a) indicated the direction of change of states is:

$$0 \rightarrow 1 \rightarrow 2$$

CHARACTER 29, geniohyoideus medialis muscle: *state 0*, muscle contiguous medially; *state 1*, muscle separated medially.

Heyer (1975a) indicated *state 0* is the primitive state.

CHARACTER 30, sternohyoideus ventralis muscle insertion: *state 0*, muscle insertion near lateral edge of hyoid body; *state 1*, muscle insertion extending to midline of hyoid body.

Heyer (1975a) indicated *state 0* is the primitive state.

CHARACTER 31, petrohyoideus anterior muscle: *state 0*, muscle insertion on lateral edge of hyoid plate; *state 1*, muscle insertion on ventral body of hyoid.

Heyer (1975a) indicated *state 0* is the primitive state.

CHARACTER 32, petrohyoideus posterior muscles: *state 0*, three slips present; *state 1*, two slips present.

Most frogs have *state 0* (Trewavas, 1933; Liem, 1970); the state is assumed primitive (Criterion II of Heyer, 1975a).

CHARACTER 33, dilatator laryngis muscles: *state 0*, one pair of slips present; *state 1*, some species with one pair, others with two pairs of slips present; *state 2*, two pairs of slips present.

The usual state for frogs is *state 0* (Trewavas, 1933); *state 0* is assumed the primitive state (Criterion II of Heyer, 1975a). The direction of change of states is:

$$0 \rightarrow 1 \rightarrow 2$$

CHARACTER 34, pupil shape: *state 0*, pupil vertical; *state 1*, pupil horizontal.

Heyer (1975a) indicated *state 0* is the primitive state.

CHARACTER 35, abdominal skin texture: *state 0*, skin of abdomen smooth; *state 1*, skin of abdomen coarsely granular in some or all species.

The majority of frogs have *state 0*; it is assumed primitive (Criterion II of Heyer, 1975a).

CHARACTER 36, tongue: *state 0*, tongue free posteriorly; *state 1*, tongue adherent to mouth floor.

About 10 genera of frogs have *state 1*; the state is considered derived (Criterion II of Heyer, 1975a).

CHARACTER 37, toe webbing; *state 0*, toes webbed; *state 1*, toes fringed in some or all species; *state 2*, toes free in some or all species.

Heyer (1975a) indicated the direction of change of character states to be:

0 → 1 → 2

CHARACTER 38, inner metatarsal tubercle: *state 0*, inner metatarsal tubercle not enlarged and shovel-shaped; *state 1*, inner metatarsal tubercle enlarged, shovel-shaped, compressed, and keeled.

State 0 is considered primitive (Heyer, 1975a).

CHARACTER 39, outer metatarsal tubercle: *state 0*, absent; *state 1*, absent in some species, present in others; *state 2*, present, unmodified; *state 3*, present, strongly compressed.

Heyer (1975a) indicated state 0 to be the primitive state. The direction of change of character states is:

0 → 1 → 2 → 3

CHARACTER 40, intermandibularis muscle: *state 0*, no intermandibularis-submentalis connection; *state 1*, intermandibularis-submentalis connection present.

The generalized distribution of state 0 (Tyler, 1971) suggests this state to be primitive (criterion II of Heyer, 1975a).

CHARACTER 41, egg mass: *state 0*, not foamy; *state 1*, foamy.

Heyer (1975a) indicated state 1 to be derived.

CHARACTER 42, site of egg development: *state 0*, aquatic; *state 1*, non-aquatic, including terrestrial and parental brooding.

Heyer (1975a) indicated that state 0 is primitive.

The distribution of states among the taxa is presented in Table 1. The recoding of states as used in the next section is presented in Table 2.

Analysis of Relationships

The combinatorial method of Sharrock and Felsenstein (1975) was used to organize the data. The combinatorial method locates all monothetic clusters in the data set and prints them out. Information from the character state trees was included; the clusters were formed with derived states only. The construction of the first phylogeny (Figure 1) maximized the number of shared derived states at each clustering point. Certain

conclusions can be drawn from the phylogeny of Figure 1. There are three major groupings of myobatrachid frogs: *Rheobatrachus* forms a group by itself and apparently has little if any relationship to the remaining genera; the remaining genera form two major clusters, corresponding with taxonomic proposals made by previous workers. The cluster including *Myobatrachus* corresponds with the subfamily Myobatrachinae; the cluster including *Limnodynastes* corresponds with the subfamily Limnodynastinae (Liem, in press) (=Cyclorantinae of Lynch, 1971, and Parker, 1940, except for the exclusion of *Cyclorana*). The basal clusters defining the two groups each contain unique state appearances within the tree. As discussed later, three of the muscle characters may be miscoded; nevertheless, each cluster still has unique state appearances within the tree. These two groups are convincing sister groups in terms of Hennig's (1966) terminology. There are no other meaningful arrangements of these two groups.

There are several rearrangements possible within each group, however, that need detailed comment.

The cluster of *Assa*, *Metacrinia*, *Pseudophryne*, and *Pseudophryne occidentalis* is the strongest cluster in the data set, indicating that the closest relationship of any of these taxa is with the other three. Characters not used in the analysis provide evidence to suggest a rearrangement within the cluster. First, however, the cluster of *Pseudophryne occidentalis* and *Pseudophryne* is substantiated: all members lack tympani and columellae, have a unique locomotion of crawling (except *P. douglasi*) (Liem, in press), and have a uniform mating call (Liem, in press). *Pseudophryne* does form a sister group with *P. occidentalis*; all *Pseudophryne* (except *P. occidentalis*) have the derived state of the depressor mandibulae muscle and have femoral glands (a derived condition, Heyer, 1975a), while *P. occidentalis* has narrow sacral diapophyses, a compressed outer metatarsal tubercle, and two slips of the dilatator laryngis muscles (Liem, in press). These morphological differences indicate different adaptive complexes in these two groups, differences best reflected at the generic level. Liem (in press) pointed out the distinctiveness of *P. occidentalis* but preferred not to recognize it at the generic level. Blake (1973) did not include *P. occidentalis* in his analysis.

Blake (1973) proposed placing *Metacrinia* in the

TABLE 1.—Distribution of character states among genera as used for computer coding ("9" indicates no information)

Genus	Character Numbers and States																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Adelotus	1	0	0	1	0	0	0	0	1	0	0	1	1	1	1	0	0	1	1	0	1
Assa	0	0	0	0	1	1	2	1	0	1	0	0	1	0	1	0	1	0	1	0	1
C. georgiana	0	0	0	0	1	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	1
C. haswelli	0	0	0	0	1	1	2	1	0	1	0	1	1	0	0	0	1	0	0	0	1
Geocrinia	0	0	0	0	1	1	1	1	0	1	0	1	1	0	0	0	1	0	0	0	1
Ranidella	0	0	0	0	1	1	3	1	0	1	0	1	1	0	0	0	1	0	0	1	1
Glauertia	2	0	1	0	1	1	4	1	0	0	0	1	1	0	1	1	1	0	1	1	2
Heleioporus	0	0	2	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	1
Kyarranus	0	0	2	0	0	1	0	0	1	0	0	1	1	0	1	0	0	1	1	0	1
Lechriodus	0	0	2	1	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	0	0
Limnodynastes	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	1
Metacrinia	2	0	0	0	1	1	2	1	0	1	0	1	1	0	1	0	1	0	1	0	1
Mixophyes	0	1	2	1	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	0
Myobatrachus	2	1	0	0	1	1	4	1	0	0	0	1	1	0	1	0	1	0	1	0	1
Neobatrachus	0	0	1	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	1
Notaden	2	0	1	0	1	1	0	0	1	0	0	1	1	0	1	1	0	1	1	0	1
Philoria	0	1	2	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	1	1	2
Platyplectron	0	0	2	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	1
Pseudophryne	2	0	0	0	1	1	3	1	0	1	0	0	1	0	1	0	1	0	1	2	1
P. occidentalis	2	0	0	0	1	1	4	1	0	1	0	1	1	0	1	0	1	0	1	0	1
Rheobatrachus	1	0	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Taudactylus	0	0	0	1	1	1	2	1	0	1	0	0	1	0	0	0	1	0	1	0	1
Uperoleia	1	0	2	1	1	1	3	1	0	1	0	0	1	0	1	0	1	0	1	2	1

Genus	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Adelotus	1	1	2	1	1	2	2	0	1	0	0	0	1	0	1	0	0	2	1	1	0
Assa	1	0	1	0	0	0	2	1	1	1	1	0	1	0	0	2	0	2	0	0	1
C. georgiana	1	0	1	0	0	0	0	1	1	1	0	0	1	1	0	2	0	2	0	0	0
C. haswelli	1	0	1	0	0	0	2	1	1	1	0	2	1	0	0	1	0	2	0	0	0
Geocrinia	1	0	1	0	0	0	1	1	1	1	0	1	1	0	0	2	0	0	0	0	1
Ranidella	1	0	1	0	0	0	0	1	1	1	0	0	1	1	0	2	0	2	0	0	0
Glauertia	1	0	1	0	0	0	2	1	1	1	0	2	1	1	0	0	0	3	0	0	0
Heleioporus	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1
Kyarranus	1	1	0	1	0	2	2	0	1	0	0	0	1	0	0	2	0	0	1	1	1
Lechriodus	1	1	2	1	1	1	0	0	0	0	0	0	1	0	0	2	0	0	1	1	0
Limnodynastes	1	1	2	1	0	2	2	0	0	0	0	0	1	0	0	2	0	1	1	1	0
Metacrinia	1	0	1	0	0	0	2	1	1	1	1	0	1	1	0	2	0	2	0	0	1
Mixophyes	0	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Myobatrachus	0	0	1	0	0	0	2	0	1	1	1	2	1	0	0	2	0	0	0	0	1
Neobatrachus	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Notaden	1	0	0	0	1	0	2	0	1	0	0	0	0	0	0	0	1	1	1	0	0
Philoria	0	1	0	1	0	2	2	0	1	0	0	0	1	0	0	2	0	0	1	1	1
Platyplectron	1	1	2	1	1	2	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0
Pseudophryne	1	0	1	0	0	0	2	1	1	1	0	0	1	0	0	2	0	2	0	0	1
P. occidentalis	1	0	1	0	0	0	2	1	1	1	0	0	1	0	0	2	0	3	0	0	1
Rheobatrachus	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	2	0	0	1
Taudactylus	0	1	0	0	0	1	0	1	1	1	0	1	1	0	0	1	0	2	0	0	0
Uperoleia	1	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	3	0	0	0

synonymy of *Pseudophryne*. This action is not supported by the present study. *Metacrinia* and *Pseudophryne* (including *occidentalis*) form robust sister groups: *Pseudophryne* lacks a columella and crawls (except *P. douglasi*); *Metacrinia* has the derived state of the posterior petrohyoideus muscle, a granular belly, and terrestrial larvae. These differences are best expressed at the generic level. The relationships of *Metacrinia* appear to lie closest with *Assa*, in fact. Within the characters used for analysis, all of the derived states of *Assa* are shared with *Metacrinia*. Thus, within the cluster of four, *Assa* and *Metacrinia* together share the derived state of the posterior petrohyoideus muscle. In addition, both taxa have the derived condition of reduction of a phalanx in the first finger, a state found additionally only in *Uperoleia*. *Metacrinia* and *Assa* do form sister groups when more life history information is added: *Metacrinia* has narrow sacral diapophyses and a granular belly; *Assa* has male brooding pouches. This distinctive life history pattern is best expressed at the generic level as currently recognized.

In the phylogeny of Figure 1, *Crinia georgiana* does not form a monothetic cluster with *Geocrinia*. A better arrangement, in which all clusters are monothetic, involves pairing *C. georgiana* with *Ranidella*, and *Geocrinia* with *C. haswelli*. Interestingly, a combination of these four taxa does not form a monothetic cluster. The combination of all four with *Assa*, *Metacrinia*, and *Pseudophryne* (including *occidentalis*) is a monothetic cluster, as is a cluster of either *C. georgiana*-*Ranidella* or *Geocrinia*-*C. haswelli* with *Assa*, *Metacrinia*, and *Pseudophryne*. There is no clear advantage to be gained from choosing between these last alternatives in terms of numbers of shared states within clusters, or number of convergent states. Thus, while all of the above taxa seem to be most closely related among themselves, the combination of *C. georgiana*, *C. haswelli*, *Geocrinia*, and *Ranidella* is a poor cluster since it is not monothetic.

Placement of *C. haswelli* with *Geocrinia* agrees with Liem (in press), but disagrees with Blake (1973), who placed *C. haswelli* together with *C. georgiana*. *Crinia georgiana* and *C. haswelli* do not form a monothetic cluster in the present data set, indicating that they are not most closely related. *Geocrinia* and *C. haswelli* appear to be a robust sister group (Figure 2) because *C. haswelli*

has 5 unique states and *Geocrinia* 2. However, many of these states are the uniform expression of a variable state. For example, the omohyoideus is absent in *haswelli*, but it is also absent in some *Geocrinia*. Thus these kinds of states can not be used to define clear cut sister groups. Each taxon has one unique state: *C. haswelli* has an outer metatarsal tubercle; *Geocrinia* has terrestrial egg deposition. A further complication in attempting to deduce relationships is occasioned by the fact that *C. haswelli* actually shares two more derived states with the cluster of *Assa*, *Metacrinia*, and *Pseudophryne* (including *P. occidentalis*) than with *Geocrinia*. The taxonomic decision of whether to recognize *C. haswelli* as a distinct genus has a parallel, in part, with the *Ranidella* complex; the decision involving *C. haswelli* will be deferred until the situation with *Ranidella* is described.

On the basis of the characters analyzed for this study, all of the derived states of *Crinia georgiana* are found within *Ranidella*, suggesting that these two taxa are most closely related to each other. Once the individual characters are examined in detail, it becomes apparent that *R. riparia* is distinctive within *Ranidella*, and for purposes of present discussion should be separated. The best placement of *Ranidella riparia* is with *C. georgiana* and the remaining *Ranidella* Liem (in press) examined (Figure 2). States 9, 10, and 11 separate *C. georgiana* from *Ranidella* (restricted sense). All these states involve reduction of the vomer and vomerine teeth. Vomerine teeth are absent in *Ranidella* (restricted sense), the vomer is present or absent. Since there is a trend within *Ranidella* (restricted sense), it is not unreasonable to carry the trend back one step further to include *C. georgiana* within the same genus. The larval evidence (Watson and Martin, 1973) does not support inclusion of *C. georgiana* in with *Ranidella* (restricted), because *C. georgiana* has a stream adapted tadpole (as do *R. riparia* and *R. tasmaniensis*). Of the species examined in this study, *R. riparia* is distinctive from a cluster of *C. georgiana* and *Ranidella* (restricted sense) in mandibular musculature, terrestrial egg placement, and possibly loss of the columella (Blake, 1973, so indicates; Liem, in press, does not). The mating call of *C. georgiana* is a unique quacking call, distinctive within the *Ranidella* complex (Main, 1968).

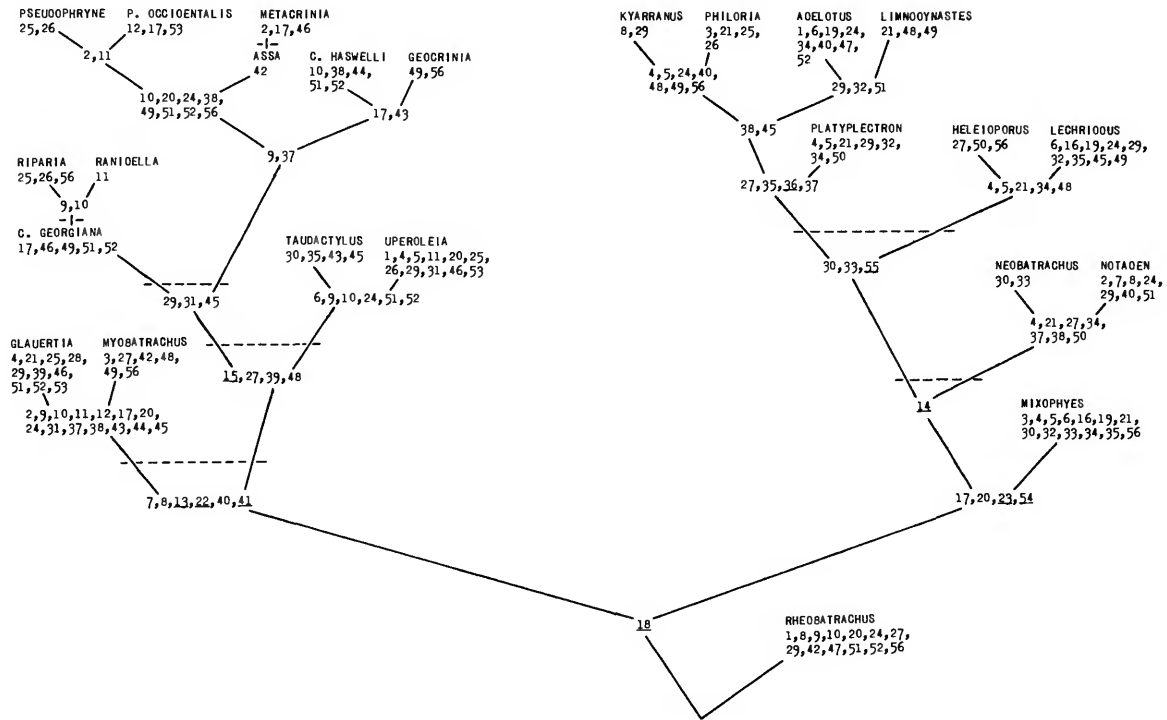


FIGURE 2.—Alternate phylogenetic relationships among the myobatrachid genera. (Underlined states = unique appearances within phylogeny; dashed lines = lineages are not sister groups; see text.)

In attempting to determine the relationships among *Crinia georgiana*, *C. haswelli*, *Ranidella riparia*, *Geocrinia*, and *Ranidella*, certain characters are keys to understanding the relationships: vomer and vomerine teeth, omohyoideus muscle, outer metatarsal tubercle, belly texture, and egg placement. There is no way to group the myobatrachine taxa so that two of the derived states of these characters define the same assemblage. Rather, a grouping which results in a cluster having all the taxa with the same derived state of one character leads to convergence of states in the other characters. The most reasonable assumption is that the common ancestor of the group had the genetic potential to produce the states in question, but, in part, the results were a mosaic pattern. Based on this assumption, the most reasonable taxonomic criteria to describe the situation is the recognition of the following as distinct genera, indicating separate evolutionary lineages: (1)

Geocrinia, (2) *Crinia haswelli*, (3) *Crinia georgiana*, (4) *Ranidella*, and (5) *R. riparia* and *R. tasmaniensis* (latter was not included in Liem's, in press, study sample). This arrangement is consistent with the available larval evidence (Watson and Martin, 1973) and has the advantage that each unit is homogeneous with respect to life history mode. Separation of *tasmaniensis* from *Crinia*, sensu lato, has been previously suggested (Littlejohn, 1970).

Of the remaining myobatrachine taxa, *Taudactylus* and *Uperoleia* are most closely related, and when joined with the taxa mentioned above, form a monothetic cluster with a unique state appearance (Figure 2). *Glauertia* and *Myobatrachus* are closely related and can also form a monothetic cluster at the same level as *Taudactylus* and *Uperoleia* of Figure 2, but the cluster does not have a unique state appearance.

The proposed relationships among the limnodynastines of Figure 1 contain one non-monothetic

cluster. If clusters are chosen to maximize the number of appearances of unique states within the total phylogeny, one major difference in placement occurs: the location of *Mixophyes*. With *Mixophyes* removed basally, the remaining limnodynastines have fused cervical and second vertebrae. *Mixophyes* is unique in that the nervus mandibularis lies between the levator mandibulae externus and subexternus muscles, it is the only myobatrachid genus with axillary amplexus (DSL), the genus is unique in egg placement (Liem, in press) and tadpole morphology (Watson and Martin, 1973), further supporting the basal dichotomy as represented in the phylogeny of Figure 2.

Liem (in press) thought *Heleioporus* and *Neobatrachus* to be closely related. This hypothesis is not substantiated by this study; in fact, the two taxa do not share a monothetic cluster. Assuming that *Neobatrachus* has closest relationships with *Notaden*, then the remaining limnodynastines are characterized by eggs laid in foam nests.

Liem (in press) indicated a close relationship between *Adelotus* and *Lechriodus*. Apparently this was occasioned by shared primitive states, since analysis of the derived states indicates the closest relationships of *Adelotus* and *Lechriodus* lie elsewhere rather than with each other (Figure 2).

Liem (in press), following the lead of Littlejohn (1963), proposed placing *Kyarranus* in the synonymy of *Phyloria*. These two taxa share the most derived states among the limnodynastines. Further, the two taxa uniquely share the derived life history pattern of nonaquatic, nonfeeding larvae among the limnodynastines. Within this study, *Kyarranus* and *Phyloria* form sister groups, *Kyarranus* having derived states of the squamosal and the supracoracoideus muscle, *Phyloria* having derived states of the nasal and frontoparietal relationship, prehallux, and depressor mandibulae muscle. *Phyloria* has undergone a separate evolutionary history from *Kyarranus* although both had a common ancestor. It seems rather a point of personal preference whether the emphasis is on the common ancestry, resulting in recognition of a single genus, or on the evolutionary divergence, suggesting two genera. In fact, we disagree on this one point: the first author prefers to recognize two genera, the second author prefers to recognize one. For purposes of this study, *Kyarranus* and *Phyloria* are

considered as separate generic units in order to present more information.

SISTER GROUPS WITHIN THE PHYLOGENY

Within the phylogeny of Figure 2, those dichotomies not representing sister groups (Hennig, 1966) are indicated by dashed lines. In two cases, additional information is needed to recognize sister groups. In the case of *Mixophyes* and the remaining limnodynastines, the life history information has been presented previously. In the case of *Rheobatrachus* compared with the rest of the genera, *Rheobatrachus* has a unique sacro-coccygeal articulation (Liem, 1973) and a unique developmental pattern of gastric larval incubation (Corben, Ingram, Tyler, 1974). As argued elsewhere (Heyer, 1975a), the weakest areas in the phylogenies occur where sister groups are not present. It seems reasonable to assume that higher taxa recognized in an analysis of this sort should be sister groups.

COMPARISON WITH PREVIOUS SCHEMES

Lynch (1971) summarized the classificatory schemes of the myobatrachids, with the exception of *Rheobatrachus*, which was unknown to science at that time. Parker (1940) was the first to recognize the distinctiveness of the myobatrachines and limnodynastines. Lynch's (1971) study, as well as the present study, supports Parker's conclusions. Lynch (1971) further recognized two tribes in the limnodynastines. The present study does not support that conclusion, since Lynch included *Heleioporus*, *Mixophyes*, *Neobatrachus*, and *Notaden* in a single tribe. The results of this study point to the distinctiveness of *Mixophyes* within the limnodynastines.

Liem (in press) included *Rheobatrachus* in the subfamily Myobatrachinae. In contrast to the present study, Liem (in press) also drew some different systematic conclusions at the generic level, as did Blake (1973) in his study of the Myobatrachinae. Differences between this study and Liem's and Blake's studies are due to the different analytic procedures used. Both Liem (in press) and Blake (1973) used a phenetic approach in which primitive and derived states were used to produce phylogenetic hypotheses. In this study, only derived state information was used to produce phylogenetic

hypotheses. We think that clusters based on shared primitive states are weak, since there is no information with respect to change from an ancestral condition. All taxa can be systematically thought of as collections of primitive and derived character states. The primitive states indicate no change in that character from the ancestral condition. The derived states do indicate a change from an ancestral condition. If groups of taxa share the same derived states, they may form a common evolutionary lineage. From a philosophical point of view, we think the approach used in this study is superior for deducing relationships than is a phenetic analysis, which indiscriminately uses primitive and derived character state information. The approximation of reality in the kind of analysis presented herein depends on the correctness of determination of primitive and derived states.

Systematic Conclusions

The relationships, as presented in the phylogenies (Figures 1, 2), are best represented by recognizing three subfamilies: one for *Rheobatrachus*, one for the myobatrachines, and a third for the limnodynastines. The limits of this study preclude an evaluation of the familial status of these three units. It may be that all three units are actually familial units. Some authors (Liem, in press; Watson and Martin, 1973) suggest that the myobatrachines and limnodynastines are familial units; this study demonstrates that *Rheobatrachus* is very distinctive from the myobatrachines and limnodynastines. Recognizing each as a subfamily has the advantage of pointing out the major differences within the total study group, while not adding taxonomic confusion to any future situation (a suprageneric taxon is available for a family name).

The only possible formal classification below the subfamily level that could be proposed confidently would be to recognize a tribe for *Mixophyes*. There seems, however, to be no advantage to emphasizing the distinctiveness of *Mixophyes* in a formal action.

The new taxonomic categories or combinations arising from this study are presented formally. Diagnostic definitions only are provided since the full character complements of the taxa are presented elsewhere within the paper (Table 1).

The genera of each of the subfamilies as recognized in this study are:

NEW SUBFAMILY	New genus for <i>Ranidella</i>
<i>Rheobatrachus</i>	<i>riparia</i> and <i>tasmaniensis</i>
MYOBATRACHINAE	LIMNODYNASTINAE
<i>Asa</i>	<i>Adelotus</i>
<i>Crinia</i>	<i>Heleioporus</i>
<i>Geocrinia</i>	<i>Kyarranus</i>
<i>Glauertia</i>	<i>Lechriodus</i>
<i>Metacrinia</i>	<i>Limnodynastes</i>
<i>Myobatrachus</i>	<i>Mixophyes</i>
<i>Pseudophryne</i>	<i>Neobatrachus</i>
<i>Taudactylus</i>	<i>Notaden</i>
<i>Uperoleia</i>	<i>Philoria</i>
New genus for <i>Pseudophryne occidentalis</i>	<i>Platyplectron</i>
New genus for <i>Crinia howelli</i>	

RHEOBATRACHINAE, new subfamily

TYPE-GENUS—*Rheobatrachus* Liem, 1973.

DIAGNOSIS—Maxillary teeth fanglike; fontanelle not roofed over by frontoparietals; columella present; cervical cotyles narrowly separated; sacral diapophyses broad; sacro-coccygeal articulation monocondylar; coccygeal prezygapophyses and transverse processes present; cricoid a complete ring; alary process of hyoid broad and winglike; pupil vertical; tongue adherent to mouth floor; outer metatarsal tubercle present; female gastric brooding of young.

CONTENT.—Monotypic, *Rheobatrachus silus*.

MYOBATRACHINAE Schlegel, 1850

Crinia Tschudi, 1838

TYPE-SPECIES.—*Crinia georgiana* Tschudi, 1838.

DIAGNOSIS.—A myobatrachine genus; cervical cotyles widely separated; vomer and vomerine teeth present; narrow sacral diapophyses; depressor mandibulae muscle with slip from dorsal fascia; omohyoideus muscle present; tympanum present; belly smooth; toes without fringe or web; outer metatarsal tubercle present; eggs placed in water; stream larvae.

CONTENT.—Monotypic, *Crinia georgiana*.

Geocrinia Blake, 1973

TYPE-SPECIES.—*Pterophrynus laevis* Günther, 1864.

DIAGNOSIS.—A myobatrachine genus; cervical cotyles widely separated; vomer present, vomerine teeth present or absent; narrow sacral diapophyses; depressor mandibulae muscle with slip from dorsal fascia; omohyoideus muscle present or absent; tympanum present; belly smooth; toes lacking fringe or web; outer metatarsal tubercle absent; eggs laid in concealed sites on land; pond larvae or terrestrial, non-feeding larvae.

CONTENT.—*Geocrinia laevis*, *leai*, *lutea*, *rosea*, *victoriana*.

Pseudophryne Fitzinger, 1843

TYPE-SPECIES.—*Phryniscus australis* (in part) Duméril and Bibron, 1841 (= *Pseudophryne semimarmorata* Lucas, 1892).

DIAGNOSIS.—A myobatrachine genus; cervical cotyles widely separated; vomer present or absent, vomerine teeth absent; broad sacral diapophyses; depressor mandibulae muscle lacking a slip from dorsal fascia; omohyoideus muscle absent; columella absent; belly smooth; toes free, no fringe or web; outer metatarsal tubercle present; eggs placed on land (except *P. douglasi*, which places eggs in water); pond larvae.

CONTENT.—*Pseudophryne australis*, *bibroni*, *coriacea*, *corroboree*, *dendyi*, *douglasi*, *guentheri*, *major*, *semimarmorata*.

Ranidella Girard, 1853

TYPE-SPECIES.—*Ranidella signifera* Girard, 1853.

DIAGNOSIS.—A myobatrachine genus; cervical cotyles widely separated; vomer present or absent, vomerine teeth absent; narrow sacral diapophyses; depressor mandibulae muscle with slip from dorsal fascia; omohyoideus muscle present; tympanum present; belly granular; toes fringed or free; outer metatarsal tubercle present; eggs placed in water; pond larvae.

CONTENT.—*Ranidella glauerti*, *insignifera*, *parinsignifera*, *pseudinsignifera*, *remota*, *signifera*, *sloanei*, *subinsignifera*, *tinnula*.

Paracrinia, new genus

TYPE-SPECIES.—*Crinia haswelli* Fletcher, 1894.

DIAGNOSIS.—A myobatrachine genus; cervical cotyles widely separated; vomer present, vomerine

teeth absent; narrow sacral diapophyses; depressor mandibulae muscle with slip from dorsal fascia; omohyoideus muscle absent; tympanum present; belly smooth; toes fringed; outer metatarsal tubercle present; eggs placed in water; pond larvae.

CONTENT.—Monotypic, *Paracrinia haswelli*.

ETYMOLOGY.—From the Greek *para* (= beside), indicating the fact that the relationships of this genus fall within the *Crinia* complex. The genus is feminine in gender.

Australocrinia, new genus

TYPE-SPECIES.—*Pterophrynus tasmaniensis* Günther, 1864.

DIAGNOSIS.—A myobatrachine genus; cervical cotyles widely separated; vomer present, vomerine teeth present or absent; narrow sacral diapophyses; depressor mandibulae muscle lacking slip from dorsal fascia; omohyoideus muscle present; tympanum present; belly granular; toes fringed or free; outer metatarsal tubercle present; eggs placed on land or water; stream or pond larvae.

CONTENT.—*Australocrinia riparia*, *tasmaniensis*.

ETYMOLOGY.—From the Latin *australis* (= southern), indicating the southern geographic distribution of this member of the *Crinia* complex. The genus is feminine in gender.

Kankanophryne, new genus

TYPE-SPECIES.—*Pseudophryne occidentalis* Parker, 1940.

DIAGNOSIS.—A myobatrachine genus; cervical cotyles widely separated; vomer and vomerine teeth absent; narrow sacral diapophyses; depressor mandibulae muscle with slip from dorsal fascia; omohyoideus muscle absent; columella absent; belly smooth; toes free of fringe or web; outer metatarsal tubercle present; eggs placed on land; pond larvae.

CONTENT.—Monotypic, *Kankanophryne occidentalis*.

ETYMOLOGY.—From the Greek *kankanos* (= dry), in reference to the arid distribution of this genus. The genus is feminine in gender.

Phyletic Character Analysis

The analysis of characters into primitive and

derived states seems overall to be intuitively sound, since the recognition of the myobatrachines and limnodynastines as distinct units is in agreement with every other systematist that has worked with the myobatrachids in any detail.

As discussed in detail elsewhere (Heyer, 1975a), an analysis of the phylogenetic usefulness of each character state can be made after the fact. This is done by using the information from the better phylogenetic tree to determine the number of appearances of each state (as printed) on the tree divided by the total number of taxa that actually have that state. The numeric values for each state are then ranked and grouped into categories. A value of 1 indicates no phylogenetic information; the smaller the number, the better the state links the taxa as found in the preferred phylogeny.

The phylogeny of Figure 2 was used for analysis, except that *riparia* and *Ranidella* were considered as a single unit to be consistent with the original data. For multistate characters, averages are used. Best characters have values of 0.04 to 0.20, good characters have values of 0.25 to 0.42, average characters have values of 0.50 to 0.60, poor characters have values of 0.67 to 1.00.

The best characters with a unique appearance in the phylogenetic tree are: intervertebral disc, cervical vertebral fusion, cervical cotyles, coccyx, cricoid, alary process of the hyoid, anterior petrohyoideus muscle, intermandibularis muscle, egg mass type. The best characters with two or more appearances in the tree are: sphenethmoid and geniohyoideus muscle.

Good characters are: squamosal, sacral diapophyses, carpals, adductor longus muscle, adductor magnus muscle, omohyoideus, sternohyoideus, pupil shape, and toe webbing.

Average characters are vomer and vomerine teeth, anterior process of the hyale, supracoracoideus muscle, semitendinosus muscle.

Poor characters are: maxillary teeth, nasal contact with frontoparietal, carotid canal, frontoparietal fontanelle, transverse process width, dorsal crest of ilium, prehallux, depressor mandibulae muscle, adductor mandibulae muscle, extensor cruralis brevis muscle, petrohyoideus posterior muscles, dilatator laryngis muscle, belly texture, tongue, inner metatarsal tubercle, outer metatarsal tubercle, site of egg development.

There are seven multistate characters in which

the states of a given character differ with respect to clustering behavior. State 1 of the vomer-vomerine teeth complex (character 7) has good clustering behavior, states 2 and 3 are average, state 4 is poor. State 1 of the adductor mandibulae muscle (character 21) has good clustering behavior, state 2 is poor. State 1 of the semitendinosus is good (character 24), state 2 is poor. State 1 of the abductor brevis plantaris hallucis muscle (character 27) is average, state 2 is best. State 1 of the dilatator laryngis muscle (character 33) is average, state 2 is poor. State 1 of toe webbing (character 37) is good, state 2 is average. States 1 and 2 of the outer metatarsal tubercle are average, state 3 is poor.

Examination of the characters indicates a discrepancy with respect to the hyoid complex. As noted in the character analysis, the broad, wing-like state of the alary process is thought to be the primitive state, in contrast to previous coding (Heyer, 1975a). The associated muscles, corresponding with broad winglike alary process, however, were coded as derived states, as in the previous study (Heyer, 1975a). The distribution of states indicates that in order to be consistent, the primitive and derived states should be reversed for the following characters: geniohyoideus medialis muscle (character 29), sternohyoideus muscle (character 30), and anterior petrohyoideus muscle (character 31).

The purpose of this entire analysis is to produce a likely phylogenetic hypothesis for the myobatrachids. The analysis thus far concludes that there are several changes that could be made in the original data set that would improve the phylogenetic hypothesis. The changes are: (1) deletion of *Rheobatrachus*, since its evolutionary history appears to be distinct from the evolutionary history of the other two subfamilies; (2) addition of *Australocrinia*; (3) reversal of direction of character states for character numbers 29, 30, and 31; (4) deletion of characters in the poor category (as analyzed above). The purpose of making the changes in the data set is not to draw new taxonomic conclusions. Taxonomic conclusions were drawn on the basis of the entire original data set. Rather, the purpose of making the changes is to determine whether the changes allow new insights into the relationships among the taxa.

The best arrangement of the taxa in terms of maximization of character states at each cluster,

a phylogenetic tree that differs from the trees produced by the original data set. We think the phylogeny based on the revised data set is a more plausible phylogenetic hypothesis, representing the best fit of the data with the probable phylogeny of the group.

Evolutionary Zoogeography

GENERIC DISTRIBUTION PATTERNS

The known geographic distributions of the genera, summarized in map form, are essential data for the determination of distribution patterns. This information for all genera is not available in a single source. Since the discussion that follows is based upon the basic distribution data, those data are presented here (Figures 5–28). In grouping the individual distribution maps into similar clusters and attempting to associate those patterns with features of the Australian climate, landscape, and/or vegetation, certain facts become apparent. No genus of myobatrachid frog is primarily adapted to the desert habitat (compare Figure 20, *Notaden*, the genus with the most extensive desert distribution, with Figure 4). In associating the distribution patterns with other features, the distributions can be understood best in terms of the vegetation types found in the region. The geographic distributions of the genera (Figures 5–28) show four major patterns associated with broad vegetational categories:

1. Distributions primarily restricted to the antarctic vegetation unit (temperate rainforest and subtropical rainforest), > 1520 mm rainfall isohyet. *Assa*, *Kyarranus*, *Lechriodus*, *Rheobatrachus*, and *Taudactylus* share this pattern.

2. Distributions limited to wet forest vegetation types (wet sclerophyll forest), ± 1000 mm isohyet. The genera are either found only in the eastern wet forest (*Adelotus*, *Mixophyes*, *Paracrinia*, *Phyllorhina*), the southwestern wet forests (*Crinia*, *Metacrinia*), or both eastern and southwestern wet forests (*Geocrinia*).

3. Distributions in both wet forest and sub-humid woodland, about 500 mm to 1000 mm isohyets. The distributions are either primarily eastern (*Australocrinia*, *Limnodynastes*), western (*Myobatrachus*), or eastern and western (*Heleioporus*, *Platyplectron*, *Pseudophryne*, *Ranidella*, *Uperoleia*).

4. Open woodland and shrubland distributions, neither wet forest nor primarily desert, < 500 mm isohyet. *Glauertia*, *Kankaphryne*, *Neobatrachus*, and *Notaden* share this pattern. Of these genera, *Notaden* has the most arid distribution pattern, being found in shrubland, spinifex plains, and sand dunes in the rainfall distribution region < 360 mm isohyet. For zoogeographic purposes, the arid distribution pattern of *Notaden* is not recognized as a distinct pattern because there is only one genus demonstrating the pattern.

The historical record of vegetation types in the Australian region allows some generalization on evolutionary trends and sequences within the Myobatrachidae. Details of past vegetation type distribution and paleoclimates in the Australian region are not well known. The following summary, which appears to be sufficient to explain major evolutionary and zoogeographic trends in myobatrachids, seems reasonably substantiated by the available data. The antarctic forest type (*Notho-*

(Continued on p. 22)



FIGURE 4.—Broad vegetation zones critical to analysis of myobatrachid distribution patterns. (Solid areas = antarctic vegetation unit; hatched areas = wet forests; stippled areas = sandy deserts.)



FIGURE 5.—Geographic distribution of the myobatrachid genus *Adelotus*.



FIGURE 6.—Geographic distribution of the myobatrachid genus *Assa*.



FIGURE 7.—Geographic distribution of the myobatrachid genus *Australocrinia*.



FIGURE 8.—Geographic distribution of the myobatrachid genus *Crinia*.



FIGURE 9.—Geographic distribution of the myobatrachid genus *Geocrinia*.



FIGURE 10.—Geographic distribution of the myobatrachid genus *Glauertia*.



FIGURE 11.—Geographic distribution of the myobatrachid genus *Heleioporus*.



FIGURE 12.—Geographic distribution of the myobatrachid genus *Kankanophryne*.



FIGURE 13.—Geographic distribution of the myobatrachid genus *Kyarranus*.



FIGURE 14.—Geographic distribution of the myobatrachid genus *Lechriodus*.



FIGURE 15.—Geographic distribution of the myobatrachid genus *Limnodynastes*.



FIGURE 16.—Geographic distribution of the myobatrachid genus *Metacrinia*.



FIGURE 17.—Geographic distribution of the myobatrachid genus *Mixophyes*.



FIGURE 18.—Geographic distribution of the myobatrachid genus *Myobatrachus*.



FIGURE 19.—Geographic distribution of the myobatrachid genus *Neobatrachus*.



FIGURE 20.—Geographic distribution of the myobatrachid genus *Notaden*.



FIGURE 21.—Geographic distribution of the myobatrachid genus *Paracrinia*.



FIGURE 22.—Geographic distribution of the myobatrachid genus *Philoria*.



FIGURE 23.—Geographic distribution of the myobatrachid genus *Platyplectron*.



FIGURE 24.—Geographic distribution of the myobatrachid genus *Pseudophryne*.



FIGURE 25.—Geographic distribution of the myobatrachid genus *Ranidella*.



FIGURE 26.—Geographic distribution of the myobatrachid genus *Rheobatrachus*.



FIGURE 27.—Geographic distribution of the myobatrachid genus *Taudactylus*.



FIGURE 28.—Geographic distribution of the myobatrachid genus *Uperoleia*.

fagus, podocarps) has had a long history in the Australian region and during the early Tertiary, at least, had a broader distribution than present. Cookson (1953), Cookson and Pike, (1953, 1954), and Darlington (1965) have shown that fossil remains of the antarctic vegetation have been found at several localities across southern Australia, suggesting a former continuous forest belt. It is probable that the extent of this forest unit has been affected by world wide climatic changes, especially glaciation cycles. Arid environments have long been a feature of the Australian continent. The Great Dividing Range was formed at the end of the Mesozoic, and arid environments have been present in Australia throughout the Tertiary to the present.

One of the most striking features in the evolution of myobatrachid frogs has been the lack of radiation in the strict desert environment. The desert habitat has been present in Australia for a long enough time to allow a radiation. The Australian deserts are apparently too harsh an environment for frogs; some particular species can tolerate desert conditions, but none are primarily adapted for desert life. A similar situation occurs with the Namib desert anuran fauna in South Africa (Channing, 1974).

The antarctic forest vegetation appears to be the vegetation type associated with the ancestral myobatrachid stock. This assumption is supported by the historical presence of this vegetation type and by the distributions of several genera limited strictly to this vegetation type. The genera presently restricted to the antarctic vegetation type represent the descendants of the original stock which was associated with the temperate antarctic forests. If a generalized life history pattern is assumed for the ancestral stock, then the following major evolutionary trends have occurred within the beech and podocarp forests: trends toward nonaquatic larvae; either direct development, inguinal pouch brooding, or gastric brooding; and a stream adapted life history.

A second stage in the historical zoogeography of the myobatrachids was the association with temperate wet forest (including *Eucalyptus*) types. The same adaptive trends are seen in this assemblage of genera as in the previous assemblage: trends toward direct development and stream adaptations.

A third stage was the evolution of forest forms

that could also live in more open formations. Adaptive trends in this group of genera include stream adaptations, burrowing, and possibly direct development.

A fourth stage in the evolutionary history of the myobatrachids involved adaptations leading to a primary radiation in open, rather arid vegetation types. The genera with this pattern either show a distribution associated with water (oasis effect) within a more arid region (*Glauertia*, *Kankano-phryne*), or burrowers that can utilize temporary bodies of water (*Neobatrachus*, *Notaden*).

To summarize, the major adaptations associated with the four generic distribution patterns are as follows:

Pattern 1 (Temperate/subtropical rainforest)

Gastric brooding: *Rheobatrachus*

Inguinal pouch brooding: *Asa*

Terrestrial egg

Nonfeeding larvae: *Kyarranus*

Stream adapted larvae: *Taudactylus*

Montane stream adaptations: *Rheobatrachus*, *Taudactylus*

Pattern 2 (Wet sclerophyll forest)

Terrestrial egg

Stream adapted larvae: *Crinia*, *Mixophyes*

Nonfeeding larvae: *Philoria*

Trend toward direct development: *Geocrinia*, part (*leai*, *laevis*)

Direct development: *Geocrinia*, part (*lutea*, *rosea*), *Metacrinia*

Pattern 3 (Wet forest and subhumid woodland)

Rapid egg development: *Platyplectron*, part (*ornatus*, *spenceri*)

Burrowing adaptations: *Heleioporus*, *Platyplectron*

Terrestrial egg

Stream adapted larvae: *Australocrinia*

Advanced larval development: *Pseudophryne* (except *douglasi*)

Foam nest in burrow: *Heleioporus*

Possible direct development: *Myobatrachus*

Pattern 4 (Open woodland and shrubland)

Short larval life: *Kankano-phryne*, *Neobatrachus*, *Notaden*

Burrowing adaptations: *Neobatrachus*, *Notaden*

Opportunistic breeding: *Neobatrachus* (part), *Notaden*

All four stages occurred roughly contemporaneously, early in the Tertiary at the latest. If the four stages occurred in sequence, there should be an overall reduction in the average number of primitive states per genus from the first to the fourth stage. This is not the case. The first three groups all have an average of 55% primitive states per genus, the fourth group has an average of 54%.

A rough indication of recency of evolutionary

activity can be gained by examining the average number of species per genus. The assumption is that lower number of species per genus represents an older radiation, a higher number of species per genus represents more recent speciation. The first distribution pattern group has an average number of species per genus of 2.6, the second group an average of 2.0, the third group an average of 5.0, and the fourth group an average of 3.25. If the difference between the first and second group is real, it could be interpreted in the following way. The general wet forest associated group has had a more continuous habitat available since the Tertiary, while the antarctic forest associated group has had a more fragmentary distribution, with populations of frogs becoming isolated in forest fragments sometime in the Tertiary. The isolation of these latter populations has led to relatively more speciation in this group than in the more general wet forest associated group. This hypothesis is supported by the fact that most of the antarctic forest associated genera that are not monotypic typically have allopatrically distributed species. The fourth group, primarily arid adapted, has an intermediate amount of relatively recent speciation, while the forest-open formation group has the greatest amount of recent speciation. Apparently, in terms of fluctuating environments there has historically been greater fragmentation and coalescing of open formation habitats. This has allowed speciation to continue throughout the Tertiary to the present. The phenomenon of more recent speciation in open eucalypt habitat compared to rainforest habitat has also been observed in Australian birds (Schodde and Calaby, 1972).

In summary, it appears that the major expansion from the ancestral temperate antarctic forest habitat into other habitat types occurred more or less synchronously; that the radiations within the major habitats are old, stemming from the early Tertiary; and that the most recent evolutionary activity is associated with open formation habitats, intermediate between forest and desert environments.

Another overall trend is that direct development is approached or attained only in wet forest genera, as pointed out previously by Main, Littlejohn, and Lee (1959). The only possible exception is *Myobatrachus*, which has huge ovarian eggs, suggesting direct development.

EVOLUTIONARY TRENDS WITHIN THE SUBFAMILIES

When the historical zoogeography of the myobatrachids is viewed in terms of evolutionary relationships, additional trends can be postulated.

SUBFAMILY RHEOBATRACHINAE.—The sole member of this subfamily, *Rheobatrachus silus*, represents an early stream adaptational complex from the ancestral myobatrachid stock. *Rheobatrachus* has remained in the temperate antarctic forest vegetation and represents a combination of a large number of primitive states (67%) together with some of the most bizarre derived states known involving life history (Corben, Ingram, and Tyler, 1974).

SUBFAMILY MYOBATRACHINAE.—Members of the Myobatrachinae demonstrate all four geographic patterns; however, there are definite emphases within the patterns, most of the genera being associated with wet forests. *Taudactylus* represents, within the antarctic forest type, an early specialization to stream adaptations, with respect to the larvae of all known species and all adults (Liem and Hosmer, 1973). The *Crinia*-complex, represented by *Assa*, *Australocrinia*, *Crinia*, *Geocrinia*, *Paracrinia*, *Ranidella*, all appear to represent more or less independent specializations from the ancestral wet forest myobatrachine stock. Each generic unit likely represents a previous isolation in a wet forested area with concomitant adaptational responses to that given environment. The result of several independent adaptational responses in a generalized myobatrachine is a mosaic pattern of derived states. The generalized myobatrachine morphology has been retained, so the similarity among these taxa is based on a suite of primitive, rather than derived, states. *Ranidella* had the genetic plasticity to adapt to environments bordering the wet forest habitat. The genera demonstrating the arid adaptation geographic pattern, *Glauertia* and *Kankanophryne*, are exploiting local mesic habitats within an arid landscape. The divergence of *Glauertia* into this specialized habitat type probably occurred earlier than for *Kankanophryne*. *Pseudophryne*, *Ranidella*, and *Uperoleia* have adapted in part to open formation vegetation types. The large terrestrial egg of *Pseudophryne* with initial development out of water has adaptive value in areas of unreliable rainfall. There are no particular obvious adaptations in the life history

patterns of *Ranidella* and *Uperoleia* to predict a habitat shift to open formation vegetation. *Myobatrachus* is a very specialized form, a subterranean termite eater. It is the only burrowing myobatrachid that can burrow head first and is restricted to sandy areas in southwest Australia. Within the Myobatrachine, it appears that *Taudactylus*, *Glauertia*, and *Myobatrachus* represent the earliest specializations and divergences from the common myobatrachine ancestral stock. The remainder of the myobatrachine genera appear to have had a common ancestor that was widespread throughout the late Mesozoic-early Tertiary wet temperate forests, and that fragmentation of this common stock associated with fragmentation of the temperate forests, with evolution proceeding independently in each unit, gave rise to the mosaic complex of genera present today.

SUBFAMILY LIMNODYNASTINAE.—*Mixophyes* appears to be an early specialization of the limnodynastine ancestral stock to the stream environment. *Neobatrachus* and *Notaden* represent early specializations to the arid environment involving fossoriality in the adult stage. *Notaden* and *Neobatrachus* are the most arid adapted myobatrachid genera and, interestingly, have almost completely allopatric distributions. The evolutionary history of the remaining limnodynastines is associated with the foam nest. Four of the genera having a foam nest are wet forest genera, the other three are forest and open formation forms. Either the foam nest was initially evolved in response to selective pressures associated with wet forest environments or open formation environments. The evidence points to the original adaptive significance of the foam nest as having been associated with wet forests. None of the genera that are primarily arid adapted have a foam nest, while several of the genera with foam nests are found only in wet forest habitats. The wet forest foam-nesting genera have an average of 2.5 species per genus, contrasted with a 5.7 average for the open formation foam-nesting genera, suggesting the wet forest radiation is older than the open formation radiation. The foam nest, then, served as a preadaptation for exploitation of a more seasonal environment associated with open formation vegetations. *Lechriodus* is noteworthy among the myobatrachids in that it is the only genus in which more species are found outside of Australia than within Australia.

Lechriodus seems to be associated with the podocarp vegetation unit of the temperate antarctic vegetation and has undergone a minor radiation associated with, in part, the podocarp forests of New Guinea. There is no evidence, however, to suggest that the genus arose in New Guinea; in fact, the Australian species is the most primitive in the genus (Zweifel, 1972).

MAJOR TRENDS AMONG SUBFAMILIES

Even though the adaptive trends within the Myobatrachinae and Limnodynastinae are similar in that they include adaptational complexes associated with open formations and arid environments, direct development and stream habitats, the adaptations associated with these shifts are different. The myobatrachines have no truly arid adapted genera; the limnodynastines have two. Direct development involves a foam nest in the limnodynastines; a foam nest is not involved in direct development in the myobatrachines. The foam nest is the key preadaptation to open formation utilization by some of the limnodynastines; the foam nest is not a feature of the open formation myobatrachines.

Within all three subfamilies, the ancestral pattern appears to be an association with temperate antarctic vegetation and a generalized life history pattern involving a free living larva. The most parsimonious explanation of the early evolution of the myobatrachids is that the present myobatrachids represent three very early divergences in the myobatrachid ancestral stock. One lineage became adapted as adults to the stream habitats with an extremely specialized life history pattern of gastric brooding. The degree of specialization apparently led to an evolutionary dead end represented in *Rheobatrachus silus*. The early divergence of the myobatrachine and limnodynastine stocks involved morphological features which at present are difficult to associate with adaptive trends. Both groups were associated with the temperate antarctic vegetation, and they likely had a generalized life history pattern. The basic morphological differences between the two stocks allowed their evolution to act in independent ways in relation to the same environmental changes of increasing aridity in the late Mesozoic to present.

COMPARISONS WITH PREVIOUS ZOOGEOGRAPHIC SCHEMES

Previous workers in discussing the zoogeography of the Australian anuran fauna have proposed three major ideas. The first is that a segment of the anuran fauna is old, stemming at least from the early Tertiary. The second is that the anuran fauna can be explained best by using a modified Spencerian (1896) scheme of four faunal subregions in Australia. The third is the proposal of a mode of speciation in some genera involving evolution of species in southeast Australia with dispersal to southwest Australia.

This study confirms the importance of recognizing the antiquity of the myobatrachid frog fauna. The myobatrachids were certainly present in the Australian region by late Mesozoic and much of the radiation of the group may well have occurred in early Tertiary.

The faunal subregions used by most workers to explain the geographic distribution are as follows (from Littlejohn, 1967:152):

(1) Bassian—coastal, cool temperate, relatively uniform rainfall; east and south-east of the Eastern Highlands and south of the Clarence River; (2) Torresian—northern and eastern tropical area north of the Clarence River with a summer maximum rainfall; (3) Eyrean—all the drier inland portions of the continent, including the north-west coast; (4) South-west—the humid south-western corner of Western Australia which receives a reliable winter maximum rainfall.

Moore (1961) has been the only recent worker that did not use the above scheme. Moore's scheme, in part, recognized two additional regions and he emphasized that only one of his regions was truly distinctive: that corresponding with the South-west pattern described above.

None of the myobatrachids have a strictly Torresian distribution. Several of the genera have distributions combining Bassian and Torresian distributions. Most of the genera with distributions in the Eyrean region also are found in the Bassian, the Torresian, and/or the South-west regions. Neither the modified Spencerian nor the Moore (1961) schemes adequately describe the distribution patterns of the myobatrachids. We think the key to understanding the zoogeography of the myobatrachids is the recognition of the temperate antarctic vegetation associated myobatrachid fauna as a distinctive unit.

The Spencerian scheme appears to account much better for reptile distributions than for myobatrachid distributions (e.g. Keast, 1959; Kluge, 1967). We think that the Spencerian subregion scheme associates best with those faunal units having a tropical origin. For those faunal units having a temperate origin, such as the myobatrachids, the scheme proposed herein apparently is a more realistic zoogeographic hypothesis.

Lee (1967:428-429) summarized the speciation scheme proposed for certain genera:

Faced with the incongruous situation of a multiplicity of species within *Heleioporus* and two other genera of frogs (*Crinia* and *Neobatrachus*) in the topographically featureless south-western pocket, Main, Lee, and Littlejohn (1958) suggested the following explanation for their origin:

- (1) Within each genus two elements or species groups were recognized and identified as bassian and eyrean elements (after the terminology of Serventy and Whittell (1951). The breeding biology of the bassian frogs was adapted to uniform rainfall or continuously moist situations, and that of the eyrean species to seasonal rainfall and seasonally arid conditions. Designation of the eastern species based on these adaptations presented no problems, but with the specialization of the western fauna to the pronounced seasonal conditions of the area, use had to be made of similar morphology to provide clues of relationship. Judged by their morphological dissimilarity, this division into two elements was a pre-Pleistocene event.
- (2) South-eastern rather than south-western Australia was favoured as the centre of origin of the genera. The south-east is more diverse topographically and ecologically, and despite the greater number of species in these genera in south-west, there are more species and genera of frogs in the south-east.
- (3) The multiplicity of species within each genus in the south-west resulted from a series of invasions of the eastern representatives of each element into the south-western pocket where some persisted. The invasions were separated by periods of isolation of sufficient duration for the populations to retain separate identity when brought together again.
- (4) The invasions were considered to be coincident with the pluvial or glacial phases, and isolation with the arid interglacial phases of the Pleistocene. The Pleistocene events of the northern hemisphere were probably paralleled in the southern hemisphere, but only with minor continental glaciation. Browne (1957) and Browne and Vallance (1963) have been able to recognize three phases of glaciation in southeastern Australia, and this corresponds to the number of western eyrean representatives in each genus, but not to the number of bassian species, of which there are either one or two. Main, Lee, and Littlejohn (1958) suggested that early bassian invaders may have succumbed to the marked arid conditions of later interglacial phases.

- (5) Finally, the disproportionate number of species in eastern and western Australia was attributed to the failure of the western representatives to reinvade the east after specialization during isolation.

The speciation scheme includes recognizing species pairs in southeast and southwest Australia. The kinds of information used to determine relationships have been morphological similarity, mating call similarity, and hybridization results. The authors who support this mode of speciation do not distinguish primitive and derived states; thus the morphological and mating call similarities could be based on primitive states and contain no information regarding relationships. Hybridization data as an index to relationships among anurans must be used with great caution. There are many examples of viable intergeneric crosses. Postmating isolating mechanisms involving hybrid inviability may only be selected for in closely related forms that have had historical overlap in geographic ranges. We present these arguments not to invalidate the conclusions of the authors who have proposed this mode of speciation, but to indicate that there is room for another hypothesis.

The hypothesis we favor is that for such genera as *Heleioporus*, during glacial periods, when the mesic forests would have had an expanded distribution, local arid habitats may have persisted due to such factors as drainage peculiarities of the soil. These isolated arid habitats would serve as refugia for the arid adapted fauna. Due to the isolated nature of these arid refugia, evolution could operate independently on the faunas of each of them allowing allopatric speciation to occur. The origin of the species would be within the same general region where they are found at present, not in southeast Australia exclusively.

MYOBATRACHID-LEPTODACTYLID COMPARISONS

The leptodactylid radiation in the Neotropics resulted in at least 47 genera and 500 species. The vastness of this radiation appears to overwhelm the myobatrachid radiation which resulted in 24 genera and about 80 species. The comparison of the total leptodactylid and myobatrachid radiations is in one sense unrealistic, since the myobatrachids have not radiated into tropical environments in the way that leptodactylids have. A more meaning-

ful comparison is to compare that portion of the leptodactylid radiation that corresponds with the myobatrachid radiation. The myobatrachid history includes original association with temperate forests and evolution into open formations and arid environments. A comparable situation is found in South America in the case of the anuran fauna of Chile and adjacent Argentina, including the Gran Chaco, but excluding Misiones and east coastal Argentina. In this Neotropical region, the original association of the leptodactylids was with the temperate forests and radiations have occurred into the open formations and arid environments.

Although the fauna of southern South America is reasonably well understood, the leptodactylids of Chile and Argentina are not as well understood systematically as are the myobatrachids of Australia. There are 15 genera and 50 species of leptodactylids found in the area of comparison in Chile and Argentina. This larger number of taxa indicates that the myobatrachid radiation has been larger than the leptodactylid radiation in similar habitats. Interestingly, both the southern leptodactylids and myobatrachids have the same average number of species per genus, $3\frac{1}{3}$, suggesting that the radiations are of equivalent age.

A feature of the myobatrachid radiation is that there are relatively few species per genus, *Ranidella* and *Pseudophryne* being high with 8 and 9 known species. This compares poorly with the 300 plus Neotropical species of *Eleutherodactylus* or even the 20-40 species in such Neotropical genera as *Leptodactylus* and *Physalaemus*. When one examines the leptodactylid fauna of Chile and Argentina, the situation is exactly that found in the myobatrachids. *Leptodactylus*, *Pleurodema*, and *Telmatobius* are all high with a total of 8 known species.

The more extensive radiation of the myobatrachids than the southern leptodactylids appears to be valid. The only other group of frogs with extensive distributions in Australia is the tree frog family Pelodyadidae. The tree frog family Hylidae is well represented in southern South America. In addition, there are two bufonid genera, two microhylid genera, and one pseudid genus with extensive distributions in Chile and Argentina. This last set of genera appears to have ecological equivalents among the myobatrachids. The most striking example is the fossorial termite eating

myobatrachid *Myobatrachus* and the fossorial termite eating microhylid *Dermatonotus mulleri*. There is, incidently, only one such species in each region. If this last set of genera is added to the leptodactylids, there is a total of 20 genera and 64 species. This figure is rather close to the myobatrachid figure, taking into account the fact that the southern South American anuran fauna is not as well known as the Australian anuran fauna and the total area of comparison is smaller for southern South America. It appears as though the total anuran frog faunas of these two regions are equivalent and that the myobatrachid radiation has been more extensive than the leptodactylid.

Convergence of adaptive complexes between the myobatrachids and southern leptodactylids is striking. In both groups there are riparian forms, fossorial forms, and trends toward and including direct development. Certain of these are worth more detailed comment.

Parental brooding of the larvae is found in both the myobatrachids and southern leptodactylids. The evolution of this pattern, however, has clearly occurred three different times. The myobatrachid *Assa* has male inguinal brooding pouches, the myobatrachid *Rheobatrachus* has a female gastric brooding pouch, and the leptodactylid *Rhinoderma* has a male vocal sac brooding pouch.

The evolution of the foam nest has had a similar, but independent, evolutionary history in both the myobatrachids and leptodactylids. In both groups, the original adaptive significance of the foam nest was in response to selective pressures associated with wet forest environments. The presence of the foam nest then served as a preadaptation allowing radiation into open formation

habitats. The known methods of foam nest formation are very different, as pointed out by Martin (1970). In the myobatrachids, the fingers of the female are modified to whip the jelly into foam, while in the leptodactylids the hind legs of the male whip the jelly into foam.

Recently, a complex association of specialized larval microhabitats and morphology has been described for *Leptodactylus pentadactylus* (Heyer, McDiarmid, and Weigmann, 1975). Briefly, *L. pentadactylus*, a foam nest breeder, utilizes small aquarium sized puddles as larvae. These puddles, occurring in wet environments, are replenished by almost daily rainfall, so they do not dry up. The larvae are facultatively carnivorous, a rare condition among tadpoles. It was postulated that the carnivorous tadpole mode is possible in these particular microhabitats because there are no fish in these small puddles (see Heyer, McDiarmid, and Weigmann, 1975, for a fuller explanation). *Lechriodus fletcheri*, a wet forest associated, foam nest breeding myobatrachid, also utilizes small aquarium sized puddles and has facultatively carnivorous larvae.

The myobatrachids and leptodactylids most likely had a common ancestor that was widespread throughout the Antarcto-Tertiary Geoflora of Gondwanaland. Both the myobatrachids and leptodactylids have members that are still associated with this vegetation. Arid centers developed independently in Australia and South America. The convergence of life histories and morphologies of the myobatrachids and leptodactylids with derivative temperate forests, open formation vegetations, and arid environments is nothing short of spectacular.

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