FAUNA *of* AUSTRALIA

1. GENERAL DESCRIPTION AND DEFINITION OF THE CLASS AMPHIBIA

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The word Amphibia is derived from *amphi* (double) and *bios* (life), implying a double life part of which is spent in water, and part on land. Amphibians vary in the number of pairs of limbs (two, one or none), but all have a skull that articulates with the vertebral column via two rounded condyles—reptiles have one.

The skin of amphibians is highly complex and embodies numerous types of glands which produce a diverse range of secretions

CLASSIFICATION OF THE AMPHIBIA

There has been considerable confusion over the classification, and therefore the definition, of the class Amphibia. The areas of contention centre upon the number of subclasses that should be recognised, and the distribution of orders between them. For example, Swinton (1973) associated the three extant orders within two separate subclasses—the Aspidospondyli and the Lepospondyli. Within his scheme the fossil labyrinthodonts were considered an aspidospondyl superorder. Currently, the classification of Romer (1966) is more popular. He recognised the subclasses Labyrinthodontia, Lepospondyli and Lissamphibia. Following Gadow (1901), the extant orders are referred to, and constitute, the Lissamphibia.

Much of the problem of determining the relationships of extant orders to those known only from the fossil record, is a reflection of the magnitude of differences between the Lissamphibia and the other subclasses. Carroll (1977) notes, 'One of the most profound gaps in all of vertebrate phylogeny separates the Palaeozoic and Triassic labyrinthodonts and lepospondyls from the modern amphibian orders'. Effectively the Lissamphibia is isolated structurally.

GENERAL DESCRIPTION AND DEFINITION OF THE LISSAMPHIBIA

The most well-known synapomorphic feature uniting the members of the Lissamphibia is the possession of pedicellate teeth (Fig. 1.1). The characteristic feature of this kind of tooth is a crown, that is usually bicuspid, seated upon a cylindrical basal pedicel, and separated from it by a layer of uncalcified dentine

A B

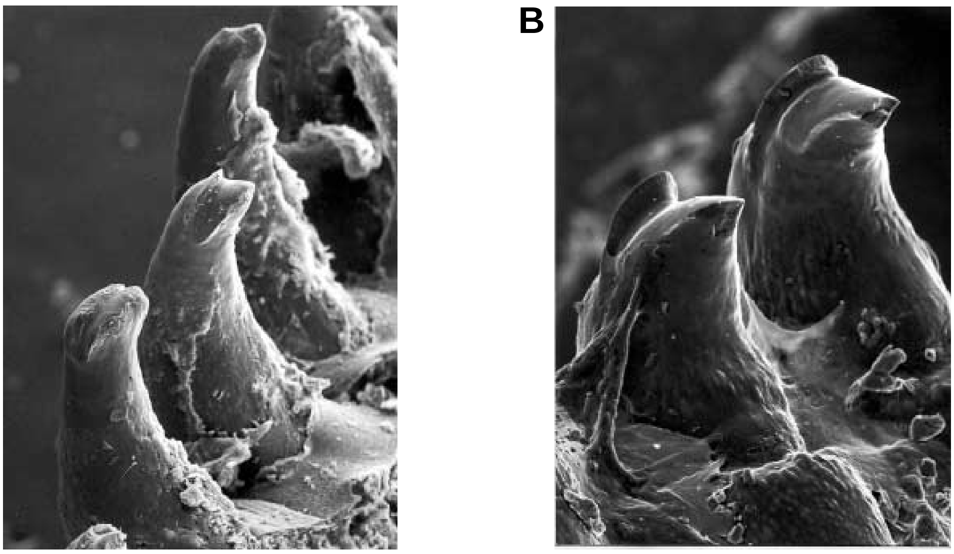

Figure 1.1 Scanning electron micrograph of maxillary teeth . **A**, *Cyclorana australis*; **B**, *Rheobatrachus vitellinus*. (From Tyler 1989a) [photo ©M.J. Tyler]

or a ring of fibrous connective tissue. Similar teeth have been found only in two small (assumed juvenile) labyrinthodonts, *Doloserperton annectens* and *Tersomius texensis* (Bolt 1969, 1977). Because of the difference in form from the hollow, conical teeth with labyrinthine dentine that characterise adult labyrinthodonts, the apparent ontogenetic transition has led to the suggestion that the lissamphibian form is paedomorphic, and that the Lissamphibia is derived from a dissorophoid labyrinthodont. Duellman & Trueb (1986) list 13 other features that either characterise lissamphibians, or are considered to show distinct trends among them. These features include the possession of a columella and an operculum to transmit sound to the inner ear, the structure and diversity of skin glands, and the various specialisations that are associated with cutaneous respiration.

Duellman & Trueb (1986) list the significant papers that address the issue of lissamphibian origins. Although they concede that the monophyletic origin of the extant Amphibia 'cannot be defended unequivocally', they clearly favour such an hypothesis.

Concepts of a diphyletic origin requires derivation of the Amphibia from separate ancestral fish stocks. Jarvik (1963) and other works argue that caudates are derived from the porolepiforme fish stock, and anurans from osteolepiform fish. He bases his hypothesis principally upon assumed homologies amongst cranial characters, and on a comparison of features of the Intermandibular Division comprising the mandibles, intermandibular musculature and hyoid components including the tongue. Amongst the more fanciful inferred homologies is that of the ventral, dermal, and bony plates of osteolepiform fishes with the supplementary elements of the *m. intermandibularis* of anurans. To deduce elaborate muscle derivation from retrogression of bone is wholly unsupportable. Jarvik does not mention the issue of the origin of the Gymnophiona.

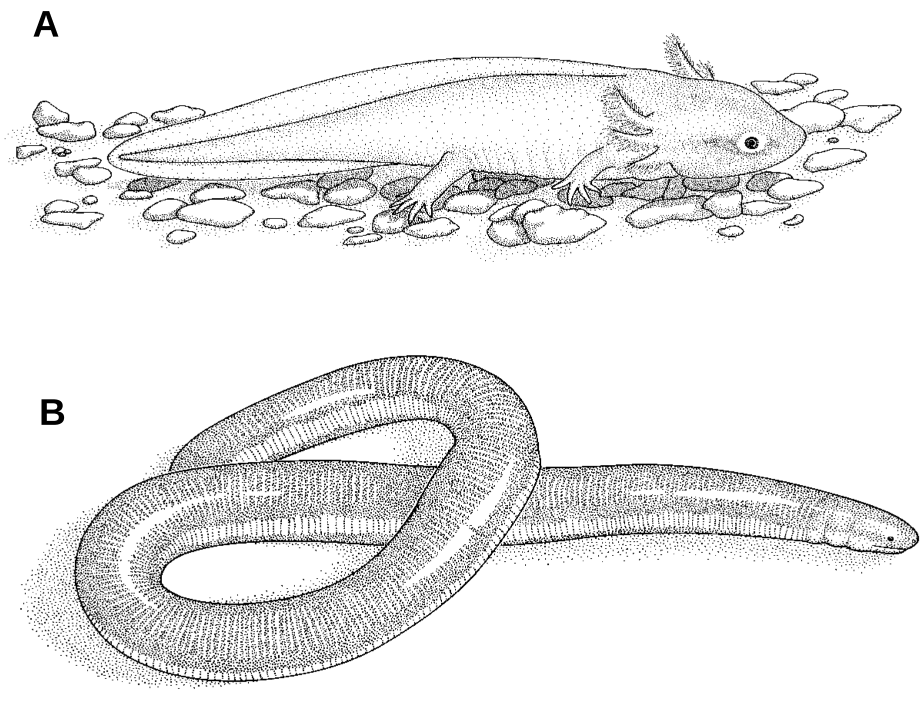

Figure 1.2 Orders Caudata and Gymnophiona. **A**, the Mexican Axolotl, *Ambystoma mexicanum*; **B**, the caecilian, *Ichthyophis kohtaoensis*. (After Nussbaum 1992) [C. Eadie]

CLASSIFICATION OF THE LISSAMPHIBIA

There is almost universal acceptance that the Lissamphibia (modern Amphibia) represent three orders: the Anura (frogs and toads), Caudata or Urodela (newts and salamanders) and the Gymnophiona or Apoda (caecilians). The only deviation from the above scheme is that of Goin & Goin (1962) who placed the caudate family Sirenidae in a separate order (Trachystomata) on the basis of the absence of hindlimbs and pelvic girdle. The Anura is the only order endemic to Australia.

Caudata

Adult caudates have long tails and, except for the sirens (family Sirenidae) of the southern United States of America, two pairs of limbs. Sirens lack hindlimbs and a pelvic girdle.

The smallest caudates are *Thorius* species of Mexico which are adult at as little as 27 mm from the tip of the snout to the end of the tail; the largest is *Andrias davidianus* of Japan which can grow to a total length of slightly more than 1.5 m. Members of the latter genus are the longest living amphibians, attaining ages of up to 55 years.

Caudates have elaborate courtship patterns and external or internal fertilisation. The majority lay eggs that hatch into aquatic larvae and commonly have branched external gills, but a number of species exhibit direct development within the egg membranes. Metamorphosis is incomplete in several species so that sexual maturity is attained in a larval form.

At least three species have been imported into Australia. The Mexican axolotl, *Ambystoma mexicanum*, has been released in Tasmania. Its impact upon the native fauna has yet to be assessed.

Gymnophiona

Commonly known as caecilians, these fossorial animals are limbless and have cylindrical bodies and a short, pointed tail. The largest known, *Caecilia thompsoni*, may reach a total length of 1.5 m. The eyes of caecilians are exceptionally small, often covered with bone and, presumably, of limited visual sensitivity. The body wall is divided externally into a series of segments and there are scales in some species. Between the eye and the nostril is a sensory tentacle. Caecilians have internal fertilisation. Development is either direct, within the egg membranes, with the young feeding upon yolk, or there are free living larvae. Parental care in the form of females remaining with their eggs has been reported in the family Ichthyophiidae of India and Southeast Asia (Nussbaum 1992).

DEFINITION AND GENERAL DESCRIPTION OF THE ANURA

There are two approaches to the definition of the Anura resulting from the lack of a consensus on the status of the Early Triassic tailed-amphibian *Triadobatrachus massinoti* of Madagascar (Fig. 1.3). Duellman & Trueb (1986) consider *T. massinoti* to be ancestral to the Anura, or at least exhibiting features shared by pre-anurans rather than anurans. The body is far more elongate than extant anurans and the ischium is much larger and unlike any anuran, but bears a striking resemblance to the form of the labyrinthodont. They place the fossil in a separate order, the Proanura. Together, the Proanura and the Anura constitute the superorder Salientia.

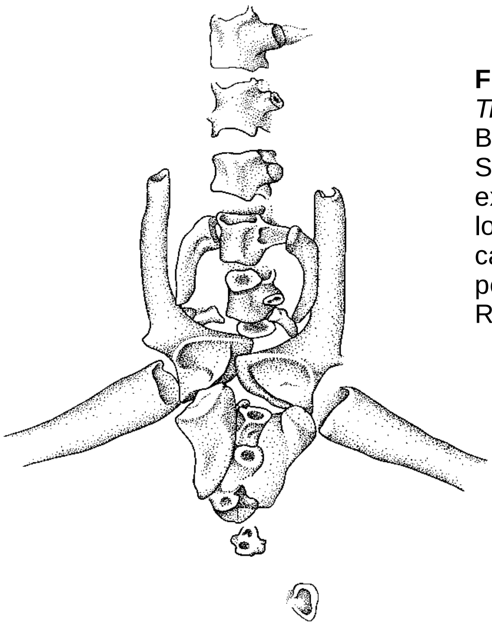

Figure 1.3 The fossil of *Triadobatrachus massinoti* from Betsieka in northern Madagascar. Specimen is complete but for the extreme anterior end of the skull, the loss of an unknown number of distal caudal vertebrae, and the distal portions of the hands and feet. (After Rage & Rocek 1989) [D. Wahl]

By contrast, Rage & Rocek (1986, 1989) consider *T. massinoti* to be an anuran, based on the remarkable similarity to the anuran skull, especially the number, shape and disposition of individual bones. They placed the taxon in the Proanura, a suborder of the Anura. The inclusion of *T. massinoti* with the anurans necessitates a broader definition of the Anura.

The view of Duellman & Trueb (1986) is followed here because it at least permits the Anura to be defined in a more rigourous manner.

The Anura is characterised by the presence in the adult of two pairs of limbs (hindlimbs elongate) and the lack of a tail. The hind feet are extended by elongate proximal tarsal elements and the tibiale and fibulare. There are usually five toes and four fingers; further reduction of phalanges is usually associated with specialised fossorial activity. There are five to nine presacral vertebrae. The ribs are free or fused with one to six of the proximal vertebrae. Post-sacral vertebrae are fused into a largely cylindrical urostyle (coccyx) bearing or lacking processes on the lateral surface. The oto-occipital region consists of prootics and exoccipitals.

The extent of skeletal ossification is highly variable. At the one extreme there is exostosis and dermal ossification and at the other incomplete ossification of adjacent bones, so leaving vast areas of cartilage and the persistence of juvenile (paedomorphic) characteristics.

Anurans are unique in the functional and structural specialisations of the skin and of the myointegumental contact. The skin is complex and highly glandular dorsally, containing mucous and granular glands, and lipid glands in some (Duellman & Trueb 1986). In numerous species the granular glands are aggregated locally to produce elevated, hypertrophied glands such as the parotoid, submental, inguinal and mandibular glands (Tyler 1987a).

The nature of the secretion of the granular glands of anurans includes a vast variety of novel polypeptides and alkaloids, with functions as diverse as toxins and antibiotics (Bevins & Zasloff 1990). Species having toxic secretions commonly have aposematic colouration whereas the majority of species have a variety of chromatophores and fundamentally cryptic colouration.

The skin of anurans is loose and, other than on the head, is not in direct contact with the underlying musculature. Instead, contact is maintained via a series of very thin, transparent septa (Tyler 1971b). The sites of attachment of the septa are consistent within families. The space between the muscle wall of the body and the limbs is occupied by a series of subcutaneous lymphatic sacs which are most highly developed in the aquatic genera *Xenopus* and *Rheobatrachus* (Carter 1979).

Vocal communication is well developed in males and inflatable vocal sacs, formed from the floor or sides of the buccal cavity, serve as resonance chambers. Behaviour patterns are often elaborate with distinct evidence of territoriality and aggression towards competitors.

Most species lay their eggs in water and have a free-living tadpole. Larval development ranges from less than two weeks to 18 months. A significant number of species lay large eggs in sheltered sites on land and the larval period is spent entirely within the egg membranes. The wide variety of reproductive modes involve elaborate investment of parental care, including nest construction and egg and larval transport. There are examples of viviparity and ovoviviparity.

CLASSIFICATION OF THE ANURA

The most recent assessment of the Anura (December 1992) recognises 25 families, 334 genera and 3967 species (Duellman 1993). There has been an increase of 484 species recognised (14%) since the last list was produced by Frost (1985).

The Australian anuran fauna comprises representatives of five of the families—the Bufonidae, Hylidae, Microhylidae, Myobatrachidae (Leptodactylidae) and Ranidae. The Ranidae and introduced Bufonidae are each represented by a single species. The Hylidae, Microhylidae and Myobatrachidae include 3, 2 and 17 genera, respectively.

There is controversy about whether the dominant component of the Australian fauna merits recognition at a family level. Following the contribution of Savage (1973), some Australian workers adopted the names Pelodryadidae for the frogs formerly recognised as members of the Hylidae and Myobatrachidae for those previously considered to represent the Leptodactylidae. Tyler (1979a) challenged these concepts, arguing that his contribution that formed the substance of Savage's work on the Pelodryadidae had been misinterpreted, as is discussed further in Chapters 6 and 8. Although the Myobatrachidae has been generally accepted, and is adopted in this volume, there is no single anatomical character or other evidence to distinguish this group from the leptodactylids, and the concerns expressed by Tyler (1979a) have not been refuted. It would appear that the Myobatrachidae is a geographic but not the systematic unit. The issue is discussed in Chapter 7.

Three subfamilies of myobatrachids are recognised in the key (Myobatrachinae, Limnodynastinae and Rheobatrachinae). However, *Rheobatrachus* the only genus of the Rheobatrachinae, is sometimes included within the Limnodynastinae (see Chapter 7). Tyler (1991) listed a total of 197 species of anurans in Australia, to which may be added two species of *Geocrinia* and one species each in the genera *Neobatrachus*, *Uperoleia* and *Litoria* (Davies, Watson, McDonald, Trenerry & Werren 1993; Ingram & Corben 1990; Roberts, Wardell-Johnson & Barendse 1991), raising this total to 202 species.

KEY TO THE ADULTS OF AUSTRALIAN ANURANS

The inherent morphological conservatism of adult anurans creates considerable problems when attempting to produce useful dichotomous keys. Whereas the ideal key solely employs external features, this goal is unachievable to distinguish anuran families and genera. It would therefore seem desirable to employ internal characters that can be revealed with minimum dissection. This has been our major goal in attempting to distinguish the families and genera. The key to the Microhylidae follows Burton (1984).

Familial and Subfamilial Features

The condition of *m. intermandibularis* features in family and subfamily keys. This throat muscle is the largest in the submandibular (throat) region. It can be revealed by incising the skin from the sternum to the tip of the lower jaw, and from the sternum to a position posterior to the angle of the jaws. When the muscles beneath this area are wet it is often difficult to detect the direction of the bundles of fibres. It is therefore best to mop up excess moisture with a tissue. If the direction still cannot be detected, it will be necessary to apply two or three drops of the iodine/potassium iodide stain described by Bock & Shear (1972), which stains the perimysium orange.

The undersurface of the skin is connected to the underlying pectoral muscles by *m. cutaneous pectoris*. Its presence can be detected by a 1 cm midline incision along the sternum, accompanied by a transverse 1 cm incision to one side. If the skin flap created is then lifted gently, the longitudinal fibres of *m. cutaneous pectoris* will be seen, contrasting with the transverse orientation of the pectoral musculature.

Generic Features

In morphological terms, several myobatrachid genera are distinguished on very flimsy grounds, and their distinctiveness supported by biological data. *Geocrinia* is thus distinguished principally by the morphological feature of fringing on the toes and the biological character of terrestrial oviposition. Conversely, though *Kyarranus* is subsumed into *Philoria* in most texts, distinctive features of the ilium warrant its recognition (Tyler 1991a). *Paracrinia* is considered a synonym of *Crinia*.

Key to the families of the order Anura

1(a) The *m. intermandibularis* differentiated by the presence of supplementary elements 2

(b) The *m. intermandibularis* muscle not differentiated, supplementary elements lacking 3

2(a) The *m. intermandibularis* with supplementary apical element; transverse prepharyngeal folds absent . . . . Hylidae

(b) The *m. intermandibularis* with lateral element; transverse prepharyngeal folds present . . . . Microhylidae

3(a) Pectoral girdle arciferal; *m. cutaneous pectoris* absent 4

(b) Pectoral girdle firmisternal; *m. cutaneous pectoris* present . . . . Ranidae

4(a) Elevated, bony, post-ocular bar present; Bidder's organ present . Bufonidae

(b) Elevated, bony, post-ocular bar absent; Bidder's organ absent . . . . Myobatrachidae

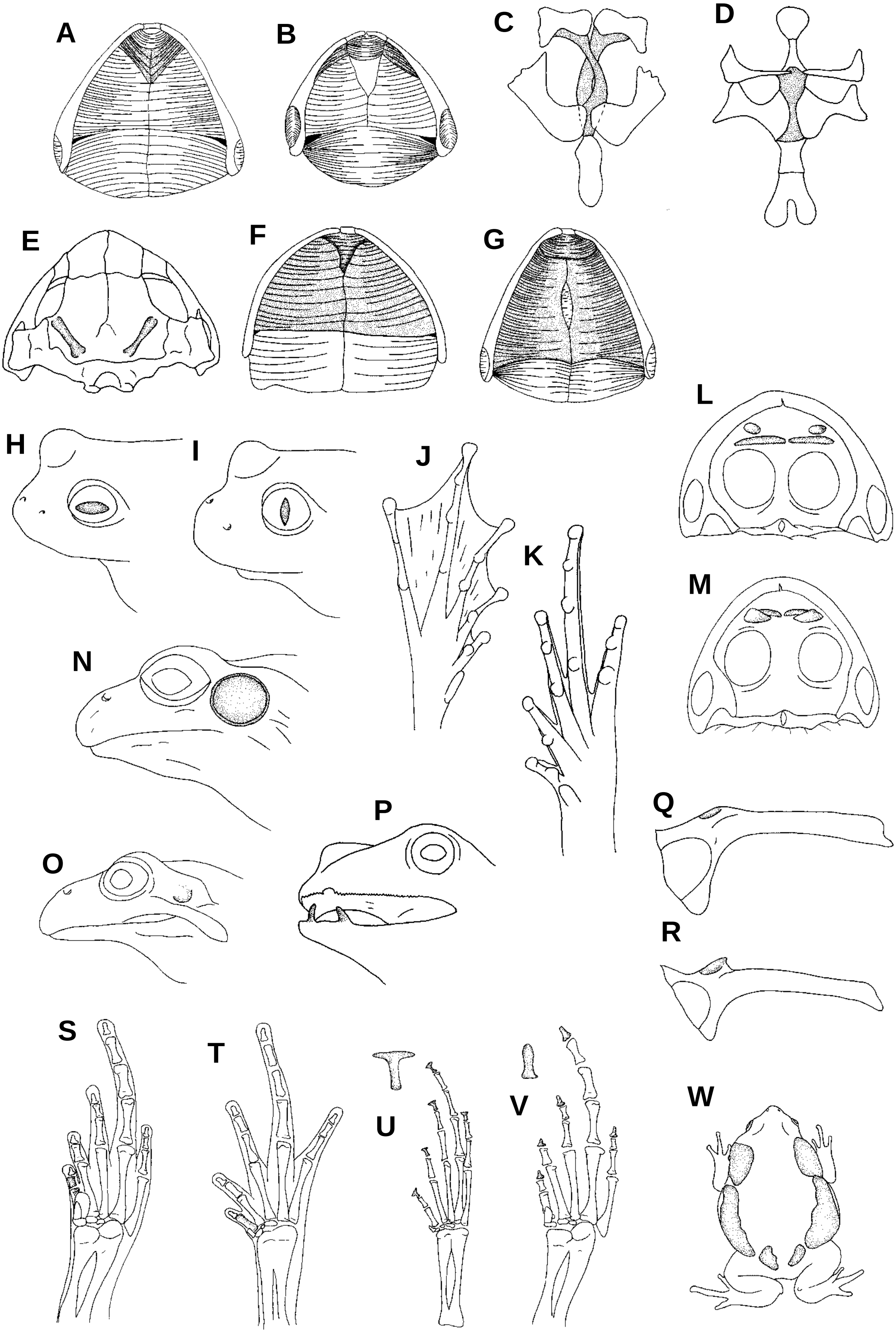

Figure 1.4 Key characters for adult anurans. Pertinent features of elements **A-W** are noted in the adjacent Keys to the anuran families, and myobatrachid subfamilies and genera. (A, B, F, G, after Tyler 1972b; C, after Davies 1984; L, M, after Burton 1984; P, after Barker & Grigg 1977). [M. Davies]

Key to the subfamilies of the Myobatrachidae

1(a) The *m. intermandibularis* underlies at least a portion of *m. submentalis* . . . 2

(b) The *m. intermandibularis* does not underlie *m. submentalis* Myobatrachinae

2(a) Tongue completely attached to floor of mouth; totally aquatic . . . . Rheobatrachinae

(b) Tongue free posteriorly, not completely attached to floor of mouth; not totally aquaticLimnodynastinae

Key to the genera of the subfamily Limnodynastinae

1(a) Constricted pupil a horizontal slit 5

(b) Constricted pupil a vertical slit 2

2(a) Inner metatarsal tubercle compressed and shovel shaped 3

(b) Inner metatarsal tubercle not compressed and shovel shaped 4

3(a) Tympanum not visible; spawn laid in a foam nest . . . . *Heleioporus*

(b) Tympanum visible; spawn laid in long strings . . . . *Neobatrachus*

4(a) Toe webbing extensive . . . . *Mixophyes*

(b) Toe webbing rudimentary . . . . *Lechriodus*

5(a) Vomerine teeth in long rows posterior to the choanae 6

(b) Vomerine teeth in short rows, variously located with respect to the choanae 7

6(a) Tympanum large and prominent . . . . *Megistolotis*

(b) Tympanum small, hidden or indistinct . . . . *Limnodynastes*

7(a) Upper jaw toothed 8

(b) Upper jaw lacking teeth . . . . *Notaden*

8(a) Odontoids on Mentomeckelian bones present . . . . *Adelotus*

(b) Odontoids on Mentomeckelian bones absent 9

9(a) Sub-dermal glands hypertrophied; dorsal prominence and dorsal protuberance of ilial shaft poorly developed . . . . *Philoria*

(b) Sub-dermal glands not evident; dorsal prominence and dorsal protuberance of ilial shaft prominent and hook-like . . . . *Kyarranus*

Key to the genera of the subfamily Myobatrachinae

1(a) Upper jaw toothed 2

(b) Upper jaw lacking teeth 7

2(a) First toe with two phalanges; male lacking inguinal brood pouches 3

(b) First toe with one phalanx; male possessing inguinal brood pouches . . . *Assa*

3(a) Terminal phalanges T-shaped . . . . *Taudactylus*

(b) Terminal phalanges knobbed 4

4(a) Parotoid and inguinal glands poorly developed or absent 5

(b) Parotoid and inguinal glands well developed . . . . *Uperoleia* (in part)

5(a) Ventral surface smooth to slightly granular . . . . *Geocrinia*

(b) Ventral surface moderately to coarsely granular 6

6(a) Vomerine teeth present . . . . *Crinia georgiana*

(b) Vomerine teeth absent . . . . *Crinia* (*Ranidella*)

7(a) Throat and abdomen of both sexes pigmented 8

(b) Ventral surface pigmentation confined to throat in males 9

8(a) Columella present; tympanum distinct . . . . *Metacrinia*

(b) Columella absent; tympanum absent. *Pseudophryne*

9(a) Fourth finger with three phalanges; metatarsal tubercles . . . . compressed . . . . *Uperoleia* (in part)

(b) Fourth finger with two phalanges; metatarsal tubercles not compressed . . 10

10(a) First toe with one phalanx; eyes conspicuous; body robust . . . *Arenophryne*

(b) First toe with two phalanges; eyes very small and inconspicuous; body bulbous . . . . *Myobatrachus*

Key to the genera of the family Hylidae

1(a) Palpebral venation present; constricted pupil a vertical slit . . . . *Nyctimystes*

(b) Palpebral venation absent; constricted pupil a horizontal slit or a rhomboid 2

2(a) Inner metatarsal tubercle large and compressed; intercalary structures . . . . . absent. . . . . *Cyclorana*

(b) Inner metatarsal tubercle small and rounded or absent, rarely compressed; intercalary structures present. . . . . *Litoria*

Key to the genera of the family Microhylidae

1(a) Supplementary slip of *m. intermandibularis* narrow, arising from either a posterior tendon or from the dentary, and oriented parallel to the mandible. . . . . *Cophixalus*

(b) Supplementary slip of *m. intermandibularis* broad, arising from ventral fascia of angulosplenial and oriented medially and only slightly anteriorly. . . . . *Sphenophryne*

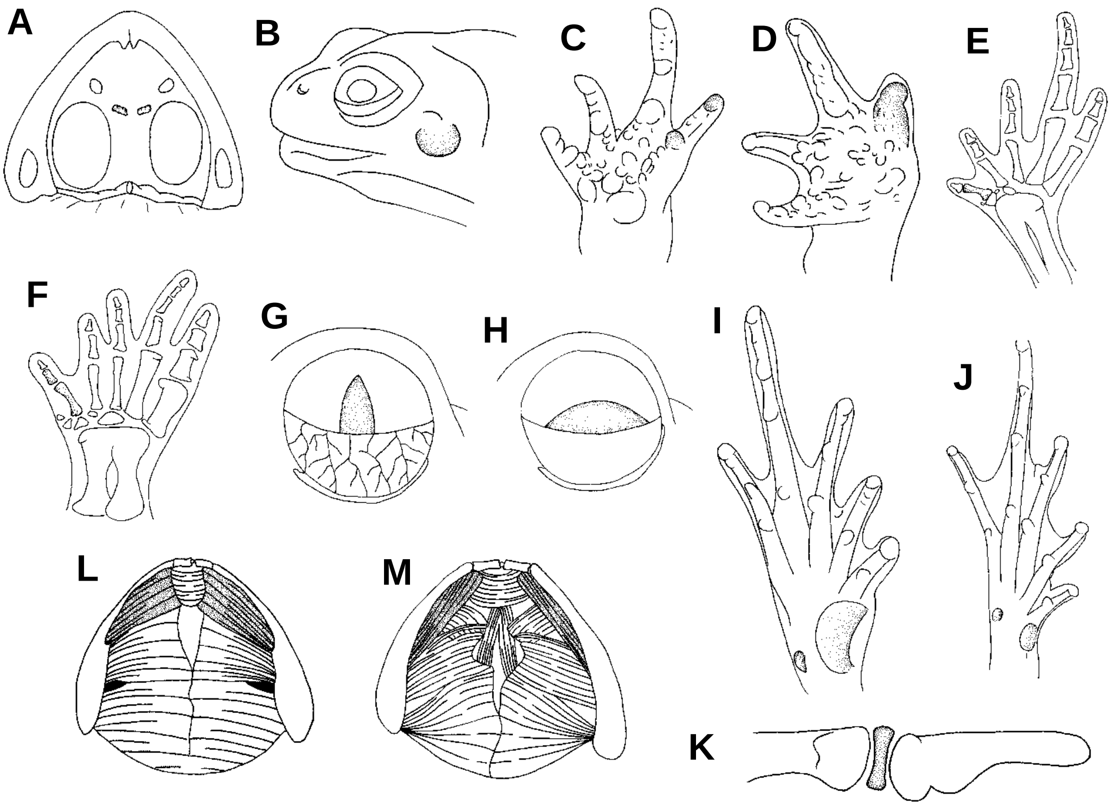

Figure 1.5 Key characters for adult anurans. Pertinent features of elements **A–M** are noted in the Keys to the genera of the Myobatrachinae (in part), Hylidae and Microhylidae. (C–F, after Davies 1984) [M. Davies]

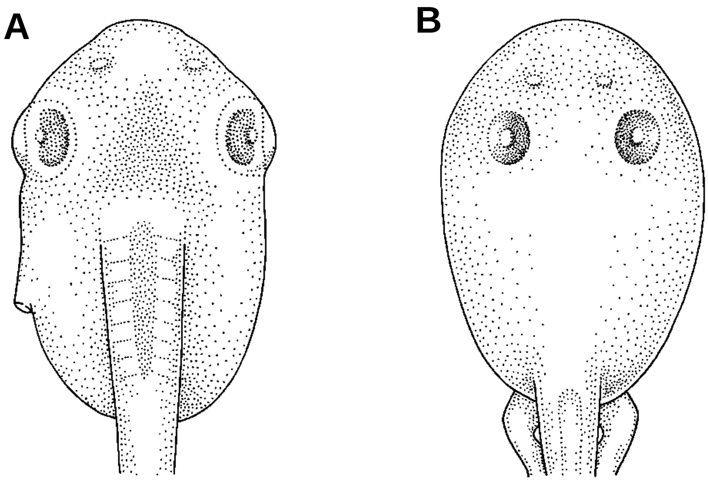

Figure 1.6 Generalised dorsal views of tadpoles that may help in quick familial identification. **A**, hylid tadpole; **B**, myobatrachid tadpole. (After Altig 1970) [R. Plant]

KEY TO THE LARVAE OF AUSTRALIAN ANURANS

At present, it is not possible to provide a complete treatment of this conspicuous and biologically important component of inland freshwater ecosystems, because the tadpole fauna of Australia is poorly known. Some detailed regional keys to local tadpole faunas are available, for example, that of Tyler, Crook & Davies (1983). However, subsequent to the general key to myobatrachid frog larvae by Watson & Martin (1973) there have been no attempts to provide comprehensive keys to Australian tadpoles. Since then, major systematic rearrangements of the fauna have been made, several new genera have been described and a considerable amount of new information has become available.

The degree of adaptive radiation of life history patterns in the Australian frog families is markedly different, particularly in the ancient Gondwanan families, the Hylidae and Myobatrachidae. Even though representatives of both families have successfully colonised most available habitats in Australia, adaptation to these diverse environments by the hylids is not reflected in striking alterations to life-history patterns. In contrast, many life histories of myobatrachids are ‘atypical’ and generally show a trend towards increasing independence of free water for larval development.

The morphological conservatism of Australian hylid tadpoles and our current inadequate knowledge of the fauna make it extremely difficult to identify characters that will key out the various taxonomic groups. The most conspicuous adaptations seen within the hylids are those associated with stream living; and similar morphological changes are evident in both *Litoria* and *Nyctimystes*. Similar adaptations are seen in stream-dwelling myobatrachids (Davies 1989b).

General body form is a useful, though not definitive, means of separating tadpoles of Australian frogs (Fig. 1.7A, B; 1.8, 1.9). However, the following key is based on Watson & Martin (1973), who utilised patterns of life history and the detailed structure of the oral disc. Morphology of the oral disc is one of the few, easily determined characteristics of tadpoles that assist in separating many Australian genera (Watson & Martin 1973; Tyler 1989a).

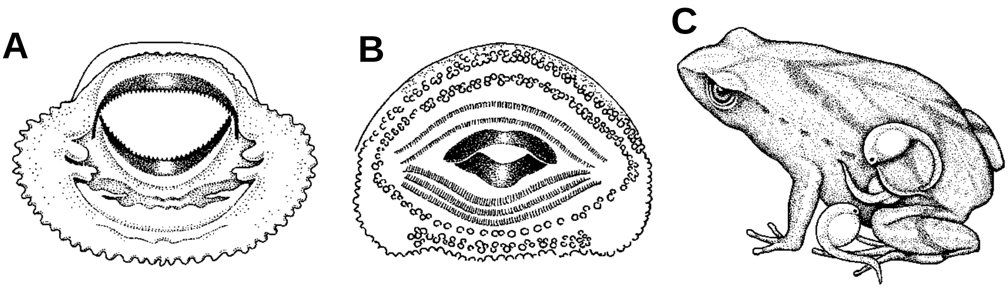

Figure 1.7 Key characters for larval anurans. **A**, mouth disc of *Kyarranus sphagnicolus* tadpole without labial teeth; **B**, mouth disc of *Litoria nannotis* tadpole with labial teeth; **C**, adult male *Assa* with tadpoles. (A, B, after Watson & Martin 1973; C, after photo by H. Ehmann/NPIAW)
[A, B, R. Plant; C, T. Wright]

Key to genera of Australian anuran larvae

1(a) Larvae free-living for at least part of the life cycle 2

(b) Larvae never having a free-living aquatic existence 3

2(a) Labial teeth absent 8

(b) Labial teeth present 11

3(a) Larval development within egg capsule or jelly mass. 5

(b) Not as above 4

4(a) Larvae develop in stomach of female . . . . *Rheobatrachus*

(b) Larvae develop in lateral pouches of male . . . . *Assa*

5(a) Larvae confined within egg capsule 6

(b) Larvae hatch, but remain in jelly mass in depressions under dense vegetation . . . . *Geocrinia rosea* group

6(a) Groups of generally discrete capsules buried deep in sand (8–1.2 m) 7

(b) Groups of capsules often held together by mucilaginous cords in short chains, in tropical forest litter . . . . *Sphenophryne*
. . . . *Cophixalus*

7(a) Capsule diameter greater than 7 mm . . . . *Myobatrachus*

(b) Capsule diameter less than 6 mm . . . . *Arenophryne*

8(a) Length of tail more than twice the body length. . . . . *Kyarranus*

(b) Length of tail less than twice the body length (Figs 1.8D, F, H; 1.9B, D, F, H) 9

9(a) Larvae with funnel-shaped, suctorial mouth 10

(b) Without suctorial mouth, restricted to Mt Baw Baw plateau . . . . . . *Philoria*

10(a) Beak lacking; array of finely-pointed papillae surrounds oral opening (Fig. 8.3D) . . . . *Litoria subglandulosa*

(b) Beak horny; restricted to streams and creeks above 400 m in central and south-eastern Queensland . . . . *Taudactylus eungellensis*,
. . . . *Taudactylus diurnus*

11(a) Deep-bodied larvae having two upper and two lower rows of labial teeth . . . . *Crinia haswelli*

(b) Shallow-bodied larvae having three lower rows of labial teeth 12

12(a) Larvae with two upper rows of labial teeth. 13

(b) Larvae with more than two upper rows of labial teeth 15

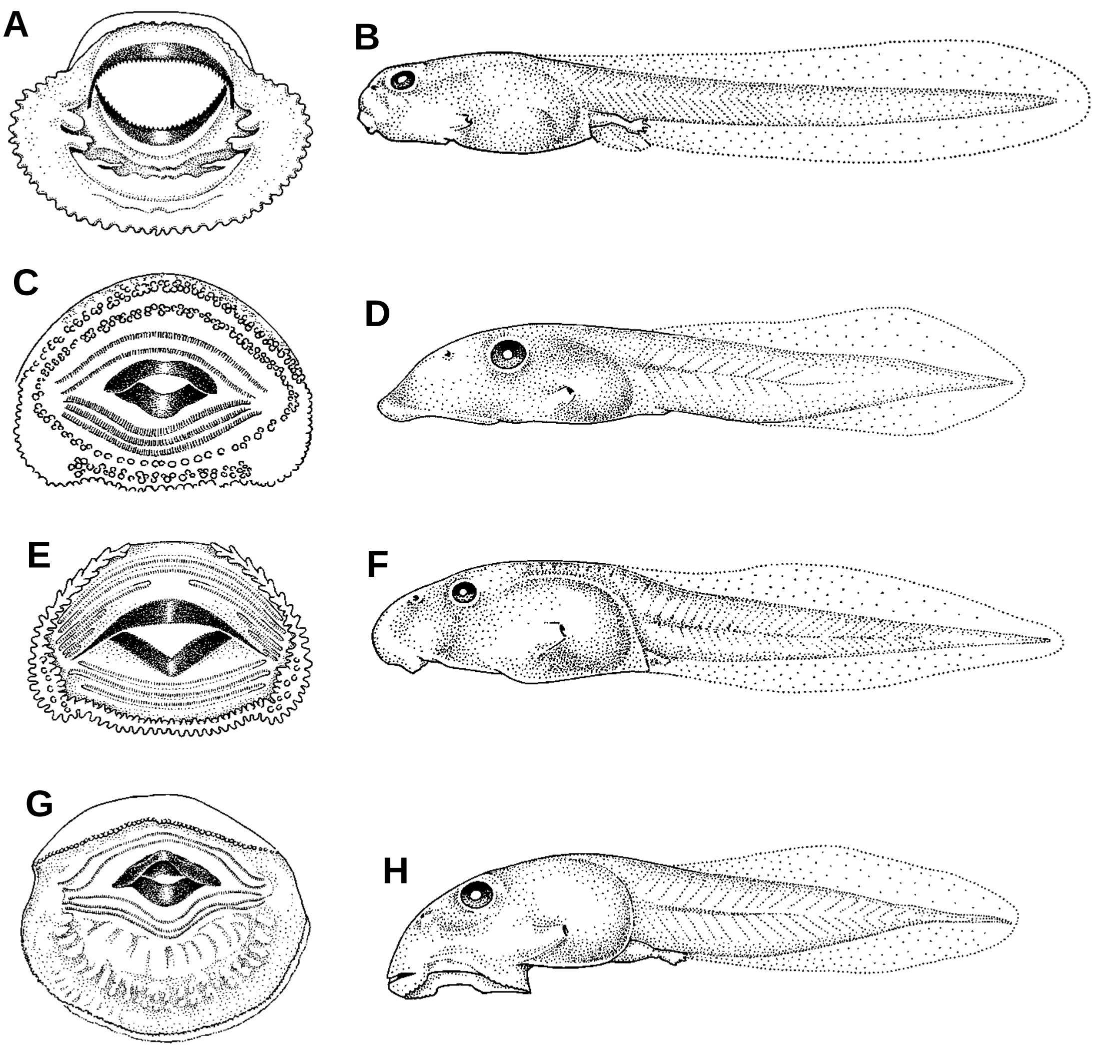

Figure 1.8 Tadpoles and mouth discs of anurans. **A**, *Kyarranus sphagnicolus* mouth disc; **B**, *Kyarranus sphagnicolus* tadpole; **C**, *Litoria nannotis* mouth disc; **D**, stream-adapted tadpole of *Litoria nannotis*; **E**, *Megistolotis lignarius* mouth disc; **F**, stream-adapted tadpole of *Megistolotis lignarius*; **G**, *Nyctimystes dayi* mouth disc; **H**, stream-adapted tadpole of *Nyctimystes dayi*. (A–C, after Watson & Martin 1979; D, after Liem 1974; E, F, after Tyler *et al*. 1979; G, H, after Davies & Richards 1990) [R. Plant]

13(a) Papillary border complete; usually found in streams . . . . . .*Litoria* (in part), ... *Nyctimystes*

(b) Papillary border incomplete. 14

14(a) Papillary border with an anterior gap . . . . *Litoria* (most species)
. . . . *Cyclorana*
. . . . *Limnodynastes spenceri*
. . . . *Taudactylus acutirostris*

(b) Papillary border with both anterior and posterior gaps
. . . .*Geocrinia* non-*rosea* group
. . . . *Notaden melanoscaphus*
. . . . *Crinia* (most species)
. . . . *Bufo*
. . . .*Uperoleia*

15(a) Papillary border complete; usually found in streams . . . . *Mixophyes*

(b) Papillary border incomplete. 16

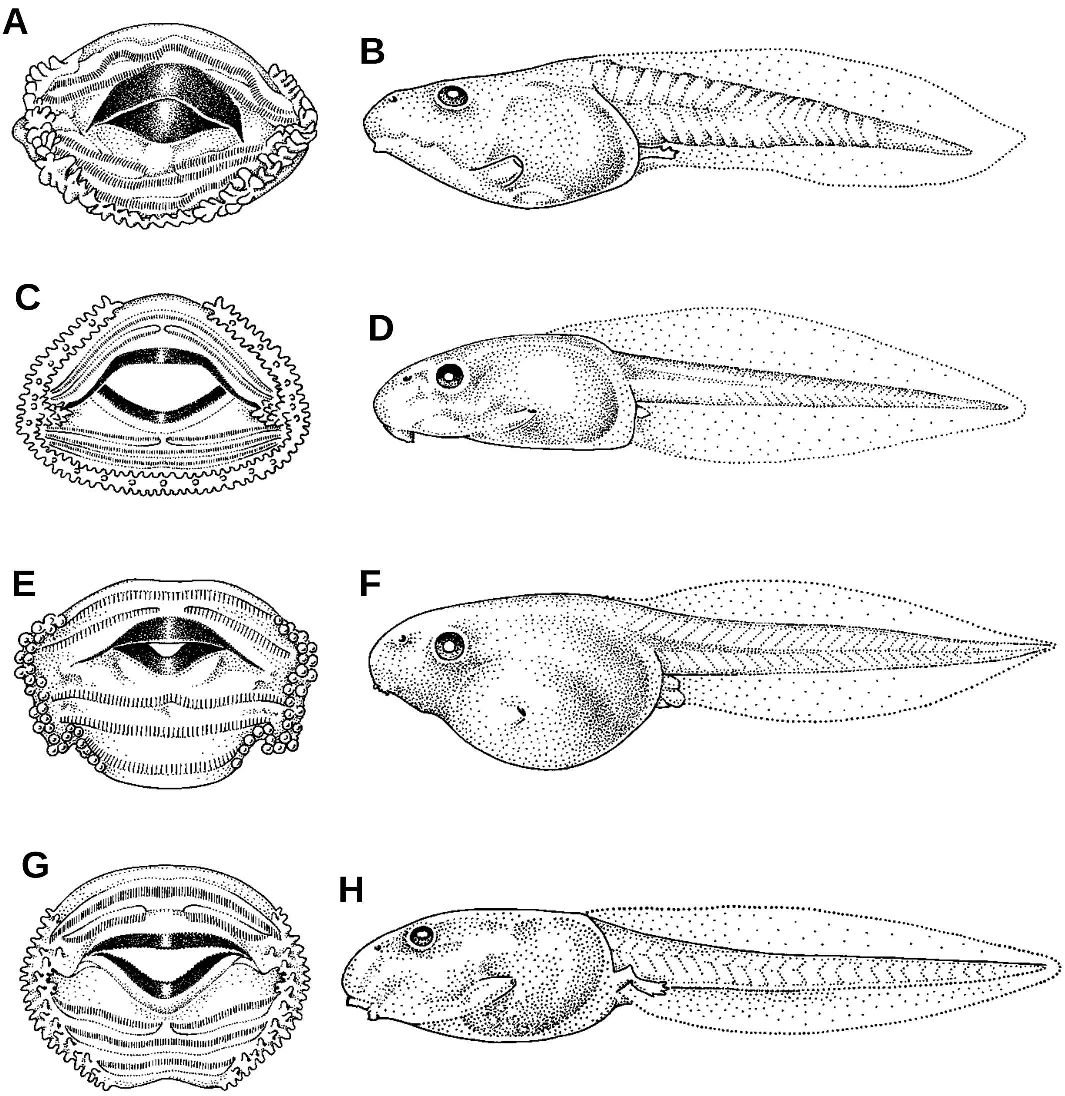

Figure 1.9 Tadpoles and mouth discs of anurans. **A**, *Cyclorana longipes* mouth disc; **B**, *Cyclorana longipes* tadpole; **C**, *Litoria gracilenta* mouth disc; **D**, *Litoria gracilenta* tadpole; **E**, *Bufo marinus* mouth disc; **F**, *Bufo marinus* tadpole; **G**, *Geocrinia laevis* mouth disc; **H**, *Geocrinia laevis* tadpole. (A, B, after Tyler *et al*. 1983; C, D, G, H, after Watson & Martin 1979; E, F, after Breder 1946) [R. Plant]

16(a) Papillary border with an anterior gap 17

(b) Papillary border with both anterior and posterior gaps . . . . *Crinia georgiana*

17(a) Mouth with three or four upper rows of labial teeth 18

(b) Mouth with more than four upper rows of labial teeth . . . .
. . . . *Limnodynastes* (most species)
. . . . *Megistolotis*
. . . . *Heleioporus*
. . . . *Lechriodus*

18(a) Larval anal opening dextral . . . . *Adelotus*

(b) Larval anal opening median or nearly so. . . . . *Limnodynastes ornatus*
. . . . *Limnodynastes peronii*
. . . . *Notaden nichollsi*
. . . . *Neobatrachus*