



FAUNA *of* AUSTRALIA



4. MORPHOLOGY AND PHYSIOLOGY OF THE ANURA

**Margaret Davies &
Philip C. Withers**

EXTERNAL CHARACTERISTICS

In general, the Anura exhibit remarkable conservatism in body form — the variation that occurs is usually related to the life style of the species. Useful general references on external characteristics include Duellman (1970), Tyler (1982, 1989a), Tyler, Smith & Johnston (1984), and Tyler & Davies (1986).

Male frogs are generally smaller than females, except in the monotypic limnodynastine *Adelotus* (Pl. 2.4). The smallest Australian frogs are the hylid, *Litoria microbelos*, (males ranging 14 to 16 mm snout-vent length (S–V), females 15 to 16 mm S–V) and the myobatrachines, *Crinia remota*, (males 13 to 16 mm, females 14 to 19 mm S–V) and *C. deserticola* (males 13 to 18 mm S–V). The largest species are the hylids *Litoria caerulea*, *L. splendida* and *L. infrafrenata* (Pl. 1.4), females of which can grow as large as 140 mm S–V.

Fossorial (burrowing) species tend to have globose bodies with short snouts, elevated heads and short limbs (Pls 1.6, 2.1, 2.8, 2.12). Ground-dwellers and scansorial species (ground-dwellers adapted for climbing) tend to be more streamlined with longer, sharp snouts, depressed heads and long legs (Pls 1.1–1.3, 1.5, 2.4–2.6, 2.9–2.11, 2.13). In contrast, arboreal species are intermediate with moderately rounded snouts, moderately depressed heads and legs of intermediate length (Pl. 1.7).

The head is triangular or hemispherical when viewed from above. External nares are usually dorso-lateral and vary in location along the length of the snout. These lead internally to the choanae on the roof of the palate. The junction between the lateral and dorsal surfaces of the snout, or canthus rostralis, is straight, or gently curved and varies in prominence. The loreal region is straight or concave. The eyes are prominent, vary slightly in size and tend to be lateral rather than dorsal. When constricted, the pupil is usually horizontal, but may be vertical or rhomboidal.

The lower jaw is edentate, though *Adelotus brevis* bears a pair of odontoids, or ‘tusks’, on the mentomeckelian bones that vary in prominence between the sexes. The upper jaw is usually dentate in most species except the myobatrachid genera *Notaden*, *Pseudophryne*, *Arenophryne*, *Myobatrachus* and some *Uperoleia* and in the microhylids *Cophixalus* and *Sphenophryne*. The teeth are usually small, bicuspid and are continuously replaced.

Vomerine teeth are extensive in *Limnodynastes* and *Megistolotis*, and occur as small paired elevations in the choanal region in most genera. They are absent in the microhylids, *Pseudophryne*, *Myobatrachus*, *Arenophryne*, all *Crinia*, some *Uperoleia* spp. and some small *Litoria*. Vomerine teeth are thought to assist in grasping prey prior to swallowing.

The external ear, or tympanum, is situated behind the eye surrounded by a rim or annulus, and is flush with the skin (Fig. 4.1C). In many species it may be partially obscured by a conspicuous supratympanic fold, and in others it is indistinct or covered with skin and not visible externally.

The tongue is elongate or cordiform and its anterior attachment allows it to protrude during prey capture. In males, slits leading to the submandibular vocal sacs lie laterally to the tongue. These apertures and vocal sacs are absent in *Litoria lesueuri*, *L. nannotis*, *L. rheocola*, *L. nyakalensis*, *L. lorica*, *L. eucnemis*, *Taudactylus diurnus*, and the genera *Heleioporus* and *Neobatrachus*.

Relative limb length (the ratio of tibial length to snout-vent length) is related to the lifestyle of the frog. All frogs have four fingers and five toes (Fig. 4.1A, B), though phalanges are reduced in some myobatrachine species (see Chapter 7). The digits are rounded or flattened, may be fringed, and terminate in discs of varying widths (Fig. 4.1A, B). Expansion of the discs aids in climbing and is usually associated with extensive webbing between the fingers and toes, which increases the surface area of contact and improves adhesion (Fig. 4.1A, B). Most

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species have non-webbed fingers, but toe webbing varies from the extensive webbing of the aquatic *Rheobatrachus*, *Litoria dahlia* and, surprisingly, of the desert-adapted, fossorial *Cyclorana platycephala*, to the minimal webbing of many species of *Uperoleia* and the Microhylidae.

Subarticular tubercles occur at the junctions between the phalanges, and large palmar tubercles occur on the hand (Fig. 4.1A, D, E). There are often supernumerary tubercles on both the hands and feet. The feet of backwards burrowing species have pairs of cutting structures, the inner metatarsal tubercles, which are raised and compressed and often keratinised to provide a hard edge. A second pair, the outer metatarsal tubercles also are sometimes compressed. Metatarsal tubercles are variously developed in non-fossorial species and in some, the outer metatarsal tubercle is absent.

Secondary sexual characteristics in the form of nuptial excrescences are developed on the thumbs of males of most species. They are unpigmented glandular pads in *Uperoleia*, pigmented pads as in *Limnodynastes convexiusculus*, or spiny thorns in members of the *Litoria nannotis* group, *Heleioporus* and *Megistolotis*. Fine structure of these excrescences varies greatly (Tyler & Lungershausen 1986). Secondary sexual spines can extend along the forelimbs and onto the chest, as in *Litoria nannotis* and *L. lorica*.

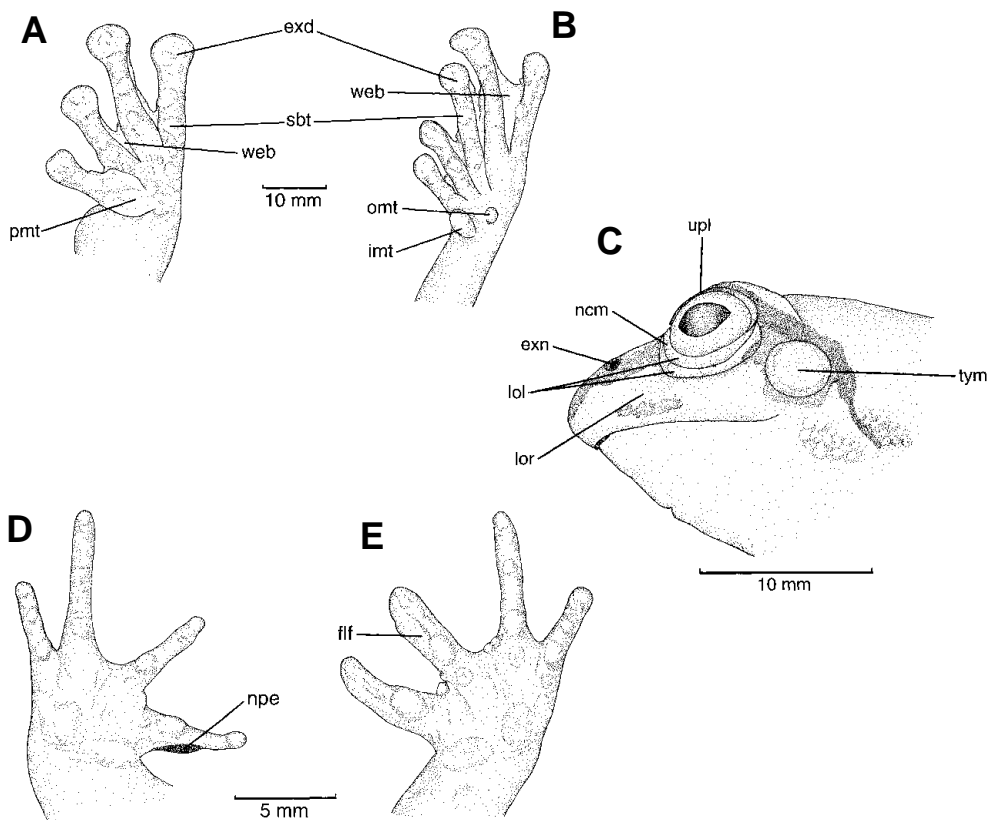


Figure 4.1 External features of frogs. **A**, palmar view of the hand, and **B**, plantar view of the foot of *Litoria splendida*; **C**, lateral view of the head of *Cyclorana longipes*; **D**, palmar view of the hand of a male *Limnodynastes convexiusculus*, **E**, palmar view of the hand of a female *L. convexiusculus*. **exd**, expanded discs; **exn**, external naris; **flf**, flanged finger; **imt**, inner metatarsal tubercle; **lol**, lower lid; **lor**, loreal region; **ncm**, nictitating membrane; **npe**, nuptial excrescence; **omt**, outer metatarsal tubercle; **pmt**, palmar tubercle; **sbt**, subarticular tubercles; **tym**, tympanum; **upl**, upper lid; **web**, webbing. [M. Davies]

Male secondary sexual characteristics usually develop seasonally. Females of species that lay eggs in a foam nest usually develop flanges on the first and second fingers, as discussed in Chapter 7.

BODY WALL

The skin is usually permeable to water and is an important respiratory and osmoregulatory organ. Dorsal skin may be smooth or tubercular to varying degrees. Dorso-lateral skin folds are present in some species. The skin is highly glandular, comprising mucous and granular glands scattered across the surface or hypertrophied in the parotoid, inguinal, coccygeal, suprarostrals, supralabial, or dorsal tibial areas (Fig. 4.2A, B, C). Ventral skin is smooth or finely to coarsely granular. Granularity is often confined to a patch in the pelvic region, associated with water uptake. The structure of the anuran skin has been reviewed by Duellman & Trueb (1986).

Colour varies considerably, often with disruptive colouration providing camouflage. Many arboreal species are green, and a dark canthal stripe, which disrupts the outline of the eye, is common in ground-dwelling species. Bright yellow, or orange, and black markings that occur on the backs of the thighs of many species are thought to startle predators, as would the inguinal patches of red, yellow and orange of many ground dwelling species. Colouration is even more startling and possibly aposematic in many myobatrachids (see Chapter 7; Pls 2.5, 2.12).

Chromatophores (pigment cells) in amphibian skin are responsible for colour. Duellman & Trueb (1986) review studies of these pigments, and analysed colour change. Morphological colour change, caused by the synthesis or destruction of pigment, is a slow process (taking days to months). Physiological colour change, the result of intracellular pigment movement within chromatophores, is rapid (seconds to minutes).

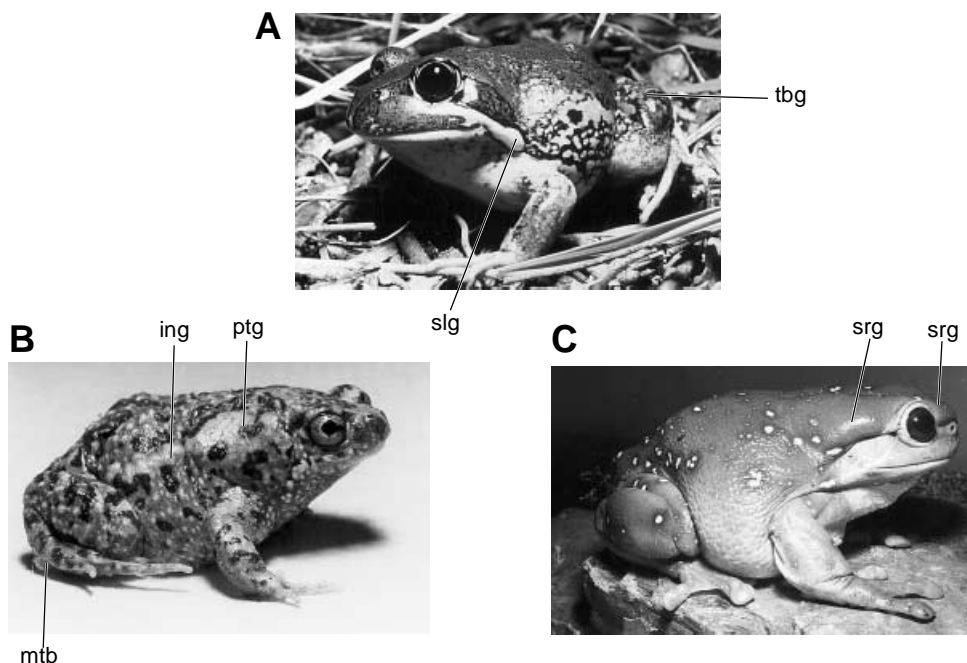


Figure 4.2 Skin glands of frogs. **A**, *Limnodynastes terraereginae*; **B**, *Uperoleia littlejohni*; **C**, *Litoria splendida*. **ing**, inguinal gland; **mtb**, metatarsal tubercle; **ptg**, parotoid gland; **slg**, supralabial gland; **srg**, suprarostrals; **tbg**, tibial gland. [Photos © P.C. Withers]



Figure 4.3 Water-conserving posture of *Neobatrachus sutor*.

[Photo ©P.C. Withers]

The epidermal glands are alveolar, with a duct system leading to the skin surface, and are of two general types. Smaller, more numerous mucous glands continually secrete mucopolysaccharides that keep the skin moist. Granular glands secrete a variety of bioactive compounds in response to sympathetic neural or endocrine stimulation, including biogenic amines such as indolealkylamine and serotonin, and bioactive peptides such as uperolein from *Uperoleia* and caerulein from *Litoria* (Erspamer *et al.* 1984).

The stratum corneum of the skin is periodically moulted, or sloughed, every few days to several weeks, depending on the species. The shed skin is ingested. Moulting is under hormonal control of the pituitary.

Cocoon-forming frogs, such as species of *Cyclorana* and *Neobatrachus* typically moult frequently, about every two days to maximise the rate of cocoon formation, whereas frogs which do not form cocoons, such as *Heleioporus* spp., shed about every six to eight days (Withers unpub. obs.).

The rate of evaporative water loss (EWL) of frogs depends on many complex variables, including body mass, posture, exposed body surface area, temperature, humidity, wind velocity, and activity (see Heatwole 1984; Warburg 1965, 1967). Many frogs press closely the ventral surface of the head and body to the substratum and tuck the limbs into the side of the body when exposed to dehydrating conditions. This characteristic ‘water-conserving’ posture minimises the exposed surface area and EWL. Activity level affects EWL, because it increases the exposed surface area and reduces the boundary layer, for example, *Notaden bennettii* (Heatwole *et al.* 1971). *Heleioporus eyrei* loses 22% of its mass by water loss when active during the night (Lee 1968).

Aggregation of individuals in contact with each other effectively reduces the surface area/volume ratio of the group, and lowers EWL. The EWL of aggregated juvenile *Limnodynastes* spp. can be reduced by over 50% for groups of over five individuals (Johnson 1969a).

There is no general relationship between EWL and aridity for Australian frogs (Clyne 1968; Heatwole 1984). Most, though not all, frogs evaporate water as if they have a free water surface, equivalent to a resistance to evaporation of about 1–3 sec/cm. EWL increases with body mass, but the mass-specific EWL declines with mass, reflecting both the lower mass-specific surface area of larger frogs and changes in air flow patterns and boundary layer thickness.

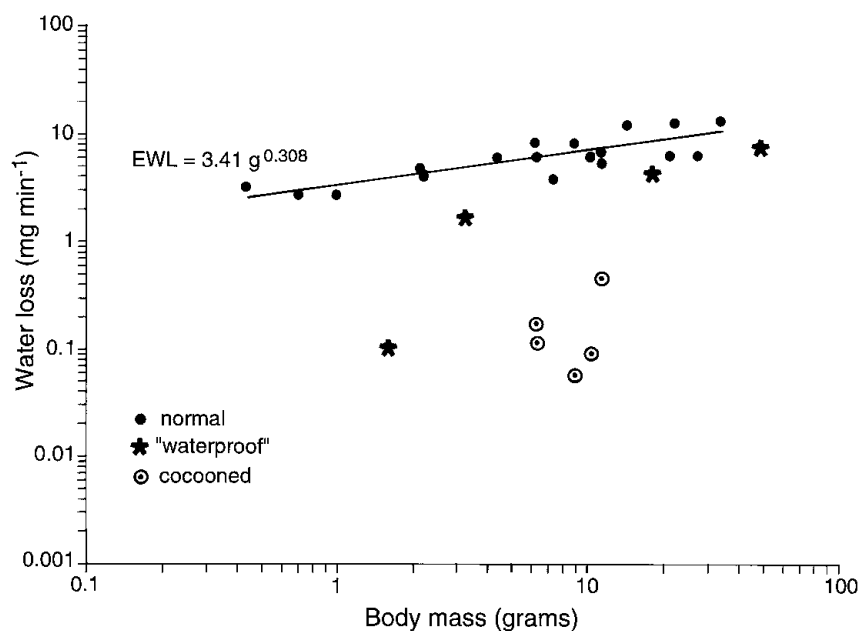


Figure 4.4 Relationship between rate of evaporative water loss, EWL, and body mass for a variety of Western Australian frogs, for cocooned *Cyclorana* and *Neobatrachus*, and for water-proof *Litoria*. (From Withers unpub. data; van Beurden 1984; Buttemer 1990) [P.C. Withers]

Some 'water-proof' Australian tree frogs have an EWL that is much lower than that of a free water surface. For example, *Litoria gracilentia* has a resistance of 118 sec/cm (Withers *et al.* 1984); *L. caerulea* has a resistance of about 9 sec/cm and *L. chloris* about 39 sec/cm (Buttemer 1990).

A number of arid-adapted Australian frogs (*Cyclorana platycephala*, *C. australis*, *C. maini*; *Litoria alboguttata*; *Neobatrachus pictus*, *N. sutor*, *N. wilsmorei*, *N. kunapalari*, *N. pelobatooides*, *N. fulvus*) form a water-proofing cocoon while buried underground and dormant (Lee & Mercer 1967; van Beurden 1984; Withers unpub. data; Fig. 4.5A). *Limnodynastes spenceri* has also been reported to form a cocoon (Lee & Mercer 1967) but this has not been verified subsequently (Withers unpub. data). The cocoon remains loosely attached to the surface of the skin, and covers the entire frog, including eyes, mouth and cloaca, except for the external nares. It is a hygroscopic structure that markedly reduces the EWL and is formed by the accretion of numerous layers of shed stratum corneum; the single cell layers are cemented together by mucopolysaccharides. The resultant multi-layered cocoon is formed at about one layer every two days, and may contain from one to over fifty layers, depending on its age.

Heleioporus and *Notaden* spp. do not form a cocoon while dormant (Withers unpub. data). These semi-arid and arid frogs presumably burrow deeper than *Cyclorana* and *Neobatrachus* into moister, sandier soils (Main 1968), and this prevents desiccation. *Arenophryne rotunda*, which inhabits arid coastal sand dunes near Shark Bay, also does not form a cocoon; it apparently remains in water balance by absorbing soil moisture (Roberts 1990).

Amphibians do not drink, but absorb water across their skin. Australian frogs assume a typical water-uptake posture, with the tarsus beside the knee rather than the usual postural position underneath the knee (Johnson 1969b). Cutaneous water uptake is more rapid across the ventral skin, particularly the pelvic patch region of the groin, than across the dorsal skin.

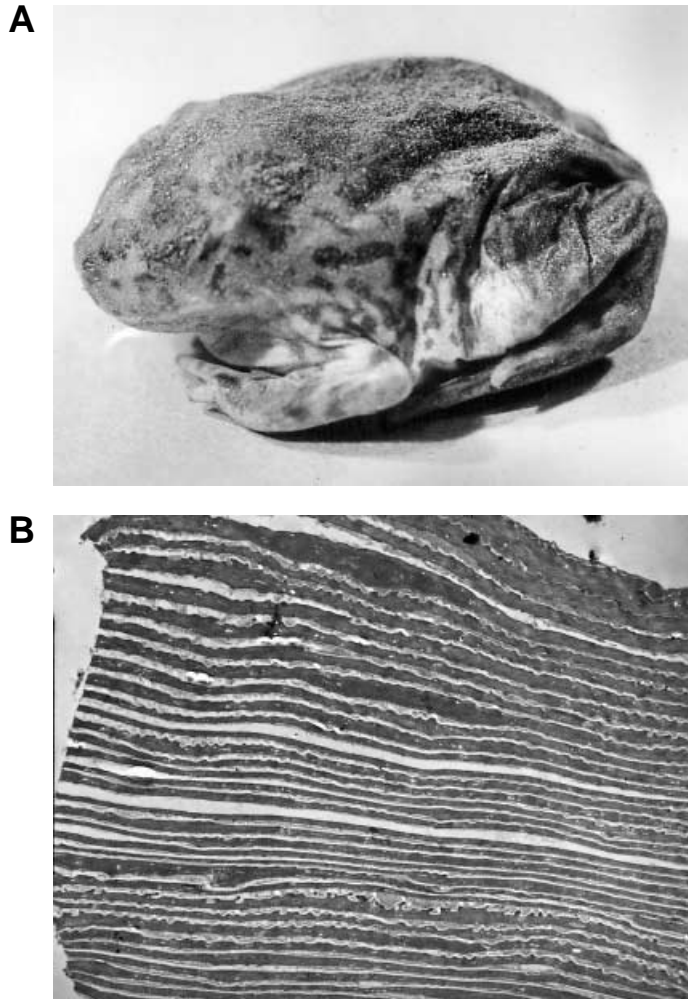


Figure 4.5 Structure of the cocoon of fossorial frogs. **A**, *Neobatrachus sutor* in a cocoon; **B**, transmission electron micrograph of a section of a cocoon from *Neobatrachus sutor*, showing the multiple layers of single-cell thick stratum corneum. [Photos ©P.C. Withers]

Dehydrated frogs absorb water through the skin faster than hydrated frogs, reflecting, at least in part, the role of endocrine systems in regulating water absorption. The hydration rate is initially highest, and declines during rehydration (Johnson 1971b; Warburg 1965, 1967). The rehydration rate varies dramatically for different Australian frogs from about 30 mg/cm²/h to over 140 mg/cm²/h (Cree 1985; Main & Bentley 1964; Packer 1963; Johnson 1971b; Bentley *et al.* 1958; Clyne 1968; Warburg 1965, 1967). The rehydration rate of *Neobatrachus* species, which have short burrows in clay soil and form a cocoon to minimise EWL, is well-correlated with their aridity (*N. pelobatoides* < *N. centralis* < *N. sutor* < *N. wilmorei*; Bentley *et al.* 1958). There is no correlation between aridity and water uptake rate in a comparison of *Heleioporus psammophilus*, *H. inornatus*, *H. eyrei*, *H. barycragus* and *H. albopunctatus*, which have deep burrows in sandy soil and do not form a cocoon.

Frogs can absorb water from soil if the water potential difference between the body fluids and the soil is favourable. Rehydration from moist soil is considerably slower than from water for *Taudactylus diurnus* (Johnson 1971b) and *Heleioporus eyrei* (Packer 1963) although the rate is similar in water and moist soil for *Litoria caerulea* (Johnson 1971b). *Notaden bennettii* loses less mass in moist soil than in drier soil, and is reluctant to burrow in very dry soil, preferring to stay on the surface and aggregate in groups (Heatwole *et al.* 1971).

SKELETAL SYSTEM

The bones and their arrangement in adult Australian frogs follow the basic anuran pattern. Variations reflect the reduction or loss of some elements. The most labile elements of the skull are the vomers, quadratojugal, elements of the ear, especially the columella, and dentition on the maxillary arch.

Reduction in skeletal elements is usually greatest in myobatrachine species, although the limnodynastine *Notaden* shows the greatest reduction in cranial elements of all known Australian species. Reduction or loss of some cranial elements in some genera has been attributed to the influence of heterochrony in frogs (Davies 1989a). Reduction in postcranial elements is usually restricted to phalanges in the fingers and toes (Davies 1984) and to elements in the pectoral girdle (Burton 1986).

Skeletal elements generally begin to ossify in the later stages of amphibian metamorphosis (Davies 1989a). Hyperossification and calcification occurs in senescent animals, particularly in species known to have long life spans, such as *Litoria caerulea* (Davies unpub. data).

The osteology of the Anura has been analysed by Trueb (1973) and Duellman & Trueb (1986). The following discussion applies strictly to Australian Anura.

The cranium consists of elements of dermal bones, formed within membranes, and endochondral bones derived from cartilaginous primordia. The skull is roofed by two pairs of dermal bones, the frontoparietals and the nasals.

The frontoparietals vary in the extent to which they roof the underlying frontoparietal fontanelle. At maximal ossification, they abut along their medial edge and roof the fontanelle completely (for example, *Uperoleia minima*; Tyler *et al.* 1981). At the other extreme, they are narrow slivers of bone which edge the orbit and totally expose the frontoparietal fontanelle, as seen in *Pseudophryne bibronii*; see Lynch 1971). Anteriorly their terminations vary from truncated to acutely pointed. They may articulate with the posterior extremities of the nasals and overlie the sphenethmoid dorsally, or be separated from the nasals and overlie only a portion of the sphenethmoid. The orbital edges may be straight or angled postero-laterally and supraorbital flanges occur in some species, for example, *Litoria infrafrenata* (Davies 1978). Extensive exostosis occurs, as in *Cyclorana australis* (Lynch 1971). Posteriorly they overlie the prootic, but do not fuse with other elements of the cranium.

The nasals overlie the olfactory region of the skull. They vary in the extent of ossification. Those of *Notaden nichollsi* are narrow (Lynch 1971), whereas those of *Uperoleia rugosa* are well-ossified and provide strong protection for the snout (Davies & McDonald 1985). Postero-laterally, a maxillary process may reach the maxilla and often is confluent with the preorbital process of the pars facialis of this bone. Medially they can abut each other or be separated to varying degrees. The nasals are free from contact with other bones, roof the sphenethmoid to a greater or lesser extent or abut with the anterior extremities of the frontoparietals.

The bones of the palate, the parasphenoid, the paired vomers, palatines and pterygoids, are all of dermal origin.

The triradiate parasphenoid comprises an anterior cultriform, or dagger-shaped, process and postero-lateral alae, and invests the base of the neurocranium. The cultriform process varies in length, width and shape of its termination. The alae vary in orientation and in their relationships with the medial rami of the pterygoids.

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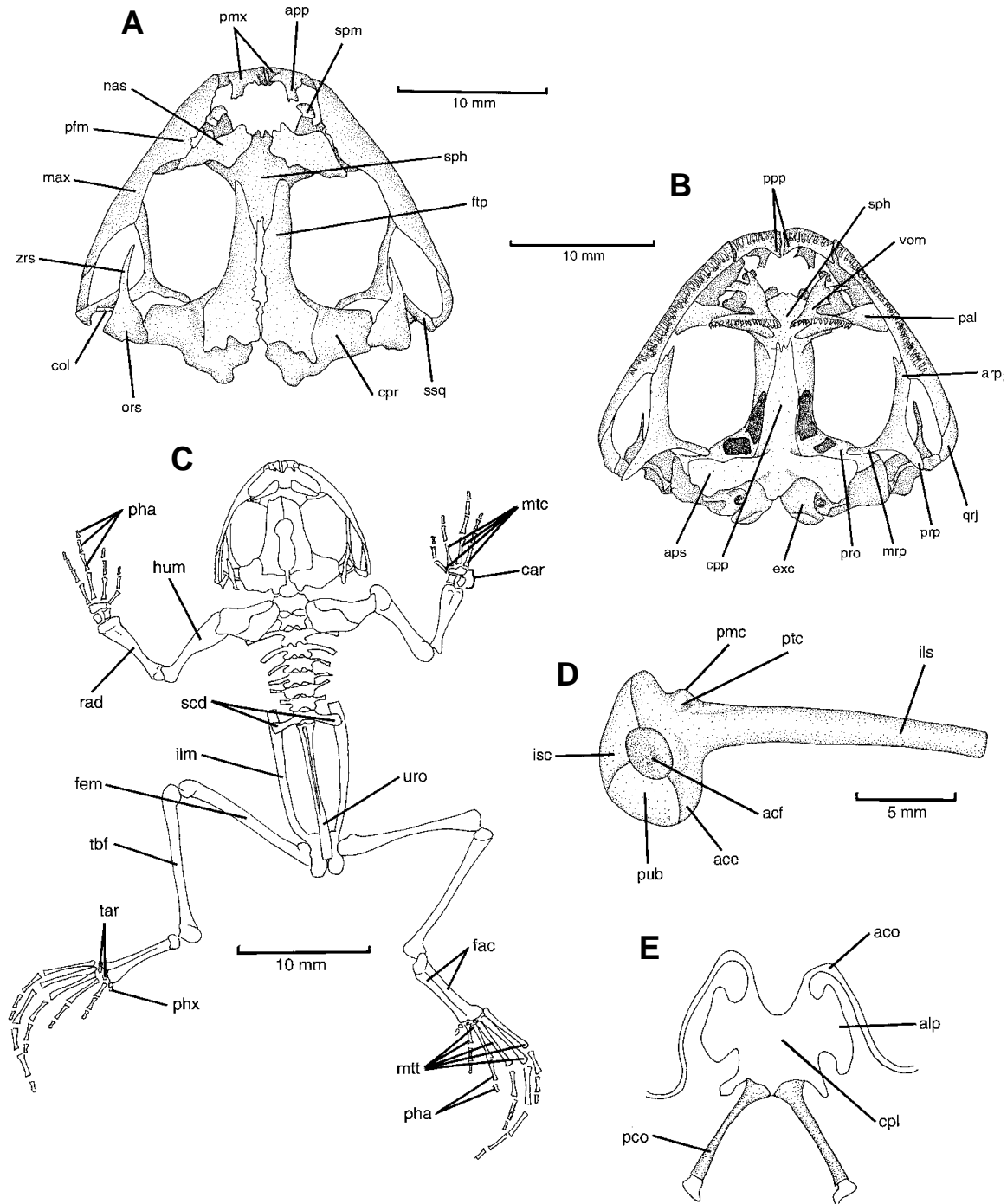


Figure 4.6 Skeletal components of frogs. **A**, dorsal, and **B**, ventral views of the skull of *Limnodynastes peronii*; **C**, skeleton of *Crinia haswelli* in dorsal view; **D**, lateral view of the ilium of *Heleioporus inornatus*; **E**, ventral view of the hyoid of *C. haswelli*. **ace**, acetabular expansion; **acf**, acetabular fossa; **aco**, anterior cornu; **alp**, alary process; **app**, alary process of premaxilla; **aps**, alae of parasphenoid; **arp**, anterior ramus of pterygoid; **car**, carpal bones; **col**, columella; **cpl**, central cartilaginous plate; **cpp**, cultriform process of parasphenoid; **cpr**, crista parotica; **exc**, exoccipital; **fac**, fused astralagus and calcaneum; **fem**, femur; **ftp**, frontoparietal; **hum**, humerus; **ilm**, ilium; **ils**, ilial shaft; **isc**, ischium; **max**, maxilla; **mrp**, medial ramus of pterygoid; **mtc**, metacarpal bones; **mtt**, metatarsal bones; **nas**, nasal; **ors**, otic ramus of squamosal; **pal**, palatine; **pco**, posterior cornu; **pfm**, pars facialis of maxilla; **pha**, phalanges; **phx**, prehallux; **pmc**, dorsal prominence; **pmx**, premaxilla; **ppp**, palatine process of premaxilla; **pro**, prootic; **prp**, posterior ramus of pterygoid; **ptc**, dorsal protuberance; **pub**, cartilaginous pubis; **qrj**, quadratojugal; **rad**, radioulna; **scd**, sacral diaphragm; **sph**, sphenethmoid; **spm**, septomaxilla; **ssq**, shaft of the squamosal; **tar**, tarsal bones; **tbf**, tibiofibula; **uro**, urostyle; **vom**, vomer; **zrs**, zygomatic ramus of squamosal.

[M. Davies]

When present, the vomers underlie parts of the nasal capsule (Fig. 4.6B). They are highly variable between taxa and may or may not bear true teeth. Dentigerous processes vary in length and in position with respect to the palatines. Lateral alae usually form bony supports for the edges of the choanae. The vomers and palatines are fused in the microhylid genera *Cophixalus* and *Sphenophryne*.

Lying on the ventral surface of the neurocranium anterior to the orbit, the palatines extend from the maxillae to meet medially and overlie the ventral sphenethmoid. They are reduced both medially and/or laterally in many species. When present, ventro-medial ridges are occasionally serrated.

The triradiate pterygoids comprise anterior, posterior and medial rami which vary in length and form of their articulation with the maxillae, the quadrate and the prootic respectively. A dorso-medial flange occurs at the junction of the three rami in some species, for example, *Rheobatrachus silus* (Davies & Burton 1982). The posterior ramus usually shows greatest reduction, for example, *Notaden* spp. (Lynch 1971).

The lower jaw articulates with the squamosals, which are paired dermal bones situated postero-laterally on the skull. They comprise a shaft, an anterior (zygomatic) ramus and a posterior (otic) ramus. Extremes of development of the zygomatic rami range from absence, as in some *Uperoleia* spp. (Davies *et al.* 1986) to broad extension to the maxillae with which they articulate, as in *Cyclorana australis* (Lynch 1971). Otic rami may be absent (for example, *Notaden weigeli*; Shea & Johnston 1988), short, narrow and not in contact with the lateral extremities of the crista parotica, as in *Uperoleia capitulata* (Davies *et al.* 1986), or expanded slightly but not in contact with the crista parotica (*Rheobatrachus* spp.; Mahony *et al.* 1984). The otic rami may overlie the crista parotica, forming a complete or partial arch, for example, in *Litoria piperata* (Tyler & Davies 1985) and *Cyclorana australis* (Lynch 1971). A medially expanded otic plate (*sensu* Lynch 1971) has not been observed.

The neurocranium comprises the endochondral sphenethmoid, paired exoccipitals and paired prootics. The sphenethmoid houses the anterior portion of the brain. It is ossified to a greater or lesser extent or not ossified at all, as in *Notaden weigeli* (Shea & Johnston 1988). Maximal ossification extends anteriorly between and beyond the nasals, including portions of the septum nasi (for example, in *Cyclorana*) whilst in some myobatrachine genera, medial ossification is absent and the bone appears as two blocks (Davies 1989a).

The otoccipital comprises the prootics and exoccipitals which are fused indistinguishably in ranids, bufonids, hylids and most limnodynastines but remain separate in the Australian microhylids and in most myobatrachines. It also varies in the shape of its lateral extremities (the crista parotica) and in the disposition of the occipital condyles (Lynch 1971). The auditory capsule forms part of the otoccipital. This comprises a cartilaginous operculum that lies in the posterior portion of the fenestra ovalis, and a plectrum (or columella). The plectrum is absent in some myobatrachine genera and species, and is sinusoidal in shape in limnodynastine genera.

Three pairs of dermal bones, the premaxillae, maxillae and quadratojugals form the maxillary arch, or upper jaw. The premaxillae lie at the anterior extremities of the cranium. Their base comprises a dentate or edentate pars dentalis extending lingually as a pars palatina. The postero-medial extensions of the pars palatina form the palatine processes, which vary in extent, width and medial separation. The premaxilla extends dorsally as alary processes which vary in width, length and orientation.

The maxillae form the major part of the maxillary arch. Like the premaxillae, they extend lingually as an edentate or dentate pars dentalis and a pars palatina. Dorsally, each maxilla extends as a facial flange (pars facialis), which varies in

its development. Posteriorly, this flange may extend further as a preorbital process, which may articulate with the maxillary process of the nasal. The maxillae always articulate anteriorly with the premaxillae, and posteriorly they usually articulate with the quadratojugal. The maxillae may also articulate with the anterior rami of the pterygoids and with the lateral extremities of the palatines.

The quadratojugal completes the maxillary arch in most Australian frogs. Anteriorly it articulates with the maxilla, except when it is reduced, for example, in some species of *Litoria* (Tyler & Davies 1978), or absent, as in the genus *Notaden* (Lynch 1971). Posteriorly the quadratojugal articulates with the base of the squamosal shaft.

In most Australian species, teeth are present on the premaxillae and maxillae. Exceptions are the microhylid genera, some myobatrachine genera and in the limnodynastine *Notaden*. The lower jaw or mandible, comprises the angulosplenic, the dentary and the mentomeckelian bones and cartilages. Dorsal processes are present posteriorly on the angulosplenic in many species, such as the *Litoria citropa* species group (McDonald & Davies 1990).

The hyolaryngeal skeleton consists of a central cartilaginous plate, from which arise a pair of recurved cornua (or anterior hyale) that attach to the ventral surface of the otic capsule. A pair of antero-lateral alary processes are important diagnostically at the family and subfamily levels. A pair of postero-lateral processes also usually occur together with a pair of bony postero-medial processes, the posterior cornua. Trewavas (1933) provided the most comprehensive analysis of the hyolaryngeal skeleton in the Anura.

The postcranial skeleton comprises the vertebral column and the pelvic and pectoral girdles. The vertebral column consists of seven or eight presacral vertebrae and a coccygeal region comprising a single bone, the urostyle. All Australian frogs have eight procoelous presacral vertebrae, except the Limnodynastinae (excluding *Mixophyes* and *Rheobatrachus*) in which vertebrae I and II are fused. These are usually non-imbricate and always lack ribs. Intervertebral discs remain free in adult Myobatrachinae. The sacral diapophyses are dilated in the Hylidae, Microhylidae and Myobatrachidae, expanded in the Bufonidae and rounded in the Ranidae (Trueb 1973). The urostyle articulates with two condyles of the sacrum in all Australian frogs. Coccygeal transverse processes occur in *Rheobatrachus* and the Microhylidae, occasionally appearing as anomalies in other species.

The pectoral girdle comprises the osseous clavicles, coracoids, scapulae, suprascapulae and the epicoracoid and procoracoid cartilages, the omosternum and the sternum (xiphisternum and mesosternum). Amongst Australian families, the Ranidae and Microhylidae have firmisternal pectoral girdles. These lack epicoracoid horns, the epicoracoids are fused, and, if present, the clavicles and coracoids are narrowly separated. The other families have arciferal (or modified arciferal, as in *Rheobatrachus silus*; Davies & Burton 1982) pectoral girdles, with epicoracoid horns which are directed posteriorly, free overlapping epicoracoids, and divergent clavicles and coracoids.

The midventral prezonal omosternum may be present or absent, and the xiphisternum varies considerably in its expansion. In the frontwards burrowing genera *Myobatrachus* and *Arenophryne*, the coracoids are relatively massive and widely separated from each other (Davies 1984) (Fig. 4.7B; Chapter 7). The microhylid genus *Cophixalus* lacks clavicles (Fig. 9.2; Burton 1986). The degree of ossification of the suprascapula varies between species.

The forelimb comprises the humerus, radioulna, carpal bones, metacarpals and phalanges. Humeral crests vary between species, for example, in the *Litoria nannotis* species group (Davies & McDonald 1979), and often between sexes. The basic phalangeal formula of the hand is 2,2,3,3, but variation occurs in

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myobatrachines (see Chapter 7) and some hylids (see Chapter 8). Flanges sometimes occur on the metacarpal and phalangeal bones, as in the *Litoria dorsalis* group (Tyler & Davies 1977). The carpus usually consists of five or six bones, for example, in *Uperoleia* (Davies & Littlejohn 1986; Davies *et al.* 1986), although a systematic study of the carpus of Australian frogs has yet to be undertaken.

The pelvic girdle consists of paired ilia, ischia and cartilaginous pubes. Characters of the ilium are useful diagnostic features of genera and species (Tyler 1976) and have provided information on all the fossil fauna of Australian anurans (Tyler 1989a, 1989b, 1991a, 1991b, 1991c). The form of the ilium in *Rana*, two microhylid, three hylid and 19 myobatrachid genera is illustrated by Tyler (1976). The ilial shaft may bear crests and ridges and the shape and nature of the preacetabular zone is highly variable. Location and nature of the dorsal prominence and dorsal protuberance provide further diagnostic characters. The bony ischium and the pubis, which is usually cartilaginous but often is calcified in larger and older frogs, do not appear to provide diagnostic features.

The hind limb consists of the femur, tibiofibula, fused astragalus/calcaneum, the distal tarsals, metatarsals and phalanges. Terminal phalanges are knobbed in most Myobatrachidae, though T-shaped in *Taudactylus* (Fig. 1.15A; Straughan & Lee 1966). They are clawed in the Hylidae (except *Cyclorana*), T-shaped or Y-shaped in the Microhylidae and rounded in the Bufonidae and Ranidae.

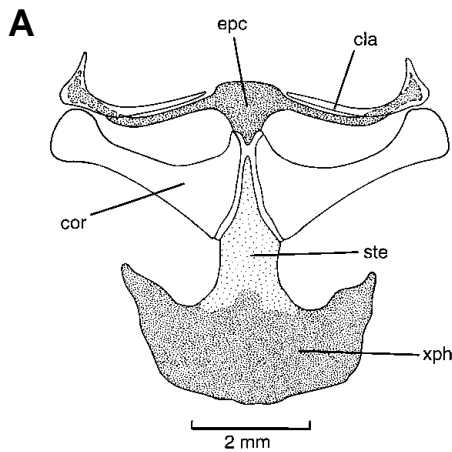
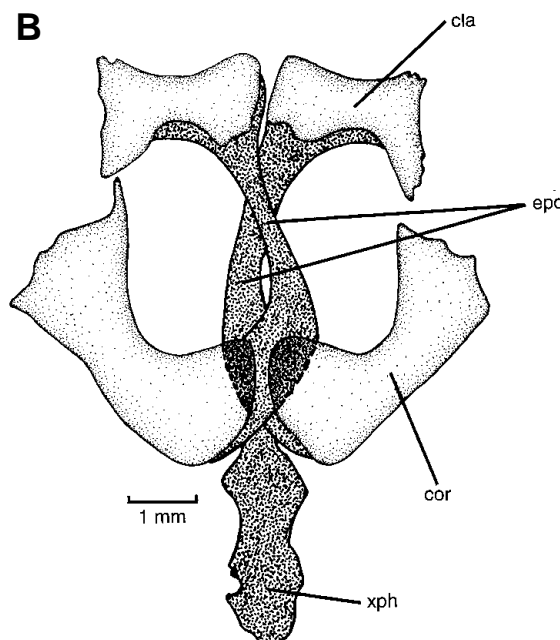


Figure 4.7 Pectoral girdles of frogs. **A**, firmisternal girdle of the microhylid *Sphrenophyne fryi*; **B**, arciferal girdle of the myobatrachid *Myobatrachus gouldii*. **cla**, clavicle; **cor**, coracoid; **epc**, epicoracoid cartilage; **ste**, sternum; **xph**, xiphisternum. [A, C. Eadie; B, M. Davies]



MUSCULAR SYSTEM

Duellman & Trueb (1986) provide a comprehensive overview of anuran musculature. The only full description of an Australian species is that of the gastric brooding frog *Rheobatrachus silus* Davies & Burton 1982; Burton 1983).

Studies on a number of muscle systems have added considerably to the knowledge of Australian species. Such systems include the hindlimb of *Litoria (Hyla) aurea* (Briggs 1940), cranial musculature of several Australian species (Kesteven 1944), the superficial mandibular musculature of the Hylidae and the Myobatrachidae (Leptodactylidae) (Tyler 1971a, 1972b), the tongue (Horton 1982), hyolaryngeal musculature (Trewavas 1933), the depressor mandibulae (Griffiths 1954), and cutaneous muscles (Tyler 1971c; Burton 1980). Broad studies of the hind limb were made by Dunlap (1960) and Sanders & Davies (1984), and by Starrett (1968) of jaw musculature in frogs.

The anuran jaw musculature is complex, but usually comprises two sets of muscles, adductors and depressors, responsible for opening and closing the jaw (Duellman & Trueb 1986).

Muscular communication between the hyoid and the mandible is through the tongue and *m. geniohyoideus* and *m. genioglossus*. There are three continuous superficial throat muscles — *m. submentalis* arises from the lateral surface of the mandible and fibres either traverse from one side to the other, or meet in a median raphe; *m. intermandibularis* and *m. interhyoideus* comprise the two superficial ventral constrictor muscles of the lower jaw.

In the Pelodyadinae, *m. submentalis* is moderate in size and lacks a raphe, and *m. intermandibularis* has a supplementary apical element (Tyler 1971a; Tyler & Davies 1978). In the Limnodynastinae, but not in the Myobatrachinae, the most anterior fibres of *m. intermandibularis* attach upon the ventral surface of *m. submentalis*. In all Myobatrachidae, *m. intermandibularis* is not differentiated into separate elements (Tyler 1972b; Davies & Burton 1982; Burton 1983). The nature of supplementary slips of *m. intermandibularis* can be used to separate the two Australian microhylid genera *Cophixalus* and *Sphenophryne* (Burton 1984) (Fig. 4.8D; Chapter 9). A median aponeurosis is present in the Bufonidae, whilst the superficial mandibular musculature varies within the Ranidae (Tyler 1974).

The tongue consists of two muscles, *m. genioglossus* and *m. hyoglossus*. Horton (1982) recognised four distinct states in the arrangement of the genioglossus (see Chapter 7).

The only detailed survey of the pectoral musculature is that of Jones (1933). Included in this study were *Cyclorana australis*, *Limnodynastes tasmaniensis*, *L. peronii* and *Uperoleia 'marmorata'*. Davies & Burton (1982) and Burton (1983) provided a comprehensive description of the pectoral musculature of *Rheobatrachus silus*.

The well-developed thigh musculature of anurans moves the femur and, in some instances, flexes the knee joint. Some leg muscles are constant in form and are useful in phylogenetic studies (Dunlap 1960; Heyer & Liem 1976; Thompson 1981), whilst others are clearly adaptive and vary according to function. Shank musculature of myobatrachid frogs is correlated with mode of burrowing (Sanders & Davies 1984). Thigh and shank musculature was described by Duellman & Trueb (1986).

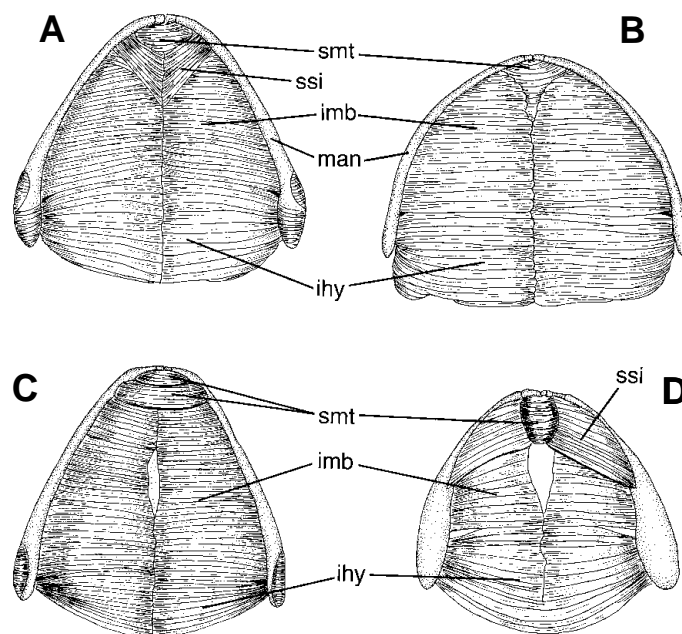


Figure 4.8 Superficial mandibular musculature of frogs. **A**, *Litoria aurea* (Hylidae: Pelodyadinae); **B**, *Limnodynastes tasmaniensis* (Myobatrachidae: Limnodynastinae); **C**, *Taudactylus acutirostris* (Myobatrachidae: Myobatrachinae); **D**, *Sphenophryne* species (Microhylidae: Microhyliinae). **ihy**, *m. interhyoideus*; **imb**, *m. intermandibularis*; **man**, mandible; **smt**, *m. submentalis*; **ssi**, supplementary slip of the *m. intermandibularis*; (A–C after Tyler 1974, D after Burton 1986) [M. Davies]

The skin of amphibians is attached to the body wall at intervals by cutaneous muscles. The *m. cutaneous pectoris* is unique to the Ranidae (Tyler 1971c), and the *m. cutaneous dorsalis* is restricted to the Microhylidae and some members of the Leptodactylidae (Burton 1980). The *pars anteroflecta* is restricted to the Microhylidae (Burton 1980).

LOCOMOTION

Modes of locomotion of anurans vary with lifestyle. Most frogs hop or leap, although some also run, climb or burrow. All can swim, although some terrestrial species, such as the myobatrachine *Arenophryne rotunda* and many microhylid species never encounter bodies of water. Methods of swimming vary greatly. Some species swim using a powerful ‘frog-kick’ with their hindlimbs while the forelimbs are adpressed to the sides of the body (for example, *Cyclorana australis*). Others, such as *Notaden nichollsi*, paddle with alternate strokes of the forelimbs coupled with similar action of the hind limbs, and yet others use a combination of these strokes to manoeuvre themselves through the water. Some dive, others restrict their swimming to surface activity.

On land, hopping or leaping is the most common form of locomotion, and the length and height of these movements is related to the length of the hind limbs and the shape of the body. Frogs with streamlined bodies and long hind limbs are often prodigious leapers, while frogs with shorter limbs usually have shorter hops. The hind limbs provide forward propulsion, and the pectoral girdle absorbs the shock on landing (Emerson 1983). Some frogs such as *Notaden nichollsi* scuttle like mice. *Pseudophryne bibronii* and *Arenophryne rotunda* are amongst those that walk rather than hop; the latter leaves characteristic tracks in the sand, indicating the direction of travel (Tyler *et al.* 1980).

Burrowing species are short legged and generally globose in body shape. Those that burrow frontwards have reduced phalanges on the fingers so that the hand is broad and digs easily (Chapter 7) and/or have a thickening of skin over the snout to allow the head to push into the substrate, such as burrowing microhylids. The latter also have modified premaxillae to provide bony protection for the vulnerable portions of the snout (Burton 1986) while the nasals of burrowing myobatrachines fulfil this role (Davies 1984).

There are two kinds of backwards burrowing. Backwards sliding burrowers enter the ground at an angle and remain facing the same direction while they descend, whereas circular burrowers change direction as they burrow (Sanders & Davies 1984).

The metabolic cost of hopping increases linearly with velocity, to a maximum of about nine times the resting metabolic rate (Walton & Anderson 1988). Proportionately, the cost of hopping is similar to that for other terrestrial vertebrates. The average metabolic rate for Australian frogs burrowing in dry, sandy soil, is 6.1 times the resting rate for *Neobatrachus kunapalari* and 5.2 times for *Myobatrachus gouldi* (Withers unpub. data). These values are less than their maximal metabolic rate, and correspond to a net cost of burrowing (0.0308 ml and 0.405 ml O₂ per cm burrowed per gram body mass in *M. gouldii* and *N. kunapalari* respectively).

FEEDING AND DIGESTION

Most adult frogs are unspecialised, opportunistic predators that feed on a variety of small terrestrial invertebrates, particularly insects, snails and collembolans (Main 1968; Tyler 1989a). The muscular, sticky tongue is flicked at terrestrial prey. Aquatic prey are either grasped and pushed into the mouth by the forelimbs, or snapped by the jaws. Small teeth facilitate grasping and crushing of the prey in preparation for digestion by enzymes.

Little is known of the digestive physiology of Australian frogs apart from *Bufo* and the gastric-brooding frogs *Rheobatrachus*. However, the general structure and function of the digestive tract is similar for most frogs (Reeder 1964; Duellman & Trueb 1986). That of *Litoria (Hyla) aurea* was described by Briggs (1940).

The digestive tract of anurans is relatively simple. The rear of the buccal cavity is the pharynx. Medially a slit-like entry to the larynx lies alongside the muscular opening to the short oesophagus. Glandular secretions, described by Duellman & Trueb (1986), mix with large food items that are swallowed by the combined actions of the tongue, retraction of the eyes into the buccal cavity, and contraction of circum-pharyngeal muscles, then peristaltic contractions of the oesophagus. Small items pass to the oesophagus by ciliary action of the buccal and pharyngeal cilia.

The structure of the stomach of *Rheobatrachus silus* is described by Fanning *et al.* (1982) and the nature of gastric secretions in anurans, by Duellman & Trueb (1986). The gastric epithelium and glands of the stomach secrete mucus, pepsinogen and hydrochloric acid. Gastric secretion, which is stimulated about 40 to 60 min after food is swallowed, has a pH less than two (Taylor *et al.* 1985). The low pH converts pepsinogen to the active proteolytic enzyme, pepsin, which has a low pH optimum of about two in *Bufo marinus* (Taylor & Tyler 1986).

Weak gastric peristalsis moves food from the fundus to the pylorus. Strong gastric peristalsis macerates the stomach chyme, and forces it through the pyloric sphincter into the small intestine.

The structure of the intestine, pancreas and liver is described for *L. aurea* by Briggs (1940) and for anurans generally by Duellman & Trueb (1986). Digestion of stomach chyme is completed in the small intestine using pancreatic and biliary secretions, and nutrients are also absorbed. The alkaline intestinal secretion (pH 7.5 to 9.0) from the epithelium and glands contains mucus, bicarbonate, and intestinal enzymes. Pancreatic secretion contains bicarbonate to buffer a neutral pH, and a variety of enzymes including proteases, amylase, lipase, DNAase and RNAase. The main pancreatic protease, trypsin, is secreted as an inactive precursor, trypsinogen, which is activated in the small intestine by enterokinase. The other pancreatic proteases, chymotrypsin and carboxypolypeptidase, are also secreted as inactive precursors (chymotrypsinogen and procarboxypolypeptidase) and are activated by trypsin. The pancreatic proteases have a pH optimum about 7. Bile secreted by the liver cells neutralises the acidic chyme in the small intestine and inhibits bacterial growth. Bile salts emulsify fats into small droplets called micelles, aiding in digestion.

The ileum abruptly widens to form the rectum which runs posteriorly and opens externally via the cloaca. A flap-like valve between the ileum and the rectum prevents retrograde movement. The rectum reabsorbs ions and water from the remaining undigested material and forms faeces. Faecal material is enclosed by a thin membrane of mucus and cellular detritus, and is extruded in a spiral fashion from the hind-gut. This neat elimination of the faeces prevents contamination of the cloaca and its other orifices.

Gastric function is dramatically modified in gastric-brooding frogs, *Rheobatrachus* spp. The female swallows eggs or early-stage larvae, and uses her stomach as a brood sac (Corben *et al.* 1974; Tyler & Carter 1981; McDonald & Tyler 1984). Brooding is accompanied by structural changes of the stomach that reflect its marked distension, and additionally in *R. silus* by separation of the smooth muscle cells from the connective tissue matrix, atrophy of the epithelium to a single layer of low columnar-cuboidal cells with shallow gastric pits and few glandular acini, and regression of the HCl-secreting cells (Fanning *et al.* 1982). Similar degenerative changes are not observed in *R. vitellinus* (Leong *et al.* 1986). The brooded embryos appear to secrete a potent inhibitor of gastric secretion, prostaglandin E₂ (Tyler *et al.* 1983; de la Lande *et al.* 1984; Taylor *et al.* 1985).

CIRCULATORY SYSTEM

The circulatory system of Australian frogs, other than *Litoria aurea* and *Bufo marinus*, is poorly known, but presumably resembles that of other frogs, because there is considerable similarity in cardiovascular structure and function in anuran amphibians (Briggs 1940; Foxon 1964; Brady 1964; Duellman & Trueb 1986).

Nucleate red blood cells contain haemoglobin, and their principal role is O₂ transport. They tend to be large, as in *Neobatrachus sutor* (a diploid species), in which the red blood cells are about 17 mm × 11 mm, and *N. kunapalari* (a tetraploid) with even bigger red blood cells about 21 mm × 13.5 mm. There are generally about 5 × 10⁵ to 10⁶ red blood cells/mm³ of blood. The haematocrit varies considerably, from <10 to >30%.

The less numerous white blood cells (about one per 50 red cells) include agranular leucocytes (lymphocytes and monocytes) and granular leucocytes (basophils, neutrophils and eosinophils), which provide defence against foreign material or microorganisms by phagocytosis and an immune response. The blood clotting mechanism involving thrombocytes, or nucleated 'spindle' cells, resembles that of mammals, although it occurs at lower temperatures.

The amphibian heart has two atria and a single ventricle (see Duellman & Trueb 1986). Deoxygenated blood from the body, and oxygenated blood from the skin, drains to the right atrium, and oxygenated blood from the lungs drains to the left atrium. Trabeculations of the ventricle and the spiral valve of the conus functionally separate the flow of oxygenated and deoxygenated blood. The structure of the truncus has been described for some Australian frogs by Oliver (1909).

The amphibian heart muscle obtains its O_2 and nutrient supply from the blood passing through its chambers; it does not have a separate coronary blood supply.

The detailed arrangement of the vascular system of *Litoria aurea* (Briggs 1940) and *Bufo marinus* (Smith & Campbell 1976; Snyder *et al.* 1990) is representative for frogs.

The arterial system supplies the body via the carotid and systemic arches, and the lungs via the pulmonary arch. The left and right common carotid arteries each form an internal and external carotid artery and supply blood to the jaws, thyroid, brain, eyes and associated structures. Each systemic arch gives rise to several arteries before they unite posteriorly to the heart to form a dorsal aorta. Branches from the aorta supply the viscera. The aorta divides posteriorly into the left and right common iliac arteries, which supply blood to each hind-limb. The pulmonary artery delivers deoxygenated blood to the lungs for oxygenation, and to the skin of the dorsal and lateral body wall via the cutaneous magnus artery.

Blood drains from the body via the veins and venae cavae, and from the lungs via the pulmonary veins. The sinus venosus receives the large postcaval vein draining the posterior part of the body, and the short precaval veins draining blood from the head and forelimbs. All veins other than the pulmonary and hepatic and renal portal veins drain into these large veins. The pulmonary veins arise from the lungs, and carry oxygenated blood to the left atrium.

The lymphatic system collects interstitial fluid that is filtered across the tissue capillaries, and returns it to the veins. Anuran amphibians have extensive subcutaneous lymph sacs, into which the lymph drains from the tissues. The role of the lymphatic system in regulation of water distribution is recorded by Baustian (1988). Aquatic frogs have more extensive lymph sacs than do terrestrial frogs. Water absorbed across the skin may be circulated via the lymphatic spaces and posterior lymph hearts to the renal portal system, thence the kidneys (Carter 1979).

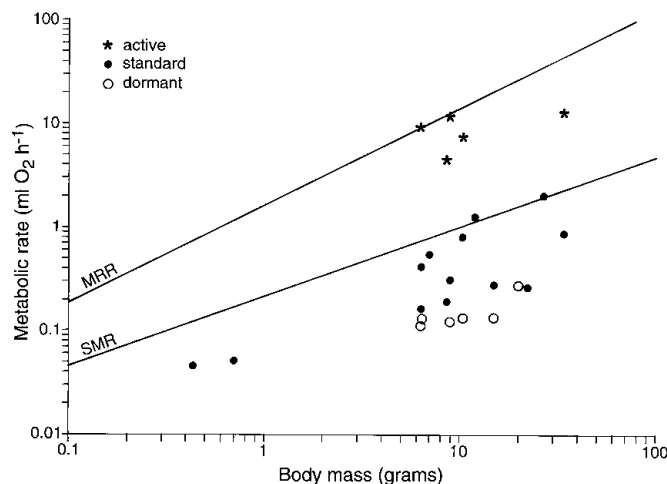


Figure 4.9 Relationship between metabolic rate and body mass for resting Western Australian frogs, and for dormant, cocooned frogs. **MRR**, maximal metabolic rate; **SMR**, standard metabolic rate. (From Withers unpub. data) [P.C. Withers]

Cardiovascular physiology has been extensively studied for *Bufo marinus*. Oxygen delivery to the tissues by the circulation depends on the O₂ content of arterial and venous blood, and the blood flow rate. The O₂ content of blood is determined by the blood haemoglobin content and the oxygen dissociation curve which indicates the relationship between % saturation of oxygen and partial pressure of oxygen. Amphibian haemoglobin binds about 1.34 ml O₂/gram (Hillman 1976). The oxygen dissociation curve is generally sigmoidal, but the P₅₀ value (the partial pressure of O₂ for 50% saturation) varies dramatically depending on the partial pressure of CO₂, pH and temperature. For *Bufo marinus*, the P₅₀ is about 5.9 kPa (pH 7.4, 25°C; Hall 1966). The P₅₀ varies for tadpoles and adults, and also for different species. The Bohr shift increases the O₂-unloading capacity of the blood to the tissues.

Dramatic adjustments of cardiovascular and respiratory function during activity increase O₂ delivery to tissues to match their increased O₂ requirements. Blood flow increases because of elevated arterial blood pressure and decreased peripheral resistance. The arterial blood O₂ level increases during activity, facilitating O₂ delivery. Most of the increased O₂ demand of activity is met by increased O₂ extraction from the blood (A–V O₂ difference) rather than elevated blood flow (Withers *et al.* 1988b).

Cardiovascular adjustments during moderate dehydration compensate for the resultant decreased blood volume and elevated haematocrit, but eventual cardiovascular failure may limit the dehydration tolerance of frogs (Hillman 1987; Hillman *et al.* 1987). Cardiovascular adjustments during haemorrhage maintain blood pressure and blood flow to essential tissues (Hillman & Withers 1987; Baustian 1988).

The anuran immune system consists of the thymus, aggregations of lymphoid tissue (spleen; procoracoid, prepericardial and epithelial bodies; jugular body) and other sites of blood cell synthesis (bone marrow, liver, kidney; Cooper 1976). These lymphoid tissues filter blood and lymph, form antibody-forming and antibody-carrying lymphocytes, and are sites for synthesis of antibodies (immunoglobulins M and G).

RESPIRATION

The Respiratory System

The primary role of the respiratory system is gas exchange, although it is also important for sound production or buoyancy in some frogs. The structure and function of the respiratory system is described by Foxon (1964), Tyler (1982) and Duellman & Trueb (1986).

A complex cycle of buccal air-pumping ventilates the lungs (Vitalis & Shelton 1990). Respiratory gas exchange also occurs across the skin and lining of the buccal cavity and pharynx in adult amphibians, and via gills, skin and/or lungs in tadpoles. Frog eggs rely on gas exchange by diffusion through the egg capsule from the surrounding water.

The moist, well-vascularised skin of most frogs is an effective gas exchange surface, particularly for CO₂. Cutaneous gas exchange can support much, or even all, of the gas exchange for small, resting frogs, but large and/or active frogs require a significant pulmonary contribution to O₂ exchange. For resting *Bufo marinus*, the resting VO₂ is about 0.048 ml/g/h, of which about 20% is cutaneous and 80% is pulmonary (Bentley & Shield 1973). Cutaneous gas exchange is estimated to be only about 4% of the O₂ uptake for active *Bufo marinus* whereas pulmonary exchange is 96% (Withers & Hillman 1988).

Energetics

The aerobic metabolic rate of anuran amphibians is variable, depending on species, habits, body mass, temperature and activity level. Anurans also rely extensively on anaerobic metabolism for unsteady-state activities such as rapid locomotion, prey capture and avoidance of predators.

The standard metabolic rate (SMR) of anuran amphibians is strongly determined by body mass, and the SMR of Australian frogs conform well to this relationship. Walking, hopping, burrowing, swimming and calling are the principal energy-requiring activities of anurans. Burrowing and calling especially are sustained aerobic activities. Walking and hopping would be sustained aerobic activities for widely-foraging species, but would have an important anaerobic component for frogs that rely on short bursts of activity. The 'maximal' metabolic rate (MMR) of anurans is about 8 to 10 times resting metabolic rate. MMR values for Australian frogs are consistent with those for other anurans. MMR has often been measured during enforced exercise (Walsberg 1986) but this does not necessarily elicit the maximal metabolic capacity of the frog. For example, in sustained calling, the metabolic cost can exceed the MMR measured during activity (Taigen & Wells 1985; Taigen *et al.* 1985).

Many anurans, especially fossorial arid species that spend considerable periods underground, show a considerable metabolic depression when inactive. For example, the metabolic rate of *Neobatrachus pelobatoides* declines by about 80% from the resting rate over about four weeks from the onset of dormancy (Flanigan *et al.* 1990). The metabolic rate of dormant *C. platycephala* is 30 to 40% of that of a resting frog (van Beurden 1980, 1982). A similar metabolic depression has been reported for *C. maini* and a variety of *Neobatrachus* species (Withers 1993). The metabolism of some developing terrestrial embryos is also depressed prior to hatching, by hypoxia (Bradford & Seymour 1988b). During dormancy, a low respiratory quotient (about 0.73) indicates a reliance by *Cyclorana platycephala* on lipid stores; this is consistent with the initially high abdominal fat pad content of the frogs (up to 20% body mass) and the observed pattern of decline in fat pad lipid and total body lipid, carbohydrate and protein content (van Beurden 1980). The mechanism for metabolic depression is not clear, although it does not involve a lowered body temperature or hypoxia (Flanigan *et al.* 1992). Some changes in enzyme function accompany metabolic depression in *N. pelobatoides* (Flanigan *et al.* 1990) but it is not clear whether these are responsible for, or are biochemical sequelae of, the metabolic depression.

The anaerobic metabolic capacity of anurans is considerable, but the accumulation of lactate and alteration of body fluid pH make anaerobiosis a nonsteady-state mechanism for ATP production. The whole-body lactate content (WBL) of anurans (after four minutes of activity) generally increases in approximate proportion to body mass, although there are significant inter-specific differences (Taigen *et al.* 1982).

The particular combination of aerobic and anaerobic capacity for a frog reflects the complex energy requirements of a wide spectrum of activities (Taigen & Pough 1985), including predator avoidance behaviour (active or static), locomotory mode (hopping, jumping, walking, burrowing), predatory behaviour (sit-and-wait versus widely-foraging), reproductive behaviours (calling, wrestling, amplexus, nest-building).

As most frogs are nocturnal and semi-aquatic, external sources of heat are limited, and body temperature (T_b) tends to be similar to the ambient water or air temperature. In general, arid zone and tropical frogs experience a higher field T_b than temperate frogs, but even desert amphibians tend to have only a moderate T_b , from 20° to 30°C (Mayhew 1968; Brattstrom 1970). Field body

temperatures vary from 4.2°C (*Neobatrachus sudelli*) to 27.8°C (*Litoria caerulea*) for southern and eastern Australian frogs to 33.0°C (*Crinia pseudinsignifera*), 33.6°C (*Notaden nichollsi* and *Uperoleia (Glauertia) mjobergi*) and 39.2°C (*Cyclorana cultripes*, *C. platycephala*, *Litoria rubella*) for Western Australian frogs (Johnson 1970, 1971a, 1971b, 1971c, 1972; Main 1968). The highest T_b 's recorded are for frogs and tadpoles in shallow ponds, which heat up considerably during the day. Tadpoles of *L. coplandi* have been reported in water at 45°C (Tyler 1989a).

There is a general trend for arid-zone and tropical frogs to have a higher critical thermal minimum temperature (CT_{min}) and critical thermal maximum temperature (CT_{max}). The actual CT_{max} value depends somewhat on the geographic range and temperature at which the frog was acclimated before measurement. For example, the CT_{max} of *Litoria rubella* varies from 38.2° to 40.4°C, depending on locality and acclimation temperature (Warburg 1967). There is rapid acclimation of CT_{max} for tadpoles of *Limnodynastes peronii* (Marshall & Grigg 1980). The thermal preferendum and CT_{max} for whole organs and tissues of frogs is also correlated with the latitude of collection (Stephenson 1968). For example, *Crinia tasmaniensis* has a thermal maximum of 30° to 37°C at 45° latitude, compared to 45°C for various tropical frogs at 19° latitude.

EXCRETION

The mean water content of Australian frogs (expressed relative to fat-free mass, with the bladder empty) is about 78.7%, with a range from 75 to 85% (Main & Bentley 1964; Clyne 1968; Main 1968; Johnson 1970, 1971a). There is no evidence for a trend of higher body water content for arid-adapted frogs.

Frogs can tolerate a marked loss of body water and an increase in solute concentration. There is generally a correlation for amphibians between the level of terrestriality and tolerance of dehydrational mass loss, or vital limit. Mesic frogs tend to have a low vital limit, and arid frogs have a higher vital limit (Heatwole 1984). For example, the rain-forest frog *Taudactylus diurnus* has a low mass loss (26.2%) at its vital limit, whereas *Heleioporus* spp. have a mass loss of about 40% at their vital limit (Bentley *et al.* 1958; Johnson 1971a).

The paired kidneys of frogs are located on either side of the dorsal aorta. Duellman & Trueb (1986) describe their structure.

The general functioning of the kidneys is similar in all anurans (Shoemaker & Nagy 1977). Urine is formed by ultrafiltration from the glomerular capillaries. Half or less of the primary filtrate is reabsorbed during passage through the nephron, but typically more than 90% of the solutes are reabsorbed, producing copious dilute urine (about 0.5 ml/g/day). This can be reabsorbed to replace body fluids and is an important water store, especially for desert species.

Most frogs become essentially anuric when removed from water. Both glomerular filtration and urine flow are greatly reduced (Bakker & Bradshaw 1977). The ultrafiltration rate declines even more rapidly, because renal reabsorption of filtrate is increased above the normal value.

The control of osmoregulation in dehydrated frogs is discussed by Duellman & Trueb (1986). In most adult frogs, the kidney has numerous ciliated funnel-like openings, or nephrostomes, that collect fluid from the coelomic cavity. The nephrostomes apparently connect only to the renal venous system, and would return coelomic fluid directly to the circulatory system. Some adaptive variations in renal structure for Australian arid frogs are associated with a burrowing habit and storage of large volumes of bladder urine. The number of nephrostomes per kidney varies markedly, from about 30 for *Litoria lesueuri*, 100 for *Neobatrachus (Heleioporus) pictus*, 200 for *Litoria (Chiroleptes)*

alboguttata and over 1000 for *Notaden bennettii* (Sweet 1907). The nephrostome ducts of *N. bennettii* connect, not only to the renal venous system, but also to the nephrons, thus providing a direct passage of coelomic fluid to the bladder for storage. The more medial nephrons of *Cyclorana platycephala* and *L. alboguttata* tend to be aglomerular, or at least to have markedly reduced glomeruli (Dawson 1951). This would reduce the glomerular filtration rate and diminish the circulation of water between the plasma and bladder during dormancy.

Tadpoles and aquatic adults generally excrete ammonia (>70% of nitrogenous wastes excreted as ammonia). Despite its high toxicity, it is very soluble and is readily lost to the external environment. Terrestrial amphibians tend to excrete urea rather than ammonia (<10% excreted as ammonia) which is less toxic, although there is a metabolic cost to urea synthesis from ammonia via the urea cycle. This shift from aquatic ammonotelic to terrestrial ureotelic has been documented for the Australian tree frogs *Litoria raniformis* and *L. ewingii* (Cree 1985). There is a similar shift for *Pseudophryne corroboree* from ammoniotelic as aquatic tadpoles to ureotelic as adults (Domm & Janssens 1973). No Australian frog is known to excrete uric acid.

SENSE ORGANS AND NERVOUS SYSTEM

Little information is available on the sense organs of Australian frogs. Their structure and function has been reviewed by Duellman & Trueb (1986). Anuran olfactory organs are well documented (Scalia 1976) and function in chemoreception (Madison 1977).

Larval anurans and adults of some aquatic species possess lateral line systems with mechanoreceptors called neuromasts. Such a system is absent in *Rheobatrachus silus* (Tyler & Davies 1983b).

The anuran auditory system is unique amongst vertebrates because the ear is capable of receiving airborne transmissions only at very limited frequencies. This filtration of sound allows species to recognise the calls of their own kind in mixed choruses. Loftus-Hills and his colleagues have provided information on ear structure and function for the Australian fauna in Chapter 7.

Briggs (1940) described the brain and nervous system of *Litoria (Hyla) aurea*. Sweet (1896) examined the spinal nerves of the same species and of *Neobatrachus (Heleioporus) pictus*, *Limnodynastes tasmaniensis*, *L. ornatus* and *Cyclorana (Chiroleptes) platycephala*, but found little difference between these species in the distribution and position of the nerves. Duellman & Trueb (1986) reviewed information on the anuran brain and nervous system.

ENDOCRINE SYSTEMS

The endocrine glands of amphibians are responsible for the regulation and coordination of many organ systems, by the secretion of hormones into the circulatory system for distribution via the body fluids to specific target organs (Bentley 1971; Gorbman 1964; Turner & Bagnara 1976).

Neurohypophyseal hormones from the posterior pituitary target the kidney tubules, bladder and skin. In the bladder, they promote water reabsorption from the bladder and potentiate the water balance response. Arginine vasotocin (AVT) is the main antidiuretic hormone, although oxytocin is also present and has antidiuretic effects. AVT reduces glomerular filtration rate and increases water reabsorption from the nephron tubules and across the skin (Pang *et al.* 1982). It increases the cutaneous water permeability for *Crinia georgiana* from 3.4 to 13.5 ml/cm²/h, and for *Bufo marinus* from 28 to 85 ml/cm²/h (Bentley & Main 1972). The sympathetic nervous system probably also regulates glomerular

filtration and urine flow rate. Another neurohypophyseal hormone, mesotocin, may elevate glomerular filtration rate and urine flow rate in hydrated frogs (Pang & Sawyer 1978).

The roles of the intermediate pituitary, anterior pituitary, thyroid, parathyroids, ultimobranchial bodies, pineal organ, thymus and the endocrine portion of the pancreas and their hormonal secretions were reviewed by Duellman & Trueb (1986). The roles of the adrenal glands and their catecholamines were also discussed by these authors, and Tufts *et al.* (1987) and Withers *et al.* (1988a) described the circulating levels of the catecholamines in *Bufo marinus* during physical activity, haemorrhage and dehydration.

In addition to their role in reproduction, the testes and ovaries are important endocrine glands. Control of their endocrine activity is described by van Oordt (1974), Lofts (1974) and Duellman & Trueb (1986).

REPRODUCTION

Genetics

The diploid chromosome complement of Australian frogs varies from the basic number for frogs of $2n=26$ chromosomes, as in *Cyclorana*, to $2n=24$ in the genera *Adelotus*, *Limnodynastes* in part, *Mixophyes*, *Notaden*, *Pseudophryne*, *Crinia*, *Rheobatrachus*, *Taudactylus*, *Uperoleia*, *Litoria infrafronata*, and $2n=22$ for some *Limnodynastes* species (Morescalchi 1977). Bisexual tetraploidy occurs in some *Neobatrachus*; examples are *N. sudelli*, *N. aquilonius*, *N. kunapalari* and *N. centralis*, in which $2n=48$ (Mahony & Robinson 1980; Mahony & Roberts 1986). The karyotype of *Bufo marinus* is $2n=22$. This species shows no sexual dimorphism in its sex chromosomes (Benirschke & Tsu 1971).

Genetic sex determination in frogs is not uniformly of the heterogametic male–homogametic female system (XX, XY). In some species, females are heterogametic (ZZ, WZ). Sex determination is further complicated by the potential effects in some species of environmental variables on the development of the gonads, irrespective of the genetic sex of the individual (Gallien 1974). For example, in some species, all tadpoles have ovaries, including the males in which testes differentiate only after metamorphosis. High ambient temperature may induce testis formation in females, and low temperature may induce ovarian development in males. Temperature apparently influences the medullary development of the gonads, overriding the genetic sex determination.

The ovaries are paired, sac-like structures with a highly-folded wall and a narrow cortical region of germinal epithelium (Lofts 1974). They become enormously distended with eggs at the beginning of the breeding season. Freshly ovulated eggs enter the Mullerian oviduct, where they are coated with up to five layers of jelly before extrusion during mating.

The testes are paired, ovoid bodies attached to the dorsal body wall, in the body cavity (Lofts 1974). The numerous secondary sexual characteristics, such as high red cell count, lung size, behaviour and nuptial excrescences, are directly stimulated by the testicular androgenic hormones.

EMBRYOLOGY AND DEVELOPMENT

The size of eggs varies widely for Australian frogs, from about 1 mm for many aquatic eggs to over 5 mm for *Arenophryne* and 7.4 mm for *Myobatrachus*. Amphibian eggs consist of the ovum, surrounded by the tough, thin vitelline

membrane and a variable number of concentric egg capsules (Salthe 1963). There is a perivitelline chamber between the vitelline membrane and the innermost egg capsule.

Frog eggs swell immediately after deposition in water, the extent depending on the osmotic concentration of the external medium. The vitelline membrane functions as a semi-permeable membrane (Salthe 1965). There is a further increase in egg diameter during development.

Clusters of eggs, in close proximity, can deplete the local O_2 , and this is exacerbated by the limited rate of diffusion of O_2 through the jelly and foam of egg masses. Submerged egg masses can sustain O_2 delivery to eggs within about 1.5 cm of the surface, but eggs deeper within the egg mass experience hypoxia and have retarded development, or die (Seymour & Roberts 1991). The limitation of O_2 delivery to eggs in masses is alleviated if the egg mass is suspended by vegetation at the water surface, if it is foamy and floats at the water surface, or if there is convective oxygenation of the interior of the egg mass by water flow induced by wind or thermal gradients.

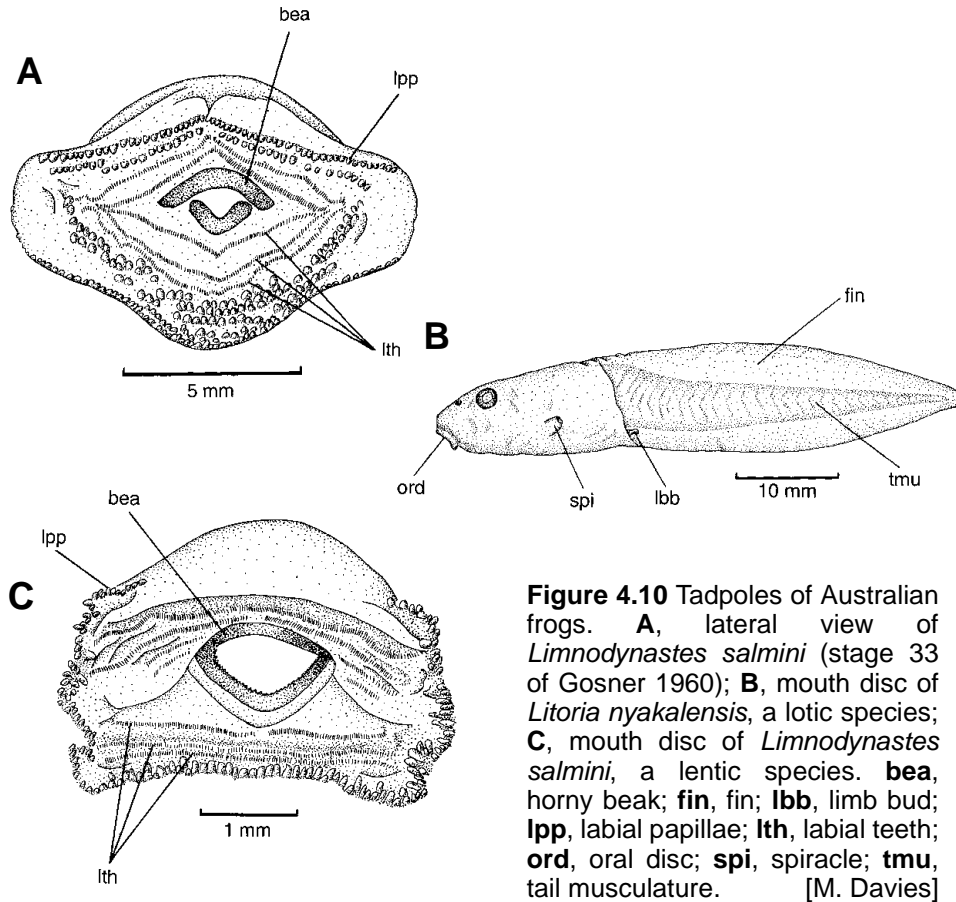
Terrestrial eggs are susceptible to desiccation, and their survival is extremely dependent on the external hygric conditions. Eggs of *Geocrinia (Crinia) victoriana* lose water, even in saturated air, at a rate dependent on the ambient humidity (Martin & Cooper 1972). The egg capsule is not a barrier to water loss. Eggs lose water by evaporation from the egg capsule as if it is a free water surface. For example, the resistance to water loss of eggs of *Pseudophryne guentheri* is about 1 sec/cm (Withers unpub. data). The volume, embryonic growth rate and survival of *Pseudophryne bibronii* is greatest at high water potentials (Bradford & Seymour 1988a). The metabolic rate of *Pseudophryne bibronii* eggs increases in an exponential fashion during development, until either stage 26 or 27 is reached, and development ceases. Metabolic rate is then depressed until the eggs are flooded, and hatch into tadpoles.

The O_2 conductance of the egg capsule increases in concert with metabolic rate during development of terrestrial eggs, because the capsule becomes thinner as the egg swells; the internal pO_2 remains constant, and high enough to prevent hatching (Bradford & Seymour 1985). However, the internal pO_2 is sufficiently low for ready-to-hatch embryos that it depresses their metabolic rate; this prevents further development and conserves energy until hatching. The stimulus for hatching is a depressed internal pO_2 (Bradford & Seymour 1988b). Flooding of terrestrial eggs lowers the pO_2 at their surface to less than a critical value, and they hatch. *Pseudophryne bibronii* eggs hatch in air if the external air pO_2 falls below 5.2 kPa, and hatch when flooded at an external air pO_2 less than 29.9 kPa.

Most aquatic embryos excrete their nitrogenous wastes as ammonia. However, ureotelism may be common for terrestrial and arboreal eggs, which lack copious amounts of water for ammonia excretion. For example, urea accounts for up to 86% of the nitrogen excreted by embryos in the terrestrial eggs of *Geocrinia victoriana* (Martin & Cooper 1972).

Larval forms of frogs are morphologically and physiologically very different from adults. Developmental stages are recognisable, but life tables have been constructed for few Australian amphibians and illustrated only for *Litoria rubella* (Tyler 1989a). Gosner (1960) provided a generalised staging table for species that develop aquatically, but it is not applicable to species which develop directly, such as *Myobatrachus gouldii* and *Arenophryne rotunda* (Roberts 1981, 1984).

The early stages of development of anuran larvae are conservative, and interspecific and intergeneric variation are slight. The major morphological features that vary in these early stages are the nature of the external gills and the condition of the ventral adhesive organs, when these are present.



Species hatch at different stages, usually around stages 18 to 20 of Gosner (1960). Feeding usually commences at stage 25, but in some species that have relatively large yolky eggs, the tadpole gut does not differentiate until some time after hatching.

External gills rapidly become incorporated into the branchial chamber. This opens sinistrally by way of a single operculum, the spiracle, located laterally or ventro-laterally. It is reduced to a simple aperture in the branchial wall in *Rheobatrachus silus* tadpoles, which are not aquatic or free swimming (Tyler & Davies 1983a).

Initially an anterior or antero-ventral depression marks the position of the mouth, or stomodaeum, which eventually perforates and may become relocated more ventrally. In all aquatic tadpoles, except *Litoria subglandulosa* (Tyler & Anstis 1975), *Taudactylus diurnus* and *T. eungellensis* (Watson & Martin 1973; Liem & Hosmer 1973), the mouth comprises a keratinised beak surrounded by rows of denticles (Fig. 4.10B, C). The number and arrangement of these tooth rows is species specific and is also a useful diagnostic feature at the subfamily and family level (Martin & Watson 1971; Watson & Martin 1973). The oral disc is surrounded by rows of papillae and again the nature and arrangement of these papillae are diagnostic. Lentic species have oral discs that are least differentiated (see Watson & Martin 1973) whilst lotic species have elaborations of the discs that enable larvae to attach to the substrate in fast flowing waters. Such adaptations vary between species (Martin & Watson 1971; Liem & Hosmer 1973; Liem 1974; Watson & Martin 1973; Tyler *et al.* 1979, 1983; Davies 1989b, 1991; Davies & Richards 1990).

Species which develop directly rely upon yolk reserves for nutrition and hence the oral disc is undifferentiated (Tyler & Davies 1983a).

The nostrils of larvae perforate just before or just after hatching. They can be sessile or elevated slightly above the surface of the snout and generally open antero-laterally. The eyes lack lids and are relatively small.

The body of a tadpole is short and characteristically ovoid (Fig. 4.10A). It is attached to a laterally compressed tail consisting of an axis of musculature, the depth and width of which are adaptive, and dorsal and ventral fins. The depth of these fins, the shape of their terminal confluence and the positions from which they arise are also adaptive. The anus usually opens dextrally or medially near the confluence of the body and tail. The hind limbs first appear as buds at the posterior end of the body closely applied to the tail musculature. These develop as the tadpole grows and eventually are clearly differentiated as five-toed hind limbs with subarticular and metatarsal tubercles and differentiated discs. The forelimbs develop in the branchial chamber and the first erupts through the spiracular opening, closely followed by the second which ruptures autolysed skin of the branchial chamber just prior to metamorphosis.

The larval mouthparts break down and dramatic changes occur to the chondrocranium which ossifies and assumes the shape and structure of the adult skull and jaws (see Duellman & Trueb 1986 for a summary of these events). The mouth forms and the larval gut differentiates into an adult digestive tract. During these final stages of transformation, larvae do not feed. The tail is reabsorbed into the body by apoptosis and the four-legged, tailless froglet emerges to face life on land.

Tadpoles generally feed on small to microscopic food particles, often by filter feeding. Many supplement the filterable food by rasping the surface of plants, dead animals, and the substrate. The branchial basket of tadpoles forms a filter that is covered by a layer of mucus, that is directed by ciliary currents in a spiral fashion into the oesophagus. The tadpole foregut is undifferentiated, and has a storage role but no digestive role; it serves primarily to direct food to the small intestine. Consequently, there is a lack of peptic protein digestion. The tadpole small intestine, in contrast to that of the adult, is long and coiled, the relative length varying interspecifically and with the nature of the diet. Symbiotic microorganisms may be involved in the digestion of food eaten by herbivorous or omnivorous tadpoles.

Tadpoles have internal gills, a well-vascularised skin, and some have lungs well before they metamorphose. The contribution to gas exchange of these respiratory surfaces varies with ambient conditions (temperature, water pO_2), and tadpole size, stage of development and activity. Tadpoles of *Heleioporus* and *Pseudophryne*, which hatch and remain in a jelly mass in burrows or depressions in the soil until flooded, must rely on diffusion of O_2 through the jelly mass to their body surface. Survival of the hatched larvae is also affected

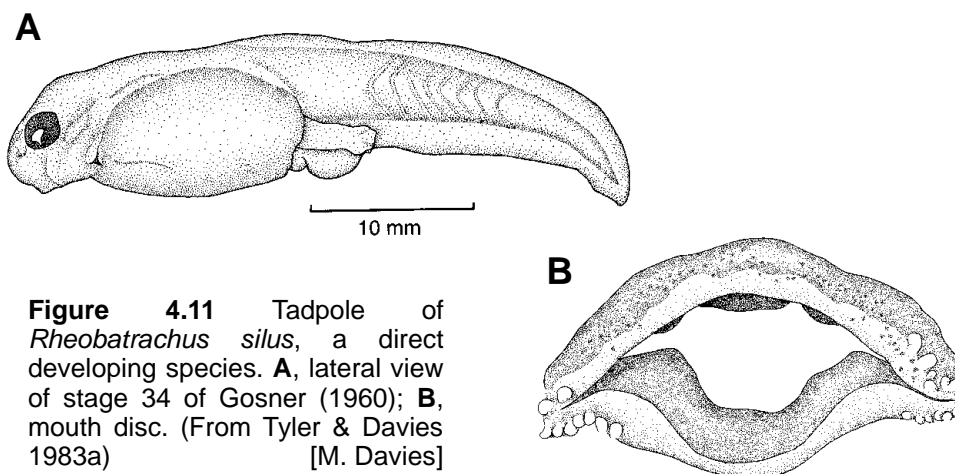


Figure 4.11 Tadpole of *Rheobatrachus silus*, a direct developing species. **A**, lateral view of stage 34 of Gosner (1960); **B**, mouth disc. (From Tyler & Davies 1983a) [M. Davies]

4. MORPHOLOGY AND PHYSIOLOGY OF THE ANURA

by the water potential of the substratum, as well as by the temperature (Geiser & Seymour 1989). Many tadpoles cannot survive out of water. For example, tadpoles of *Bufo marinus* only survive 10 hours out of water, even if kept moist (Valerio 1971).