



# FAUNA *of* AUSTRALIA



## 6. BIOGEOGRAPHY AND PHYLOGENY OF THE ANURA

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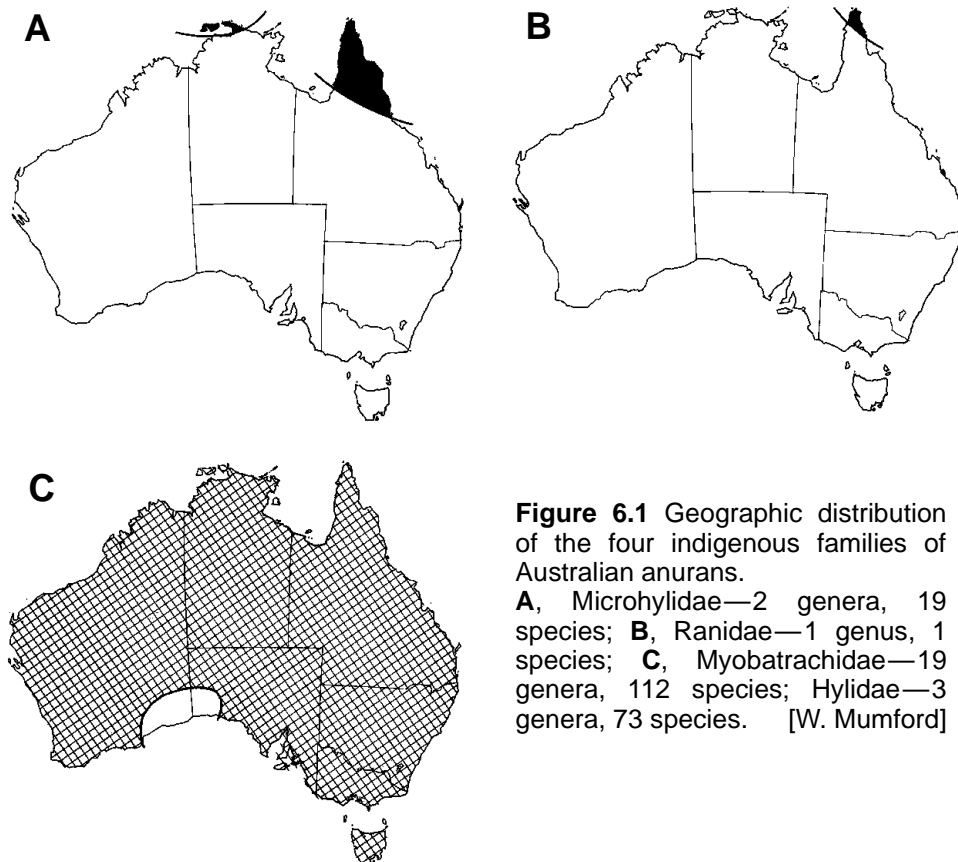
## 6. BIOGEOGRAPHY AND PHYLOGENY OF THE ANURA

The amphibian fauna of Australia is depauperate, and only the Anura is represented in the extant biota. Within this group, two distinct faunal strata are recognised. These are an ancient, gondwanan element and a more recent faunal element having affinities with South-East Asia. While there is general agreement on this broad pattern of historical biogeography and phylogeny, there is little uniformity of views on the detail of these relationships.

Four families of frogs are native to Australia—the Microhylidae, the Myobatrachidae (or Leptodactylidae), the Hylidae (or Pelodryadidae) and the Ranidae. A fifth family, the Bufonidae, is represented by the introduced cane or marine toad, *Bufo marinus*. Two of these families (Microhylidae and Ranidae) are derived from Asian groups that colonised the area following collision of the Australian and Asian continental plates (Tyler 1989a). The remaining two families, which include most of the Australian anuran fauna, have Gondwanan origins. Even though the general phylogenetic and biogeographical relationships of the Australian anuran fauna are established, their systematic positions are far from settled.

Continuing controversy surrounds the nomenclature and status of the two ancient, austral groups. Indeed, the two authors of this chapter hold conflicting views. One of us (GFW) agrees with the case argued by Tyler (1989a) that, apart from geography, there is insufficient evidence currently available to justify removal of Australian species from the families Hylidae and Leptodactylidae. An opposing view (supported by JDR) suggests that the two groups are best recognised as distinct families to which the names Pelodryadidae (for Australian ‘treefrogs’) and Myobatrachidae (for Australian leptodactyloid frogs) are appropriate.

It is not our intention in this chapter to resolve the nomenclatural status of these units but rather to point out that how the groups are recognised inevitably influences perceptions of their phylogenetic and biogeographic relationships. For example, as Tyler (1989a) points out, because the families Hylidae and



**Figure 6.1** Geographic distribution of the four indigenous families of Australian anurans.

**A**, Microhylidae—2 genera, 19 species; **B**, Ranidae—1 genus, 1 species; **C**, Myobatrachidae—19 genera, 112 species; Hylidae—3 genera, 73 species. [W. Mumford]

Leptodactylidae have extensive distributions outside Australia, application of these names to Australian families implies a close relationship to frogs of other continents. Two groups, however, deserve special mention. *Cyclorana*, a genus of primarily burrowing frogs, widespread in the arid zone and wet-dry tropics, was formerly considered a myobatrachid, and its name was used to define the subfamily Cycloraninae (Lynch 1971). Extensive evidence from studies of chromosomes and musculature led Tyler (1978) to transfer this genus to the Hylidae. This move was supported by later immunological studies based on serum albumin (Maxson, Tyler & Maxson 1982). The second controversial group is the genus *Rheobatrachus* which has been given variously familial status, subfamilial status or simply considered as a myobatrachid genus (see section on Myobatrachidae).

The biogeography of Australian frogs has been treated at three levels. These are: broad scale patterns of intercontinental relationships (for example, Savage 1973; Tyler 1979a), analyses of biogeographic patterns within Australia (for example, Moore 1961; Tyler, Watson & Martin 1981c) and detailed analyses of patterns within genera or geographic regions (for example, Main, Lee & Littlejohn 1958; Littlejohn 1967, 1981; Main 1968; Roberts & Maxson 1985, 1988; Watson & Littlejohn 1985).

Phylogenetic studies are available over a similar array of levels. They include: families within and between continents (for example, Savage 1973; Lynch 1971), within families within the Australian and New Guinean region (for example, Heyer & Liem 1976; Farris, Kluge & Mickevich 1982), and within and between related genera (for example, Tyler & Davies 1978a; King 1981; Roberts & Maxson 1986; Hutchinson & Maxson 1987a).

### **APPROACHES TO PHYLOGENETIC AND BIOGEOGRAPHIC RELATIONSHIPS**

Traditionally, hypotheses of relationships between groups have been based on detailed morphological analyses of the included taxa. The Australian anuran fauna has been extensively and intensively studied in this regard, based in particular on external characteristics and muscular and skeletal morphology (see Chapters 7 and 8 for reviews). Cladistic methodologies, rather than those based on phenetic methods, have also been applied to data sets drawn from comparative morphological and ecological studies (for example, Heyer & Liem 1976; Farris *et al.* 1982).

More recently, a range of complementary and modern technologies has been applied to obtain further character data in order to elucidate phylogenetic and biogeographic relationships among the Australian anuran fauna. These techniques include comparisons of mtDNA, as used by Dennington (1990), and karyological studies, such as those of King (1980, 1981), King *et al.* (1979), Mahony & Roberts (1986) and Mahony & Robinson (1980, 1986).

The most influential of a variety of biochemical analyses (for example, Barendse 1984; Gartside 1982), and one that has had profound effects on our understanding of the systematic biology of Australian frogs, is the immunological technique of micro-complement fixation (MCF), using serum albumin (Maxson *et al.* 1982; Maxson, Ondrula & Tyler 1985; Maxson & Roberts 1985; Hutchinson & Maxson 1987a, 1987b, 1987c; Maxson & Maxson 1990). MCF analyses have been used to elucidate systematic relationships, as well as to define temporal sequences in phylogenies based on assumptions of a molecular clock.

One of the authors (JDR) has been a leading proponent of this technique, and has made a major contribution to the extensive application of MCF technology towards re-interpreting the phylogeny and biogeography of many groups of



Australian frogs. The other author (GFW) believes that these data are inappropriate and inapplicable to these problems, a point of view that is receiving increasing support in the systematic literature (for example, Scherer 1990). As these different viewpoints inevitably influence our interpretations, we have separated our systematic contributions on the myobatrachids and the hylids, which were prepared by JDR and GFW respectively. Both viewpoints are put in our consideration of regional biogeographic patterns.

## MYOBATRACHIDAE

The intercontinental relationships of this family are not resolved. The myobatrachids represent a leptodactyloid lineage (Lynch 1971) and may therefore be related to South American leptodactyloid lineages. Savage (1973) presents very detailed arguments about the probable origins of the Australian family (see also Heyer & Liem 1976; Tyler 1979a; Tyler, Watson & Martin 1981c). The myobatrachids are a gondwanan element but little more can be added to their explicit relationships. However, most recent authors have considered the Myobatrachidae as a monophyletic lineage (for example, Heyer & Liem 1976; Farris *et al.* 1982), though this treatment may be by default as they were dealing with genera of common geographic origin in Australia and New Guinea.

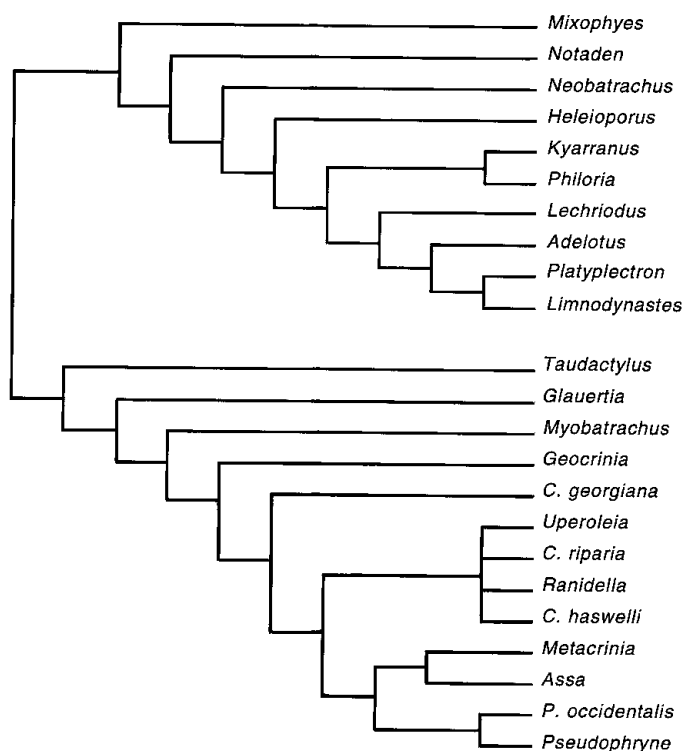
### Relationships of Genera

Two major analyses of the relationships within this family have been made, by Heyer & Liem (1976) and, in a subsequent treatment of much of the same data, by Farris *et al.* (1982).

The relationships of genera recognised by Heyer & Liem are shown in Figure 6.2. Several of these genera have now been synonymised: *Glauertia* with *Uperoleia* (Tyler, Davies & Martin 1981a), *Australocrinia* with *Ranidella* (Thompson 1981), *Ranidella* with *Crinia* (Heyer, Daugherty & Maxson 1982), and *Kankanophryne* with *Pseudophryne* (Tyler & Davies 1980). The one general feature which emerges from this analysis is a fundamental division into two subfamilies, the Myobatrachinae and the Limnodynastinae. This subdivision is consistent with earlier taxonomic treatments (Parker 1940; Moore 1961) and a recent immunological analysis (Maxson 1992). However, within these two subfamilies there is no clear pattern. Part of this stems from the quality of the data. For example, direct development is equated in all species, whereas later field data indicate that in some species there is intracapsular development (for example, *Myobatrachus*; Roberts 1981), but in others the eggs hatch and develop without feeding, as in some species of *Geocrinia* (Main 1968). The analyses by Tyler & Davies (1980) of the status of *Kankanophryne* and Thompson (1980) on *Australocrinia* are also consistent with poor quality data in Heyer & Liem's (1976) study.

The analysis produced by Heyer & Liem (1976) has been heavily criticised by Farris *et al.* (1982) on three grounds. First, they questioned the use of the South American Leptodactylidae as an outgroup, and argued that Heyer used the Australian myobatrachids as the outgroup for his analyses of relationships in American leptodactylids, indicating that the argument about primitive and derived character states was circular. They queried the status of many characters used and ultimately reduced the characters from 42 to 23. They also noted major deficiencies in the methodology used by Heyer & Liem to generate their phylogeny.

Farris *et al.* (1982) re-analysed both the complete and the reduced data sets in two ways. The phylogeny shown in Fig. 6.3 is their preferred tree. The same basic pattern of two subfamilies noted by Heyer & Liem is present, but there are



**Figure 6.2** The preferred phylogenetic arrangement of Heyer & Liem (1976) of the myobatrachid genera. *Crinia georgiana*, *C. riparia*, *Crinia haswelli* and *Pseudophryne occidentalis* were named *Crinia*, *Australocrinia*, *Paracrinia* and *Kankanophryne* in the original illustration. (Modified from Heyer & Liem 1976) [D. Wahl]

many discrepancies. For example, their results associated *Myobatrachus* with *Assa* and *Metacrinia*, but in Heyer & Liem's analysis *Myobatrachus* was only distantly related to these other two genera. However, some of the earlier deficiencies in the data, for example, those relating to breeding biology, are perpetuated. Farris *et al.* conclude their paper with the following: 'It seems necessary to conclude that these characters offer only weak evidence on kinship. Given such weak data, we see little value in generalising further about the relationships among myobatrachid frogs'.

Subsequent attempts to examine relationships within this family have concentrated on relationships within selected genera or between sets of closely related genera. Many studies since 1981 have compared the structure of serum albumin using MC'F (Maxson & Maxson 1990). MC'F generates a measure of immunological distance (ID) which is generally believed to reflect differences in the amino acid sequence of the albumins compared (Maxson & Maxson 1990; Maxson 1992). There are a number of methods for generating phylogenetic information from pair-wise distance comparisons (Swofford & Olsen 1990).

Farris *et al.* (1982) considered the genus *Rheobatrachus* as related other genera of the Limnodynastinae, but placed it as a very old derivative of this subfamily. Heyer & Liem (1976) also saw *Rheobatrachus* as distinct and erected a new subfamily to recognise this fact. Hutchinson & Maxson (1987b) compared the albumins of the two known species, *R. vitellinus* and *R. silus*, and compared *Rheobatrachus* both with other Australian myobatrachid genera and other leptodactyloid frogs (*sensu* Lynch 1971) from South America. They concluded that the two species of *Rheobatrachus* are closely related, and that the genus is also not closely related to any other genera or lineages within the Myobatrachidae, but it is more closely related to Australian lineages than to any

other leptodactyloid group. However, the data obtained are at the limits of resolution for the MCF methodology. The distinctness of this genus is unquestioned, but its relationships are still unclear. The antiquity of the split of this genus from other Australian frogs may make this position unresolvable until techniques capable of resolving ancient divergences are applied (Hutchinson & Maxson 1987b).

The analysis of relationships using data from MCF, within genera or apparently related genera, has generated partial tests of relationships proposed by the tree of Farris *et al.* (1982). These pieces of information are summarised below.

### The Subfamily Myobatrachinae

The *Myobatrachus* lineage: *Myobatrachus*, *Metacrinia* and *Arenophryne*. Only the first two of these were included in the analysis of Farris *et al.* (1982). However, *Metacrinia* was seen as closely related to *Assa*. MCF data presented by Maxson & Roberts (1985) and Roberts & Maxson (1989) suggested that *Metacrinia*, *Myobatrachus* and *Arenophryne* are closely related, but these analyses give no information on relationships to *Assa*. Maxson & Roberts (1985) noted several major differences in the breeding biology of *Assa* and the other three genera under consideration here and argued that a close relationship to *Assa* was unlikely. Of the array of genera considered by Maxson & Roberts (1985) and Roberts & Maxson (1989) (*Uperoleia*, *Pseudophryne*, *Geocrinia* and *Crinia*), *Pseudophryne* is the genus most closely related to the *Metacrinia*, *Myobatrachus*, *Arenophryne* cluster.

The *Pseudophryne*, *Uperoleia* lineage. The ten described species of *Pseudophryne* are closely related (Roberts & Maxson, 1989). Generic comparisons that included *Crinia* and *Geocrinia* suggested that the sister group of *Pseudophryne* is probably *Uperoleia* (Maxson & Roberts 1985). This contrasts with the placement by Farris *et al.* (1982) of *Uperoleia*, *Crinia*, *Ranidella* and *Crinia haswelli* (previously *Paracrinia*) in a monophyletic group with *Glauertia*.

The *Crinia* lineage: *Crinia*, *Ranidella*, *Paracrinia*, and *Geocrinia* were once included in the genus *Crinia* (Parker 1940), until split by Blake (1973) and Heyer & Liem (1976). Farris *et al.* (1982, Fig. 7b) clustered *Crinia haswelli*, *Ranidella* and *Crinia georgiana* in a monophyletic group but *Geocrinia* was not seen as closely related to these genera or species. The close relationship of *Crinia* and *Ranidella* is confirmed by albumin comparisons (Daugherty & Maxson 1982), by electrophoretic data (Barendse 1984) and in comparisons of the shape of the ilium (Tyler 1991a). The albumin similarities were the primary basis for the decision by Heyer *et al.* (1982) to synonymise *Ranidella* with *Crinia*. The status of *Paracrinia* has only been assessed indirectly using MCF. It was the second most distant genus from *Crinia signifera* (ID 140) (*Assa* was most distant, ID 160) in one-way comparisons and based on comparisons to a single species from all known myobatrachine genera (Daugherty & Maxson 1982). The albumin data do not support a close relationship of *Paracrinia* and *Crinia* (*sensu* Heyer *et al.* 1982), nor do these one-way comparisons support a close relationship of *Crinia* and *Geocrinia*. The immunological distance between *Geocrinia victoriana* and *Crinia signifera* is 133. In reciprocal MCF comparisons, *Crinia* is more closely related to *Pseudophryne* than to *Geocrinia* (Maxson & Roberts 1985). This suggests three lineages: *Crinia*, *Geocrinia* and *Paracrinia*.

The relationships of *Taudactylus* have not been examined using biochemical methods. Farris *et al.* (1982) placed it close to *Pseudophryne* while Heyer & Liem (1976) saw *Taudactylus* as an early derivative of the myobatrachine lineage and not closely related to any other genus.

### The Subfamily Limnodynastinae

Only some of the genera in this subfamily have been investigated using studies of albumin using MCF. Therefore, a complete picture for comparison with other analyses is not available.

*Limnodynastes*, *Platyplectron* and *Megistolotis*: Roberts & Maxson (1986) rejected the use of *Platyplectron* (*sensu* Heyer & Liem 1976) to include all burrowing species of *Limnodynastes*. MCF comparisons of albumin showed clearly that *L. ornatus* and *L. spenceri* were closely related but very distantly related to any other *Limnodynastes* lineage; specifically the *dorsalis* group (*sensu* Martin 1972a). No member of the well-defined *dorsalis* group is more closely related to any species of *Limnodynastes* outside the group. Unlike *L. ornatus* members of the *dorsalis* group have albumins quite similar to those of other *Limnodynastes* species (Roberts & Maxson 1986). *Limnodynastes ornatus* and *L. spenceri* form a sister group to all other species of *Limnodynastes* but the immunological distance is only marginally smaller than that to *Notaden* or *Heleioporus* (Roberts & Maxson 1986). Farris *et al.* (1982) found that *Platyplectron* was not closely related to *Limnodynastes*. Roberts & Maxson (1986) used *Platyplectron* to include all burrowing species of *Limnodynastes*: *L. dorsalis*, *L. dumerilii*, *L. interioris*, *L. terraereginae*, plus *L. ornatus* and *L. spenceri* following the distribution map of Heyer & Liem (1976, Fig. 23). These authors, however, did not list the content of this genus. Roberts & Maxson (1986) did not investigate relationships of *Limnodynastes* to *Adelotus*, *Kyarranus*, *Philoria* or *Lechriodus*, the genera that Farris *et al.* (1982) associated with *Limnodynastes* more closely than *Platyplectron*.

Hutchinson & Maxson (1987c) showed that *Megistolotis* falls within the genus *Limnodynastes* and suggested that these two genera should be synonymised. This is not surprising, as Tyler *et al.* (1979) noted many similarities between *Megistolotis* and the *Limnodynastes tasmaniensis* group. The unique features of *Megistolotis* are derived and convergent with *Heleioporus* (Hutchinson & Maxson 1987c; *cf.* Tyler *et al.* 1979).

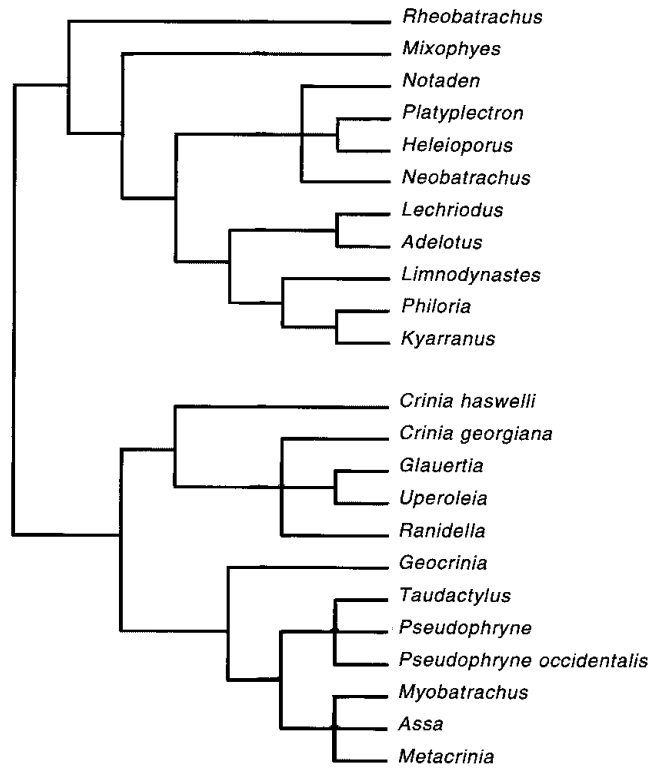
One-way MCF comparisons of *Neobatrachus pictus* of albumins of *Heleioporus*, *Notaden* and *Limnodynastes* suggest that *Neobatrachus* and *Heleioporus* are closely related and that the next closest group is *Notaden* (Roberts & Maxson 1986). This is consistent with the placement of these three genera by Farris *et al.* (1982) and with earlier treatments, for example, Parker (1940), who synonymised *Neobatrachus* and *Heleioporus*. However, the breeding biologies of *Neobatrachus* and *Heleioporus* are strikingly different (Main 1968).

Relationships of other genera within the Limnodynastinae are untested. The tree in Fig. 6.3 (after Farris *et al.* 1982) represents the best hypothesis of relationships for these remaining groups.

The relationships of genera within the family Myobatrachidae are still not clearly resolved, despite the detailed analyses available from MCF studies and the analysis of 23 morphological and biological characters used by Farris *et al.* (1982). However, the status of two subfamilies Limnodynastinae and Myobatrachinae is not questioned.

## HYLIDAE

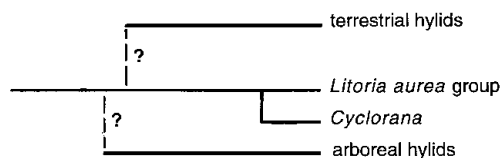
The Australopapuan tree frogs of the genera *Litoria* and *Nyctimystes* form a monophyletic group defined by the presence of a supplementary apical element of the intermandibularis muscle (Tyler 1971b, 1979a). However, the status of this group relative to other hylid lineages worldwide and to the Australian



**Figure 6.3** Wagner tree based on a twenty-three character, restricted dataset. *Ranidella* includes *R. riparia* (now placed in *Crinia*), *Limnodynastes* excludes burrowing species treated as *Platyplectron* (see text) and *Pseudophryne* excludes *P. occidentalis*. (After Farris, Kluge & Mickevich 1982) [D. Wahl]

myobatrachid lineages has been questioned. Tyler (1979a) suggested that Australian hylid and myobatrachid frogs might share a common ancestor. This claim was partly based on the status of *Cyclorana*, at that time considered a myobatrachid, but now clearly shown to be a hylid frog (see above, and also Tyler & Davies, Chapter 8).

Tyler, Watson & Martin (1981c) suggested that the Australian tree frogs fall into four lineages: the terrestrial hylids, the *Cyclorana* group, the *Litoria aurea* group (closely allied to the *Cyclorana* group) and the arboreal hylids. This scheme was presented as a speculative phylogeny, shown in Figure 6.4. Hutchinson & Maxson (1987a) demonstrated by MCF studies that the Australian and New Guinean hylids in *Litoria* and *Nyctimystes* form a monophyletic lineage, relative to South American forms. They showed also that this group might be closely related to hyline lineages from South America. However, they did not test relationships to any myobatrachid lineages.



**Figure 6.4** Possible phylogeny of Australian Hylidae. (After Tyler, Watson & Martin 1981c) [D. Wahl]



Hutchinson & Maxson (1987a) placed *Cyclorana* with *L. aurea*, supporting the view of Tyler (1979a) and Tyler, Watson & Martin (1981c), and consistent with the karyological analysis of King *et al.* (1979). Likewise, the MCF analysis placed *Nyctimystes* within the *L. freycineti* assemblage (Hutchinson & Maxson 1987a) that also included montane *Litoria*. This relationship is consistent with the suggestion of Tyler & Davies (1979b) that *Nyctimystes* and montane *Litoria* are closely related, although the latter authors argued that this grouping was derived from a *Litoria eucnemis*-like ancestor. The MCF phylogeny of Hutchinson & Maxson (1987a) placed *L. eucnemis* (as *L. serrata*) in the separate and distinct *L. lesueuri* assemblage.

The MCF analysis of Hutchinson & Maxson (1987a) formed the basis of the only formally published phylogeny of selected species of Australian hylids. Nevertheless, other investigations have suggested various categorisations of species groups among Australian hylids. These groupings have been based on life history and larval characteristics (for example, Moore 1961; Martin & Watson 1971), morphological, osteological and ecological similarities (Tyler & Davies 1978a) and details of chromosome morphology and banding patterns (King 1981).

It is clear from a comparison of the phylogeny of Hutchinson & Maxson (1987a, Fig. 2) and the most extensive of the other categorisations of species groups within Australian hylids (Tyler & Davies 1978a) that no general consistency exists between groupings based on more traditional methods and those based on MCF comparisons. Such discrepancies can be resolved only by further analyses of phylogenetic groupings using independent data sets, as well as by clarifying the appropriateness of techniques such as MCF for determining phylogenies. Until such analyses are undertaken, generic and subgeneric characterisation of Australian hylids will remain an area of contention even though there seems to be general agreement that the speciose genus *Litoria* contains divisions large enough to justify taxonomic separation.

## SPECIATION MECHANISMS IN THE AUSTRALIAN ANURAN FAUNA

Allopatric speciation models have dominated writing about speciation mechanisms in the Australian anuran fauna. In such models, major geographic barriers develop and isolate populations. Subsequently, the isolated populations diverge until they are recognised as separate species (Futuyma 1986). Many of these models have involved repeated expansions from source areas, with subsequent isolation after climatic change or rise in sea level. Models of this type have been used to explain speciation in the anuran fauna of south-western Australia (for example, Main *et al.* 1958) and in south-eastern Australia (Littlejohn 1967, 1981; Watson & Littlejohn 1985).

Although many genera exhibit patterns of geographically isolated species which are apparently closely related, such as *Uperoleia*, *Crinia* and *Pseudophryne*, and consistent with an allopatric speciation model, in some instances the detail of these models has not been justified by critical analysis of relationships.

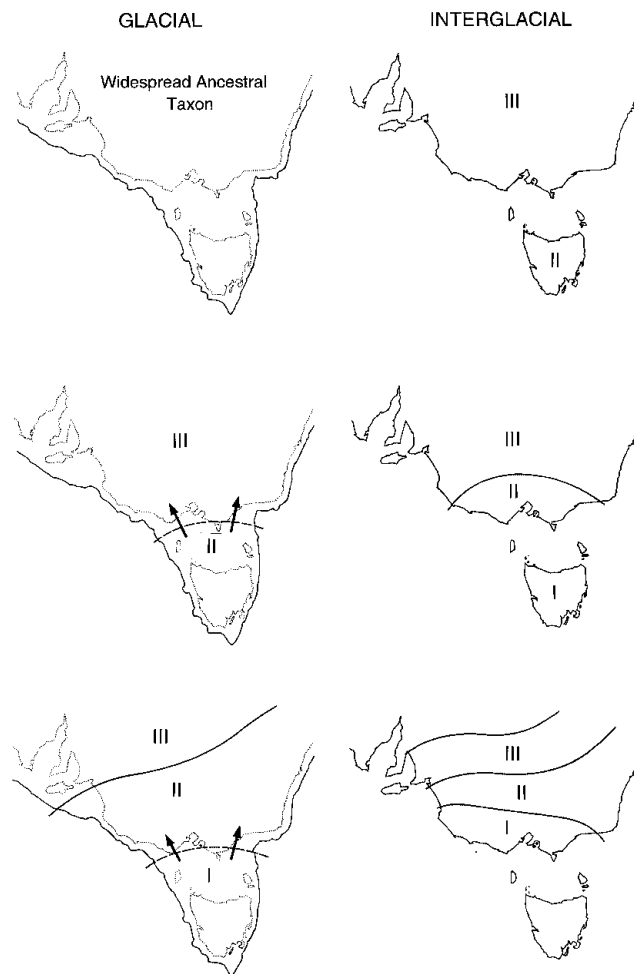
Main *et al.* (1958), for example, argued that the high species richness in south-western Australia in the three genera *Heleioporus*, *Neobatrachus* and *Crinia*, could be explained by repeated invasion of an eastern stock with subsequent isolation and differentiation in south-western Australia. Roberts & Maxson (1985) reviewed relationships in these south-western genera, using data from gel electrophoresis, MCF studies and chromosome analysis. They showed that the data contradicted the relationships suggested by Main *et al.* (1958) in some instances, for example, in *Crinia* and *Heleioporus*, or that alternative modes of speciation had not been considered, such as polyploidy in *Neobatrachus*. They

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concluded that most of the data were consistent with an *in situ* speciation model despite the lack of geographic barriers within south-western Australia. The possibility of speciation within this area is now clearly demonstrated, however, by the discovery of four species of *Geocrinia* in far south-western Australia. These taxa have clear differences in colour, call, and in genotype as determined by electrophoresis (Wardell-Johnson & Roberts 1991).

A critical review of speciation processes in south-eastern amphibians by Roberts & Maxson (1988) reached conclusions similar to those for south-western Australia. Not all species pairs were as closely related as had been predicted and there was little evidence to support multiple invasions of the mainland from Tasmania. However, Watson & Littlejohn (1985) provided strong evidence of repetitive patterns of distribution and relationships within the various species groups of south-eastern Australian amphibians. These are consistent with repeated periods of differentiation between Tasmanian and mainland populations while isolated geographically, interspersed with periods of northward expansion of Tasmanian populations when land was continuous across Bass Strait.

In their review, Watson & Littlejohn (1985) proposed phylogenetic relationships based on a variety of factors. Levels of genetic compatibility between taxa were determined through *in vitro* hybridization experiments (for example, Watson & Martin 1968; Littlejohn, Watson & Loftus-Hills 1971). Also examined were morphological differentiation (for example, Littlejohn & Martin 1964; Martin



**Figure 6.5** Hypothetical model of taxonomic divergence giving rise to species groups with three taxa in south-eastern Australian amphibians. (After Watson & Littlejohn 1985) [W. Mumford]

1972a), quantitative differences in advertisement calls (for example, Littlejohn 1964, 1965); and the structure of the various zones of intertaxonomic interaction. The latter ranged from extensive hybridization between interacting taxa, which indicates close genetic and ecological similarity, to extensive spatial coexistence with little or no hybridization, indicating considerable genetic and/or ecological differentiation (for example, Littlejohn *et al.* 1971; Littlejohn & Watson 1985; Watson 1972; Watson *et al.* 1985). While any one of these factors may not provide strong evidence of phylogenetic relationships, together they provide a substantial body of evidence to refute the view put by Roberts & Maxson (1988).

Watson & Littlejohn (1985) considered eight groups of species in Tasmania and on the mainland of south-eastern Australia. Seven of these groups provide clear evidence of a southern taxon showing a pattern of distribution that includes the southern mainland and Tasmania, with one or more additional mainland taxa. In the eighth group, the *Crinia signifera* complex, a more complicated but consistent pattern of distribution is evident. The proposed pattern of speciation requires the southern (Tasmanian) taxon to disperse northwards across the Bassian land bridge—a suggestion that is not unreasonable, given that the cooler glacial conditions would be expected to favour the cold-adapted southern taxon. Watson & Littlejohn (1985) considered that the commonality of these repetitive patterns provide compelling evidence of repeated patterns of allopatric speciation within south-eastern Australia, for which the sequence of Pleistocene glaciations provided an appropriate geographic and temporal framework.

What are the alternatives to major geographic barriers, such as Bass Strait, being involved in speciation processes? Wardell-Johnson & Roberts (1991) suggested a continental pattern of allopatric speciation for south-western Australia in an area with no obvious geographic barriers. They suggested further that speciation may occur in small isolated populations with minimal geographic separation. These suggestions are supported by data for *Geocrinia* in south-western Australia. *Geocrinia vitellina* occupies a range of 6.0 km<sup>2</sup>, of which about 0.2 km<sup>2</sup>, largely in one creek system, Spearwood Creek, is suitable breeding habitat. *Geocrinia vitellina* is separated from the range of *G. alba* by only 10 to 12 km of unsuitable habitat. However, *G. alba* has a range of around 120 km<sup>2</sup> (Wardell-Johnson & Roberts 1991). Climates in the ranges of these two species differ significantly in several respects, though there is no suggestion that this is necessarily a causative factor in the evolution of these two species (Wardell-Johnson & Roberts 1993). Less well-documented differentiation within mainland ranges, which may also involve small isolated populations, has been reported in *Limnodynastes*: the subspecies *L. dumerilii fryi* in the Snowy Mountains, New South Wales (Martin 1972a) and the race of *L. tasmaniensis*, in which egg masses lack foam, from south-eastern South Australia (Roberts & Seymour 1989). Roberts & Maxson (1989) suggested that speciation in the genus *Pseudophryne* on the continental mainland of Australia, may have also been by an allopatric mode with isolates developing at several sites simultaneously.

The only demonstrated alternative is the role of chromosomal change in the speciation process. There are several tetraploid species in the genus *Neobatrachus* (Mahony & Robinson 1980) and Mahony & Roberts (1986) have shown that some of these differ in chromosome morphology, specifically in the placement of the nucleolar organiser region. As tetraploids are derived from a diploid ancestor or ancestors, this must be a form of sympatric speciation (Futuyma 1986), although the tetraploid may later spread, generating parapatric distributions. However, *Neobatrachus* is the only Australian anuran genus in which there is any evidence for significant involvement of chromosomal alterations in the speciation process (King 1981; Mahony & Robinson 1986).

## DISTRIBUTION PATTERNS

The distribution patterns of Australian frogs have been dealt with extensively. Older schemes were based on recognising four major biogeographic regions: the cool-temperate, southern Bassian area; the central desert Eyrean; the tropical, northern and north-eastern Torresian; and a separate cool-temperate South-Western region (Littlejohn 1967). This scheme has been criticised by Heyer & Liem (1976) who argued that this set of biogeographic regions does not adequately explain the distribution of myobatrachid frogs. They contended that this group represents a derivative of an ancestral fauna associated with temperate Antarctic vegetation. Given that the myobatrachids may be most closely related to leptodactylid lineages in South America, and previously connected to South America via Antarctica, this is not a particularly surprising suggestion.

Tyler, Watson & Martin (1981c) rejected analysis based on biogeographic regions and, instead, delineated nine regions with significant amphibian diversity. Areas of highest diversity are the Kimberley and adjacent Northern Territory, north-eastern Queensland, and a sub-tropical area of high diversity in New South Wales. South-eastern Australia (Victoria and Tasmania) and south-western Australia are cool-temperate centres of diversity (see Fig. 5.1). They argued that the Nullarbor Plain and the Great Sandy Desert in the north-west of Western Australia represented significant barriers to frog dispersal. Pianka & Schall (1981) also analysed amphibian distribution patterns. They showed that regional species diversity was essentially similar to the pattern described by Tyler, Watson & Martin (1981c), but they looked also at the impact of five climatic variables as determinants of species richness. These were annual total hours of sunshine, annual average precipitation, annual average temperature, frost-free days and the coefficient of variation in annual precipitation. Precipitation was the most important variable, followed by the number of frost-free days, but all factors made a significant contribution in a multiple regression analysis. Species richness increased with rainfall up to about 90 cm/year, above which there was no further increase in the number of frog species.

## FOSSIL RECORD

Regrettably, the fossil record for Australian anurans is poor, for many questions about distribution patterns and the phylogenetic relationships of modern taxa might be answered with a more complete fossil record. For example, the ages of divergence events could be accurately dated, providing a test of the application of molecular clocks, and the considerable homoplasy evident in analyses by Farris *et al.* (1982) might be removed if alterations in character states could be resolved.

Fossils have been detected mainly as disarticulated ilia, as these bones stand out in much of the material available for analysis (Tyler 1989a). In general, anuran fossil material falls in two age classes. The several Holocene and Pleistocene collections, primarily from cave deposits (summarised in Tyler 1989a, 1990; Tyler, Aslin & Bryars 1992), are all referable to locally occurring modern species. Iliia collected in Tantanoola Cave in south-eastern South Australia are of *Limnodynastes tasmaniensis*, *L. dumerili*, *Crinia signifera*, *Neobatrachus pictus* and *Litoria ewingii*, all species presently known in this area (Tyler *et al.* 1992). Earlier material is confined mainly to Miocene or late Oligocene deposits from two major areas: Lake Palankarinna in north-eastern South Australia and Riversleigh in northern Queensland (Tyler 1989a, 1990, 1991a, 1991b, 1991c; Tyler, Hand & Ward 1990). The Miocene material reveals the existence of one myobatrachid and three hylid frogs at Lake Palankarinna, a deposit dated as mid-Miocene (13 million years old). Fossils of about the same age representing



*Crinia*, *Kyarranus*, *Lechriodus*, *Limnodynastes* and *Litoria*, have been reported from Riversleigh (Archer *et al.* 1989; Tyler 1989b, 1990, 1991a, 1991b, 1991c) indicating a considerable, early radiation of modern genera (*cf.* Maxson 1992).

*Limnodynastes archeri* and *L. antecessor* have affinities with *L. ornatus* and *L. peronii* respectively (Tyler 1982c, 1990). The existence of these two fossil species is consistent with the predictions of the age of lineages in *Limnodynastes* made from studies of albumin evolution by Roberts & Maxson (1986), who argued that the *L. ornatus* group represents a very old divergence from the remainder of the genus. The existence of fossil material comparable to *L. tasmaniensis* and *L. peronii* at Riversleigh may also be consistent with the molecular clock estimates of divergence of these two species about 11 million years ago in the mid-Miocene (Roberts & Maxson 1986). Tyler (1990) did not specify an age for the fossils comparable with *L. tasmaniensis* but they come from sites labelled R.S.O., Upper Site and C.S. site. These all appear to be in the System B sediments dated at early to mid-Miocene (Archer *et al.* 1989).

Tyler (*pers. comm.*) has recently identified ilia of *Lechriodus* from early Tertiary deposits (54 million years old) from Murgon, southern Queensland. These are the oldest anuran fossils known from anywhere in Australia and confirm the pattern of antiquity of modern genera discussed above.

Cave deposits of Pleistocene age from both south-eastern and south-western Australia contain examples of many extant anuran species (Tyler 1989a). Pleistocene cave deposits from the southern edge of the Nullarbor Plain lack any anuran material (Lundelius 1963), thus contradicting claims of trans-Australian migrations at that time. However, this absence should be put in context. The caves are well north of the continental margin formed by the exposed continental shelf—the probable migration route during Pleistocene glacial periods and the material may not have been surveyed in sufficient detail to detect bones as small as anuran ilia.

The occurrence of genera such as *Kyarranus* and *Lechriodus* in the Riversleigh fauna, well outside their modern ranges (Tyler 1989b, 1991a), indicates radically different distribution patterns in the past associated with different vegetation and climate patterns (Archer *et al.* 1989; Tyler *et al.* 1990). The decline in abundance of *Lechriodus* at Riversleigh from the Oligocene-Miocene boundary to the late Miocene is consistent with the increasing aridity of Australian climates during that interval (Bowler 1982).

Although giving some interesting insights into the history of Australian anurans, existing fossil material is not sufficiently representative in time, space and phylogenetic spread, to resolve clearly any of the current controversies in the biogeography and evolutionary history of the Australian anuran fauna.