



FAUNA *of* AUSTRALIA



8. FAMILY HYLIDAE

Michael J. Tyler & Margaret Davies



PI 1.4. *Litoria infrafrenata* (Hylidae): a species that frequents houses; found along the coast of Cape York. [H. Cogger]



PI.1.5. *Litoria wotjulumensis* (Hylidae): a ground dwelling species of northern Australia. [J. Wombey]



Pl. 1.6. *Cyclorana novaehollandiae* (Hylidae): a burrowing species present in a wide range of habitats in Queensland and New South Wales. [J. Wombey]



Pl 1.7. *Nyctimystes dayi* (Hylidae): a large-eyed, arboreal species endemic to the wet tropics of northern Queensland. [J. Wombey]

DEFINITION AND GENERAL DESCRIPTION

Tree frogs of the family Hylidae have eight procoelous, non-imbricate, presacral vertebrae, the first two of which are unfused. The atlantyl cotyles of presacral I articulating with the skull are widely separated. Ribs are absent and the sacral diapophyses are dilated. The sacrococcygeal articulation is bicondylar. The pectoral girdle is arciferal with a cartilaginous omosternum and sternum. Palatines are present, parahyoid absent and the cricoid ring is complete. The maxillae and premaxillae are dentate. The astragalus and calcaneum are fused proximally and distally. There are two tarsalia, and osseous or cartilaginous intercalary elements are present between the penultimate and terminal phalanges (except in *Cyclorana*). The tendon of the *m.semitendinosus* inserts ventral to the *m.gracilis* and the *m.adductor magnus* has an accessory head.

Amplexus is axillary. Spawn is normally laid in water. Larvae normally have keratinised beaks and denticles, and a sinistral, lateral or ventro-lateral spiracle. Diploid chromosome complement is 26, except for *L.infracrenata* in which it is 24.

Currently the Hylidae includes five subfamilies. The Hylinae occurs in the Americas, Europe, Asia and North Africa, the Phyllomedusinae, Hemiphractinae and Amphignathodontinae are confined to South America, and the Pelodyadinae is confined to Australia, New Guinea and adjacent islands.

In the Australian region, the endemic subfamily Pelodyadinae comprises the genera *Litoria*, *Nyctimystes* and *Cyclorana*. Pelodyadines are arboreal, ground-dwelling, scansorial (*Litoria* and *Nyctimystes*) or fossorial (*Cyclorana*). The digits of arboreal species have dilated terminal discs and interdigital webbing on the hands, but terrestrial species have undilated fingers and lack webbing.

The subfamily is characterised by possession of a differentiated *m.intermandibularis*, in which a completely separate apical element, supplementary to the principal body of the muscle, lies at the apex of the mandibles on each side of, and adjacent to, the *m.submentalis* (Fig. 1.4A; Tyler 1971a, 1972b).

HISTORY OF DISCOVERY

A hylid, named *Rana caerulea* by White (1790), and now known as *Litoria caerulea*, was the first frog reported from Australia. The specimen was included in the collections of Joseph Banks, and was destroyed when the Hunterian Museum at the Royal College of Surgeons in London was hit by a bomb during World War II (Tyler & Dobson 1973). Understandably, early collections were all sent to Europe and emanated principally from the early settlements at Botany Bay and Port Essington. Type localities commonly are imprecise, for example, 'New Holland' and 'Van Diemen's Land'.

The catalogues of the collections of the British Museum by Günther (1858) and Boulenger (1882), the latter including 25 species, provided the first syntheses of hylids, and have formed the basis for all subsequent contributions. Towards the turn of the century, Fletcher (1890, 1891, 1893, 1894, 1897) reported the results of a collecting campaign by residents of New South Wales, and confirmed identifications by sending specimens to Boulenger.

The first Australian to specialise in the study of hylids was S.J. Copland, who travelled extensively in New South Wales and assembled a large collection. Although encouraged by overseas herpetologists, such as H.W. Parker of the British Museum, Copland worked largely in isolation. His descriptions of species were extremely elaborate, even by modern standards (Copland 1957). Numerous subspecies described by Copland were suppressed by Moore (1961), several of which have proved to be distinct species subsequently.

The first records of *Nyctimystes* in Australia were based on a specimen in the Naturhistorisches Museum in Vienna, and a conspicuously coloured frog from north-eastern Queensland collected by W. Hosmer. Both were referred to new species (Tyler 1964).

In the 1970s, collections in Queensland, principally by C.J. Corben, G.J. Ingram, W. Hosmer and K.R. McDonald revealed numerous new species, whilst M. Davies, A.A. Martin and M.J. Tyler found many more in the Kimberley Division of Western Australia and in Arnhem Land.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Australian hylids range in size from 14 to 140 mm snout to vent length. The dilated pupil of *Cyclorana* and *Litoria* is horizontal, and may also be rhomboid in the latter genus. In *Nyctimystes* the dilated pupil is vertical and a reticulated venation pattern is present on the lower eyelid.

Three morphotypes are recognisable, reflecting the lifestyle of the respective species—arboreal, ground-dwelling and fossorial (Plate 1.4–1.8).

Arboreal species (Plate 1.7) have dilated digital discs with clearly delineated, circum-marginal grooves. The fingers are webbed, at least basally, but often more extensively. Interdigital webbing on the toes is extensive and often reaches the tips of all digits except the fourth. The head is usually broad and gently rounded in dorsal view. The tympanum is large and usually has a well-defined annulus. A well-developed supratympanic fold is present in many arboreal species and hypertrophied parotoid and rostral glands occur in *L. caerulea* and *L. splendida*. The skin is generally smooth.

Ground-dwelling species tend to have an elongate body, long legs and a pointed snout (Plate 1.5). Fingers are slender and lack webbing, and discs rarely extend laterally much beyond the width of the proximal phalanges. The toes are slender also, have small discs, and may be extensively webbed. The tympanum is usually discrete and supratympanic folds are not as well developed as in arboreal species. The skin is smooth, rugose or bears longitudinal folds.

Most fossorial species have a globose body, short limbs and a relatively sharp snout (Plate 1.6). The fingers and toes are similar in shape and webbing to those of the ground-dwelling species. The well-developed, compressed, inner metatarsal tubercle of *Cyclorana* and *L. alboguttata* is used for digging.

Body Wall

Variation in skin structure principally involves the development of hypertrophied, localised areas of granular secreting glands. The nature, nomenclature and position of these glands are reviewed by Tyler (1987).

Briggs (1940) produced a dissection guide (including an account of the muscular system) of *Litoria aurea*. The same species featured in reviews of individual muscle divisions, such as Kesteven's (1944) study of the ontogeny of vertebrate cephalic muscles and Starrett's (1968) work on the mandibular adductor musculature. Horton's (1982) study of tongue musculature was based on numerous species. With the exception of the apical element supplementary to the *m. intermandibularis*, none of these muscular structures is unique to Australian hylids (Tyler 1971a, 1972b).

Skeletal System

Cranial features of note, in some species, include incomplete maxillary arches caused by reduction of the quadratojugal (Fig. 8.1B), and exostosis of the frontoparietals and squamosals in *Cyclorana australis* (see Tyler 1989a), *C. novaehollandiae* (Fig. 8.1C) and to a lesser extent, in *C. platycephala* and *Litoria alboguttata*.

The frontoparietal fontanelle is usually widely exposed except in the *L. aurea* group and *Cyclorana*. The *tectum nasi* of *Cyclorana* and *L. alboguttata* is partly ossified giving an 'arrowhead' expansion to the sphenethmoid. It is absent in other *Litoria* species and in *Nyctimystes*. The prootic is complete in all hylids and the columella is present.

Vomerine teeth are present in all except very small *Litoria* such as *L. microbelos*. Supraorbital flanges of the frontoparietals are present in the *L. caerulea* group (*sensu* Tyler & Davies 1978a, 1979b) and in *L. infrafronata*.

Litoria and *Nyctimystes* have cartilaginous intercalary structures between the clawed terminal and the penultimate phalanges. Ossification of these structures in some *Litoria* species increases the phalangeal formulae to 3,3,4,4 and 3,3,4,5,4 on the fingers and toes respectively. *Cyclorana* is unique within the Hylidae in lacking intercalary elements.

The hylid ilium lacks a dorsal crest and the dorsal protuberance and prominence tend to be developed laterally.

Subsequent to Gilles & Peberdy's (1917a, 1917b) early work, hylid osteology has been important more recently in studies on Australian fossil frogs (Tyler 1974a, 1976c) and taxonomy of extant taxa, especially species of *Litoria* (Davies 1978; Davies, Martin & Watson 1983; Davies & McDonald 1979a,

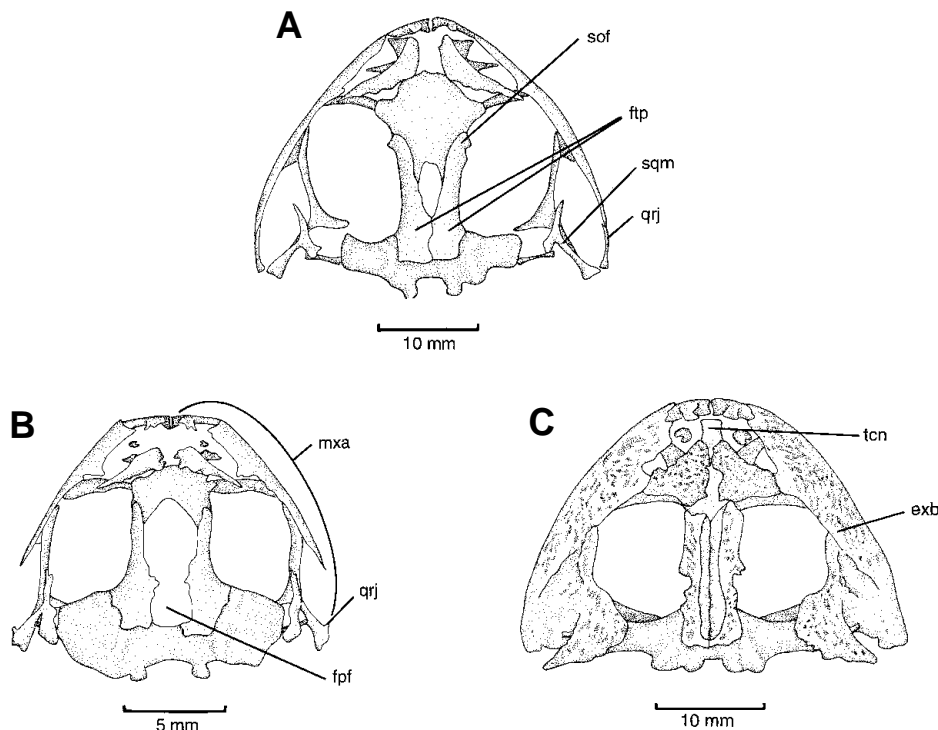


Figure 8.1 Dorsal view of the hylid skull. **A**, *Litoria splendida*; **B**, *Litoria verreauxii*; **C**, *Cyclorana novaehollandiae*. **exb**, exostosed bone; **fpf**, frontoparietal fontanelle; **ftp**, frontoparietal; **mxs**, maxillary arch; **qrj**, quadratojugal; **sof**, supraorbital flange; **sqm**, squamosal; **tcn**, *tectum nasi*.
[M. Davies]

1979b; Davies, McDonald & Adams 1986a; McDonald & Davies 1990; Tyler & Davies 1977, 1978a, 1978b, 1979a, 1979b, 1985; Tyler, Davies & King 1978; Tyler, Davies & Martin 1977, 1978, 1981b, 1982).

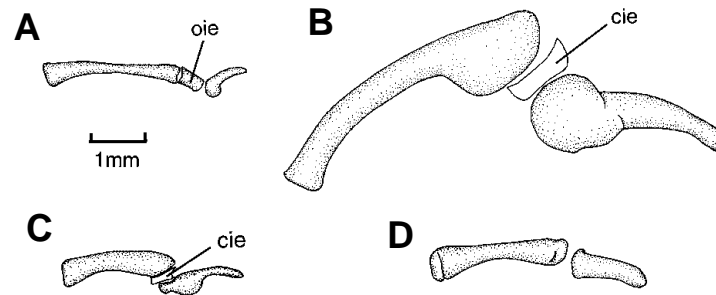


Figure 8.2 Terminal phalanges of hylid frogs. **A**, *Litoria nasuta*; **B**, *L. caerulea*; **C**, *Nyctimystes dayi*; **D**, *Cyclorana australis*. **cie**, cartilaginous intercalary element; **oie**, ossified intercalary element. [M. Davies]

Locomotion

The widely expanded finger and toe discs, and extensive webbing increase adhesion and are locomotory adaptations to arboreal or scansorial life. The structure and function of the discs in the Australian Hylidae were reviewed by Tyler (1989a).

The length of the leap in ground-dwelling hylids is related to the relative length of the hind limbs. Amongst Australian frogs, *Litoria nasuta* and *L. freycineti* show the greatest capacity to jump (Tyler 1982b). Hylids will leap into water to escape predators and tend to be strong, 'frog-kick' type swimmers.

Burrowing is common to *Cyclorana* and *L. alboguttata*. *Cyclorana australis*, *C. longipes*, and *L. alboguttata* are 'backwards sliding' burrowers (Fig. 4.4; Sanders & Davies 1984).

Feeding and Digestive System

Feeding is facilitated by an elongated or broadly cordiform tongue. Larger species (for example, *L. caerulea* and particularly *L. dahlii* and *C. australis*) use the hands to push food items into the buccal cavity. *Litoria dahlii* can capture and swallow food underwater. Beyond the brief report of Briggs (1940) there have been no studies of the digestive system of hylids. Superficial examination has not revealed any difference from the generalised anuran pattern.

Circulatory System

The only Australian hylid in which the circulatory system has been described is *L. aurea* (Briggs 1940). It conforms with the general anuran pattern (Duellman & Trueb 1986).

Respiration

The respiratory system and respiratory movements in *L. aurea* have been described by Briggs (1940). During dormancy, low respiratory quotients and depressed metabolic rates have been recorded in the cocooning fossorial hylids, for example *Cyclorana platycephala* and *C. australis* (van Beurden 1980; Withers unpubl. data; Chapter 4).

Excretion

Interest in the excretory system of hylids has focussed upon structural and behavioural factors that reduce water loss in exposed arboreal species. Following the discovery of uricotelism in an African frog by Loveridge (1970), it was believed that comparable adaptations may also occur in Australian species. However there is no evidence that any Australian frog excretes uric acid. Waterproofing behaviour in *Litoria splendida* consists of frenetic wiping of granular gland secretions across the dorsum.

Sense Organs and Nervous Systems

There are no studies on the sense organs of Australian hylids. The only complete description of the nervous system is that of Briggs (1940) on *L. aurea*. Variation in the mandibular branch of the trigeminal nerve (V) is reported by Tyler (1974b).

Endocrine and Exocrine systems

Most of the research on these systems has been devoted to the kidney and the adrenal glands. Several *Litoria* species were included in a comparative study of the renin-angiotensin system by Taylor, Scroop, Tyler & Davies (1982), whilst the predominance of adrenalin was demonstrated by Robinson & Tyler (1972).

Reproduction and Development

Most males have unilobular submandibular vocal sacs, but some species of *Litoria* and *Nyctimystes* lack vocal sacs. The species lacking vocal cords tend to be riparian and call near broken water (for example, *Litoria nannotis*, *L. rheocola*). Calling sites may be high in trees, in low vegetation to ground level, and adjacent to, overhanging or removed from water.

Hylids spawn in streams, permanent ponds and ephemeral pools, except for *L. longirostris*, which may lay eggs on vegetation overhanging water. Amplexus is axillary. Eggs are laid as mats on the water surface, as small bunches attached to submergent vegetation, or to the undersurface of rocks, or singly (Martin 1967b; Davies & Richards 1990).

Australian hylids exhibit one of two reproductive modes. Small eggs with little yolk reserves, laid in water, hatch at an early stage and develop aquatically. Eggs of species with the first reproductive mode range from 0.8 mm in diameter in *L. microbelos* to 2.9 mm in *L. bicolor* (Tyler *et al.* 1982). Alternatively, eggs, which are laid with a moderate yolk reserve in a lotic environment, hatch and then feed as later stage, motile larvae and develop aquatically (Horton 1984; Davies 1989b; Davies & Richards 1990). Eggs of such species range from 2.25 mm in *L. eucnemis* (Davies 1989b) to 3.4 mm in *L. nannotis* (Liem 1974), and are usually unpigmented (Liem 1974; Davies & Richards 1990). Eggs of *Nyctimystes* are also unpigmented.

Larvae tend to fall into one of three categories illustrated in Figure 8.3. The generalised, central type (*sensu* Orton 1953) is deep bodied with moderately high fins and moderately well-developed tail musculature. This type of larva is exemplified by *L. rubella* (Spencer 1896; Tyler, Crook & Davies 1983a; Tyler 1989a). The deep bodied, high finned, actively swimming nektonic type is exemplified by *L. aurea* and *L. ewingii* (Martin 1965), *L. rothii* (Tyler *et al.* 1983a), *L. peronii* (Martin, Watson, Gartside & Loftus-Hills 1979), and *L. infrafrenata*, whilst those of the mountain stream type have flattened bodies, narrow tail fins, a well-developed tail musculature and a large suction mouth

with numerous labial papillae, for example, *L. lesueuri* (Martin 1967a); *L. eucnemis* (Davies 1989b), *Nyctimystes dayi* (Davies & Richards 1990) and *L. nannotis*.

The single spiracle drains both branchial chambers and is lateral or ventro-lateral. In *L. infrafrenata* it is ventro-sinistral. The anus opens dextrally except in some lotic species in which it opens medially. The anal opening and developing hindlimbs are enclosed in a membranous sac in *N. dayi* and *L. nannotis* (Davies & Richards 1990). The papillary border is complete in some species, but interrupted anteriorly in others. *Litoria subglandulosa* lacks labial teeth and a horny beak (Tyler & Anstis 1975). The majority of Australian hylid larvae have a tooth row formula of

$\frac{1}{1} \frac{1}{2} \frac{1}{1}$ and $\frac{2}{3} \frac{2}{3} \frac{1}{2} \frac{1}{2} \frac{1}{2} \frac{1}{2}$ are typical modifications (Tyler 1989a).

Larval life span varies considerably. Most species in the wet/dry tropics complete their larval life rapidly, and *Litoria meiriana* and *L. nasuta* take about 30 days at 30°C (Tyler *et al.* 1983a). Other species overwinter in streams at stage 25 of Gosner (1960), for example, *L. eucnemis* (Trenerry 1988). Temperate species may complete larval development over a longer period, for example, 6–7 months in *L. ewingii* (Martin & Watson 1971; Martin & Littlejohn 1982).

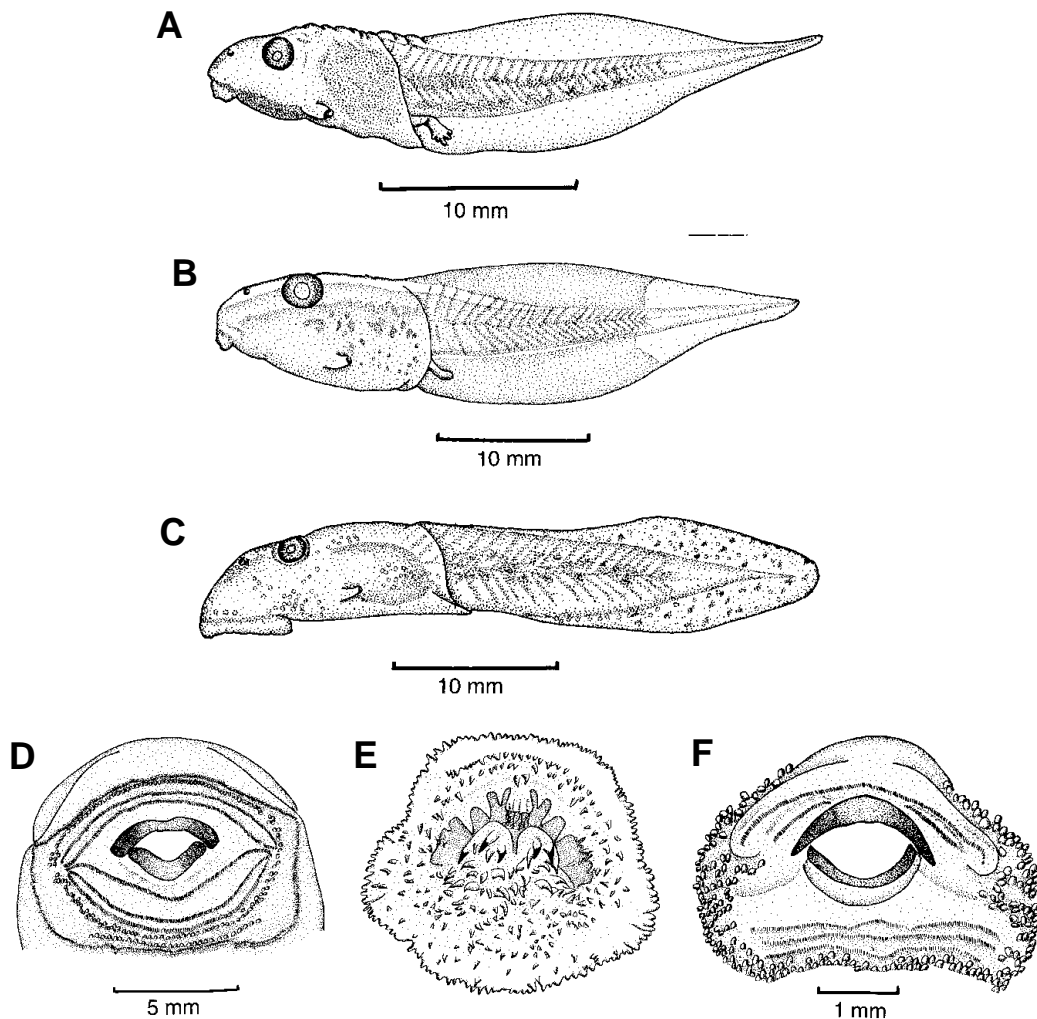


Figure 8.3 Lateral views (A–C) and oral discs (D–F) of hylid tadpoles. Lateral view of A, *Litoria rubella*; B, *L. infrafrenata*; C, *L. nannotis*. Oral disc of D, *L. nannotis*; E, *L. subglandulosa*; F, *L. infrafrenata*. (E, After Tyler & Anstis 1975) [M. Davies]

NATURAL HISTORY

Life History and Reproductive Strategy

In contrast to the diverse reproductive modes of Neotropical hylids and of myobatrachids, Australian hylids are remarkably conservative. With the possible exception of *Litoria longirostris*, all species deposit their eggs in water. As indicated above, fundamental adaptations are to lotic or lentic egg deposition sites. Arboreal spawning is unknown.

Longevity is associated with body size, for the largest hylids such as *L. caerulea* have been known to live for 23 years in captivity.

Ecology

Australian hylids are opportunistic predators on a wide variety of arthropods, primarily insects. Available data suggest dietary habits are non-specific, and that seasonal changes in the proportions of different prey groups in the diet are related to changes in abundance of these groups (Fig. 8.4; Tyler 1989a).

Frogs are constrained by their need to obtain moisture from the environment. Despite this limitation some frogs are able to live in seasonally arid areas and avoid desiccation by burrowing. *Cyclorana* species and *L. alboguttata* burrow and form cocoons to avoid desiccation (see Chapter 4).

Canopy-dwelling species such as *L. gracilentata*, *L. chloris* and *L. xanthomera* avoid desiccation by postural changes that protect the vulnerable ventral surfaces (see Tyler 1989a) whilst 'waterproofing' of the dorsal skin prevents water loss (Withers, Hillman & Drewes 1984). These species descend to the ground to breed during heavy rains.

Humphries (1979, 1981) studied a breeding guild of 11 sympatric species, including *L. lesueuri*, *L. aurea*, *L. flavipunctata*(?), *L. verreauxii* and *L. peronii*. He found that species respond predominantly to weather conditions to initiate breeding, rather than to the presence or absence of other frogs. There was intense intraspecific competition for calling sites and non-calling males were tolerated only if they maintained their silence.

The ability of frogs to disperse and/or migrate is dependent upon available moisture and suitable habitat for shelter. There is little doubt that some areas are constantly recolonised by frogs transported by flood waters and that many of these colonisations fail to become established (for example, in north-eastern

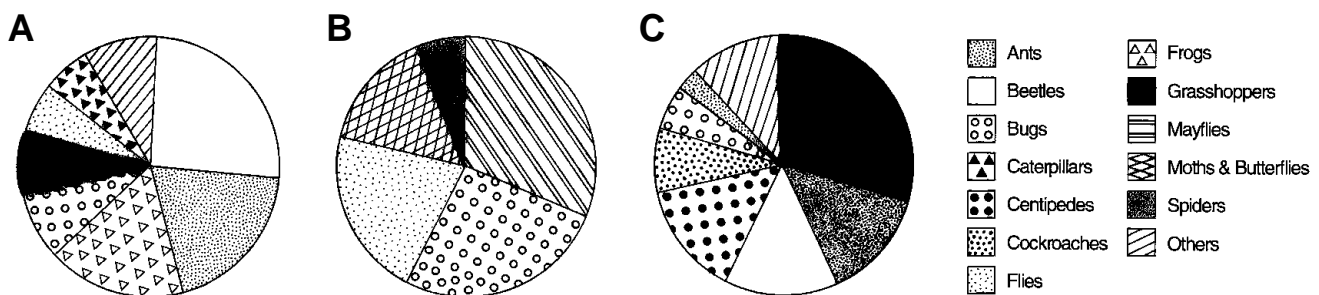


Figure 8.4 Frequency of occurrence of prey categories in the diet of *Litoria dahlia* during three periods over five months at Jabiru, Northern Territory. **A**, mid wet season; **B**, late wet season; **C**, late dry season. (From Tyler 1989a) [D. Wah]

South Australia (Tyler 1990). Anecdotal evidence of amazing homing ability in *L. caerulea* is common, but little is known of the dispersal abilities of Australian hylids.

The flies *Batrachomya mertensi* and *B. nigratarsus* are recorded as parasites of *Litoria caerulea* and *L. phyllochroa* respectively (Zumpt 1965), but knowledge of internal parasites is restricted to a few species or groups.

The acanthocephalan *Pseudacanthocephalus perrhensis* has been identified in *L. moorei* (Edmonds 1989). The nematodes, *Parathelandros mastigurus* and *P. maini*, have been found in the rectum of some Australian hylids (Inglis 1968), and Johnston & Simpson (1942) recorded *Spiroura hylae* and *Rhabdias hylae* in *L. aurea*. Trypanosomes have been found in *Nyctimystes dayi* and in 11 species of *Litoria* (Bancroft 1891; Cleland & Johnston 1910; Delvinquier & Freeland 1989).

Other blood parasites, *Lankasterella hylae* and *Haemogregarina* sp. have been found only in *L. caerulea* of 33 hylid species sampled. This suggests host specificity (Cleland & Johnston 1910; Delvinquier 1989). Marks (1960) suggested that mosquitoes transmit such parasites.

Opalinids of the genus *Protoopalina* have been recorded in two *Cyclorana* species and 32 *Litoria* species (Delvinquier 1987), and the gall bladder protozoan *Mixidium immersum* has been recorded in 12 species of *Litoria* (Delvinquier 1986).

Behaviour

Breeding behaviour is complex. Male frogs call to attract females. Breeding congresses usually comprise several related and/or unrelated species. Such congresses are acoustically separated by the nature and structure of the individual calls. Conspecifics can hear only the calls of their own kind and of species with calls of a similar frequency because the ear is tuned to a limited frequency band. Analyses and detailed descriptions of calls are available for a number of Australian hylids (Tyler 1989a; Ingram & Corben 1990).

As well as acoustic separation, spatial separation in terms of calling sites occurs. Depending on the composition of a breeding chorus, differing calling sites are occupied. *Litoria bicolor* usually calls on grasses and vegetation overhanging water. If *L. microbelos* is calling at the same site, it will call from the same vegetation, but at a lower elevation. However, if *L. bicolor* is not present, *L. microbelos* will call from the higher sites (Tyler *et al.* 1983a; Tyler, Davies & Watson 1986). *Litoria verreauxii* calls from sites on the ground or in trees close by, *L. jervisiensis* calls from emergent reeds and *L. littlejohni* is less specific, calling from low bushes, under ferns and in shallow pools (White, Whitford & Watson 1980). Other members of the *L. ewingii* complex utilise a variety of aquatic habitats for breeding including temporary or relatively permanent ponds, slow flowing streams or backwaters. The actual calling sites can vary according to the season. For example, *L. paraewingii* calls from banks or low vegetation in late spring and from water in autumn, winter and early spring (Watson, Loftus-Hills & Littlejohn 1971).

Many hylids are seasonal breeders, particularly those in the temperate regions of Australia, but others are explosive breeders, with breeding coinciding with heavy rainfall, as described in Chapter 5.

Egg laying has been described for few Australian hylids (see Watson *et al.* 1971). The male cups his feet around the batches of eggs as they are extruded, holds them against his vent, fertilises them, and then pushes them to the feet of the female who wraps them around twigs with her feet as she climbs around the vegetation.

Schooling behaviour has been observed in a number of tadpoles, in particular *L. dahlia* and *C. australis* (Tyler 1989a).

Basking has been recorded in adult frogs, particularly in *Cyclorana* spp. and members of the *L. aurea* species group (Tyler 1989a). The value of this behaviour in *C. australis* is unknown given the high ambient temperatures recorded during basking and the nocturnal feeding regime.

Tyler (1989a) reported body temperatures of 33.1° and 33.4°C at midday in *L. rothii* compared to an ambient temperature of about 40° to 45°C. Behavioural thermoregulation was dismissed as an explanation for the temperature differential, implying a more fundamental control of temperature regulation.

Economic Significance

The *L. aurea* species group was used for laboratory dissection until recently, and as a test organism for human pregnancy testing for a brief period in the 1940s.

Extensive screening of hylid skin secretions led to the discovery of caerulein in *L. caerulea* (Roseghini, Erspamer, & Endean 1976), followed by caerins in *L. splendida*. Caerulein now has a range of clinical applications. Given the modern capacity to isolate and sequence skin polypeptides from minute quantities of skin secretions, the future economic significance of hylids is likely to be as a source of structural novelties that can then be synthesised.

The economic significance of frogs as natural control organisms of pests of crops such as cotton and rice is impossible to assess. That role will be diminishing with current declines of populations.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Hylids occur throughout the continent except on the Nullarbor Plain and a portion of southern Western Australia. *Litoria* is the most widespread genus. *Cyclorana* does not occur in the south whilst *Nyctimystes* is confined to the Cape York Peninsula of Queensland.

Fletcher (1890, 1891, 1894, 1897) was the first contributor seeking to detect patterns of distribution, noting regional components within New South Wales. Moore (1961) recognised an east coast element, marked speciation in south-eastern Australia, much less in south-western Australia and a 'north-east Crescent' of species continuous from the Kimberley Division of Western Australia, across the Northern Territory and down the east coast. This broad categorisation remains supportable, except for the North East Crescent which represents the distribution of *L. nasuta*; all of its other component species have been shown to be compounded sister species.

Affinities with other Groups

Controversy about the relationships of Australian hylids with species on other continents was triggered by the action of Tyler (1971a), who resurrected *Litoria* for species formerly referred to the cosmopolitan *Hyla*. Tyler further demonstrated that *Litoria* and *Nyctimystes* comprise a monophyletic group, and argued for their recognition as a subfamily, the Pelodyadinae.

Savage (1973) interpreted these data as refuting the confamilial rather than the congeneric status of the Australopapuan element and erected the family Pelodyadidae to accommodate them. This view was followed by Laurent (1979), Dubois (1983, 1984), and reiterated by Savage (1986). Duellman (1975), who

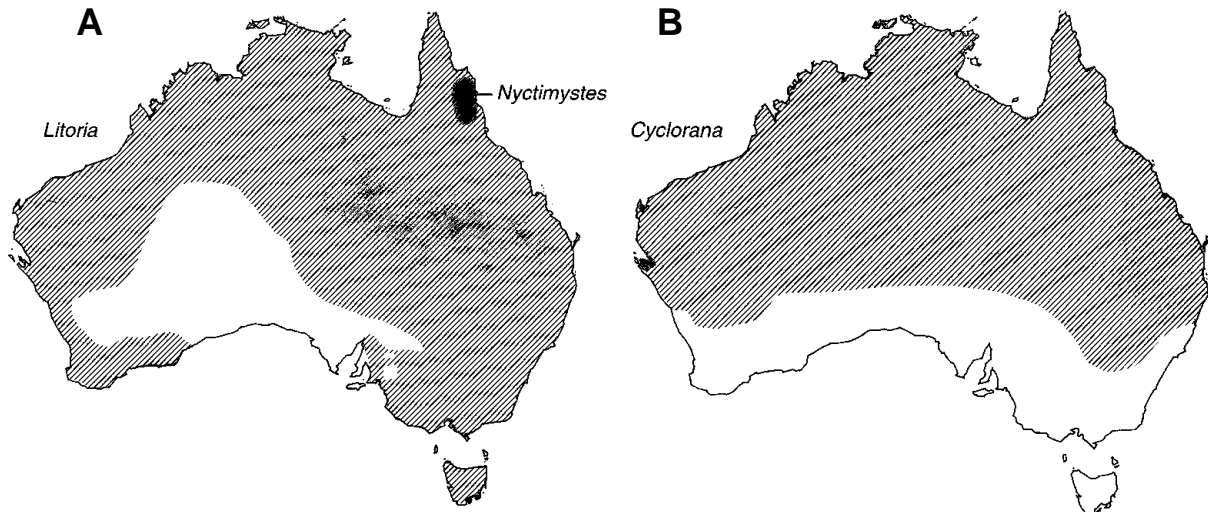


Figure 8.5 Distribution of hylid genera. **A**, *Litoria* and *Nyctimystes*; **B**, *Cyclorana*. [K. Maurice-Jones]

did not feel that available evidence warranted recognition of the Pelodyadidae as distinct from the Hylidae, and Tyler (1979a) argued strongly against such an interpretation of his data. Dubois (1985) reversed his earlier stance and supported subfamilial status within the Hylidae for the Australopapuan element.

Bagnara & Ferris (1975) noted that Australian species share with Neotropical phyllomedusine hylids the dermal pigment rhodomelanin, and suggested a close affinity between these groups. However, Tyler & Davies (1978b) found no osteological, myological or other similarities, and attributed the apparent synapomorphy to convergence.

Hutchinson & Maxson (1987a) provided evidence, from microcomplement fixation studies, that the Australopapuan hylids are monophyletic with respect to *Hyla* as an outgroup, and are properly associated with other hylids rather than with leptodactyloids (supporting the proposal of Tyler 1979a).

Affinities within the Taxon

Phylogenetic analyses within the Australian Hylidae have never considered more than a proportion of the component species of the recognised genera *Litoria*, *Nyctimystes* and *Cyclorana*.

The relationships of *Cyclorana* are probably the best resolved. Parker (1940) included it in the Leptodactylidae (now the Myobatrachidae), principally because of its fossorial adaptations. Three species originally referred to *Cyclorana* were transferred to *Litoria* because they possess intercalary elements: *L. inermis* (Straughan 1969), *L. alboguttata* (Tyler 1973) and *L. dahlia* (Tyler, Davies & King 1978).

Tyler (1978) transferred *Cyclorana* to the Hylidae on the basis of a number of characters shared with other hylids: the nature of the superficial mandibular musculature (Tyler 1972b); larval characteristics (Watson & Martin 1973); and the nature of the adrenal catecholamines (Robinson & Tyler 1972). Tyler (1979a) argued for a close relationship with the *L. aurea* species group (*sensu* Tyler & Davies 1978a), a view supported by the karyotypic data of King, Tyler, Davies & King (1979) and microcomplement fixation data (Hutchinson & Maxson 1986, 1987a; Maxson, Ondrula & Tyler 1985; Maxson, Tyler & Maxson 1982).

There is disagreement about relationships within the monophyletic group comprising *Cyclorana* and the *L. aurea* species group. The karyological data of King *et al.* (1979) and King (1980) suggested a number of lineages which are inconsistent with those recognised by Maxson *et al.* (1982, 1985) on the basis of microcomplement fixation techniques. These latter studies consider *L. alboguttata* to be more closely related to *C. australis* and *C. novaehollandiae* than to other members of the *L. aurea* group.

The position of *L. alboguttata* with respect to the *L. aurea* group and *Cyclorana* is problematical. *L. alboguttata* shares with all other *Litoria* the presence of intercalary elements (Tyler 1973; Tyler & Davies 1978a), a feature held to be a synapomorphy within the Hylidae. However, with the inclusion of *Cyclorana* in the Hylidae, this character is no longer shared by all hylid genera, although it is a feature shared by all *Litoria* and *Nyctimystes*.

Litoria alboguttata shares with *Cyclorana* an autapomorphy of an extension of ossification of the sphenethmoid to incorporate a portion of the *tectum nasi* producing an 'arrowhead' extension of the sphenethmoid (Davies unpub. data). This character supports monophyly of *L. alboguttata* and *Cyclorana*. Whether *L. alboguttata* should be returned to *Cyclorana* or whether a separate genus should be erected to accommodate it may be resolved when all data are subjected to a cladistic analysis, and the trees compared with those derived from distance matrices of microcomplement fixation data (Tyler, Davies, Donnellan & Watson in prep.).

Within *Cyclorana*, at least three distinct lineages are apparent, namely the *C. brevipes* lineage comprising *C. brevipes*, *C. cultripes*, *C. longipes*, *C. verrucosus*, *C. maculosus*, *C. vagita*, *C. manya* and possibly *C. cryptotis*; the *C. australis* lineage comprising *C. australis*, and *C. novaehollandiae* and the monotypic *C. platycephala* lineage (King *et al.* 1979; King 1980; Maxson *et al.* 1982, 1985; Davies & Tyler unpub. data).

Tyler & Davies (1978a) recognised 37 species groups within *Litoria* phylogeny, some of which may merit elevation to generic status; their species groups could be placed into three broad categories. These are: elongate, terrestrial species, with unwebbed fingers, long hind limbs and small pigmented ova; arboreal species with conspicuous finger discs, at least one third of the hands webbed, hind limbs which are rarely long and with small pigmented ova; scansorial and arboreal species with consistently well-developed finger discs and slight webbing between the fingers, hind limbs of varied length and large, unpigmented ova. The last group comprises the *L. nannotis* group and montane *Litoria* from New Guinea. Tyler (1982b) further separated the torrent-adapted Australian species from the montane Papuan *Litoria*, indicating that the Australian species acquired torrent-adapted characteristics independently of the New Guinea species.

Apart from a group designated the *L. freycineti* complex (Hutchinson & Maxson 1986), a microcomplement fixation study of 38 species of *Litoria* by Hutchinson & Maxson (1987a) accorded well with the morphologically determined species groups of Tyler & Davies (1978a). These groups were also supported by chromosome data of King (1981). However, the phylogeny derived by Hutchinson & Maxson (1987a) did not support the broad categories of Tyler & Davies (1978a). Instead, they recognised eight lineages within *Litoria*, which cut across the groupings of both Tyler & Davies (1978a) and King (1981). In particular, they recognised *L. infrafronata* as being anomalous, an observation supported by its unique karyotype within the Pelodyadinae of $2n = 24$ (Menzies & Tippet 1976).

Resolution of phylogenetic relationships within *Litoria* awaits further data analyses. It is highly likely that the number of pelodyadine genera will be increased substantially beyond the current total of three, given recognition of subgroups within *Litoria*.

Tyler & Davies (1979a) proposed that *Nyctimystes* is most closely related to montane *Litoria* and that the two lineages were derived from a *Litoria eucnemis*-like stock. Preliminary studies by Hutchinson & Maxson (1987a) suggest that *Nyctimystes* and montane *Litoria* are closely related to their *L. freycineti* assemblage within *Litoria*. No other phylogenetic studies of *Nyctimystes* have been reported.

Fossil Record

The first frog fossil reported from Australia was the hylid *Australobatrachus ilius* (Tyler 1974a). Subsequently, seven Caenozoic species of *Litoria* have been reported (Tyler 1989a). Numerous Tertiary *Litoria* have been located from freshwater limestone deposits at Riversleigh Station, Queensland, but only one species, *L. magna*, has been described (Tyler 1991e). The first fossils of *Cyclorana* have been reported recently from north-west Queensland (Tyler, Godhelp & Archer in press), but no fossils of *Nyctimystes* are known.