



FAUNA *of* AUSTRALIA



7. FAMILY MYOBATRACHIDAE

Murray J. Littlejohn,
J. Dale Roberts, Graeme F. Watson &
Margaret Davies



Pl. 2.1. *Myobatrachus gouldii* (Myobatrachidae): burrows head first into the soil, and feeds on termites; occurs in Houtman Abrolhos and southwestern Australia. [J. Wombey]



Pl. 2.3 *Adelotus brevis* (Myobatrachidae): lives under stones and logs along the coast and in mountain ranges from New South Wales to central Queensland (see also Pl. 2.4). [H. Cogger]



Pl. 2.4. *Adelotus brevis*: (Myobatrachidae): the cryptic colouration of the dorsal surface of this species belies the brilliance of colour beneath (see also Pl 2.3).
[J. Wombey]



Pl. 2.5. *Pseudophryne corroboree* (Myobatrachidae): inhabitant of alpine, grassy marshes and along forest streams, breeding in sphagnum bogs; Mt Kosciusko to the Brindabella Ranges, south-eastern Australia. [H. Cogger]



Pl. 2.6. *Megistolotis lignarius* (Myobatrachidae): the large tympanum over the ear cavity is distinctive; this species lives among rocks and in boulder fields near water; Kimberleys to Arnhem Land. [H. Cogger]

Pl. 2.7 *Rheobatrachus silus* (Myobatrachidae): a fully aquatic species, with eyes high on the head; mainly nocturnal; found only in the Blackall and Conondale ranges, south-eastern Queensland. [H. Cogger]





Pl. 2.8. *Heleioporus albopunctatus* (Myobatrachidae): a burrowing frog which breeds in ephemeral waters; coast and ranges of south-western Australia.
[J. Wombey]



Pl. 2.9. *Taudactylus acutirostris* (Myobatrachidae): a ground-dweller near mountain streams; endemic to the wet tropics.
[H. Cogger]



Pl. 2.10. *Lechriodus fletcheri*, (Myobatrachidae): a ground dwelling frog of wet forests along the eastern Australian coast.
[H. Cogger]



Pl. 2.11. *Philoria sphagnicola* (Myobatrachidae): inhabits wet mountain forests in north-eastern New South Wales.
[H. Cogger]



Pl. 2.12. *Notaden bennettii* (Myobatrachidae): a burrower in flood plains and woodland of central eastern Australia.
[J. Wombey]



Pl. 2.13. *Limnodynastes convexiusculus* (Myobatrachidae): a ground dwelling frog of coastal savannah and shrub; Kimberleys to central Queensland.
[J. Wombey]

DEFINITION AND GENERAL DESCRIPTION

The family Myobatrachidae (Leptodactylidae, in part, of some authorities) is confined to Australia and New Guinea. Between 17 and 22 genera (depending on the authority) and some 112 species occur in Australia (Frost 1985; Davies, McDonald & Corben 1986b; Donnellan, Mahony & Davies 1990), as discussed below. Five genera and eight species (three of which are shared with Australia) occur in New Guinea (Zweifel & Tyler 1982). As outlined by Tyler (1989a), there is considerable disagreement over the familial status of the Australopapuan species, for there is no clear diagnosis other than geographic occurrence. The Myobatrachidae is used in the present treatment only for consistency with the nomenclatorial arrangement of Cogger, Cameron & Cogger (1983); however, this use does not imply that all four authors accept the arrangement. For additional information and references see discussions by Frost (1985) and Tyler (1989a).

Two subfamilies are recognised within the Myobatrachidae: the Limnodynastinae with eight to 10 genera (including *Rheobatrachus*; Pl. 2.7) and 44 species, and the Myobatrachinae with nine to 12 genera and 67 species. The status of *Rheobatrachus* which was assigned to the subfamily Rheobatrachinae by Heyer & Liem (1976) and given family status by Laurent (1979), is uncertain. In this chapter the genus is considered part of the Limnodynastinae, whereas a recent cladistic study by Ford & Cannatella (1993) indicates that it may be more closely related to the Myobatrachinae (see Affinities below).

There are also differences of opinion about the status of several myobatrachine genera. The nomenclatorial status of nine genera (*Australocrinia*, *Glauertia*, *Kankanophryne*, *Kyarranus*, *Megistolotis*, *Metacrinia*, *Paracrinia*, *Platyplectron*, *Ranidella*) is in dispute. Those accepted as valid in the present work (and in Chapter 1) are *Kyarranus* (on the basis of the distinctive structure of the ilium), *Megistolotis* (Pl. 2.6) (on the basis of a large prominent tympanum and the spiny nuptial excrescences on the hands of breeding males), and *Metacrinia* (differs from the closely related genus *Pseudophryne* (Pl. 2.5) on the basis of its complete ear and other osteological features). Opinions vary on the generic status of *Ranidella* from a distinct genus (MJL) to a subgenus of *Crinia*, as it is treated in here and in other chapters of the present volume. *Australocrinia* is a synonym of *Ranidella* (after Thompson 1981), *Glauertia* is a synonym of *Uperoleia* (after Lynch 1971; Tyler, Davies & Martin 1981a), *Kankanophryne* is a synonym of *Pseudophryne* (after Tyler & Davies 1980), and *Paracrinia* is a synonym of *Crinia* because of the absence of any diagnostic attributes of the adult stage (see Heyer & Liem 1976). The status of *Platyplectron* in the sense of Heyer & Liem (1976), which includes the burrowing species previously referred to *Limnodynastes*, is uncertain (see Tyler, Martin & Davies 1979).

The following definition of the family Myobatrachidae is based on those of Lynch (1973) and Duellman & Trueb (1986). There are eight, or functionally seven, presacral vertebrae with a persistent notochord. Subadults have free intersacral discs, except in *Lechriodus* and *Mixophyes*, and these are usually fused to the posterior end of the sacrum in adults to give the procoelous condition. Ribs are lacking. The sacrum has dilated diapophyses, and a bicondylar articulation with the coccyx, which may have transverse processes proximally. The pectoral girdle is arciferal or modified arciferal. The anterior end of the scapula is not overlain by the clavicle. Palatines are present, and a parahyoid is absent. The astragalus and calcaneum are fused proximally and distally, and there are two tarsalia. The *m. sartorius* is usually distinct from the *m. semitendinosus*, the *m. gluteus magnus* has an accessory tendon, and the *m. adductor magnus* has a small accessory head.

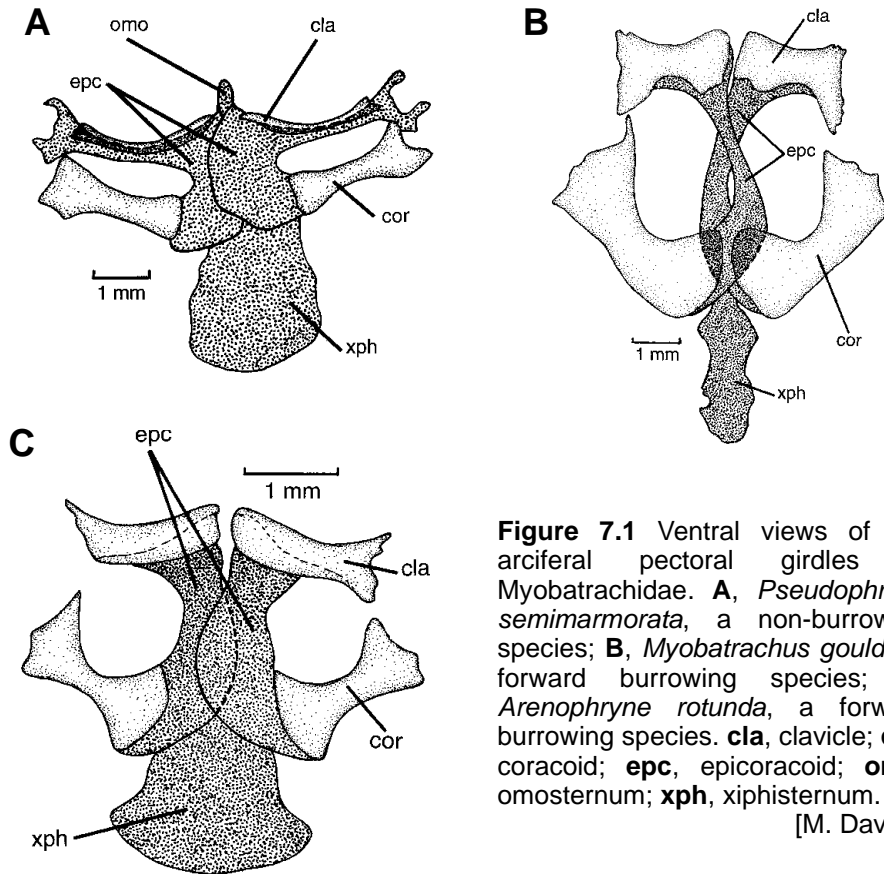


Figure 7.1 Ventral views of the arciferal pectoral girdles of Myobatrachidae. **A**, *Pseudophryne semimarmorata*, a non-burrowing species; **B**, *Myobatrachus gouldii*, a forward burrowing species; **C**, *Arenophryne rotunda*, a forward burrowing species. **cla**, clavicle; **cor**, coracoid; **epc**, epicoracoid; **omo**, omosternum; **xph**, xiphisternum.

[M. Davies]

Amplexus is inguinal, except in *Mixophyes*. In aquatic forms, the larvae are Type IV, with beaks and denticles (Duellman & Trueb 1986), and a sinistral spiracle. The chromosome number is $2n = 24$, except in four species of *Limnodynastes* where $2n = 22$, and three species of *Neobatrachus* where it is $4n = 48$ (King 1990). Adults of most species are terrestrial (except *Rheobatrachus*), and several (*Arenophryne*, *Heleioporus*, *Myobatrachus*, *Neobatrachus*, *Notaden*, *Uperoleia*, and some species of *Limnodynastes*) are fossorial. Reproductive cycles are mostly aquatic, with terrestrial oviposition and partial intracapsular development in *Geocrinia*, *Kyarranus*, *Pseudophryne* and *Heleioporus* (part). Complete or almost complete intracapsular development occurs in *Arenophryne*, *Myobatrachus*, *Kyarranus* and *Phylloria*.

HISTORY OF DISCOVERY

Two distinct phases may be recognised in the history of discovery of the Australian myobatrachid frogs. An earlier subjective morphological period predominated from 1838 to 1951, when conclusions were based largely on preserved specimens of adults. A later biological, multifactorial, biochemical and experimental period from about 1952 onwards, involved a consideration of all stages of the life history (see Chapter 2). The three primary and continuing approaches are the resolution of the higher categories (families, subfamilies and genera), the discovery and description of new species and subspecies, and investigation of their biology and ecology.

Parker (1940) provided a concise summary of the history of discovery and classification of the Australian species of myobatrachid frogs, from which the following account is derived, in part. Other information is presented by Cogger *et al.* (1983) and Frost (1985), from which works bibliographic details can be obtained, and in Chapter 2.

The first myobatrachid species to be described was *Heleioporus australiacus* (as *Rana australiaca*) by Shaw & Nodder in 1795, on the basis of a drawing. This was followed by the exhibition of a specimen of *Bombinator* (= *Pseudophryne*) *australis* by Gray in 1835, and the description of *Crinia georgiana* by Tschudi in 1838, from a preserved specimen collected near King Georges Sound, Western Australia. In the next three decades, six species in four genera were recognised and, by the turn of the century, species of nine or 10 of the presently accepted genera had been described.

Although *Crinia georgiana* was originally placed in the family Cystignathi, each subsequent new myobatrachid species was placed in one of several families. Thus, Cope (1865, 1866a, 1866b) revised the disposition of the genera into three families: Bufonidae (*Myobatrachus*, *Pseudophryne*), Asterophrynidae (*Adelotus*), and Cystignathidae (*Crinia*, *Cyclorana*, *Heleioporus*, *Mixophyes*, *Neobatrachus*, and *Uperoleia*). Boulenger (1882) arranged the genera only slightly differently: *Adelotus* (Pl. 2.4) was transferred to the Cystignathi (which was renamed the Cystignathidae); *Notaden* (Pl. 2.12) was included in the Bufonidae; and *Lechriodus* (Pl. 2.10) was placed in the Pelobatidae. Three groups were thus recognised—toothed forms in the Cystignathidae, non-toothed forms in the Bufonidae, and the Pelobatidae. Based on the work of Nicholls (1916), Noble (1922) transferred the cystignathid genera and *Lechriodus* to the Bufonidae, and later, (Noble 1931) subdivided the Bufonidae into two groups, the Bufoninae and the Criniinae, with the latter containing all of the Australian genera. On the basis of the morphology of the tongue and associated structures, Parker (1940) separated the Bufonidae of Noble (1931) into two families, Bufonidae and Leptodactylidae, the latter including the subfamily Criniinae. After a critical evaluation of the morphology, Parker (1940) recognised two clearly defined groups as subfamilies: Cycloraninae (*Adelotus*, *Cyclorana*, *Heleioporus*, *Lechriodus*, *Limnodynastes*, *Mixophyes*, *Notaden* and *Philoria*); and Myobatrachinae (*Crinia*, *Glauertia*, *Metacrinia*, *Myobatrachus*, *Pseudophryne* and *Uperoleia*). He erected the monotypic genus *Metacrinia* to include *Pseudophryne nichollii*. The review of Parker (1940) thus represents a significant synthesis of the Australian myobatrachid frogs.

An active and expanding period of research on Australian myobatrachids, with emphasis on field studies, began in 1951–1952 with the work of J.A. Moore and A.R. Main. The initial studies of Main, and subsequently those of his students, led to a reasonable understanding of the amphibian fauna of south-western Western Australia. A significant contribution from this period was the revision of the genus *Crinia* by Main (1957). Similar studies were initiated in south-eastern Australia in the late 1950s by M.J. Littlejohn and his colleagues (see Chapter 2).

Moore (1961) produced a comprehensive and critical treatment of the Australian Anura in which he recognised 16 genera, including *Kyarranus*, which he described in 1958, and 62 species, as well as six taxa of uncertain status. Although he rationalised the nomenclature at the specific level, and discarded all infraspecific categories, Moore (1961) did not attempt a revision of the genera and subfamilies. This work remains as a benchmark in studies of the Australian anurans. Other important systematic treatments were the comprehensive monographs on *Heleioporus* by Lee (1967), and on *Limnodynastes dorsalis* complex by Martin (1972a). Independently of the other schools, I.R. Straughan, and later D.S. Liem, undertook field studies in south-eastern Queensland. M.J. Tyler and his colleagues, M. Davies, A.A. Martin and G.F. Watson, pioneered field programmes in northern Australia in 1977, resulting in the discovery of many species, and the resolution of some taxonomic confusion.

A new genus and species, *Taudactylus diurnus*, was described by Straughan & Lee (1966). Tyler (1972b) erected the genus *Assa* to accommodate *Crinia darlingtoni*. Blake (1973) revised the genus *Crinia*, and re-established

Ranidella, described *Geocrinia*, and synonymised *Metacrinia* with *Pseudophryne*. *Rheobatrachus* was described by Liem (1973) to accommodate an unusual aquatic species. Heyer & Liem (1976) established several new monotypic genera, including *Australocrinia*, *Kankanophryne* and *Paracrinia*, none of which are presently recognised. *Arenophryne* was described by Tyler (1976a) to incorporate a newly discovered forward-burrowing species. The most recent new, extant genus to be described is *Megistolotis* (Tyler, Martin & Davies 1979). Cogger *et al.* (1983) recognised the monotypic genus *Metacrinia*, as had Heyer & Liem (1976), and placed *Kyarranus* in the synonymy of *Philoria*. Heyer, Daugherty & Maxson (1982) synonymised *Ranidella* within *Crinia* on the basis of immunological distance. Tyler *et al.* (1981a) placed *Glauertia* in the synonymy of *Uperoleia*. Frost (1985) recognised *Kyarranus*, *Megistolotis* and *Paracrinia*, but not *Metacrinia* and *Ranidella*. Tyler (1991a) confirmed the status of *Kyarranus* as distinct from *Philoria* on the basis of differences in the structure of the ilium.

National and regional zoogeographic syntheses were initiated by Moore (1961) and Littlejohn (1967), with subsequent reviews by Littlejohn & Martin (1974) (Bass Strait area), and Littlejohn (1981) (eastern and south-western Australia), and Tyler, Watson & Martin (1981c) (all of Australia). Detailed distribution maps were produced by Littlejohn & Martin (1974) and Martin & Littlejohn (1982) for Tasmanian anurans, and A.J. Brook produced a series of atlases of anuran distributions for Victoria, Tasmania, South Australia and Australia (Brook 1975, 1979a, 1979b, 1981, 1982, 1983). Syntheses of life history patterns and larval morphology for myobatrachines began with the work of Martin (1967), Main (1968) and Watson & Martin (1973).

An indication of the increased effort on taxonomy of the Myobatrachidae may be gained from the numbers of myobatrachine genera (excluding *Cyclorana*) and species recognised in taxonomic reviews, namely 12 and 47 by Parker (1940), 15 and 61 by Moore (1961), 20 and 96 by Cogger *et al.* (1983), and 19 and 112 in the present work.

MORPHOLOGY & PHYSIOLOGY

External Characteristics

Adult myobatrachids range from 20 to 115 mm in length. They also vary greatly in their general habitus. Fossorial species have a small head, globose body and short hind limbs (Pl. 2.1, 2.8, 2.12). Some, such as *Crinia* (*Ranidella*) species, are more streamlined, whereas others, for example *Mixophyes*, are broad bodied with intermediate-length, powerful legs.

The dorsal skin ranges from smooth in species such as *Limnodynastes tasmaniensis* and *Rheobatrachus silus* (Pl. 2.7) through tubercular skin such as found in *Notaden bennettii* (Pl. 2.12), to skin that has characteristically well-developed localised glandular areas, particularly in the parotoid, inguinal and coccygeal regions as in *Arenophryne*, *Uperoleia* or in the supralabial and tibial regions such as in the *L. dorsalis* complex. Examination of the dorsal skin of *R. silus* by scanning electron microscopy reveals a repetitive pattern of polygons with raised lateral cell margins and elongate depressions bounded by narrow, slightly raised ridges (Tyler & Davies 1983a). Ventral skin is smooth or granular with variations (sexually dimorphic and intraspecific) in the degree of granularity (Davies *et al.* 1986b).

Skin colouration is highly variable, but commonly drab brown or grey often highlighted with patches of ochre, gold or red. Many species are highly colourful with brilliant yellow and black stripes as in *Pseudophryne corroboree* (Pl. 2.5), or an intense yellow dorsum patterned in the form of a crucifix in black

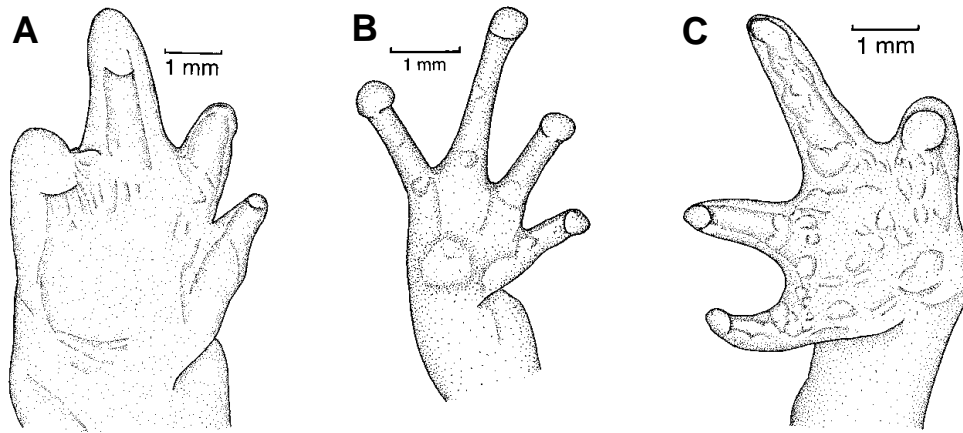


Figure 7.2 Palmar views of myobatrachid frogs. **A**, right hand of *Myobatrachus gouldii*; **B**, right hand of *Taudactylus diurnus*; **C**, left hand of *Arenophryne rotunda*. [M. Davies]

and red in juvenile *Notaden bennettii* (Pl. 2.12), or red or tan triangular head markings as in *P. australis* and *P. coriacea*. Many species have bright patches of colour (scarlet, orange, yellow) in the axillary and inguinal regions. Ventrally, many myobatrachids are highly patterned, as in examples of *Pseudophryne semimarmorata* with bold black and white marbling supplemented by brilliant orange/scarlet (illustrated by Tyler 1976b). Main (1965a) observed that *Metacrinia nichollsi* were often collected with the ventral surface uppermost, and that the ventral patterning closely resembled fungal hyphae and fruiting bodies within their habitat.

Individuals of *Pseudophryne* sp. feign death habitually and the bold ventral patterning may serve to startle potential predators (Tyler 1976b). Bright colours are generally interpreted as being aposematic or warning colourations, although supporting data to confirm these interpretations are lacking. Many colours are disruptive and may act as camouflage thus protecting frogs from predators. A dark stripe along the snout, through the eye and often to the axilla is a common feature (for example, *Mixophyes* spp.) acting to break up the outline of the prominent eye.

Secondary sexual characteristics of myobatrachids include the nuptial excrescences on the first three fingers in the males of some species and flanges on the first and/or second fingers in females associated with the production of foam nests during egg deposition. Both nuptial excrescences and flanges are subject to seasonal or ontogenetic variation.

Nuptial excrescences are usually glandular and located at the base of the first finger. In most species they are pigmented, but they lack pigment in *Uperoleia* (Davies & Littlejohn 1986). Within the Limnodynastinae, structure of the nuptial excrescences ranges from thorn-like in *Heleioporus* and *Megistolotis* to numerous and very fine spines, appearing glandular to the naked eye in *Limnodynastes convexiusculus* (Davies & Watson unpub. data). Under the Scanning Electron Microscope, the nuptial excrescences appear as conical elevations (*Lechriodus fletcheri*), pads in the form of rosettes (*Neobatrachus pictus*), radial processes (*Limnodynastes spenceri*) or alary processes (*L. ornatus*; Tyler & Lungershausen 1986). The nuptial excrescences of *L. ornatus* are found on the first three fingers (illustrated by Tyler & Davies 1986) whilst in *L. spenceri* there are several pads on the first two fingers (illustrated by Tyler, Smith & Johnstone 1984).

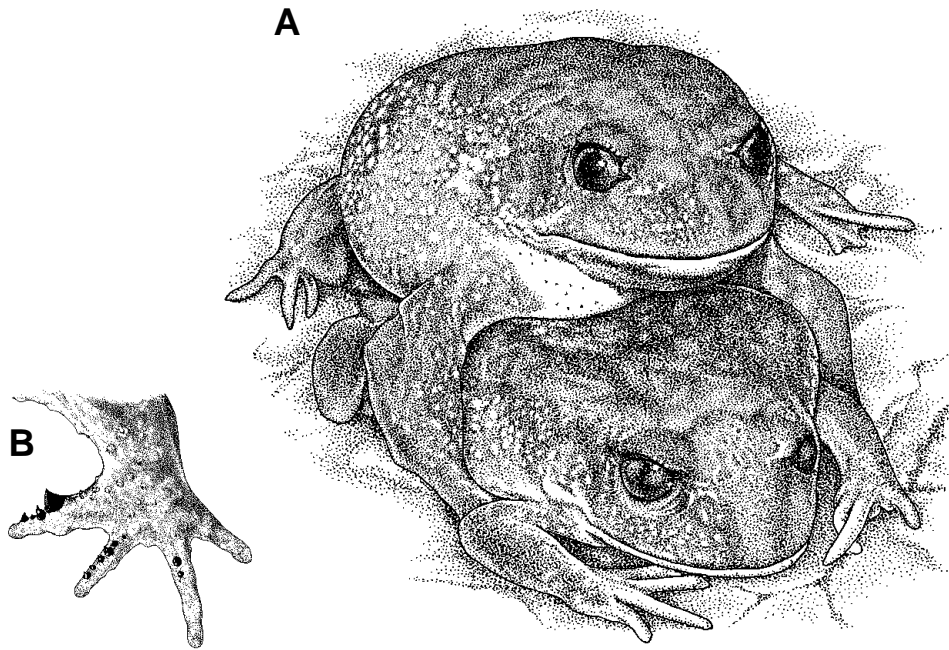


Figure 7.3 Mating behaviour **A**, amplexus in *Heleioporus australiacus*, **B**, nuptial excrescences on the hand of the male. (A, after Hoser 1989; B, after photo by F. Kristo/ANT) [K. Hollis]

Fossorial species, except forward burrowers like *Myobatrachus*, are characterised by compressed, shovel-shaped, keratinised, inner metatarsal tubercles (Fig. 7.2A, C; Pl. 2.1) which are melanic in most *Neobatrachus* and in *Notaden melanoscaphus*. *Uperoleia* spp. also have the outer metatarsal tubercle adapted for burrowing although some species such as the toothed forms *U. tyleri*, *U. martini*, *U. laevigata* and *U. fusca* that live in temperate wet areas not subjected to the same extremes of seasonal aridity, tend to have poorer fossorial development of the outer metatarsal tubercles.

Fingers and toes may be fringed or not, and terminal discs are undilated, except in *Taudactylus* (Fig. 7.2B; Pl. 2.9). Toe webbing varies from non-webbed (*Arenophryne*, *Assa*, *Crinia*, *Geocrinia*, *Kyarranus*, *Lechriodus*, *Metacrinia*, *Myobatrachus*, *Philoria* and *Pseudophryne*) (Pls 2.1, 2.10, 2.11) to almost fully webbed in the aquatic genus *Rheobatrachus* (Pl. 2.7).

Body Wall

The skin of amphibians comprises an outer stratum corneum and an inner stratum spongiosum which overlies a glandular layer comprising granular and mucous glands. Beneath these layers is the basal stratum compactum of collagen fibres. The relative thickness of these layers varies interspecifically. Tyler & Davies (1983a) recorded comparative data for the myobatrachids *Crinia (Ranidella) signifera*, *Pseudophryne bibronii*, *Limnodynastes dumerilii*, *L. tasmaniensis* and *Rheobatrachus silus*. For example, the stratum corneum of *R. silus* is only one cell thick and the epidermis only two to four cells thick. Mucous glands are large, granular and packed with circular vesicles. The basal stratum compactum is extremely narrow (Tyler & Davies 1983a).

The only myobatrachid for which a complete description of musculature is available is *Rheobatrachus silus* (Davies & Burton 1982; Burton 1983a) although particular muscle groups have been examined in various phylogenetic studies. Tyler (1972b) examined the superficial mandibular musculature of Australopapuan myobatrachid frogs and identified three muscles: the m. submentalis which is ovoid and usually araphic at the apex of the mandibles;

the *m. intermandibularis* which arises as a thin flat sheet from the lateral lingual surface of the mandibles between the *m. submentalis* and the jaw articulation; the *m. interhyoideus* arising principally from the anterior cornu of the hyoid uniting anteriorly with the posterior border of the *m. intermandibularis*. Tyler (1972b) showed that the nature of these muscles separates the Limnodynastinae and the Myobatrachinae (Figs 1.4F, G, 7.4F). In the limnodynastines the *m. intermandibularis* underlies the *m. submentalis* whilst in the myobatrachines, the *m. intermandibularis* has no contact with the *m. submentalis*. *Rheobatrachus*, a genus of contentious subfamilial placement, shares the limnodynastine condition (Tyler 1983c).

Tyler (1972b) also reported that the *m. intermandibularis* is sometimes differentiated by the presence of supplementary elements lying ventrally to the usual sheet of muscle. In the Limnodynastinae, the most anterior fibres of the *m. intermandibularis* attach on the ventral surface of the *m. submentalis* by transversely oriented fibres. Such attachments are absent in the Myobatrachinae.

Parker (1940) separated the two subfamilies on the basis of the nature of the distal tendon of the *m. semitendinosus* of the leg. In the Myobatrachinae the tendon perforates the ligamentous head of the *m. gracilis* or perforates the *m. gracilis* complex. *Rheobatrachus silus* exhibits the limnodynastine condition in this feature (Burton 1983a). Heyer & Liem (1976) used the *m. adductor longus* as a character for phylogenetic analysis, but Burton (1983a) cautioned against its use as he found intraspecific variation in its form in *R. silus*, such as he and others had found also in non-myobatrachid taxa.

Sanders & Davies (1984) showed that frogs with one of two modes of backwards burrowing have associated modifications to the muscles of the shank. In the ‘circular burrowers’ (for example, species of *Notaden* and *Neobatrachus*), the *m. cruralis* is considerably modified with an associated increase in the mass of the muscles of the lower limb when compared with the ‘backwards sliding burrowers’, *Limnodynastes ornatus* and *L. dumerilii*.

Horton (1982) examined the tongue musculature of a variety of frogs, including many myobatrachid species, and described a condition of the genioglossus found in all limnodynastines (except *Mixophyes* and *Rheobatrachus*). Two groups of fibres arising from corresponding mentomeckelian bones pass ventrally and medially to an interdigitating element. Groups of fibres extend caudally for a short distance, and then curve medially to meet in a median raphe. The result is a crescentic structure or superficial element. The fibres are free posteriorly for the remainder of the genioglossus. On the other hand, in the Myobatrachinae, the fibres are not free posteriorly from the remainder of the genioglossus. *Rheobatrachus* and *Mixophyes* lack tendinous structures that characterise the Limnodynastinae and Myobatrachinae, a state shared with members of the Hylidae and with *Ascaphus*, *Pelobates* and *Pelodytes* (Horton 1982).

Skeletal System

The maxillary arch is complete and dentate in all limnodynastines except *Notaden* (Lynch 1971; Shea & Johnston 1988). The teeth form a continuous row, except in *Adelotus* in which a distinct diastema between the maxillary and premaxillary teeth corresponds to the position of the odontoid ‘tusks’ on the lower jaw. *Adelotus* has fang-like teeth (Lynch 1971) that are found also in *Rheobatrachus* (Liem 1973; Davies 1983). In these two genera, medio-lateral extremities of the premaxillary palatal shelf extend such that they lie medial to the anterior portion of the palatal shelf of the maxilla (Davies 1983). Within the Myobatrachinae, the maxillary arch is invariably complete, but is edentate in *Pseudophryne*, *Myobatrachus*, *Arenophryne* and many species of *Uperoleia*.

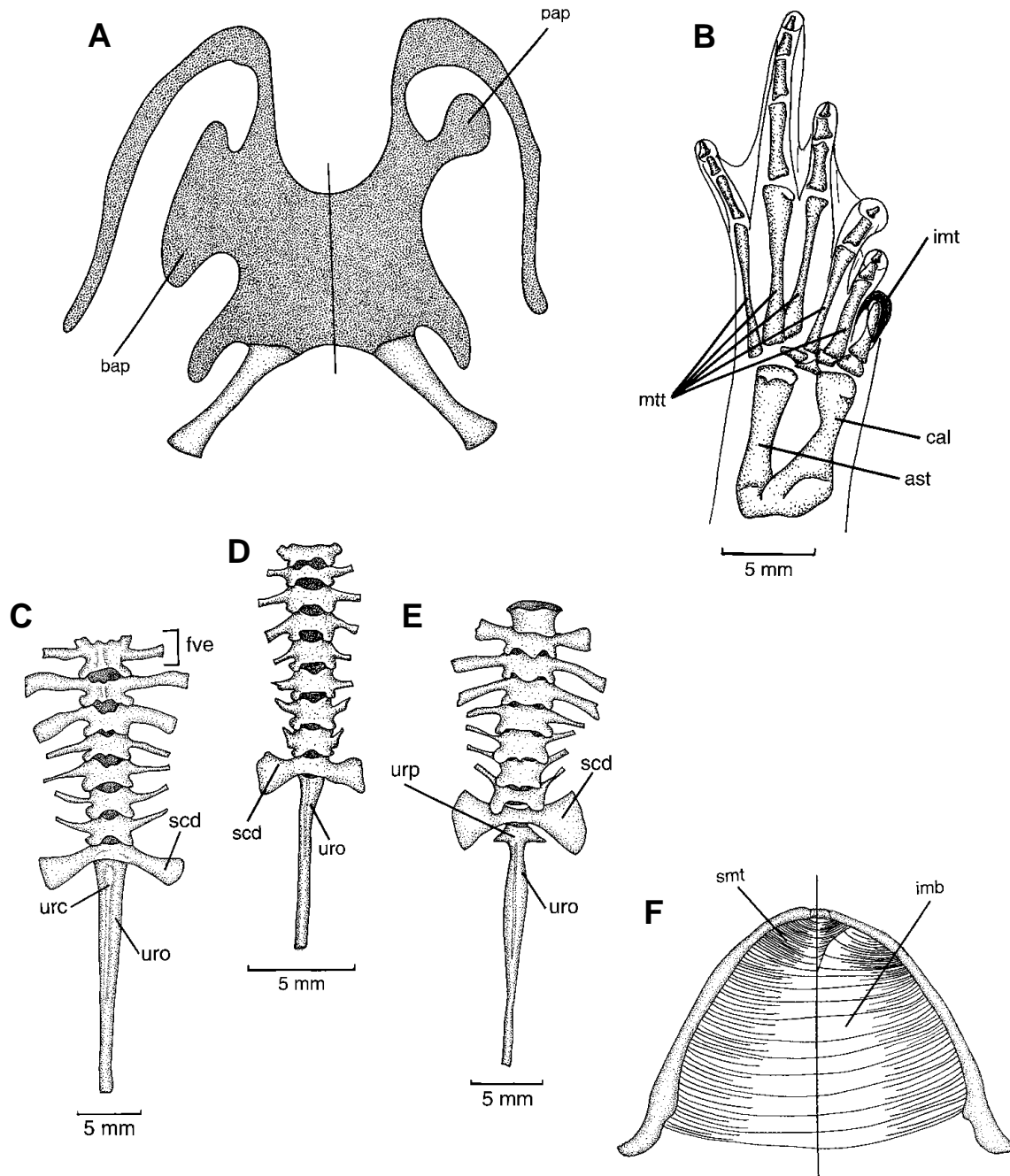


Figure 7.4 Postcranial elements of myobatrachid skeleton. **A**, composite diagram of hyoid to compare structure in the Myobatrachinae (left) and the Limnodynastinae (right); **B**, bones of the foot of *Neobatrachus aquilonius*, a backwards burrowing species with a melanic inner metatarsal tubercle; **C**, dorsal view of the seven, non-imbricate presacral vertebrae of the limnodynastine *Megistolotis lignarius*; **D**, dorsal view of the vertebral column of *Rheobatrachus vitellinus*, a possible limnodynastine species with eight imbricate presacral vertebrae; **E**, dorsal view of the vertebral column of *Pseudophryne semimarmorata*, a myobatrachine species with eight non-imbricate presacral vertebrae; **F**, composite diagram of the superficial mandibular musculature of the Myobatrachinae (left) and Limnodynastinae (right), to show structure. **ast**, astragalus; **bap**, broad alary process; **cal**, calcaneum; **fve**, fused first and second vertebrae; **imb**, intermandibularis; **imt**, melanic inner metatarsal tubercle; **mtt**, metatarsals; **pap**, pedunculate alary process; **scd**, sacral diapophysis; **smt**, submental; **urc**, urostyle crest; **uro**, urostyle; **urp**, urostyle process. (A & F after Tyler 1983) [M. Davies]

Teeth occur sparsely in *U. micromeles* and *U. altissima* (Tyler *et al.* 1981a; Davies, Watson, McDonald, Trenerry & Werren 1993). Tooth complement is influenced by heterochrony (Davies 1989a).

The facial lobe of the maxilla (*pars facialis*) is relatively deep in the Limnodynastinae. The depth of the *pars facialis* in the Myobatrachinae varies from moderately shallow, as in *Arenophryne*, (Davies 1984) to moderately deep in some species of *Uperoleia* (Tyler *et al.* 1981a).

The dorsal bones of the skull vary considerably in both subfamilies. The nasals of the Limnodynastinae vary in size and position relative to the premaxillae, sphenethmoid and frontoparietals (Lynch 1971). In *Philoria frosti* and *Mixophyes* spp., the nasals are large and in broad median contact overlying the sphenethmoid (Lynch 1971; Donnellan, Mahony & Davies 1990). Those of *Megistolotis lignarius* are slender and widely separated from each other and from the other dorsal bones of the skull (Tyler *et al.* 1979). The nasals of myobatrachines range from the relatively massive bones of *Myobatrachus gouldii* and *Uperoleia rugosa* (Lynch 1971; Davies & McDonald 1985) to the slender nasals of *Crinia (Ranidella) signifera* (Lynch 1971).

The development of the sphenethmoid in the Limnodynastinae is variable. This bone is absent in *Notaden weigeli* (Shea & Johnston 1988), but extends to the anterior extremities of the nasals in *Neobatrachus pictus* (Lynch 1971). In the Myobatrachinae, it is usually poorly developed and fails to ossify medially in most genera (Davies 1984). The exoccipital and prootic are not confluent in the limnodynastines, *Rheobatrachus silus* (Davies & Burton 1982) and *Notaden* spp. (Shea & Johnston 1988; Davies unpub. data), but are confluent in *R. vitellinus* (Mahony, Tyler & Davies 1984). Confluence of the exoccipitals and prootic is also often absent in the Myobatrachinae (for example, *Arenophryne* and many *Uperoleia*), but is present in other taxa (for example, *Crinia* and *Myobatrachus*).

The Limnodynastinae has moderately to well-developed frontoparietals, except in *Notaden*. Exposure of the frontoparietal fontanelle is moderate, or lacking, as in *Adelotus* (Lynch 1971) and *Mixophyes hihiorlo* (Donnellan *et al.* 1990). The frontoparietals of the Myobatrachinae vary from slender bones at the edges of the orbit, for example, in *Pseudophryne* and *Crinia (Ranidella)* to being well-ossified and totally roofing the fontanelle, as in *U. laevigata* and *U. rugosa* (Lynch 1971; Davies & Littlejohn 1986; Davies 1989a).

The structure of the limnodynastine squamosal and its relationship with the lateral extremities of the crista parotica is variable. It is extremely reduced in *Notaden*, lacks one or both of the zygomatic and otic rami and is widely separated from the crista parotica. It has a moderately expanded otic plate, overlying or narrowly separated from the crista parotica, in *Kyarranus sphagnicolus* and *Philoria frosti*, respectively (Lynch 1971). In the Myobatrachinae the shaft of the squamosal is usually stocky. The zygomatic ramus is long and slender in *Taudactylus* but is reduced or absent in most genera. Vomerine teeth are present in *Crinia georgiana*, *C. haswelli* and *Geocrinia*.

The palatines are robust in all limnodynastine genera except *Notaden* (Lynch 1971; Shea & Johnston 1988), and bear a medial ridge of prominent odontoids in *Mixophyes fasciolatus* (Donnellan *et al.* 1990). The palatines are reduced laterally in most species of the myobatrachine genera *Uperoleia*, *Arenophryne* and *Pseudophryne*.

In the Limnodynastinae the pterygoids vary from extremely robust in for example, *Mixophyes* (Donnellan *et al.* 1990), to reduced, with only a minute posterior ramus in *Notaden weigeli* (Shea & Johnston 1988). A ventral flange occurs on the body of the pterygoid in *Rheobatrachus* (Davies & Burton 1982; Mahony *et al.* 1984). The parasphenoid is invariably robust. The columella is

always present and is sinuous in shape in most genera (Davies unpub. data.). In the Myobatrachinae, the pterygoids are moderately robust, varying in the breadth of the anterior ramus, and the parasphenoid is invariably robust. The columella, where present, is straight. It is absent in *Arenophryne*, *Myobatrachus*, *Pseudophryne* and *Crinia* (*Ranidella*) *riparia*.

On the basis of Trewavas' (1933) studies, Parker (1940) considered that a complete cricoid ring was characteristic of the Limnodynastinae, a conclusion corroborated by Tyler (1972b). Parker (1940) also used the structure of the alary processes of the hyoid as a diagnostic character for the two subfamilies that he recognised. Within the limnodynastines, these processes are pedunculate and expanded distally, although the degree of expansion is variable. They are absent, for example, in *Notaden* spp. (Tyler 1972b; Shea & Johnston 1988). In contrast, the cricoid ring of the Myobatrachinae is incomplete ventrally (Trewavas 1933; Parker 1940; Tyler 1972a), and the alary processes of the hyoid are broadly based and 'wing-like' (Parker 1940; Fig. 7.4A).

The occipital condyles of the limnodynastine exoccipitals are not stalked and are poorly separated, so that the atlantyl cotyles of the articulating presacral vertebrae are juxtaposed (Lynch 1971). Those of the Myobatrachinae are stalked and widely separated in all genera except *Myobatrachus* and *Arenophryne*, a feature probably associated with the forwards burrowing habit (Davies 1984; Lynch 1971). Thus the atlantyl cotyles of vertebra I are widely separated.

Presacral vertebrae I and II are fused in the Limnodynastinae, except in *Mixophyes* and *Rheobatrachus*, so that there are effectively only seven presacral vertebrae. The ontogeny of the fusion of presacrals I and II is obscure as there are only seven cartilaginous primordia of presacral vertebrae at hatching (Davies unpub. data.). The neural arches of the presacral vertebrae are imbricate or non-imbricate. In some species, the first vertebrae are imbricate, whilst the others are non-imbricate. The majority of genera have free intervertebral discs as subadults (ectochordy) (Lynch 1971). Shea & Johnston (1988) reported dorsal fusion of fused presacral vertebrae I and II with presacral vertebra III, but this may be anomalous as it does not occur in congeners (Davies unpub. data.). Presacral vertebrae I and II are not fused in the Myobatrachinae, and there are eight presacral vertebrae. The vertebrae are procoelous with free intervertebral discs, in many cases persisting in the adult, and generally are non-imbricate.

Sacral diapophyses are moderately expanded in the Limnodynastinae, and transverse processes occur on the urostyle in *Rheobatrachus*; in the Myobatrachinae they are poorly expanded, and transverse processes have been recorded on the urostyle of *Metacrinia nichollsi* (Lynch 1971), although this occurrence has not been confirmed.

Within the Limnodynastinae, the phalangeal formula of the hand is uniformly 2,2,3,3 and of the foot 2,2,3,4,3. The terminal phalanges are knobbed. In *Limnodynastes fletcheri*, and to a lesser extent *L. peronii*, *L. salmini* and *Megistolotis lignarius*, metacarpal I is disproportionately long with an associated reduction in size of the phalanges (Parker 1940; Davies & Watson in ms). Parker associated this lengthening with an absence of nuptial excrescences in the *Limnodynastes* species, but such structures have since been located in *L. salmini* (Davies & Watson in ms), and they are spinous and prominent in *M. lignarius* (Tyler *et al.* 1979). Medial flanges are present on the first metacarpal of *M. lignarius*, *L. convexiusculus* and in *L. salmini* (Davies & Watson in ms.). The prehallux provides support for the inner metatarsal tubercle (Tyler, Davies & Walker 1985), and is large and hastate in burrowing species such as *Neobatrachus* and the *Limnodynastes dorsalis* group. The digital formulae are reduced in some myobatrachine species, including the forward burrowers (Fig. 7.5B, C). The terminal phalanges are knobbed except in *Taudactylus*, in which they are T-shaped (Fig. 1.4U, 7.5A). A modified

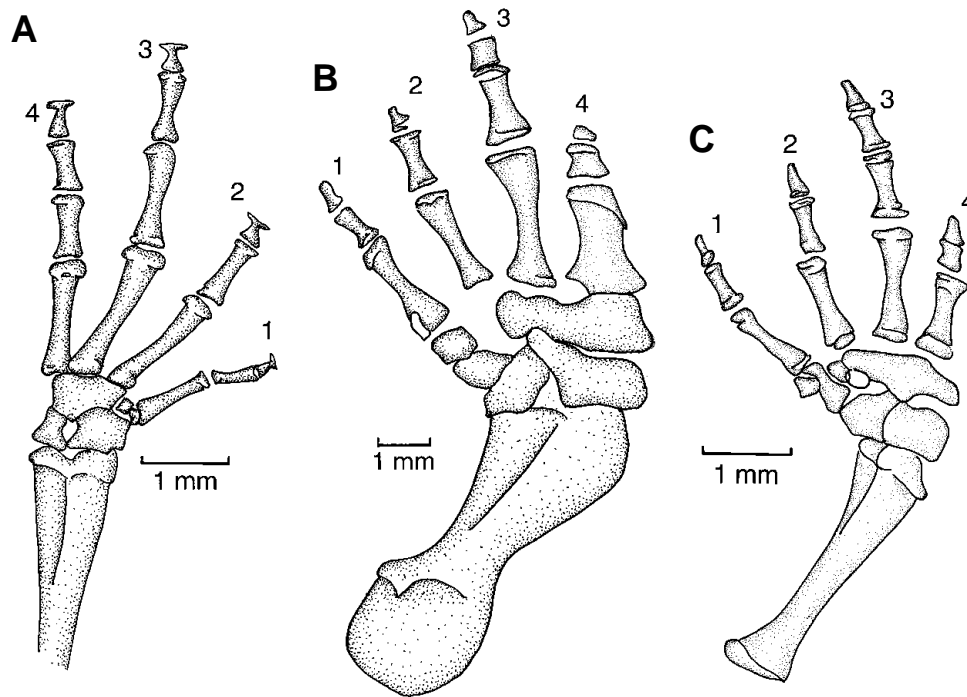


Figure 7.5 Palmar views of the bones of myobatrachid frogs. **A**, the right hand of *Taudactylus diurnus* which has no phalangeal reduction, but has T-shaped terminal phalanges; **B**, left hand of *Myobatrachus gouldii*, showing phalangeal reduction in the fourth finger; **C**, left hand of *Arenophryne rotunda*, showing phalangeal reduction in the fourth finger. [M. Davies]

prehallux supporting the inner metatarsal tubercle is present in *Uperoleia*, but there is no osteological support for the well-developed outer metatarsal tubercles in this genus.

Arenophryne and *Myobatrachus* are unique amongst the Myobatrachidae in that they burrow head first; they have particular post-cranial modifications not found in other myobatrachids (Davies 1984). The clavicles are broad, and the coracoids robust and acutely angled posteromedially (Fig. 7.1B, C). The limb bones are relatively massive in comparison with the other myobatrachines and the structure of the bones of the hands is appropriately modified for scooping the substrate when burrowing (Fig. 7.5B, C).

Tyler (1976a) provided generic diagnoses of the ilia of the Myobatrachidae, which are of particular value in identifying fossil anurans.

Locomotion

Movement amongst myobatrachids varies from the powerful and versatile swimming motions of the aquatic species *Rheobatrachus silus* (Tyler 1976b) through the walking motion of the short-legged *Pseudophryne* and *Uperoleia* species to the scuttling, mouse-like motion of the rotund, short-legged species of *Notaden* (Tyler & Davies 1986) and the leaps of the longer-legged species of *Mixophyes*. The method of locomotion is a function of the relative length of the hindlimbs and the shape of the body.

Feeding & Digestive System

Tyler (1989a) tabulated the published dietary studies on Australian frogs. Diet is, to a large extent, governed by the gape of the mouth and seasonal abundance of the prey. Prey is captured by either a biting or a grabbing action, or by tongue-flicking (Regal & Gans 1976). The tongue of *Rheobatrachus* is fused to the floor

of the mouth (Horton 1982), so that it cannot be flicked out. *Rheobatrachus vitellinus* appears to feed underwater, on the basis of its diet (McDonald pers. comm.), but studies on the diet of *R. silus* suggest that this species does not (Ingram 1983).

Vomerine teeth which lie either between or entirely behind the choanae may perforate the body of the prey by spiking it and assist the taste buds to test palatability. It is highly unlikely that they are involved in the killing of prey (Tyler 1976b). The tongue may be roughly heart-shaped, as in *Limnodynastes dorsalis* (Tyler, Smith & Johnstone 1984) or oval as in *Notaden nichollsi*. The oval form can extend for great distances, whereas the cordiform tongue is less mobile.

Excretion and Water Loss

Many arid-adapted species exhibit enhanced rates of rehydration when compared to mesic-adapted congeners as shown for *Neobatrachus* by Bentley, Lee & Main (1958), although a similar trend was not evident in *Heleioporus*. Lee (1968) demonstrated that average water losses in *H. eyrei* foraging at night during hot, arid summers, were equivalent to 22.3% of body weight. The water loss was replenished with water obtained from food or by rehydration from the sand surrounding daytime burrows. Water loss in *H. eyrei* was accompanied by significantly increased plasma sodium levels, which may facilitate rehydration, even though urine was retained in the bladder (Lee 1968).

Water stored in the bladder may be reabsorbed during periods of dehydration (Heatwole 1984). Bladder capacity (as a percentage of body weight) is generally higher in arid-adapted species, such as *Neobatrachus* and *Notaden*, although high values are also seen in some mesic-adapted species such as *Mixophyes fasciolatus* (Heatwole 1984). The subcutaneous lymph sacs do not appear to function as an auxiliary water store Carter (1979), as has been suggested previously, because aquatic amphibians tend to have large lymph sacs whereas fossorial species, including many myobatrachids (*Heleioporus albopunctatus*, *Limnodynastes dumerilii*, *Mixophyes fasciolatus*, *Neobatrachus* spp., *Notaden nichollsi*) have reduced lymph sacs.

Many myobatrachid genera show an increasing independence of free water during embryonic, and in some, larval, development, which involves many adaptations for overcoming environmental stress. The best studied genera in this regard are *Geocrinia* and *Pseudophryne*. Martin & Cooper (1972) described the ecology of terrestrial embryos and larvae of *G. victoriana*. Eggs are generally laid under litter in areas that later will be flooded by winter rains (Littlejohn & Martin 1964) but if flooding does not occur, development is suspended at stage 26 (Gosner 1960), and larvae can survive on land for up to four months. Egg capsules lose water freely by evaporation, but apparently little of this water comes from the larvae, as an hydrated egg can lose up to 90% without adverse effects on the larva (Martin & Cooper 1972). The large yolk reserves in eggs and ureotelism of the larvae of this species are presumably adaptations to prolonged terrestrial development.

A similar life history pattern is found in *Pseudophryne*. Terrestrial embryos of *P. bibronii* up to Gosner stages 26 to 28 show similar patterns of development to aquatic embryos (as measured by levels of oxygen consumption). If hatching in terrestrial eggs is delayed, then growth and development are reduced, thus extending the period of subsistence on stored energy reserves (Bradford & Seymour 1985; Seymour & Bradford 1987; Seymour, Geiser & Bradford 1991a, 1991b). Seymour & Bradford (1987) showed that increasing demands for oxygen in developing terrestrial embryos are facilitated by water absorption from the substrate into the perivitelline space, thus decreasing the thickness of

the jelly capsule and increasing the surface area. The resulting increase in oxygen conductance apparently is essential for adequate oxygenation of late-stage embryos.

Sense Organs & Nervous System

Duellman & Trueb (1986) note that species that have lost the columella tend to be fossorial or to live alongside streams. Although this holds true for *Arenophryne rotunda* and *Crinia (Ranidella) riparia*, the columella is lacking also in all species of *Pseudophryne*. There appears to be no adaptive significance in the loss. Other parts of the auditory system are not lost in those species lacking a columella, hence sound is received by a different route (see Duellman & Trueb 1986 for a summary of sound production). Lack of a tympanum appears not to inhibit sound reception (though see Wever 1973). The surface area of the tympanum has been suggested by Loftus-Hills (1973b) as affecting auditory sensitivity, although this does not hold true for all anurans (Frishkopf, Capranica & Goldstein 1968). Within the Myobatrachidae, the largest tympanum relative to the size of the frog is that of *Megistolotis lignarius*. The call of this species is a soft tapping sound with remarkable carrying capacity (Tyler, Davies, Watson & Martin unpub. data). Underlying neural mechanisms for acoustic behaviour have been investigated in *Limnodynastes dumerilii* (as *L. dorsalis*) and *Pseudophryne semimarmorata* (Loftus-Hills 1971, 1973a), and further investigations are reported by Loftus-Hills (1973b), Eggermont (1988) and Jaslow, Hetherington & Lombard (1988).

Different parts of the auditory system process different frequencies. The papilla amphibiorum processes frequencies below 1000 Hz, whilst high frequencies are processed by the papilla basilaris (Loftus-Hills & Johnstone 1970).

Exocrine Systems

Davies *et al.* (1986b) speculated that the glandular secretions of *Uperoleia* spp. may be toxic or distasteful to predators, but reported *U. mjobergii* in the stomach of the rufous (Nankeen) night heron (*Nycticorax caledonicus*). They also cited observations that secretions from *U. talpa* are toxic to other frogs sharing the same container.

Secretions from the tibial gland of *Limnodynastes dumerilii* provide some degree of protection from potential predators (Crook & Tyler 1981). Release of the secretion, however, appears only to occur in response to lateral compression of the glands.

The role of skin secretions is multifunctional and probably includes antimicrobial and antifungal activity, antipredator activity and water balance and respiratory functions.

Reproduction

Of all Australian frogs, the myobatrachids show the most radical variations from basic anuran life styles. This variation is most clearly expressed in patterns of breeding biology and egg deposition. These patterns also differ between members of the two subfamilies, the Limnodynastinae and the Myobatrachinae.

The Limnodynastinae exhibits six modes of egg deposition and breeding biology.

Eggs in jelly deposited in water. In *Neobatrachus*, the eggs are deposited in long strings, two to three eggs wide (Main 1965a; Roberts 1978). Those of *Notaden melanoscapus* are deposited in a thin film on the water surface (Tyler, Crook & Davies 1983a); egg deposition has not been described for other species of *Notaden*.

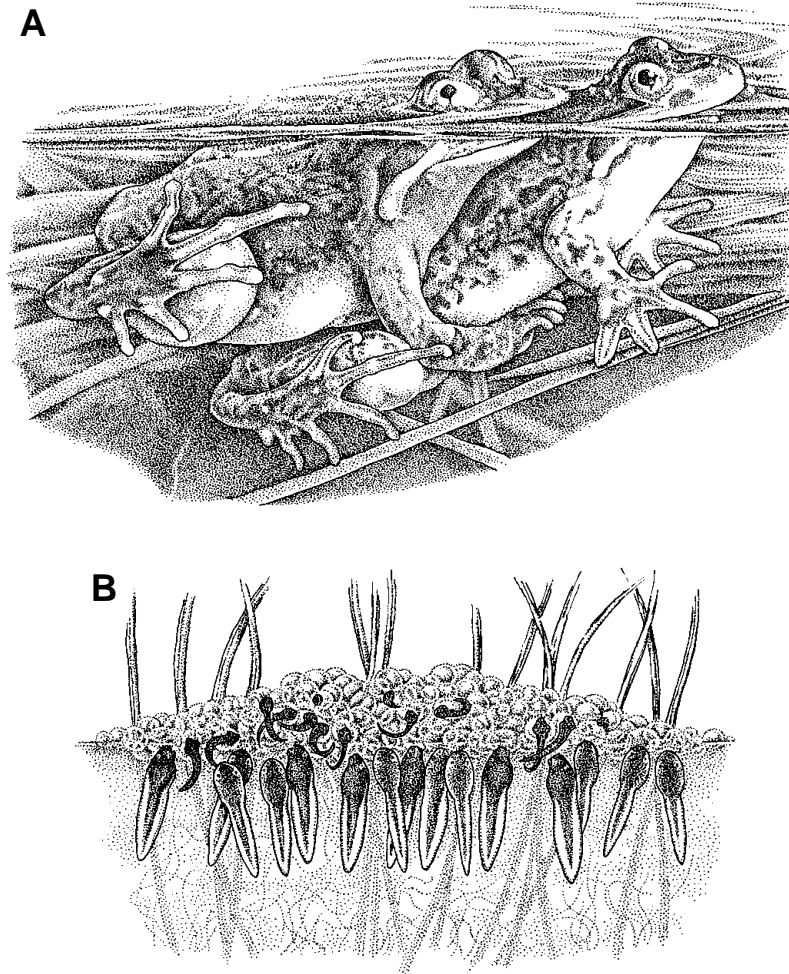


Figure 7.6 Reproduction in *Limnodynastes tasmaniensis* **A**, amplexus. Note flanged fingers of the female; **B**, tadpoles sheltering beneath foam nest. (A, B, after photos by C.A. Henley/NPIAW) [K. Hollis]

Eggs in jelly deposited on land with an aquatic tadpole. Species of *Mixophyes* deposit eggs in hollows under litter adjacent to streams, which are then are washed into the stream by heavy rain (Barker & Grigg 1977).

Eggs in a foam nest in water. All species of *Adelotus*, *Limnodynastes*, *Lechriodus* and *Megistolotis* (Fig. 7.6) use this mode (Tyler 1989a). In the southern call race of *Limnodynastes tasmaniensis*, populations in south-eastern South Australia deposit eggs masses without foam (Roberts & Seymour 1989). Foam may persist for several days in *Limnodynastes tasmaniensis* (Roberts & Seymour 1989), but in *Limnodynastes ornatus*, it breaks down within 24 hours of deposition (Tyler *et al.* 1983a). Amplectant females produce a stream of bubbles by paddling with the hands. These bubbles are incorporated in jelly released with the eggs. The first two fingers are flanged, and this modification may facilitate bubble production (Tyler & Davies 1979c; Fig. 7.6A). Flanges are absent in females of *L. tasmaniensis* where foam is not present in the egg mass, thus supporting this view.

Eggs in a foam nest out of water with an aquatic, feeding tadpole. In Western Australian species of *Heleioporus*, eggs are deposited in a foam nest at the bottom of a dry breeding burrow. These burrows are well-defined structures up to 115 cm long and up to 7 cm diameter depending on species (Lee 1967). Embryonic development proceeds in the nest until the burrow floods with the onset of winter rains. In some instances, eggs may hatch at the bottom of the burrow before full flooding occurs (Lee 1967). In *H. australiacus* from eastern

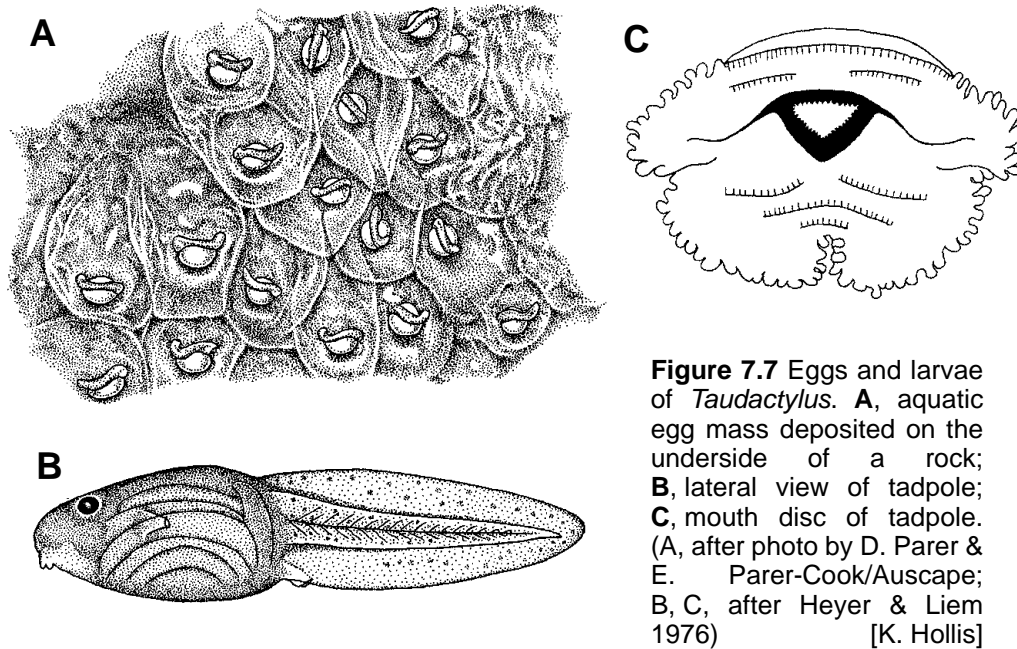


Figure 7.7 Eggs and larvae of *Taudactylus*. **A**, aquatic egg mass deposited on the underside of a rock; **B**, lateral view of tadpole; **C**, mouth disc of tadpole. (A, after photo by D. Parer & E. Parer-Cook/Auscape; B, C, after Heyer & Liem 1976) [K. Hollis]

Australia, the eggs are deposited in a foamy mass floating in water or in a flooded burrow (Watson & Martin 1973), although Barker & Grigg (1977) reported calling by males from burrows in sandy banks a few metres from water, as occurs in the western species. Eggs of all species of *Heleioporus* are non-pigmented or very lightly pigmented (Lee 1967).

Eggs in a foam nest out of water with a non-feeding tadpole. In *Kyarranus*, the foam nest is formed in a hollow under litter, or is buried up to 15 cm deep in moist sphagnum (Moore 1961). In *Philoria*, the egg mass is deposited in shallow water (Malone 1985), or in moist sphagnum (Watson & Martin 1973). In both genera, the eggs are non-pigmented, and females have flanges on the first two fingers as in *Limnodynastes*.

Gastric brooding. Eggs, or early larvae, are ingested by the female, and direct development proceeds in the stomach leading to oral birth. This process is only known for the two species of *Rheobatrachus*. The nature and location of egg deposition and ingestion in this genus is unknown (Fanning, Tyler & Shearman 1982; Gibbins & Tyler 1983; Tyler 1985a, 1989a; Leong, Tyler & Shearman 1986; Tyler, Shearman, Franco, O'Brien, Seamark & Kelly 1983b).

Within the Myobatrachinae there is also a wide variety of strategies of egg deposition, but the foam nesting which occurs in many limnodynastines is absent.

*****Aquatic eggs with a free-swimming tadpole.** This mode occurs in many species of *Crinia* (*Ranidella*), and in *Uperoleia*, *Crinia haswelli* and *Taudactylus*. Eggs may be deposited singly or in small clumps as in *C. signifera* (Moore 1961), in small clumps under rocks as in *Taudactylus* (Fig. 7.7A; Czechura & Ingram 1990), or in a broad jelly sheet on the underside of rocks in shallow water as in *C. riparia* (Tyler 1978) or close to water (Littlejohn & Martin 1965). In *Uperoleia*, eggs are attached to submerged vegetation in groups of one or two (Robertson 1986), or in water 2 to 5 cm deep—where the eggs soon sink (Tyler *et al.* 1983a). Unlike other species of *Pseudophryne*, eggs of *P. douglasi* are also deposited in water (Main 1965a).

Terrestrial eggs with an aquatic tadpole. There are two variants on this theme. Eggs may develop out of water for long periods, as in eastern species of *Geocrinia* (up to 120 days for *G. victoriana*, Martin 1967b) and all species of

Pseudophryne except *P. douglasi* (Main 1965a; Pengilley 1973). Eggs of *Geocrinia leai* are deposited above water in vegetation; after hatching, the tadpoles wriggle into water (Main 1965a), without an extended period of terrestrial development.

Direct-developing eggs. These may be deposited in shallow depressions or in short burrows hidden under leaf litter or vegetation cover as in species of the *Geocrinia rosea* complex (Roberts, Wardell-Johnson & Barendse 1990), deposited deep (80 to 120 cm) underground as in *Arenophryne* and *Myobatrachus* (Roberts 1981, 1984) or deposited in or under litter and then the young carried in inguinal pouches of the male as in *Assa* (Straughan & Lee 1966; Fig. 5.4). *Metacrinia* probably also has direct-developing eggs (Maxson & Roberts 1985). In *Myobatrachus* and *Arenophryne*, pairing and egg deposition are separated by periods of up to five months; pairing occurs in the spring, with egg deposition the following autumn (Roberts 1984).

Parental care of young has only been demonstrated clearly in *Assa* (Straughan & Lee 1966; Ehmann & Swan 1985) and *Rheobatrachus* (Tyler 1989a). In other myobatrachids, males (for example, *Pseudophryne*, Woodruff 1977) or females (for example, *Kyarranus*, Moore 1961) may be associated with egg masses. However, there is no evidence that the presence of adults enhances survival of the progeny.

Martin (1967b) and Tyler (1985b) discuss evolutionary trends away from egg deposition in an aquatic environment. Partial or complete removal of eggs from water is not an adaptation to arid environments (Main 1968). In species with terrestrial eggs and aquatic larvae, the early development on land may give the resulting advanced larvae an ecological advantage over aquatic breeders when both types enter the pond, either in terms of utilising different food items, of shorter larval periods, or because the larger size of hatchlings makes them less prone to predation (Martin 1967b; Main 1968). The shift away from aquatic egg deposition may also be in response to the rigours of the available aquatic environment, as fast-flowing streams may wash tadpoles away, or be to take advantage of soils that are reliably moist (Roberts 1984). Predation in the aquatic environment has also been seen as a strong selective force favouring terrestrial development (Martin 1967b). However, no data exist that demonstrate even the proximate value of terrestrial egg-deposition for Australian frogs.

It is likely that terrestrial egg-deposition, with or without direct-developing embryos, has evolved several times in the Myobatrachinae, and possibly twice in *Geocrinia*, as the *G. rosea* group are spring breeders, not autumn breeders as are the remaining *Geocrinia* species (Roberts *et al.* 1990). The other genera are *Arenophryne*, and *Assa*, *Metacrinia* (Maxson & Roberts 1985) and *Pseudophryne*. There is a tendency in this direction in *Crinia* (*Ranidella*) *riparia* (Littlejohn & Martin 1965) and *Crinia georgiana* (Main 1968). Although some of the genera are presumed to be closely related (for example, *Myobatrachus* and *Pseudophryne*; Maxson & Roberts 1985), and a direct-developing egg may be derived from a strategy of terrestrial egg-deposition with an aquatic larva, the details of the radically different breeding systems make this unlikely (Roberts 1984).

The members of the subfamily Limnodynastinae have evolved foam-nesting at least once (the *Limnodynastes*, *Adelotus*, *Megistolotis*, *Kyarranus*, *Philoria* and *Lechriodus* lineage), and possibly twice, as *Heleioporus* has a radically different form of foam production (Watson & Martin 1973). The function of foam is unclear, though possible options are protection from desiccation and aquatic predators, the ecological advantages of foam nesting in a terrestrial site (see above), and respiratory advantages where foam holds the egg mass close to the highly oxygenated water surface (Roberts & Seymour 1989). Though foam does

not necessarily protect against desiccation, or against predation (see Embryonic Mortality below), there is some support for the last suggestion (Roberts & Seymour 1989; Seymour & Roberts 1991).

Myobatrachids, in common with other Australian anuran species, show marked variation in breeding seasons and breeding patterns. For the 15 south-western species for which data are available on both activities, Main (1968) reported that calling and breeding periods were almost coincident in explosive breeders like *Neobatrachus*, and in autumn breeders like *Heleioporus* and *Pseudophryne*. However, in several species of *Crinia* (*Ranidella*), calling extended over several months more than breeding. For example, *C. glauerti* calls year round, but breeding females have been seen only from mid-April to mid-November. Similar patterns were seen in the Northern Territory, where *Uperoleia inundata* called from late December to late April, but breeding was observed only in January (Tyler *et al.* 1983a). There may also be wide between-year variation, with *Limnodynastes ornatus* calling and breeding from late October until the end of February in 1978–1979, and calling over a similar period in 1979–1980; but in the second season, breeding only occurred on a few days in early December 1979 (Tyler *et al.* 1983a).

The cues that initiate calling and breeding are not well known. Calling in *Myobatrachus gouldii* is absolutely dependent on rainfall, and it only occurs on the night immediately after rain (Roberts 1981). In other explosive breeders, such as *Neobatrachus*, rainfall is also a proximate trigger for calling and breeding (Main 1968; Roberts 1978). Main (1968) claims that breeding in *Heleioporus* is strictly seasonal, irrespective of rainfall, with females entering breeding burrows in late autumn. However, movement of *Heleioporus* to breeding sites and construction of burrows is correlated strongly with the onset of rain, with the exception of *H. eyrei*, which may call before opening rains in April, particularly at moist sites (Lee 1967). Applying a multiple regression model, Humphries (1979) determined that rainfall has little influence on breeding activity in *P. bibronii*, *L. tasmaniensis*, *Uperoleia laevigata* (as *U. rugosa*), *C. parinsignifera* and *Crinia* (*Ranidella*) *signifera* near Canberra. However, pond levels and changes in pond level, interpreted as measures of soil moisture and changes in soil moisture, were important for most species.

Martin (1969) reported that emergence from hibernation in *Limnodynastes dumerilii* was dependent on high soil temperatures ($>12.5^{\circ}\text{C}$), provided that some critical, high (possibly saturation) level of soil moisture was reached. If soils were dry, emergence was not synchronous and breeding was absent or spasmodic. In this species, breeding activity in years of mass emergence was highly skewed, and most breeding occurred immediately after emergence, but tailed off over the next five weeks. Humphries (1979) observed similar skews in his sets of breeding data. Although the stimuli critical to the initiation of breeding are unclear, these variations and uncertainty are not unique to myobatrachid frogs.

Observational data on breeding activity in Australian frogs indicates that in many species breeding will occur in response to rainfall irrespective of other seasonal conditions. Hero, Littlejohn & Marantelli (1991) listed predicted breeding seasons for Victorian myobatrachids, and some are prolonged, including all year for *Crinia* (*Ranidella*) *signifera* and over ten months for *Limnodynastes tasmaniensis*. Perhaps the best documented longer-term study of reproductive activity was that of R.B. Humphries working near Canberra where, for example, he found that peak breeding in successive ‘breeding seasons’ in *L. tasmaniensis* occurred in mid-September 1975 and in late February 1977 (Humphries 1977).

Embryology & Development

In terms of life history and larval morphology, the Myobatrachinae is a relatively uniform group whilst the Limnodynastinae is a more heterogeneous assemblage (Watson & Martin 1973). Members of the Myobatrachinae could be linked on the basis of their life history and larval morphology traits—eggs with discrete capsules, egg masses not foamy, no external gills at hatching, a dextral anus, two upper and three lower rows of labial teeth, and anterior and posterior gaps in the papillary border. The few exceptions that Watson & Martin (1973) recorded were in *Assa*, *Crinia* and *Taudactylus* in which larvae are modified for development in specialist niches. Odendaal & Bull (1980) showed experimentally that *Crinia* (*Ranidella*) *riparia* has a body and mouth form adapted for living in fast flowing streams and this has been inferred for *Mixophyes* species (Moore 1961; Watson & Martin 1973; Davies 1991).

Larvae of the genera *Arenophryne* and *Myobatrachus* develop directly (Roberts 1981, 1984). The myobatrachine tooth row complement of *Taudactylus acutirostris* is unlike that of its congeners *T. diurnus* and *T. eungellensis* that lack tooth rows (Watson & Martin 1973; Liem & Hosmer 1973). Given that habitat of *T. acutirostris* is riparian and similar to that of the described congeneric species, the form of the mouth disc appears somewhat anomalous. There is no gap in the labial papillae, either posteriorly or anteriorly. *Crinia georgiana* is the only myobatrachine recorded as having more than two upper rows of labial teeth (Main 1968).

Within the Limnodynastinae, external gills are present in species of *Heleioporus* (though not located in *H. albopunctatus*), *Kyarranus*, *Lechriodus*, *Limnodynastes*, *Philoria*, *Mixophyes*, *Megistolotis*, *Neobatrachus* and *Notaden*, but not in *Adelotus*. The number of upper labial tooth rows is variable. As in the Myobatrachinae, direct-developing larvae of the limnodynastine genera *Kyarranus*, *Philoria* and *Rheobatrachus* lack labial tooth rows (Moore 1961; Littlejohn 1963; Watson & Martin 1973; Ingram & Corben 1975; Tyler *et al.* 1979; Anstis 1981; Tyler *et al.* 1983a; Tyler & Davies 1983b; McDonald & Tyler 1984; Davies 1991).

Most larvae have 3 to 6 upper rows of labial teeth; exceptions are *Limnodynastes spenceri* and *Notaden melanoscapus* which have two rows, *Mixophyes balbus* with 11 upper rows, and *M. schevilli* with 11 to 12 rows. Limnodynastines have an anterior gap in the papillary border, except in *M. balbus* and *M. schevilli* in which the papillary border is complete. Tadpoles of *Mixophyes* are lotic species and a complete papillary border may be an adaptation allowing tadpoles to hold on to substrata in fast flowing streams. However, *M. lignarius* is also a lotic species and the papillary border of the larval mouth is interrupted anteriorly. The anus is usually medial, but often slightly offset or dextral in *Neobatrachus* and fully dextral in *Adelotus*, *Heleioporus* and *Mixophyes* (Main 1968; Watson & Martin 1973; Tyler *et al.* 1979; Tyler *et al.* 1983a; Davies 1991, 1992).

Standard developmental schemes for anurans (for example, Gosner 1960) apply to many myobatrachids. However, for species with terrestrial eggs or direct development, the large yolk mass may complicate the normal patterns of development. Initial cleavage and gastrulation are slower in *H. eyrei* than in *Rana*, presumably because of the relatively large yolk in *H. eyrei* (Packer 1966). Gollman & Gollman (1991) described developmental stages of *Geocrinia laevis*, *G. victoriana* and their hybrids. They noted differences from Gosner's scheme in stages 20 to 26. Gollman (1991) also described development in *Crinia* (*Ranidella*) *signifera*. In these two genera, the only major variation from Gosner's scheme is that *Geocrinia* hatch at a later stage than expected. Roberts

(1984) did not report any special adaptations or variations from expected developmental patterns in the direct-developing eggs of *Arenophryne rotunda*, except that the tail seemed to be heavily vascularised.

In both subfamilies, the survival of eggs deposited out of water is dependent on the size of the yolk reserve, and on environmental factors that will affect yolk use or embryonic survival. In most species with terrestrial egg-deposition or direct development, eggs are relatively large compared with those of frogs comparable in size with aquatic eggs (Main 1968; see also Chapter 5). The embryos of *Pseudophryne bibronii* show an initial rapid growth with associated high metabolic rates and yolk use, reach Gosner stages 26 to 28 in 33 days at 12°C, and thereafter the rate of growth and development slows to almost zero. Eggs in this latter state can survive up to 140 days, with oxygen consumption rates about a third those of aquatic hatchlings of similar age (Bradford & Seymour 1985). Similar delays in development may occur in other species with this style of egg deposition. In *Heleioporus*, speed of development may be dependent on water availability, paradoxically being faster in eggs kept free of water (Lee 1967).

Large yolk volumes are not always associated with direct development. *Geocrinia rosea*, comparable in adult size to *G. victoriana*, has a mean egg diameter of 2.35 mm compared with 3.10 mm; but *G. rosea* has a direct-developing egg (Martin 1967b). The sizes of metamorphlings in *G. victoriana* range from 8.2 to 10.3 mm (Martin 1965); in *G. rosea* the size of hatchlings (equivalent to metamorphlings for a direct developer) is about 5.1 mm (based on five froglets from a single egg-mass collected on Grey Block, near Pemberton, Western Australia). Smaller eggs may result in smaller body sizes at metamorphosis.

Detailed patterns of growth and development under conditions of field temperature have been reported for *Notaden melanoscaphus* and *Uperoleia inundata*, and under laboratory conditions for *Limnodynastes terraereginae* and *L. fletcheri* and *Heleioporus albopunctatus*. The limited data available suggest that the myobatrachid and hylid frogs show the same general patterns of growth and development (Tyler *et al.* 1983b; Davies 1991, 1992).

NATURAL HISTORY

Life History

Myobatrachid frogs may be locally abundant. For example, *Arenophryne rotunda* is extremely abundant in coastal sand dunes at Shark Bay, Western Australia (227.6 frogs per hectare) (Roberts 1985), with population densities approaching those of salamanders in North America. Population densities of *Myobatrachus gouldii* are almost as high at 176 frogs per hectare (Roberts 1985). The density of *Limnodynastes dorsalis* populations near Badgingarra, Western Australia, was much lower at only 40 frogs per hectare. By contrast, Ingram (1983) estimated population densities of the fully aquatic *Rheobatrachus silus* at only 1.11 frogs per hectare. Estimates of population size (from potential breeding sites) for species that might be less wide-ranging, also give some impressive population sizes. *Crinia (Ranidella) insignifera* at Lighthouse Swamp on Rottnest Island, Western Australia, were present in large populations (138 to 580 frogs in different years), with large inter-annual fluctuations in recruitment (Main 1965a). From the same site, Lee (1967) estimated the population size of *Heleioporus eyrei* as 202 adult males, 78 females, and for the previous year, 2 241 juveniles! Myobatrachids may be particularly abundant components of the terrestrial vertebrate fauna.

Embryonic and larval stages are subject to major mortality. Only 9% of 77 egg masses of *Philoria frosti* survived from egg to metamorphling (Malone 1985). There was no difference in mortality rates of embryonic and larval stages. Humphries (1979) reported similar survival rates for *Crinia (Ranidella) parinsignifera*, *Limnodynastes tasmaniensis*, *L. dumerilii*, *Pseudophryne bibronii* and *Uperoleia laevis* (as *U. rugosa*) from a study pond near Canberra. Survival rates in this last species ranged from zero to only 2.71%. Main (1965a) estimated that only 30 of 200 eggs of *Heleioporus inornatus* deposited in burrows survived to metamorphosis.

Woodruff (1976b) and Humphries (1979) reported separate instances of mass embryonic mortality caused by desiccation in *Pseudophryne*. However, Woodruff (1976b) suggested that embryonic mortality was generally low in *Pseudophryne* spp., ranging from 1.1% to 8.8%. Mortality was intrinsic and related to developmental or genetic problems, not to environmental impacts. Neither Woodruff nor Humphries observed any instances of predation on egg masses of *Pseudophryne*. Malone (1985) suggested that desiccation was the major cause of egg loss in the direct-developing species, *Philoria frosti*. Eggs of this species take five to eight weeks to develop, followed by a free-swimming larval stage of five to ten weeks. The larva probably does not feed because metamorphlings still have yolk in the gut (Malone 1985). Up to metamorphosis, mortality varied from 0 to 100%, with a mean of 65.4%.

Egg masses of *Heleioporus eyrei* are commonly infested with larvae of an undescribed phorid fly. One of us (JDR) has observed infestations in 19 of 66 egg masses in early June at the end of the breeding season. Fly larvae were observed inside capsules of some eggs, but most damage resulted from the removal of the foam around the eggs. This removal may cause premature hatching of tadpoles and death by desiccation. Similar infestations of egg masses of the phylomedusine frog *Agalychnis annae* by phorid flies caused significant embryonic mortality (Villa & Townsend 1983). Ehmann & Swan (1985) reported predation on eggs of *Assa darlingtoni* by carabid beetles before the eggs hatched and the tadpoles were moved into the inguinal pouches of the male. The aquatic egg masses of *Limnodynastes tasmaniensis* (Fig. 7.6B) may be subject to predation by leeches, and to dessication after water levels fall (Humphries 1979).

Developmental periods range from 16 days in *Notaden nichollsi*, a desert species, to 13 to 16 months in *Limnodynastes dumerilii* from southern Victoria (Martin 1965a). The short larval life span for *Notaden* represents an adaptation for the use of ephemeral aquatic habitats in deserts. The long larval-span for *Limnodynastes* is not so easily explained, especially when other species (for example, *Heleioporus barycragus* and *L. dorsalis*) with similar body sizes at metamorphosis and as adults have shorter larval periods of about 150 days (Main 1968).

Developing embryos and larvae of arid dwelling species can tolerate extremely high water temperatures. Tadpoles of various species, including myobatrachids, utilise high temperature ephemeral waters in northern Australia. For example, the larvae of *Uperoleia lithomoda* were found in water at 39.6°C (Tyler 1989a). Some species utilising these unpredictable habitats also exhibit particularly short larval life spans, presumably in response to the likelihood of ponds drying out, though the direct effects of higher environmental temperatures on developmental rates may be partly responsible. *Limnodynastes ornatus* and *Crinia (Ranidella) bilingua* have minimum larval lives of 21 and 13 days, respectively; in contrast, two congeners, *L. dumerilii* and *C. glauerti*, from more mesic and predictable environments, have minimum larval lives of 12 to 15 months and 130 days, respectively (Tyler 1989a).

General strategies of egg deposition and larval development for Australian frogs are discussed in Chapter 5. Larval development in *Heleioporus inornatus* may proceed in the breeding burrow, or in small pools around the burrow entrance (Lee 1967). In other species of *Heleioporus*, tadpoles move into larger water-bodies. Hatched tadpoles of *Philoria* are associated with the site where the foam nest was deposited (Malone 1985). In *Kyarranus*, the tadpoles hatch, but development may proceed in a broken-down egg-mass (Moore 1961). In myobatrachines with direct-developing eggs, development may take place in the remains of broken-down egg capsules (for example, *G. rosea*, Main 1965a), or there may be intracapsular development (*Myobatrachus* and *Arenophryne*, Roberts 1984). In *Assa*, eggs are deposited under litter, larvae hatch 11 days later, and then enter the inguinal pouches of the male (Ehmann & Swan 1985). Larvae not picked up by a male lived for up to 34 days, but eventually died, suggesting that male care is essential for survival (Ehmann & Swan 1985).

Ecology

Habitats occupied by myobatrachids vary widely, and include the driest desert regions (species of *Neobatrachus* and *Notaden*), the coldest and highest montane regions (*Pseudophryne corroboree*), temperate and sub-tropical zones with summer and winter peaks in rainfall (species of *Heleioporus*, *Uperoleia* and *Crinia*) and an array of tropical habitats, such as fast-flowing streams (*Mixophyes*) or litter habitats completely free of flowing or standing water (*Assa*).

The distributions of some species are relatively broad, covering a wide range of habitats, and those of others are restricted. For example, *Arenophryne rotunda* is common in coastal sand dunes, but also occurs on adjacent red sands in mallee scrub on the edge of the arid zone at Shark Bay, Western Australia (Anon. 1980; Roberts 1985, 1990). *Myobatrachus gouldii* is common in coastal and inland



Figure 7.8
Limnodynastes spenceri
 a 'backward sliding
 burrower'.
 [Photo ©M. Davies]



7. FAMILY MYOBATRACHIDAE

Table 7.1 Numbers of myobatrachid taxa in the 14 zoogeographic areas for anurans. Taxa include species, subspecies (*Limnodynastes dumerilii* – 5) and five informal races (*Limnodynastes tasmaniensis* complex – 3; *L. peronii* complex – 2). Codes and their derivation for zoogeographical areas are given in Figure 7.10.

Genera	SMW	SMC	SME	SMS	WMW	WMS	UNI	XNW	XSW	XNC	XSC	XNE	XCE	XSE
<i>Limnodynastes</i>	3	3	6	6	1	6	4	1	–	1	1	2	5	7
<i>Ranidella</i>	1	2	1	3	4	4	2	–	1	1	–	1	2	4
<i>Uperoleia</i>	8	4	4	4	–	–	4	4	–	2	–	2	2	1
<i>Neobatrachus</i>	–	–	–	1	2	2	1	2	5	1	1	–	2	3
<i>Notaden</i>	2	1	1	1	–	–	–	1	–	1	–	2	1	1
<i>Pseudophryne</i>	–	–	–	4	1	2	5	1	2	–	1	–	–	1
<i>Mixophyes</i>	–	–	2	4	–	–	1	–	–	–	–	–	–	–
<i>Heleioporus</i>	–	–	–	–	5	–	1	–	1	–	–	–	–	–
<i>Geocrinia</i>	–	–	–	–	5	2	1	–	–	–	–	–	–	–
<i>Megistolotis</i>	1	1	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adelotus</i>	–	–	1	1	–	–	–	–	–	–	–	–	–	–
<i>Rheobatrachus</i>	–	–	1	1	–	–	–	–	–	–	–	–	–	–
<i>Taudactylus</i>	–	–	4	2	–	–	–	–	–	–	–	–	–	–
<i>Crinia</i>	–	–	–	–	1	–	1	–	–	–	–	–	–	–
<i>Kyarranus</i>	–	–	–	3	–	–	–	–	–	–	–	–	–	–
<i>Lechriodus</i>	–	–	–	1	–	–	–	–	–	–	–	–	–	–
<i>Assa</i>	–	–	–	1	–	–	–	–	–	–	–	–	–	–
<i>Metacrinia</i>	–	–	–	–	1	–	–	–	–	–	–	–	–	–
<i>Myobatrachus</i>	–	–	–	–	1	–	–	–	–	–	–	–	–	–
<i>Philoria</i>	–	–	–	–	–	–	1	–	–	–	–	–	–	–
<i>Arenophryne</i>	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Total	15	11	20	32	21	16	21	9	10	6	3	7	12	17

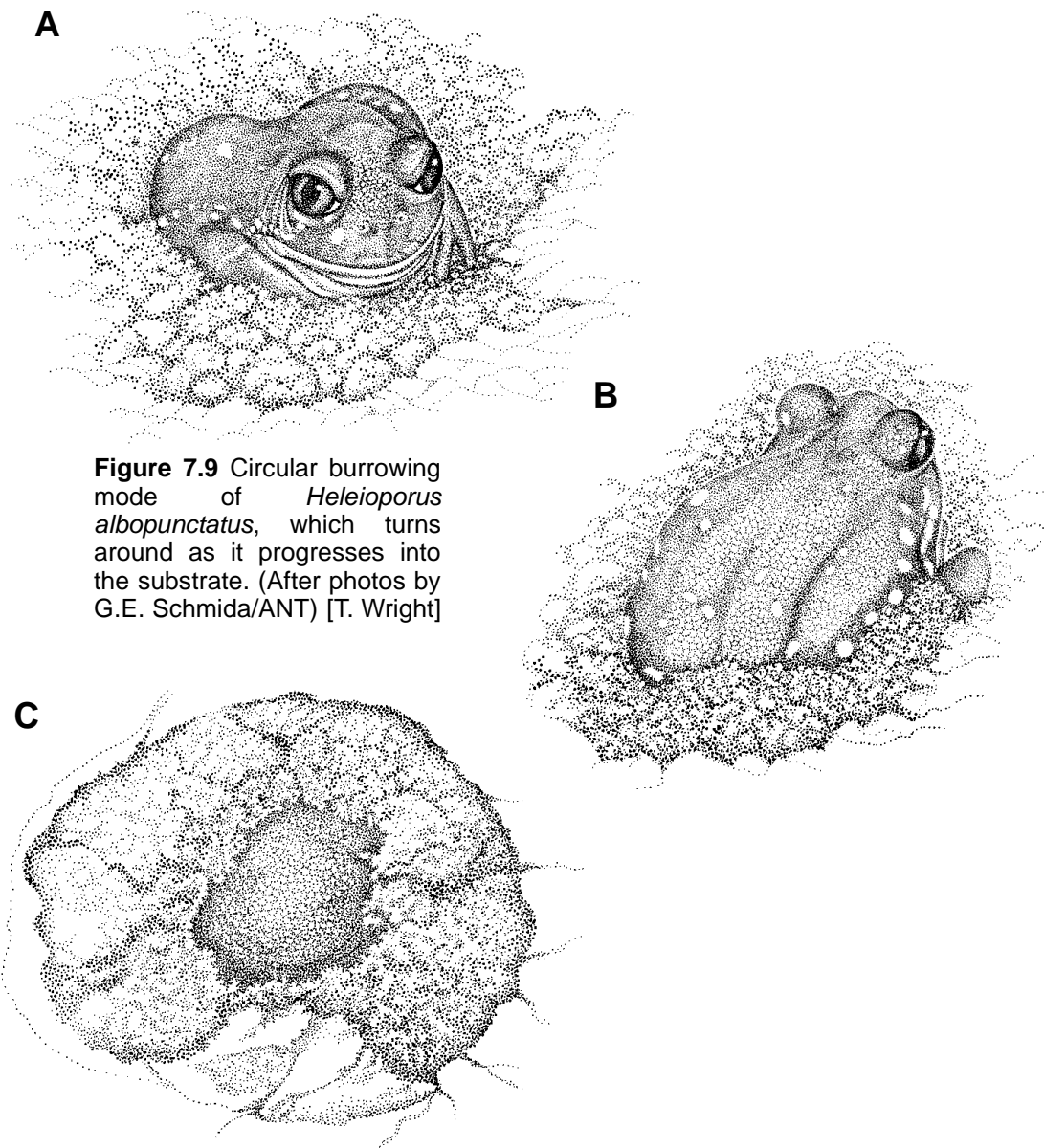
areas with reliable winter rainfall in south-western Western Australia, but is absent from the wetter forested areas, and the arid zone (Roberts 1981). *Geocrinia vitellina* and *G. alba* occur only in a limited number of flat-bottomed creek systems in far south-western Western Australia, where there are seepage systems that can supply excess soil moisture during spring breeding seasons (Wardell-Johnson & Roberts 1991).

Friend & Cellier (1990) analysed occurrence of frogs in wet and dry seasons in relation to habitat types for five myobatrachids from Kakadu National Park in the Northern Territory. Although there were some strong correlations with structural features of the vegetation community and soil condition, no myobatrachid species showed any correlation with particular plant species. For example, for flood-plain margins in the wet season, the abundance of *Limnodynastes convexiusculus* (Pl. 2.13) was negatively correlated with the abundance of hollow trees but positively correlated with the occurrence of buffalo wallows. *Crinia* (*Ranidella*) *bilingua* was common at vegetated sites, but showed a negative correlation with the amounts of leaf litter.

The significance of such of correlations lies at two levels. Many distribution patterns reflect breeding patterns that are adapted to particular rainfall distributions, or to other factors that might influence breeding success. For

example, no species of *Heleioporus* in south-western Australia occurs outside the area of reliable winter rainfall. Calling and egg deposition occur in autumn after opening winter rains, but before ponds form. Eggs develop in breeding burrows, and hatch when flooded by rising water levels (Lee 1967). This breeding system would not succeed in areas with an unpredictable winter rainfall, for example, the adjacent desert, as eggs would routinely die from desiccation or after using up yolk reserves before they were flooded. However, limits to distribution may also reflect physiological capabilities, with *Heleioporus* being unable to form water-proof cocoons (Weatherilt 1987), a feature found in desert species of *Limnodynastes* and *Neobatrachus* (Lee & Mercer 1967).

Frogs are commonly exposed to extreme temperatures. Brattstrom (1970) reported the results of an extensive study of thermal acclimation in Australian frogs, including 20 species of myobatrachids. Cold tolerant (cryophilic) species tend to have a more southerly distribution and heat tolerant (thermophilic) species a more northerly one; but species with wide (eurythermic) or narrow (stenothermic) temperature tolerances were found across all latitudes. Extent of geographic range appeared to be related to ability for thermal acclimation, and species that have restricted ranges (for example, *Kyarranus sphagnicolus* and



Philoria frosti), show no physiological ability to adjust their temperature tolerances. Even so, Marshall & Grigg (1980) found that tadpoles of the wide-ranging species *Limnodynastes peronii* show little evidence of ability to adjust temperature tolerances physiologically and they concluded that any adaptations of tadpoles to regimes of fluctuating temperatures are probably behavioural rather than physiological.

Frogs in arid environments, or mesic habitats like rainforests, where standing water other than in streams may be scarce, can exhibit a number of physiological and behavioural characteristics associated with avoiding or reducing stress brought about by water shortage. These features include burrowing and aestivation, production of relatively impermeable cocoons, water absorption, increased levels of electrolytes and urea accumulation, as well as water storage (Heatwole 1984; see sections on Excretion and Behaviour herein).

Few detailed data are available on the ecology of the tadpole stage of myobatrachid frogs — there are no detailed studies of diet. Cannibalism has been reported in *Lechriodus fletcheri* (Moore 1961), and in *Limnodynastes ornatus* (Tyler *et al.* 1983a). Both species may breed in extremely small water bodies, including shallow water-filled depressions on road surfaces. Tyler (1976b) reported the presence of plant material and several species of insects in the gut of a large tadpole of *Neobatrachus pictus*.

Behaviour

Burrowing, which is common in myobatrachids, is the most fundamental and widespread means of avoiding periods of aridity (Tyler 1989a). Three groups are recognised on the basis of burrowing pattern. *Limnodynastes dumerilii*, *L. ornatus* and *L. spenceri* are ‘backwards sliding burrowers’. *Neobatrachus* spp., *Notaden bennettii*, *N. melanoscapus*, *N. nicholli* and *Heleioporus albopunctatus* (Pl. 3.8) are ‘circular burrowers’ (Fig. 7.9; Sanders & Davies 1984). *Arenophryne rotunda* and *Myobatrachus gouldii* are the two members of a ‘forward burrowing’ group (Pl. 2.1–2.3; Tyler 1989a).

Cocoon formation has been documented in a number of arid-adapted species. In species of *Neobatrachus* evaporative water loss from aestivating frogs can be greatly reduced (to levels of less than 10% of that in individuals without cocoons), enabling prolonged periods of dormancy in burrows (Lee & Mercer 1967; Heatwole 1984). Together with reduced water loss, aestivation can be prolonged by lowering the energy expended in maintaining the basal metabolic rate. Flanigan *et al.* (1991) showed a 60 to 70% reduction in resting metabolic rates between aestivating and non-aestivating individuals of *Neobatrachus pelobatoides* (see also Chapter 4).

In most frogs, calling is an essential feature of mate attraction. Males may make advertisement calls and territorial calls, and both sexes may produce release and alarm calls. The functions of these calls are covered in detail in Chapter 5. Calling in myobatrachids has been studied extensively. Recognition of species-specific calls led to the description of many species of *Crinia*, *Heleioporus* and *Neobatrachus* (see Main 1965a; Roberts, Mahony, Kendrick & Majors 1991).

Myobatrachids demonstrate specificity of female response to calls of conspecific males. For example, females of *Geocrinia laevis* always approached broadcast calls of a conspecific male when given a choice between that and a call from *G. victoriana* (Littlejohn & Watson 1974). Females of *G. victoriana* were almost as successful, but about 12% of females chose incorrectly. In sympatric myobatrachids, call differentiation is marked. For example, five species of *Heleioporus* that breed synchronously in the same swamps in south-western Australia have distinct calls (Littlejohn & Main 1959; Lee 1967; Bailey & Roberts 1981) ranging from a slow moan in *H. eyrei* to a highly pulsed call in *H. psammophilus*. However, calls of related, allopatric species may retain strong

similarity in structure. For example, *Geocrinia alba* and *G. vitellina* both have short pulse trains, although they differ slightly in pulse rate, pulse number, and in dominant frequency (Roberts *et al.* 1990).

Males may make use of environmental features to enhance call transmission. Bailey & Roberts (1981) showed that *Heleioporus* use the burrow as a resonator, with the degree of amplification dependent on the length of burrows and the location adopted by calling males. Such a strategy may compensate for the absence of vocal sacs in frogs of this genus.

The interaction between the calls of males is described in Chapter 5. Males of *Pseudophryne semimarmorata* cease calling when calling is initiated by males of *Geocrinia victoriana* (Littlejohn & Martin 1969). These two species commonly share breeding sites. After a male of *G. victoriana* ceases to call, males of *P. semimarmorata* call again, but at a faster rate. Littlejohn, Harrison & MacNally (1985) showed that the call of *C. parinsignifera* could also inhibit calling by the sympatric males of *C. signifera*. Calls of these two species are very distinct, but they share a common frequency at around 3 kHz. Given the special sensitivity to sound at the dominant frequency of male advertisement calls seen in many anurans (for example, Loftus-Hills & Johnstone 1970), this form of interaction is not unexpected. MacNally (1979) showed that males of *C. parinsignifera* actively displaced males of *C. signifera* from preferred calling sites, and advertisement calls may be an important mechanism for that displacement.

Advertisement calls may also serve to protect male territories from take-over by conspecifics. However, many species use an encounter call for active territorial defence by acoustic signals. Males switch to this call when stimulated by a conspecific male calling close by.

Robertson (1986) showed that when calling, male *Uperoleia laevis* (reported as *U. rugosa*) heard conspecific calls at intensities above 84 dB at the receiver, they switch to an encounter call. The production of encounter calls may rapidly inhibit calling by an intruder. However, males may fight if the territorial male and the intruder are evenly matched for body weight, with the winner taking over the other's territory.

Robertson (1986) showed that males use the dominant frequency of the intruder's call to assess whether to produce encounter calls, fight or retreat. Similar playback studies by Littlejohn *et al.* (1985) with *C. signifera* and *C. parinsignifera* also elicited a switch from advertisement to territorial calls. Playback of sound stimuli similar to calls of *Crinia georgiana* also produced a response by males (Ayre, Coster, Bailey & Roberts 1984). However, in this species there is no evidence of a separate territorial or encounter call. The advertisement call was lengthened by adding notes in response to repeated stimulation (see Chapter 5). In *Geocrinia victoriana*, males produce a diphasic call with an introductory and a repeated note. The introductory note apparently serves in male-male interactions and the repeated note has a primary function in female attraction (Littlejohn & Harrison 1985). Males may alter the structure of the introductory note in a graded response, mimicking the behaviour expected when two males interact acoustically.

Choruses may be spatially organised. MacNally (1979) showed that males of two species of *Crinia* (*Ranidella*) were regularly spaced, and that males held specific calling-sites over extended periods. Non-calling, satellite males were common in these choruses. Satellites often took over calling sites when they were abandoned by resident callers. In *Uperoleia laevis* (as *U. rugosa*), males actively defend an exclusive calling zone (Robertson 1984, 1986). In this species, there are also many satellite males who cannot hold calling territories. The status of males changes predictably over time. The heaviest males hold

territories; however, as calling and territorial defence are energetically costly activities, the territorial males lose weight rapidly, and hence their ability to hold territories if challenged.

Choruses may also be temporally organised. Alternation of calls is common in anurans, and has been demonstrated clearly in *Limnodynastes dumerilii*, *Uperoleia laevis* (as *U. rugosa*) and *Crinia georgiana* (Loftus-Hills 1971; Robertson 1984; Ayre *et al.* 1984). The function of alternation is uncertain. It may help males to locate other males calling around them and it has been suggested that calling free of interference from other males will retain species-specific signal structure (for example, pulse rate), or allow easier location by females. However, the last of these suggestions is not supported by experimental evidence (Schwartz 1987).

Females may also use call structure cues to assess the potential value of males as mates. As noted in Chapter 5, female choice may be based on such cues as frequency (indicating male body-size), calling rate or intensity. Only one study has investigated female preference for call variants in an Australian frog. Robertson (1986) showed that females of *U. laevis* (as *U. rugosa*) selected the calls of heavier males in a two-choice situation. However, overall, females chose as mates males which were about 70% of their own body weight. This matching of body weights is not obviously related to the mechanics of egg deposition in this species, but may be an indicator of other male qualities, possibly sperm reserves.

Economic Significance

No species of myobatrachid has direct commercial significance as a pest, as a managed and harvested source of food, or as another utilitarian product. There are, however, a few historical references to the consumption of frogs by humans (Chapter 2). Tyler (1976b) referred to an earlier report on the use of the leg muscles of *Notaden bennettii* (Pl. 2.12) as a food by the aborigines of western New South Wales.

The glandular nature of frog skin and the function of its secretions have been investigated in the last 25 years. A number of secretions with pharmacological activity have been isolated from species of *Uperoleia* and *Taudactylus*, and from *Pseudophryne guentheri* (Erspamer, Roseghini, Endean & Anastasi 1966; Erspamer, de Caro & Endean 1966; Erspamer, Negri, Erspamer & Endean 1975; Anastasi, Erspamer & Endean 1975; Erspamer, Erspamer & Linari 1977; Nakajima, Yasuhara, Erspamer, Erspamer, Negri & Endean 1980). A physalaemin-like peptide (tachykinin) identified as uperolein was isolated from *Uperoleia rugosa* and *U. marmorata*. However, inaccurate species identification explains variation in the activity ratio among the various peptides isolated from *Uperoleia* (Erspamer *et al.* 1975). A bradykinin-like peptide was also located in *Taudactylus diurnus* and *T. eungellensis*.

The physalaemin- and bradykinin-like polypeptides were not located in *Mixophyes fasciolatus*, *Limnodynastes fletcheri*, *L. peronii* and *Lechriodus fletcheri* (Erspamer, Roseghini, Endean & Anastasi 1966). Daly, Highet & Myers (1984) and Daly, Garraffo, Pannell, Spande, Severini & Erspamer (1990) isolated alkaloids from the skin of *Pseudophryne semimarmorata*. Although not yet assayed for pharmacological properties, these compounds could be of medical significance. A further unidentified alkaloid was located in *P. corroboree* (Pl. 2.5) (Habermehl 1965) and a toxic substance was reported from *Heleioporus* (Softly & Nairn 1975). Tyler (1983a) alluded to the potential clinical applicability of the factors controlling gastric secretion in the stomach of *Rheobatrachus silus* by the developing embryos (involving a prostaglandin).

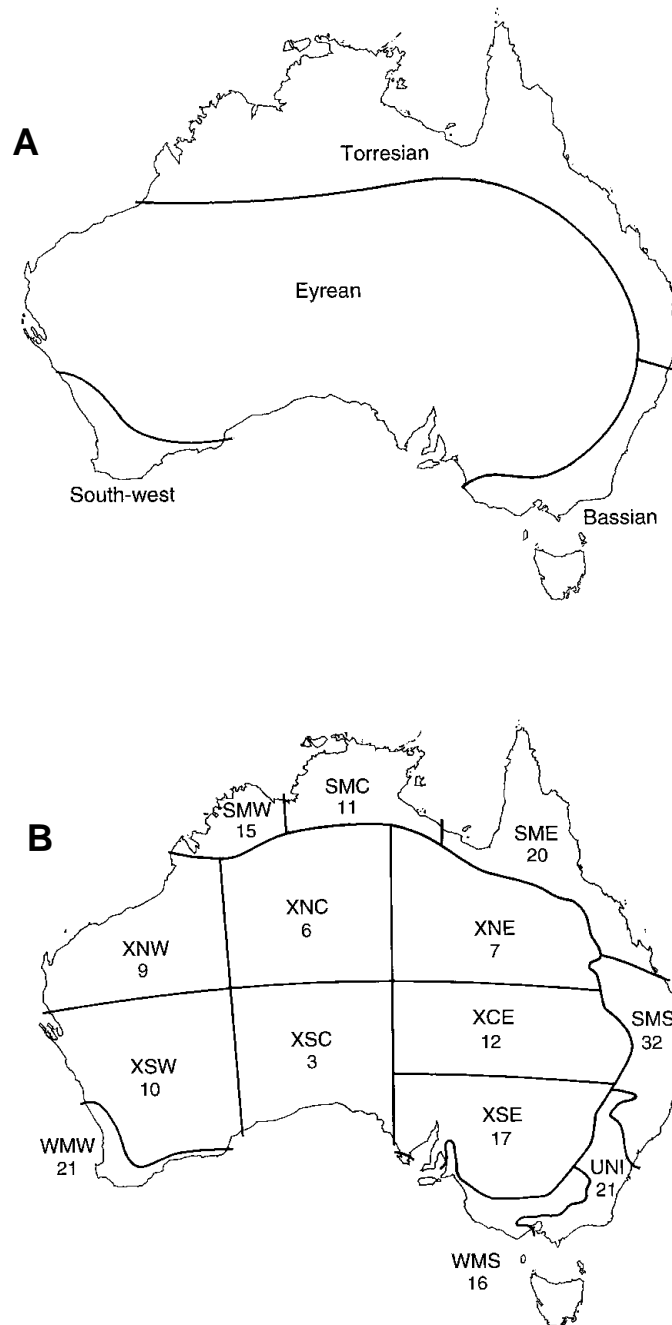


Figure 7.10 Australian zoogeographical regions. **A**, the faunal subregions of Spencer; **B**, zoogeographic areas for myobatrachid frogs. Division of three eastern areas (SMS, UNI, WMS) is based on seasonal rainfall incidence—the ratio of median rainfalls in summer and winter. The crescentic belt of summer-maximum precipitation has been arbitrarily divided at the borders between Western Australia, the Northern Territory and Queensland (SMW, SMC, SME). The eastern coastal mesic area is divided from the central xeric area along a line between the 600 to 650 mm summer maximum rainfall isohyets, or the 500 mm winter maximum rainfall isohyet. The 500 mm isohyet marks the boundary of south-western Australia (Bureau of Meteorology 1975, 1989). For convenience, the extensive xeric region of Australia has been divided arbitrarily at 125°E, 135°E, 25°S and 30°S. Codes: C, central; M, maximum; X, xeric; S and W as first letters, summer and winter; N, S, E, W are directional; UNI, uniform. (A, from Serventy & Whitell, after Spencer 1896; B, after Littlejohn 1981) [W. Mumford]

Because of their relatively permeable skins, and, generally, complex life cycles involving aquatic herbivorous larvae and terrestrial carnivorous adults, amphibians can be effective indicators of the environmental changes resulting from anthropogenic agents as discussed in Chapter 5. As frogs are top carnivores, they accumulate biocides and their byproducts along food chains. The early embryonic developmental stages and the aquatic larvae are susceptible to ionising radiation from radio-active minerals in waste water from mining operations, as well as to biocides and their byproducts. Tyler (1989a) prepared a comprehensive review of frogs as environmental monitoring organisms, and included the results of a detailed case study, carried out at Jabiru in the Northern Territory, that involved seven species of myobatrachid.

On a global scale, many amphibian taxa, including possibly 10% of the Australian species (Tyler 1991b), have declined in numbers, become rare, or have disappeared, during the last 15 years; and some taxa with previously restricted distributions are now presumed to be extinct (Blaustein & Wake 1990; Tyler 1991b). These events have been linked to the indirect effects of anthropogenic changes (Beebe 1977; Carey 1993). However, there have been very few long-term studies of the amphibians in the areas where the changes were noted, and so there are insufficient measures of variation in recruitment and survival under natural conditions (Pechmann, Scott, Semlitsch, Caldwell, Vitt & Gibbons 1991). Among the Myobatrachidae, species such as *Rheobatrachus silus*, *R. vitellinus*, *Taudactylus diurnus* and *T. eungellensis*, appear to have vanished from apparently pristine forest environments (Czechura & Ingram 1990; McDonald 1990). Osborne (1989) reported on the decline in density of *Pseudophryne corroboree* in subalpine areas of the Snowy Mountains of south-eastern New South Wales, and suggested that the declines might be due to the severe summer droughts during the period 1979–1984. He also noted that *P. bibronii*, once common at lower elevations in the Canberra area, is probably now locally extinct. He suggested that this might have been caused by the drainage of wetlands as well as droughts (Osborne 1990), though he noted that during the same period, frogs had vanished from well-watered sites that were free from grazing. Main (1990) reviewed the influence of land clearing, prolonged agricultural activity, and the associated salination, on the diminution of geographic range of *Heleioporus albopunctatus* in the wheat belt of south-western Western Australia, especially on the destruction of breeding habitats (in low-lying water courses). Main concluded that salination, in particular, had caused a decline in the distribution and/or abundance of *H. albopunctatus*.

BIOGEOGRAPHY & PHYLOGENY

Distribution

The division of the terrestrial biota of the Australian Region (*sensu* Wallace 1876) into subregions has been a continuing process since its initiation by Tate (1889). Main, Lee & Littlejohn (1958), and Jenkins (1982) have provided historical accounts for both the flora and the fauna. The major schemes are the faunal subregions of Spencer (1896), as modified by Serventy & Whittell (1951); the floristic zones of Burbidge (1960); the avian divisions of Kikkawa & Pearse (1969); the bioclimatic regions of Nix (1982); and the botanical regions of Barlow (1984; 1985). However none of the recent, objectively-based schemes is appropriate to the anurans, usually because the mesic zones are too extensive, so that their boundaries are placed in areas that are too dry for many anuran taxa.

The amount, seasonal distribution and reliability of precipitation are critical factors in determining the geographic ranges of frog species, because of their relatively permeable integuments, and the requirement for free water or sustained high humidities to complete their life cycles (Littlejohn 1981). These

factors were used in establishing a zoogeographic map for the Myobatrachidae. Boundaries to zoogeographic regions were established using isopleths for precipitation and broad climatic patterns following the criteria of Littlejohn (1981). The Seasonal Rainfall Zones established by the Bureau of Meteorology (1975, 1989) provided the basis for delimitation of climatic regions.

Geographical distributions of taxa were derived from Brook (1983), Tyler *et al.* (1984), Tyler & Davies (1986), Hero *et al.* (1991), and Tyler (1992), and the information is summarised in Figure 7.10B.

Taxonomic richness (Table 7.1) is highest on the central eastern coast (SMS; 32 taxa), south-western Western Australia (WMW; 22 taxa), the eastern area of uniform precipitation (UNI; 21 taxa) and north-eastern Queensland (SME; 20 taxa). The most depauperate areas are in the xeric region of Australia (XSC; three taxa), the north-central area (XNC; six taxa), the north-eastern area (XNE; seven taxa) and the north-west area (XNW; nine taxa). Endemism is highest in the south-west of Western Australia (WMW; 16 taxa), and the central-eastern coastal region (SMS; 14 taxa). The lowest levels of endemism are also in xeric Australia. There are no endemic taxa in the southern central area (XSC), one taxon in the northern central area (XNC) and one in the north-eastern area (XNE).

Only five myobatrachid genera and three species are common to Australia and New Guinea: *Lechriodus*, *Limnodynastes convexiusculus*, *Mixophyes*, *Crinia* (*Ranidella*) *remota* and *Uperoleia mimula* (Tyler 1972a; Zweifel & Tyler 1982; Davies *et al.* 1986b; Tyler & Davies 1986; Tyler *et al.* 1986; Donnellan *et al.* 1990).

Affinities with other Groups

There are differences of opinion over the disposition of the Australopapuan leptodactylids (*sensu* Lynch 1971) into families and subfamilies. Lynch (1971) considered several arrangements of the leptodactylids, which included the Australopapuan myobatrachids, the South American leptodactylids and the heleophrynids of southern Africa. The family Sooglossidae of the Seychelles was also considered for inclusion in the leptodactylid grouping.

Lynch (1973) proposed uniting the Old World leptodactylid subfamilies as the family Myobatrachidae and using Leptodactylidae for the four Neotropical (South American) families, building on his earlier assertion that the Myobatrachidae form a group isolated from all other leptodactylids and could be placed in a family of their own. The Sooglossidae is probably not separable from the Myobatrachinae (Lynch 1971). Lynch (1971) suggested that the cyclorine-heleophrynid relationship is somewhat tenuous and apparently not very close, but these two groups are more closely related to each other than either is to the myobatrachines or the Neotropical complex. Further he noted that it would be sounder from a cladistic point of view to place the Myobatrachinae, the Cyclorantinae and Heleophryninae, and the Neotropical families into three separate families. Eventually, the Australopapuan representatives were placed in a separate family, the Myobatrachidae which included the Myobatrachinae, Cyclorantinae (now the Limnodynastinae) and Heleophryninae (Lynch 1973). The Sooglossidae were retained as a separate family.

Savage (1973) also recognised the family Myobatrachidae. He emphasised the radiation of the leptodactylids, and proposed that one group gave rise to the tropical tree frogs of the Australian Region (Pelodyadidae - Hylidae, in part), which dominated in the northern region of Australia, while the remaining group (now represented by the myobatrachids) dominated in the temperate south. He proposed that during the Cainozoic Era, there was a northward flow of myobatrachids.

The family Myobatrachidae was also accepted by Heyer and Liem (1976), including the two subfamilies, Limnodynastinae and Myobatrachinae. They placed *Rheobatrachus* in its own subfamily (the Rheobatrachinae), which Laurent (1979, 1986) raised to familial rank as the Rheobatrachidae — a view that has not received great support.

Tyler *et al.* (1981) retained the Australopapuan leptodactylids within the family Leptodactylidae. As pointed out by Tyler (1989a), when considering the diagnoses of the two families presented by Duellman and Trueb (1986), the recognition of the family is based on very flimsy morphological evidence (if any), the main difference being their geographical separation on different continental plates (see also Chapter 1).

From an assessment of the available evidence, Ford & Cannatella (1993) concluded that there are no derived characters to ally the Australian myobatrachids any closer to the leptodactylids of the Americas than to any other taxa. They also concluded that: ‘... the myobatrachines and the limnodynastines differ from each other, and more importantly, that they share no derived features that would unite them into a single clade...’ (Ford & Cannatella 1993). Thus, the Limnodynastinae and Myobatrachinae were each considered as monophyletic. After a re-appraisal of the characters used in earlier analyses, they found that *Rheobatrachus* may be more closely related to the Myobatrachinae than to the Limnodynastinae. The sooglossids were found to share a number of derived characters with the Myobatrachinae, and they concluded that the Sooglossidae is a sister taxon to that subfamily. In contrast to Laurent (1986), who treated the heleophrynids of southern Africa as a subfamily of the Myobatrachidae, Ford & Cannatella (1993) concluded that: ‘... there seem to be no derived characters that would suggest that relationship in preference to any other...’.

Regardless of the various schemes for postulating the relationships and arrangements of these higher categories of the leptodactylid groups, it is clear that there is a zoogeographic unit of southern frogs. This southern gondwanan unit (*sensu* Savage 1973) thus would have been separated along with the break-up of the major plate, with the ancestors of the southern African heleophrynoids and the sooglossids being the first isolated from the Antarctic remnant more than 100 million years ago. The Australian plate began to separate from Antarctica as early as 95 million years ago (Veevers & Eittreim 1988), and drifted through some 25° of latitude for over 50 million years until it docked with the New Guinea region 10 to 25 million years ago (Pigram & Davies 1987). With the sequence of collisions and dockings, intermittent land bridges or shortening water gaps became available for the potential exchange of biotic elements from the two very distinctive biogeographic regions. It is interesting to note that, even though a large section of New Guinea is part of the Australian Plate, only a small component of the Australian myobatrachid fauna is present there today, as indicated above.

Affinities within the Taxon

Historical (dynamic) patterns of zoogeography and associated differentiation (speciation) of myobatrachid populations are considered in the light of the changes in climate and sea level that occurred during the late Pleistocene, from about 200 000 years before present, and the Holocene (the last 10 000 years). The timing and extent of these changes are now reasonably well understood (Chappell 1978, 1983a), so that their possible influences on the patterns and zoogeography and speciation of the Australian region may be considered.

At the height of the last glaciation, about 20 000 years ago, the global temperatures were lower than at present (by 5 to 7°C at sea level in middle latitudes) and much of the Earth’s water was incorporated into expanded polar ice-caps and continental ice-sheets. As a consequence, the world sea level was

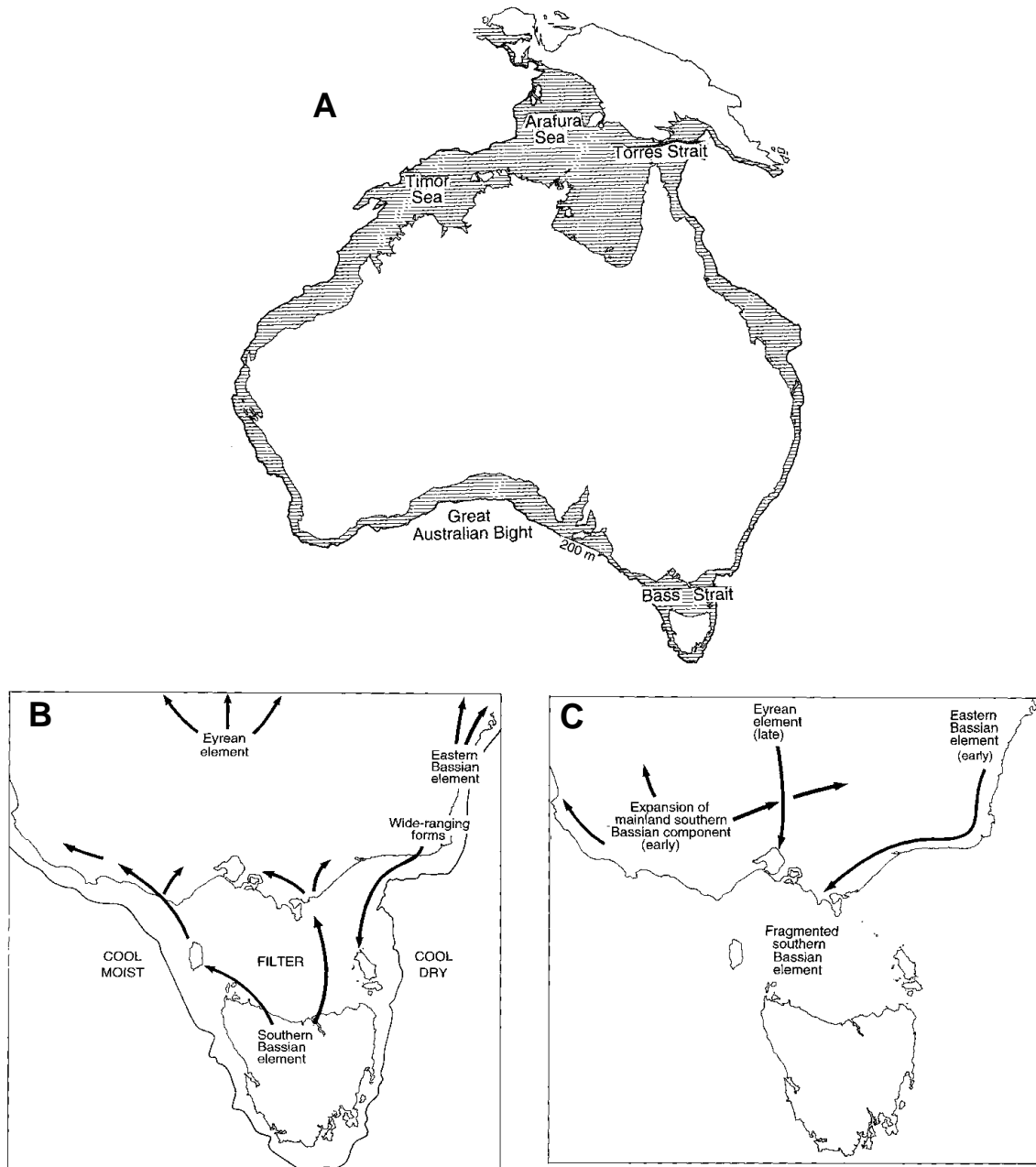


Figure 7.11 Scenarios for distributional changes in south-east Australian faunal elements. **A**, the present coastline of Australia and southern New Guinea, in which the 200 m isobath approximates the coastline some 20 000 years ago; **B**, expansion of cool-temperate (Bassian) elements, and probable contraction of xeric-adapted elements, in early, dry stage of glaciation; **C**, expansion of warm-temperate mesic elements, and contraction of the cool-temperate mesic elements, during the warmer mid-Holocene period. (A, after Jennings 1971) [W. Mumford]

lowered by some 130 to 150 metres (Chappell 1983b). Most of the continental shelf was exposed, and many of the adjacent islands were linked to the Australian mainland.

Evidence from isotope-dated changes in lake levels, stream flows, pollen profiles, etc., suggests that effective precipitation was higher than at present during the first part of the glacial period, and possibly lower than at present in the last part (see Edney, Kershaw & De Deckker 1990; Singh & Luly 1991; Nanson, Price & Short 1992 and references cited). As the glacial period ended and temperatures increased, the ice sheets began to melt, and the sea level rose

at about one metre per century until the present mean sea level was reached about 6 000 years ago (Chappell 1983b). In the mid-Holocene Epoch (about 5 000 years ago), the climate of southern Australia probably was warmer and moister than at present (De Deckker, Kershaw & Williams 1988).

During the early stage of glaciation, the cool-temperate adapted faunal elements (Bassian) could expand their ranges to the north and west, facilitated by the land bridges and extensive coastal plains, while the distributions of warm temperate xeric-adapted elements presumably contracted to the north. During the dry phase, mesic-adapted, or moisture-sensitive taxa would have reduced geographic ranges. Subsequently, during the warmer mid-Holocene, warm-temperate mesic elements could have expanded their ranges, presumably at the expense of the cool-temperate mesic elements — which would then have contracted their ranges and may have become fragmented, leading to the present patterns of distribution.

The changes outlined for the last glaciation of the Pleistocene, and for the present interglacial period (that is, the Holocene), are presumed to have been repeated during the earlier glacial and interglacial phases of the Pleistocene Epoch. But the paleoclimatic sequence of the late Quaternary Period is complicated by the possible increased frequencies of fires and consequent modification of vegetation following the colonisation of Australia by *Homo sapiens* (Kershaw 1986). In addition, the extensive and drastic alterations to the environment brought about by Europeans during the last 200 years have complicated the interpretations of patterns of geographic distribution of anurans.

The taxonomic composition and geographic distributions of frogs of northern and north-eastern Australia are still in a preliminary state, and therefore an extensive biogeographic synthesis has yet to be made. Sufficient is known, however, about the south-eastern and south-western elements of the anuran fauna to allow detailed consideration. Accordingly, zoogeographic patterns will be discussed for these regions of southern Australia, to emphasise similarities between the south-east and the south-west, and within the south-east, particularly across Bass Strait.

South-eastern and south-western Australia: the extensive coastal plains, and the cooler and presumably moister conditions at the beginning of the last glacial period, could have provided a corridor (at least along the maritime coastal strip) for the movement of mesic temperate elements between the south-east and the south-west (but see the comments of Martin 1973, and Lundelius 1983). Presumably, there was a restricted range of habitats and vegetation types available, so the bridge acted as a filter (*sensu* Simpson 1953). Such a model was developed by Serventy & Whittell (1951) to explain the distribution of disjunct conspecific populations, and the presence of closely related south-eastern and south-western species-pairs of birds. Both Eyrean and Bassian elements were considered, with postulated movements occurring in either direction, depending on the adaptations (that is, Bassian or Eyrean). At least two migrations from east to west, and one from west to east, were considered by Serventy & Whittell (1951). A similar scenario was also adopted by Keast (1958) when explaining speciation in whip birds (*Psophodes*).

Main *et al.* (1958) adopted the model of Serventy & Whittell (1951), and extended it to include three successive east-west migrations during the Pleistocene Period to explain the high diversity of south-western species in three genera of myobatrachid frogs (*Heleioporus*, *Neobatrachus* and *Crinia* (*Ranidella*)) in the absence of obvious local geographic barriers. The model of Main *et al.* (1958) was also employed by Mackerras (1962) for tabanid flies, Main (1962) for trap-door spiders, and Horton (1972) for skinks of the genus *Egernia*. Rawlinson (1974) noted the presence of eastern and western conspecific populations and species pairs of reptiles, as did Hutchinson (1990).

Thus, there seemed to be a considerable amount of supporting data from disjunct conspecific populations, and cognate species-pairs in a number of taxonomic groups that reflected recent continuous distribution across southern Australia. Lee (1967) re-examined the application of the multiple migration model to *Heleioporus*, and also considered the likelihood of *in situ* speciation in the south-west. He was also swayed against the latter model because of the apparent lack of suitable geographic barriers.

Littlejohn (1981) reviewed the situation for the frogs of south-eastern and south-western Australia, and noted that since the review by Main (1968), no new data had been advanced in support of the multiple east-west migrations. Roberts & Maxson (1985) used micro-complement fixation of albumin to demonstrate that there were closer relationships within south-western species than between south-western and south-eastern species; they also derived a pre-Pleistocene dating for the speciation events, on the basis of assumptions of a molecular clock. Information on allozymes (from Barendse 1984) was also adduced in support of their findings. Furthermore, they noted that some species of *Neobatrachus* implicated in the multiple migration model of Main *et al.* (1958) were tetraploids (Mahony & Robinson 1980; Mahony & Roberts 1986), and so must have had an origin different from the conventional process of allopatric speciation. Accordingly the pattern for this genus was no longer consistent with the hypothesis of multiple east-west migration.

The evidence refuting the model for multiple east-west migrations to explain the origin of the closely related groups of south-western species of Main *et al.* (1958) was reviewed comprehensively by Roberts & Maxson (1985). These authors then proposed that differentiation within south-western Australia is a more parsimonious hypothesis. The discovery of two new allopatric species of the *Geocrinia rosea* complex with restricted distributions in the south-west (Roberts *et al.* 1990) provided further support for *in situ* speciation. However, the refutation of molecular clocks (Melnick 1990; Scherer 1990; Baverstock, Christidis, Krieg & Birrell 1991; Gillespie 1991) and the uncertainty of serum albumin as a reliable indicator of phylogenetic relationships (Friday 1980; Hass, Highton & Maxson 1992) mean that the conclusions of Maxson & Roberts (1984) and Roberts & Maxson (1985) are less plausible. Accordingly, we are now left with two models, and insufficient information to favour either one.

Within south-eastern Australia, including the Bass Strait region: Mayr (1942) proposed a model of two north-south migrations from the mainland into Tasmania to account for the endemic and the common species of thornbill (*Acanthiza*) on the island. Moore (1954) invoked a similar model to explain the origin of the Tasmanian endemic species, *Crinia* (*Ranidella*) *tasmaniensis*, from the wide-ranging congener, *C. signifera*. Littlejohn & Martin (1964) advanced a model of speciation in Tasmania and reverse migration to the mainland for the myobatrachids, *Geocrinia* (as *Crinia laevis* and *G. victoriana*, on the basis of late Pleistocene changes in climate and sea level. This trans-Bassian model was expanded by Littlejohn (1967) (see also Fig. 6.6). Martin (1972a) employed the model of reverse migration for the derivation of *Limnodynastes dumerilii insularis* and *L. d. variegatus* from *L. d. dumerilii*. Littlejohn & Martin (1974) listed three pairs of taxa (including one pair of hylid frogs) in addition to the taxa already considered, namely: *Litoria verreauxii verreauxii* and *L. ewingii*, *Pseudophryne semimarmorata* and *P. bibronii*, and the southern and the northern call races of *Limnodynastes tasmaniensis*, as having speciated across Bass Strait. Watson & Littlejohn (1985) extended the model to include another pair of anuran taxa, the pigmented and the non-pigmented egg races of *Limnodynastes peronii*, and proposed two reverse migrations from Tasmania to the adjacent mainland for some groups of anurans.

Roberts & Maxson (1988, 1989) offered a critique on this model. They made four major points. Firstly, several relevant species had not been included in developing the phylogenies presented by Watson & Littlejohn (1985), and their inclusion might have led to a different interpretation of pattern. Secondly, they noted equivalent species richness in *Uperoleia* in a comparable area in eastern Victoria where there has never been a suggestion that multiple invasion was an explanation. Thirdly, immunological distance data from MCF studies of albumin and estimates of divergence from electrophoresis, both used as molecular clocks, generate divergence dates for several groups which are much older than the Pleistocene ages suggested by the Watson & Littlejohn models. Lastly, MCF data in several cases suggest different relationships from those proposed in the phylogenies presented by Watson & Littlejohn (1985). Roberts & Maxson (1988, 1989) explored a number of alternatives to isolation in Tasmania as models for speciation in south-eastern Australia. Among these the Great Dividing Range may have been an isolating barrier.

If albumin clocks and immunological distance data from MCF studies are rejected as useful tools then the power of this critique is diminished, though two of the four points of criticism have still not been answered. As in south-western Australia, two competing hypotheses, both with some supporting evidence, should be considered.

On both sides of the continent, there is a critical need for justifiable phylogenies, as these must be the starting point for interpretation of historical patterns of speciation (for example Cracraft 1982). It should also be clear from the discussion above that the authors of this chapter are not agreed on how such phylogenies can be generated.